Aquatic Snakes
Diversity and Natural History

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AQUATIC SNAKES

DIVERSITY AND NATURAL HISTORY

This book is dedicated to the present and future herpetologists who
will study aquatic snakes and promote their conservation.

ISBN 9798218194901

Publisher JCM Natural History
with Herpetological Conservation International

Cover Photos

The front cover photo was taken on Orchid Island (Lanyu) off the southeastern part of Taiwan on June 30, 2020. It happened to be at low tide that night, so there were many sea kraits active between the crevices of the coral reef and the tide pool (the species appeared that night including *Laticauda semifasciata*, *Laticauda colubrina* and *Laticauda laticaudata*). Since *Laticauda semifasciata* rarely crawls out of the sea surface, I crouched in a shallow tidal pool and waited for it to swim to my predetermined position. I used DSLR (Nikon D850) with a manual wide-angle lens (LAOWA 15mm f4) and off-camera flashlight shooting this photo.

Yu Sing Lin

On the back cover a Northern Water Snake, *Nerodia sipedon*, lies at the edge of a man-made canal shortly after emerging from hibernation. Will County, Illinois. JCM

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Acknowledgments

The idea for this book was initially conceived while I was working on Homalopsid Snakes, Evolution in the Mud (2007). Discussions with Harold Voris (Field Museum), Daryl Karns (Hanover College), and Myke Clarkson provided additional ideas and motivation. Rune Midtgaard (RepFocus) generously supplied the distribution maps from his website. Justin Berstein, Konrad Mebert, Myke Clarkson, Michael Jowers, and JJ Mao provide extra assistance with editing. The photographs were made possible by about 120 photographers from more than 30 countries. The co-authors provided the text to their areas of specialization, species groups and species accounts. To all my sincerest thanks. JCM

A *Python bivittatus* from Sakaerat Environmental Research Station, Thailand. Photograph JCM

Preface

> *I shall not pretend to assert that they are as numerous as land snakes; but it is very likely that one hundred species at least of this tribe exist in the waters of the ocean, lakes, and rivers.*
>
> C. S. Rafinesque 1817. ***Dissertation on water snakes, sea snakes and sea serpents.*** Philosophical Transaction

When Rafinesque wrote this, 14 species of snakes were considered water snakes. The idea for a global overview of aquatic snakes has attracted my attention since I finished the *Homalopsid Snakes, Evolution in the Mud* in 2007. Books on sea snakes are available: Malcolm Smith's classic *The Sea-Snakes*, William Dunson's *The Biology of the Sea Snakes,* Harold Heatwole's *Sea Snakes*, and Ivan Ineich and Pierre Laboutes' *Sea Snakes of New Caledonia*, to name a few. However, most information on aquatic snakes remains scattered in hundreds of journals and books.

Snakes living in fresh and brackish waters had been mostly overlooked. Snakes inhabiting marine environments were restricted to a relatively few lineages, while snakes using freshwater were found in many more lineages. Furthermore, snakes use aquatic habitats in many ways that may not cause them to be easily recognized as aquatic. For example, some North American snakes spend the winter in water-filled crayfish burrows and are terrestrial or semi-aquatic the rest of the year.

This volume is perhaps best considered an illustrated, annotated checklist of aquatic and semi-aquatic snakes in marine and freshwater environments. The biggest challenge was deciding what species to include and which to exclude. While the intent was to have accounts for all aquatic snakes, where do you draw the line on the continuum? How much evidence do you need to label a species semi-aquatic? I am confident this volume covers the range of snakes that are traditionally considered semi-aquatic. However, knowledge of some of these animals is poor or absent, while others are some of the best-studied reptiles.

Snakes are derived from lizards, but surprisingly few saurians are semi-aquatic, and no extant lizards are known to be aquatic. Bauer and Jackman (2007) found 73 species in 11 families using freshwater habitats. They found no aquatic lizards inhabiting the Nearctic or Palearctic regions. Still, the Neotropics, the Oriental, and Australian regions support the greatest diversities of freshwater forms, particularly in the families Gymnophthalmidae, Scincidae, and Varanidae. Pauwels et al. (2008) listed 153 snakes (about 5% of all snakes recognized at the time) that inhabit freshwater. This number covers 44 genera in six families (Acrochordidae, Boidae, Colubridae, Elapidae, Homalopsidae, and Viperidae), with the greatest numbers in the Oriental (64 species) and Neotropical Regions (39 species).

Here, the definition of aquatic is expanded to include marine species and species that are terrestrial, arboreal, or fossorial but enter the water and use aquatic situations and resources. I have included species considered terrestrial or fossorial because there is some evidence, they are also using aquatic habitats and resources. The marine, brackish, and freshwater snakes discussed here provide an overall picture of the extant snakes using fluid habitats. This work lists more than 420 species (about 10.3% of snakes) in 106 genera, 31 subfamilies and family-level clades. But not all these species are aquatic or semiaquatic, and they have been included because their close relatives use watery habitats. Note that I (JCM) compiled the chapters with no authors listed. The species accounts are uneven because knowledge is limited on many species, different authors have written accounts, and I have intentionally tried to keep the size of this volume down.

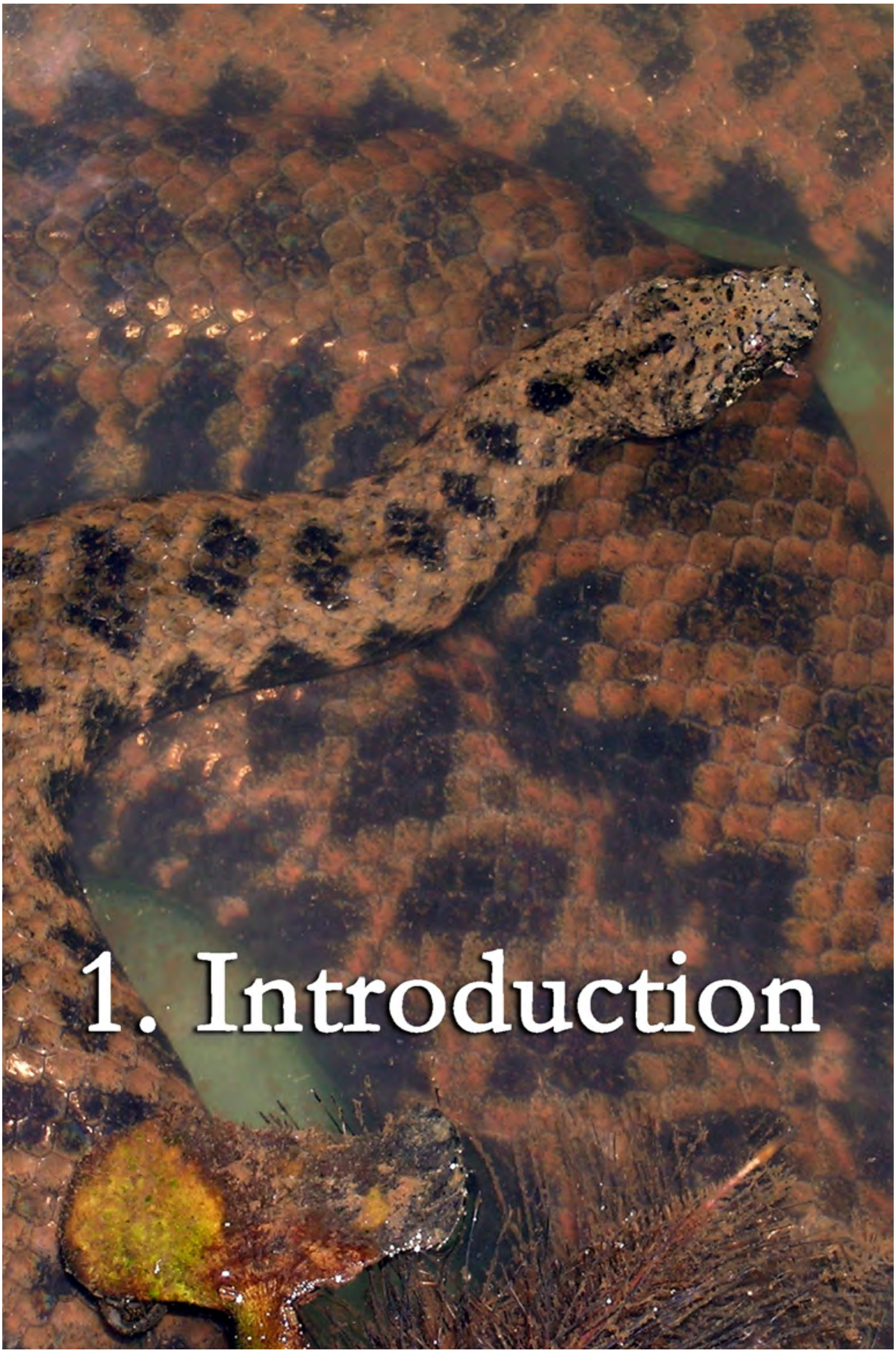
A note on species and subspecies

Definitions of species and subspecies are hotly debated. While species are frequently regarded as natural units, subspecies are considered arbitrary human constructs. This point seems to have been first argued by Wilson and Brown (1953). Others note that the "arbitrary" label could be applied against any higher taxonomic rank below the phylum (Avise and Mitchell 2007).

Zoologists have used the Linnaean system for almost three centuries, and doing away with it and replacing it with some other system seems improbable. De Queiroz (2021) has updated the subspecies concept to base them on the same criteria as species – separately evolving metapopulation lineages. They differ from species in that they have not entirely separated from each other. I have included subspecies (trinomials) in the species accounts because they are used in much of the literature – undoubtedly, some of them are invalid, others are likely valid, and yet others are likely to be elevated to species status. Some species might be synonymized once more detailed information will become available.

**Figure P.1. A *Natrix natrix* from Marchegg, Austria.
Photography by Kai Kolodziej**

**On the next page. The homalopsid snake *Enhydris jagorii*. from Bung Ka Loh.
Photography by Daryl Karns.**



1. Introduction

1. Introduction

Lake Songkhla looks like many other wetlands from the shoreline (Figure 1-1), but it is the largest wetland complex in Thailand and comprises three shallow basins. One hundred and fifty years ago, Songkhla was a bay open to the ocean. Since then, a series of barrier islands were expanded with human assistance and gradually enclosed the basins. The islands now form the Sathing-Phra Peninsula and almost wholly isolate Lake Songkhla from the Gulf of Thailand (Figure 1-2). Only one opening to the sea is located at the south end of the lake near Songkhla. Annandale (1916) described the lake as no more than 4.9 m deep. Since then, the lake has continued to accumulate silt, and today, the three basins have a mean depth of 1.2 m and a maximum depth of 2.4 m (Leelawathanagoon et al. 1997). The water levels and chemistry changes accompanying the lake's formation left an unusual mixture of freshwater and marine fauna.

Lake Songkhla has perhaps the most diverse assemblage of water-dwelling snakes globally. One sea snake (*Hydrophis brookii* family Hydrophilidae), one file snake (*Acrochordus granulatus*, family Acrochordidae), the pipe snake (*Cylindrophis* sp. family Cylindrophiidae), at least one species of keelback (Fowlea piscator - family Natricidae), and at least four species in four genera of Asian-Australasian Mud Snakes (family Homalopsidae) live in the lake or along its wet edges.

Aquatic is an easily applied label if the snake never comes out of the water, like some sea snakes or the Tentacled Snake (*Erpeton tentaculatus*). They are easily labeled semi-aquatic if they are like the North American water snakes of the genus *Nerodia*, the European *Natrix*, or the sea kraits of the genus *Laticauda*. All of these enter the water to hunt or search for mates but bask in bushes and on rocks close to the water, and some mate and lay eggs on land. Then, there are terrestrial or arboreal snakes that escape predators by diving into the water, such as *Philodryas olfersii* (Abegg and Mario-da-Rosa 2018).

Snakes have evolved aquatic lifestyles many times and to varying degrees in dozens of different lineages. Snakes living in still, turbid water and feeding on fish can be expected to have different adaptations than snakes feeding on crustaceans living in bedrock streams with boulders and fast-moving water. Making this more complex and confusing are snakes that evolved aquatic lifestyles and then returned to a terrestrial existence.

Pauwels et al. (2008) proposed that freshwater snakes forage in the water and cannot survive without aquatic prey and frequent submersion. They suggested that subtle external anatomical characters betray aquatic habits in freshwater snakes. Morphological specializations include dorsally oriented nostrils, often close together, some of which have valved nares that exclude water from the upper respiratory system and allow the snake to inhale at the surface without being seen by predators. The eyes, too, tend to be dorsally oriented so that a snake lying in the water can view the sky (or the water) above for potential prey or predators. The eyes of aquatic snakes are often reduced in size, and sometimes, the iris matches the color of the surrounding scales. Other species have a brightly colored iris that makes the eyes stand out compared to the surrounding scales. Aquatic snakes frequently have a dorsal pattern of transverse bands and keeled dorsal scales.

None of these characteristics are shared by all aquatic snakes, and some traits, like transverse bands or keeled scales, are shared with many terrestrial, arboreal, or exclusively marine species. The freshwater Tentacled Snake, *Erpeton tentaculatum,* is highly aquatic, possibly the most specialized freshwater snake, and may never leave the water or do so only on rare occasions (Figure 1-3). Its eyes are relatively large and lateral, not dorsolateral or dorsal, and it has longitudinal stripes, not transverse bands.

Figure 1.1. Lake Songkhla, the largest lake in Thailand looks very much like many other wetlands but it supports a diverse aquatic snake fauna. Photography by JCM

Figure 1.2. A view of Lake Songkhla from space is mostly isolated from the Gulf of Thailand but remains connected by an opening at the south end of the lake. Image taken 13 February 2008. Photo credit: NASA, WorldWind 1.4.0.0.

Thus, the ancestors of modern aquatic snakes were adapted for life underground, on the ground, or in the trees. Some of their descendants moved into freshwater, brackish water, or marine environments and evolved traits for those environments. Some returned to life on land, and others evolved into more specialized aquatic lifestyles.

Extant snakes are organized into about 45 family and subfamily-level clades extending backward in time. Estimated dates for snake origins are complicated by the evolution of squamate snake-like morphs that appear in the fossil record. Snakes and lizards shared an ancestor in the lower Jurassic, about 190 MYA (Harrington and Reader 2017). During this time, snake lineages branched. Some existed for a while before becoming extinct. Others survive to the present day.

The evolution and adaptations of marine snakes have received considerable attention (Dunson 1975; Heatwole 1999; Sanders et al. 2008). Sea snakes are in the subfamily Hydrophiinae – a clade nested in the larger elapid clade. All share fixed front fangs and venom glands, including coral snakes, cobras, and mambas. Marine elapids have three ancestors and have adapted to life in the oceans differently. They form two or three lineages: the sea snakes (*Hydrophis* + *Apisuryus* = hydrophiids) with 62 species and the sea kraits with eight species in the genus *Laticauda*. Both clades have paddle-like tails to improve their swimming ability, but the hydrophiids give birth to young in the water and have lost the broad ventral scales. Sea kraits are oviparous, laying eggs in terrestrial situations, and retain their broad ventral scales. The only thing sea kraits do in the water is hunt. Despite living in the oceans, sea snakes and sea kraits still rely on freshwater for drinking (Lillywhite et al. 2008; Bonnet, Brischoux 2008; Lillywhite et al. 2014). This requires the sea snakes to stay close to river deltas or areas of heavy rainfall. Freshwater draining off the land into the ocean remains on the surface before it mixes with seawater, and rainwater floats on the ocean's surface and forms a lens of freshwater before mixing with the heavier seawater.

Ambush predators can use water for concealment while retaining much of the terrestrial morphology for life on land. Other snakes hunt shorelines and search small pools without entering the water, and a few snakes hunt from branches and strike aquatic prey from a perch over the water. Arboreal snakes can use aquatic resources without the apparent morphological modifications to aquatic habitats, a reminder of the remarkable plasticity we see in snakes. Asad et al. (2020) reported that the mock viper, *Psammodynastes pictus*, is restricted to Sundaland and hunts fish of the genus Rasbora from branches overhanging the water. Trobisch and Gläßer-Trobisch (2011) observed hunting behavior in captive juvenile *Natrix tessellata* and reported hunting from branches over the water. The Burmese Vine Snake, *Ahaetulla fronticincta,* is highly arboreal but feeds exclusively on fish (Figure 1-4). It inhabits bushes and other low vegetation in mangrove forests in coastal Myanmar (Wogan and Vogel, 2020).

Snakes that hunt from branches or shorelines without entering the water are not included here because, technically, they do not spend much time in the water. However, snakes that hunt from the water are included – even though many of them are habitat generalists. And maybe taking prey from the shoreline

Not surprisingly, the largest snakes often use water. The Green Anaconda (*Eunectes murinus*) and its relatives are highly aquatic. The largest pythons (*Python sebae, P. natalensis, P. bivittatus, P. molurus,* and *Malayopython reticulatus*) are less dependent on water than the anacondas (aquatic boas). Yet the pythons still spend substantial time in the water, hunt from the water, and use the water for thermoregulation. Not only does water provide buoyancy for massive bodies, but it allows the snakes to conceal themselves from prey and predators.

One sea snake, the Yellow-bellied Sea Snake (*Hydrophis platurus)*, has become pelagic, drifting with ocean currents (Figure 1-5). The only time it is seen on land is when it

Figure 1.3. The freshwater Tentacled Snake, *Erpeton tentaculum*. Photography by Alex Mason.

Figure 1.4. Gunther's Whipsnake Snake, *Ahaetulla fronticincta,* is highly arboreal but feeds exclusively on fish. Photography by Paul Freed.

washes up on beaches from Africa's east coast to the coastlines of western North and Central America. The Yellow-bellied Sea Snake aggregates along slicks or drift lines. Floating debris accumulates in the slicks, and the snake may remain for days or weeks before a change in wind speed or current direction breaks them up. Aggregations of *Hydrophis platurus* drift, the aggregate, may contain just a few animals or several thousand, including juvenile and adult snakes. Other animals inhabiting the drifts are jellyfish medusa, fish, porpoises, sea turtles, and sea birds, often following floating debris lines. Snakes aggregate here because the slicks are a place to locate food and mates. The degree to which these snakes have adapted to the marine environment is significant, given that they represent a recent evolutionary radiation.

Figure 1-5. The Yellow-bellied Sea Snake, *Hydrophis platurus,* has become pelagic, drifting with ocean currents. Photography by May Zabe.

Was the snake ancestor aquatic?

Evidence from morphology and molecules leaves little doubt that snakes evolved from lizards. However, the transition between lizards and snakes is among the most controversial topics in evolution, partly because of the lack of well-preserved fossils. Three competing hypotheses for the lifestyle of the ancestral snake -- burrowing, aquatic, and terrestrial origins -- have been debated for more than a century.

Cope (1869) implied the snakes' ancestors could have been aquatic when he placed snakes and mosasaurs (Fig. 1-6) in the Pythonomorpha. Caldwell and Lee (1997), Caprette et al. (2004), and others who have worked on Cretaceous marine lizards also suggested an aquatic snake ancestor. Vidal and Hedges (2004) tried to rule out an aquatic origin for snakes based on the molecular results suggesting snakes were not related to varanoid lizards – the mosasauroids' closest living relatives.

Camp (1923) proposed snakes evolved from a grassland anguimorph lizard (a terrestrial ancestor). Today, anguimorph lizards remain possible candidates for the snake ancestor, and there are living grass-swimming anguimorphs. Anguimorph lizards and snakes share paired male reproductive organs with ornamentation and venom glands.

Figure 1.6. Reconstruction of living *Mosasaurus missouriensis.* The fossil remains were discovered in 2012 in a layer of shale by a mining company in southern Alberta in Canada. The lizard was about 6.5 meters long with a skull that was slightly less than a meter long. Artist credit: Nobu Tamura.

Mahendra (1938) proposed that the snake ancestor was a burrowing lizard. This hypothesis gained broad support and was the most well-accepted idea regarding the snake's ancestral lifestyle. Mahendra noted that a ring of scales surrounded the eye in most advanced snakes. Burrowing forms like the threadsnakes and blindsnakes (Leptotyphlopidae and Typhlopidae), the shield-tailed snakes (Uropeltidae), and the Amazonian pipe snakes (Anilius) have the eye covered by a single large scale. Mahendra viewed all these snakes as primitive or basal to more advanced snakes. He placed them at the evolutionary tree's base and concluded that the ancestral snake must have been fossorial. Today, these snakes are recognized as some of the oldest lineages, the dawn snakes, threadsnakes, and blindsnakes — and have been called scolecophidians – but they are not monophyletic (Heise et al. 1995).

An early terrestrial relative of snakes was the 95-million-year-old *Najash rionegrina*, which had two rear legs and a sacrum. The remains of *Najash* included partial skulls. However, other fossil snakes possessed hindlimbs, but their pelvic bones were not directly attached to the vertebrae. These are older than Najash; all were marine (*Haasiophis, Pachyrhachis*, and *Eupodophis*).

The widespread acceptance of the burrowing ancestor hypothesis was partly due to Walls' (1940) work on snake eye anatomy. In a list of differences between snake and lizard eyes, Walls clarifies that snake eye anatomy is quite distinct from lizard eye anatomy. The most dramatic difference between the lizard and snake eyes is the snakes' inability to change the shape of their lenses to focus an image onto the retina. Muscles attached to the lens for focusing in lizards are absent in snakes. Snakes must move the lens towards or away from the retina to focus their eyes using the enlarged peripheral iris muscles. Also, most snakes lack a fovea, although some Asian tree snakes have re-evolved the structure. Walls also explained the cone-like structure of rods in snake retinas (and those of other tetrapods) resulting from the loss of rods in response to diurnal activity and then secondarily redeveloping rods from cones. He thought cone cells were transformed into rod cells, which became known as the transmutation hypothesis. The modifications Walls (1940) found in snake eyes suggested to him they resulted from a burrowing lifestyle.

Shine and Wall (2008) found two ecomorphs for lizards that had lost their legs: legless burrowing lizards have elongated trunks, small heads, short tails, and constant body widths; and surface-active legless species have short trunks, broader heads, long tails, and more variable body widths. They suggested that a long tail in surface dwellers helps escape predators if the tail can be automized. Long tails are probably beneficial for locomotion when the animal uses lateral undulations (side-to-side movement). On the other hand, burrowing lizards need to push through the substrate, which requires a different arrangement of muscles and bones in which the rib cage and trunk muscles form a rigid but flexible cylinder. This pipe-like morphology transfers force to the digging head, and a long tapering tail is not well suited for this lifestyle.

Regarding the aquatic origins of snakes, Shine and Wall observe that living semi-aquatic lizards have well-developed limbs and long tails. The tails are essential in swimming and, therefore, are unlikely to be lost. Many living lizard species are burrowers, and by implication, Shine and Wall infer that snakes were more likely to have evolved from a burrowing ancestor than an aquatic one.

Molecular clock dates produced by Vidal et al. (2007) suggest lizards last shared an ancestor with snakes 166.4 MYA. Other authors using similar methods estimated that this ancestor lived 194–145 MYA. Molecular clock dates suggest the scolecophidians (leptotyphlopids, typhlopids, and anomalepidids) shared an ancestor with all other snakes about 155.6–151.9 MYA. Hugall et al. (2007) placed the snake - Anguimorph lizard divergence at about 155 MYA

Figure1.7. Threadsnakes and Blind Snakes have been long considered to be models for the ancestral snake Photography by JCM.

and the separation of the scolecophidians from the rest of the snakes at about 105 MYA. Sanders et al. (2008) place the anguimorph-snake divergence date at about 140 MYA and the divergence of the scolecophidians from the rest of the snakes at about 110 MYA.

Yi and Norell (2015) argued in favor of snakes' burrowing origin based on inner ear morphology. They noted that the fossil snake Dinilysia is a stem snake close to the most recent common ancestor of living snakes; according to most phylogenetic analyses, it has inner ear morphology like some burrowing squamates. Their model predicted that both *Dinilysia* and the reconstructed 'hypothetical ancestor of crown snakes' are classified as burrowing forms based on a comparison with modern species of known ecology. Burrowing is a predominant lifestyle in most basal lineages of crown snakes; therefore, snakes must have

Figure 1.8. The glass lizards may be readily mistaken for a snake. They are anguimorph lizards. Photography by JCM.

had a burrowing origin.

Again, looking at inner ear structure, Palci et al. (2017) used a larger dataset with more taxa and subdivided the species into five traditional ecological categories. They recognized that the closest outgroup to snakes might be iguanians, anguimorphs, or mosasauroids. The results placed *Dinilysia* close to the existing snake *Xenopeltis* and found that homalopsids were close to *Dinilysia*. The placement contradicts the claim that a sizeable spherical sacculus (their 'vestibule') is diagnostic of burrowing forms. Such morphology can also be found in semi-aquatic snakes, and it is absent in some typical obligate burrowers like scolecophidians or semifossorial snakes such as *Calabaria* and *Brachyurophis*.

Scolecophidians are often considered the most basal lineage(s) of crown snakes, historically and in recent phylogenetic analyses (Figure 1.7). Supposing this is an accurate phylogenetic position for these snakes, it might be expected that *Dinilysia* would display an inner ear morphology like scolecophidian snakes if burrowing were indeed primitive for snakes. However, the sharp differences between the inner ears of *Dinilysia* and scolecophidians are not easily understandable if all share a burrowing ancestry.

The ancestral snake's lifestyle remains uncertain; it could have been a burrower, a swimmer, a terrestrial species, or a species using a combination of these ecological lifestyles. Further discussion of this topic awaits additional fossil discoveries and studies of extant species.

Ancient Aquatic Snakes

The Eocene began at 55.8 MYA and ended at 33.9 MYA. During this time, the continents were drifting toward their present positions. It was a time when the Earth was a "greenhouse," with global warming due to increased atmospheric carbon dioxide (Bohaty and Zachos 2003). The distribution of Eocene species was remarkably different than what we see today. There were palm trees in Alaska and the northern Rockies, crocodiles on Elsmere Island above the Arctic Circle, and forests covering much of Antarctica. Primates spread from Asia to Europe and North America during this time, and the rivers, estuaries, and oceans contained snakes, including giant aquatic snakes

The snake family Palaeopheidae is known exclusively for their vertebrae and ribs. They inhabited both hemispheres, from the Upper Cretaceous to the Eocene (McDowell 1987). Their fossils are always associated with rock formed in watery environments. The vertebrae tend to be tall and narrow, and the ribs are only slightly curved, characteristics found in the most aquatic snakes living today, the sea snakes. Those who study Palaeopheidae fossils consider the group relatives of the boids, but others have suggested that they are close to the file snakes (the acrochordids).

Size estimates for the paleophids range from half a meter to nine meters or more, and while some lived in near-shore environments such as estuaries and mangroves, others were using open ocean habitats far from shore. Holman (2000) and Rage et al. (2003) have reviewed the family, known chiefly from vertebrae and ribs, and have described paleophids as booid-like.

Some species were highly modified for life in the water. They had laterally compressed vertebrae and bodies for swimming, high neural spines on all vertebrae (to aid the lateral compression of the body), synapophyses for rib articulation low on the vertebrae, and ribs that were only slightly curved (assisting lateral body compression). The vertebrae of at least one species contained marrow cavities, which may have been involved in regulating buoyancy, increased erythrocytes, or both. Moreover, like some modern sea snakes, the laterally compressed species likely could not move on land. Other family members showed only slight modifications for aquatic life and were probably somewhat terrestrial.

The extinct colubroid families Anomalophiidae and Russellophiidae are also suspected of being aquatic (Rage et al. 2003). Palaeophis colossaeus was described by Rage (1983) based on vertebrae collected in Mali. The vertebrae were 34 mm long. We do not know how many vertebrae the snake had, but given that a typical boa or python has about 270, it is likely this snake could have been 9.180 m or more than 30 feet. Another huge paleophiid is Pterosphenus schucherti, described from coastal North America. It ranged from Texas to New Jersey. Remains from Florida indicate that an individual snake died at least 300 km from the nearest mainland during the late Eocene, where it was buried with cartilaginous fish, bony fish, and an ancient whale.

Ancient aquatic snakes disappeared near the end of the Eocene, and their extinction is likely linked to a changing climate. Global cooling at the start of the Oligocene occurred as oceanic circulation was altered with Antarctica's disconnection from Australia and South America. The formation of the South Pole's continental ice sheet followed the extinction of many warm-water species

Four new fossil aquatic snake species ranging from 167–143 MYA in age were described by Caldwell et al. (2015). These four species push the earliest known snakes backward by nearly 70 million years - into the mid-Mesozoic. Thus, their origin coincided with the known radiation of most other major groups of squamates in the mid-Jurassic: the time of the final stages in the break-up of Pangaea into Laurasia and Gondwana. These new records for early snakes fill a significant chronological gap predicted by molecular phylogenetics.

In stratigraphic order, the fossil snakes Caldwell et al. recognized are Parviraptor estesi, from rocks dated at ~167 MYA, from the Middle Jurassic, from Southern England, followed by the North American *Diablophis gilmorei* dated at ~155 MYA from the Upper Jurassic of Colorado, USA; which appears to be a contemporary of Portugalophis lignites from the Upper Jurassic of Guimarota, Portugal; the youngest species was Eophis underwoodi from rocks dated at ~150–140 MYA positioned in time at the Jurassic-Cretaceous border from an outcropping near Swanage, Dorset, Southern England. *Portugalophis lignites* remains were deposited in a coal swamp. *Eophis* and *Parviraptor* remains came from mixed coastal lakes, pond systems, and riparian environments, and *Diablophis* was recovered from an epicontinental deposit several hundred kilometers from the nearest shoreline. Caldwell et al. wrote,

> "It is also possible that snakes forming these island assemblages arrived as secondarily aquatic invaders. Secondary invasions of marine environments characterize the subsequent evolutionary histories of numerous clades of fossil and modern snakes." Thus, some of the earliest known snakes – were likely semi-aquatic or aquatic.

Cretaceous (91–95 MYA) were also aquatic. *Pachyophis woodwardi* and *Pachyrhachis problematicus,* had laterally compressed bodies, small heads, and pachyostoic ribs and vertebrae (thick, dense bone lacking marrow). These fossils came from carbonate rocks deposited in an inter-reef basin, suggesting they lived in shallow water on a carbonate platform (Caldwell and Albino, 2001). A group of at least three species (*P. problematicus, Haasiophis terrasanctus,* and *Eupodophis descouensi*) had hind limbs. Their remains come from marine deposits in the Mediterranean area of the ancient Tethys Ocean or its immediate vicinity (Rage and Escuilié, 2002). Not all Cretaceous snakes were aquatic. Apesteguia and Zaher (2006) describe *Najash rionegrina,* from the Cenomanian (Upper Cretaceous) of Rio Negro Province, Argentina. *Najash* is unique among snakes (fossil and living) in that it has two sacral vertebrae that separate the trunk vertebrae with ribs from the caudal vertebrae without ribs. Thus, this animal has a

Fig. 1.9. The Green Anaconda, *Eunectes murinus,* **(Family Boidae) is the largest living snake and it is highly aquatic. Photography by William W. Lamar.**

pelvis, and articulating with the sacrum were robust functional legs. Additionally, this species was from a terrestrial deposit, with the skull showing characteristics associated with an underground lifestyle. The authors wrote that it was perhaps "…a surface-dwelling species that would occasionally use tunnels produced by burrowers."

The fossil remains of the boid, *Titanoboa cerrejonensis*, from La Guajira in northeastern Colombia, imply the snake reached 12.8 m and a weight of 1,135 kg. It is the largest snake ever discovered, and it was aquatic. The remains were dated 58 to 60 MYA (Head et al. 2009).

Extant Aquatic Snakes

Extant aquatic snakes of all lineages reach their highest diversity in tropical Southeast Asia and Australasia (Heatwole 1999). However, among the advanced terrestrial snakes, some boodontines, colubrines, dipsadids, and natricids use coastal environments and enter brackish water or full seawater. Virtually all other marine species are restricted to Asia and Australia. The only exception is the pelagic hydrophiid *Hydrophis* (*Pelamis*) *platurus,* which has dispersed into the eastern Pacific and the western Indian Ocean). Without a doubt, Asia and Australasia have the most remarkable diversity of aquatic species.

At first, this seems to be due to the abundance of shallow-water habitats. However, the answer may have more to do with the geographical origins of advanced snake lineages. The best-known and most committed aquatic snakes are the fixed front-fanged, paddle-tailed sea snakes (Hydrophiinae: Elapidae), which spend all or most of their life in water and have two or more terrestrial elapid ancestors. The unusual, semi-aquatic sea kraits (*Laticauda:*

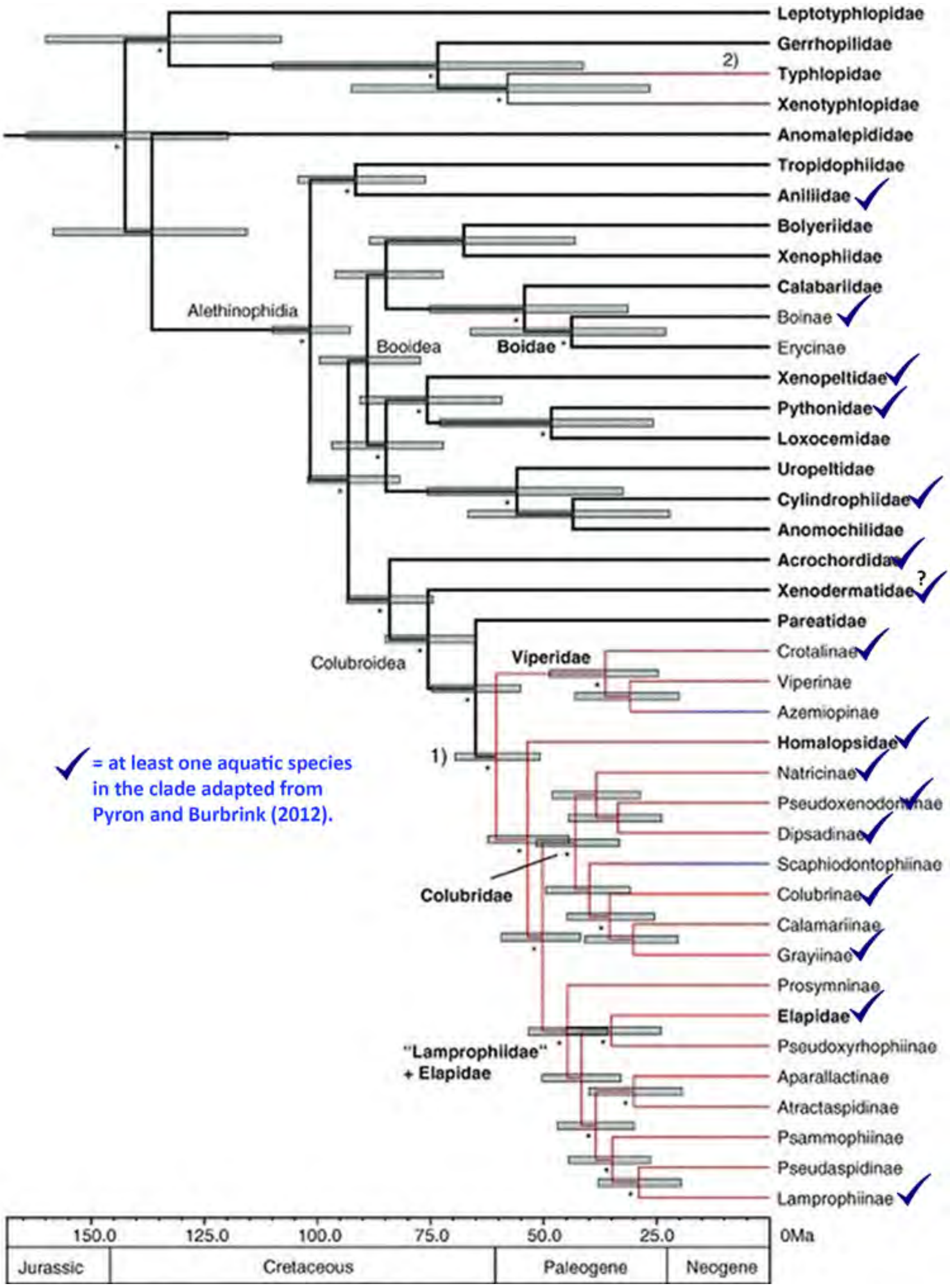


Figure 1.10. Phylogeny of the extant snakes from Pyron and Burbrink (2012) Clades with a blue check mark contain at least one aquatic or semi-aquatic species. This demostrates that aquatic life styles evolved in at least 16 subfamily and family level clades over the past 150 million years.

Elapidae) have paddle tails, broad ventral scales, and terrestrial tick parasites, and they only enter the water to feed. Instead, sea kraits bask, mate, and deposit their eggs in terrestrial locations.

The file snakes (Acrochordidae) seem to spend their entire lives in the water and show numerous adaptations to an aquatic lifestyle, suggesting they, and their ancestors, have been living in the water for an exceptionally long time. Some Oriental-Australian rear-fanged water snakes (Homalopsidae) give the impression that they spend slightly less time in the water than sea snakes and file snakes.

And, as previously mentioned, many of the natricids (Natricidae or Natricinae) are semi-aquatic. However, most species' time in the water is poorly known. This is also the case for many species in other lineages, snakes considered semi-aquatic. Life in the water changes the rules snakes face on land.

Figure 1.11. A preserved specimen of the homalopsid *Cerberus schneiderii*. Note the dorsally oriented eyes and nostrils. The nostril valve on the left side is open, the nostril valve on the right side is closed. Photography by JCM.

Water supports an animal's body weight and is slow to lose or gain heat. Salt in the ocean renders the water undrinkable for snakes and many other animals. Salt also increases the density of water, making animals more buoyant. Warm water reduces the need for basking, but some aquatic snakes live in relatively cold water that originates on mountaintops. Water may lower the risk of predation from terrestrial and aerial predators. Of course, aquatic environments expose their inhabitants to a new set of predators, parasites, and physical environmental challenges.

Aquatic habitats provide abundant food resources in the form of invertebrates, fish, and amphibians and present a variety of new hiding places, such as the intertidal burrow system, the cavities under a riverbank, or the layer of detritus covering the bottom of the pond or stream. All snakes are likely capable of swimming, but some species are much better at it than others.

Many snake lineages have at least a few species adapted to aquatic habitats. Still, five lineages (file snakes, the homalopsids, elapids, dipsadids, and the natricids) contain the most species adapted for life in water. Snake adaptations to water can include modifications to many or all organ systems. However, all adaptations for an aquatic existence do not occur in every species of aquatic snake. Some species have extreme adaptations to life in water, others appear to have very few. Dorsally positioned nostrils and eyes allow the snake to breathe and observe without exposing the head or body to the air. When diving, valves open and close the nostrils, and the trachea opens opposite the internal nares to exclude water from the respiratory tract.

Lateral compression of the body increases the surface for swimming; the ribs may be less bowed and elevated to exaggerate the surface area on the snake's sides. The tail may be flattened, compressed slightly at the base, or turned into a paddle with exaggerated fin-like flaps above and below the vertebrae. Ventral scales are broad in land-dwelling snakes so the snakes can grip surfaces; in some highly aquatic snakes, the ventral scales narrow (i.e., the file snakes), and the belly scales are similar in size to the dorsal scales. This reduction in ventral scales aids the snake in flattening its body for an increased surface area when swimming. The snakes most adapted for aquatic life swallow food while submerged and give birth in the water. Neill (1958) summarized the literature and included personal observations on snakes using brackish and seawater. In some cases, the snakes are directly observed in the water. In other instances, he assumes their saltwater use based upon their proximity to it. Many subsequent papers also discuss this phenomenon. Thus at least some semi-aquatic or mostly freshwater snakes can tolerate high concentrations of sodium ions in their blood (hypernatremia), or avoid absorbing them. This allows them to venture into brackish and marine environments to forage, find mates, or disperse into new habitats for at least a short time. Even some terrestrial species are occasionally seen swimming in the ocean. The list is extensive. The following is organized by family and based on Neill (1958) and other more recent literature.

Tropidophiidae. Neill also found the Cuban trope, *Tropidophis m. maculatus*, beneath debris at the edge of weed-grown tidal flats near Havana, Cuba.

Booids. *Candoia carinata*, Island distribution; Neil found one on Morotai Island, Moluccas, under masses of rooted coconuts at the bases of coconut trees growing above the tidal zone and notes one specimen was found swimming in the sea at Natterer Bay, New Guinea.

An African Sand Boa (*Eryx jaculus*) was found beneath logs close to the beach in Bougie, Algeria.

Pythonidae. Hart et al. (2012) found that hatchling *Python bivittatus* could survive for five months in brackish water and for more than a month in full seawater.

Colubridae. The Florida kingsnake (*Lampropeltis getula floridana*) Carr (1940) listed it as "occasional" in a salt marsh. A close ally, the speckled kingsnake (*L. g. holbrooki*) was found to be as common in the salt marsh as in the woods of southeastern Texas.

Psammophiidae. The European *Malpolon monspessulanus* has been reported multiple times from brackish and saltwater habitats (Deso et al 2021).

Natricidae. Populations of these snakes adjacent to brackish or marine environments can be expected to occur in saline waters on occasion. The green water snake (*Nerodia cy-*

Figure 1.12, *Natrix tessellata.*
Photography by Kai.Kolodziej.

Figure 1.13. *Acrochordus arafurae,* **Gregory River..**
Photography by Scott Eipper.

clopion), the Brown Water Snake, (*Nerodia taxispilota*), the Glossy Water Snake (*Lithodytes rigida*), and Graham's Water Snake (*Regina. grahami*) in brackish marshes. The European water snake (*Natrix natrix*) has been reported in the sea along the Mediterranean coast. The Viperine Water Snake (*Natrix maura*), the Eastern Garter Snake (*Thamnophis s. sirtalis*) the Ribbon Snake (*T. sauritus*) are frequent visitors to saline water. (Neill 1958)

Dipsadidae. The North American Mud Snake (*Farancia abacura*) and the Rainbow Snake (*Farancia erythrogrammus*) use tidal marshes. While the aquatic neotropical genus *Tretanorhinus* uses freshwater habitats, some inhabit mangroves.

Elapidae. The Indian cobra (*Naja naja*) is an adaptable but essentially terrestrial species, occurring in southern Asia's forests, fields, gardens, and human-modified situations. It enters the water readily and has been observed swimming in the sea (Gharpurey, 1954, p. 54). The Australian black snake (*Pseudechis porphyriacus*) has been found swimming in the middle of Botany Bay. The Australian taipan (*Oxyuranus scutellatus*) is abundant around the shores of the Gulf of Carpentaria. And other Australian elapids (species not named) may swim across estuaries (Kinghorn, 1956). And, of course, marine hydrophiids can survive in full seawater as long as they have access to freshwater for drinking.

Viperinae. The Common Viper (*Vipera berus*) is terrestrial but swims readily and has been found many miles at sea off the coast of Ireland (M. A. Smith, 1951).

Crotalinae. Some rattlesnakes (*Sistrurus* and *Crotalus*) use saline habitats. These include the Dusky Pygmy Rattlesnake (*Sistrurus miliarius barbouri*) and the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*).

Thus, freshwater snakes may take a first step into transitioning into brackish or salt water by exploring those habitats. In the reverse situation, brackish water or marine snakes may transition back to freshwater. *Cerberus microlepis*, *Laticauda crockeri,* and *Hydrophis semperi* are in genera that are mostly marine but those species live in freshwater

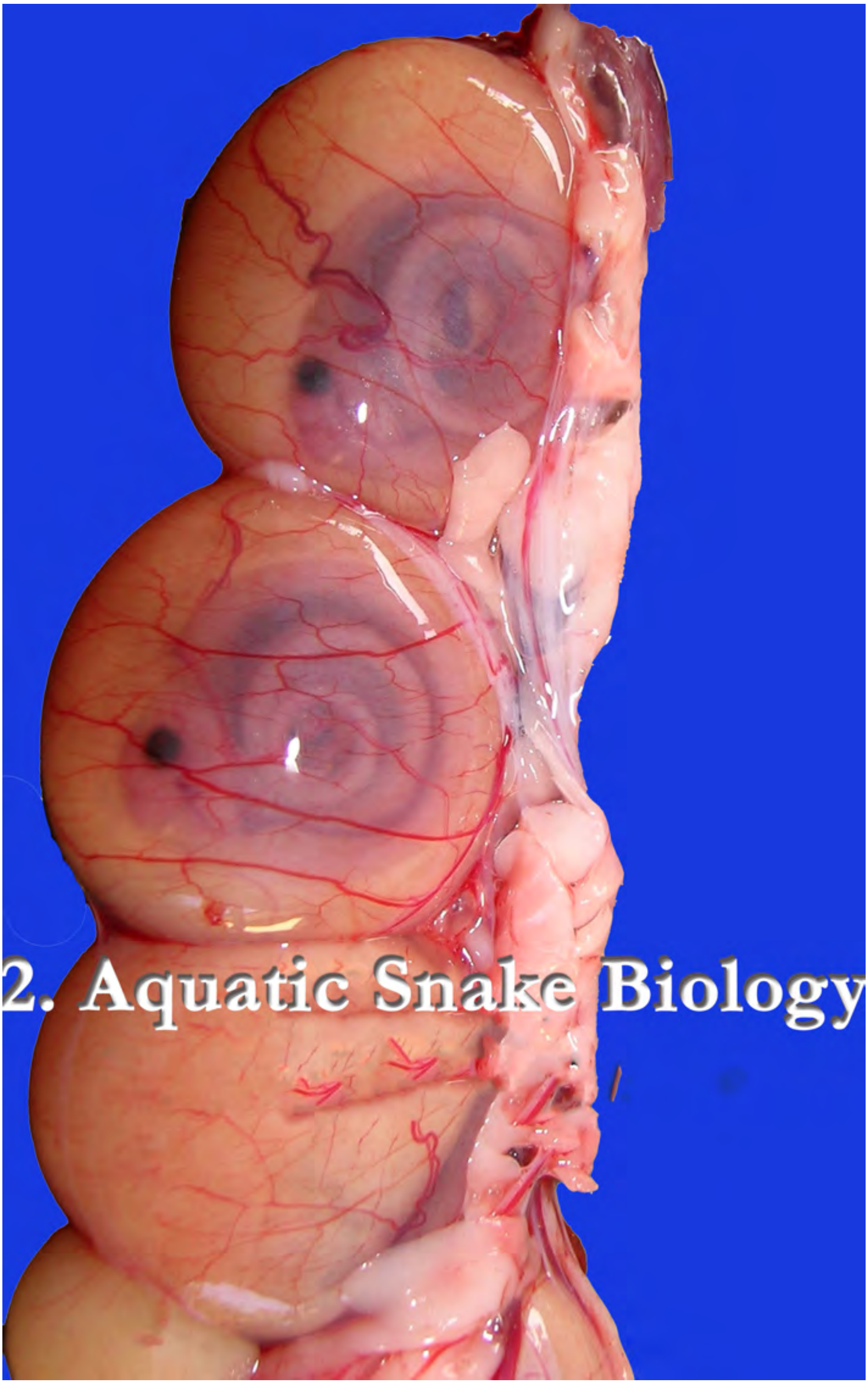
Terrestrial and Freshwater Snakes Visit the Oceans

Coastal populations of snakes that usually inhabit freshwater or terrestrial habitats may venture into brackish or full seawater. *Nerodia* spp. and in particular *Natrix tessellata* have evolved brackish- and low saline tolerant seawater populations (e.g., Mebert 2004, 2005; Tuniyev et al. 2011; Brischoux et al. 2017; Pauwels et al. 2020; Rautsaw et al. 2020). Snakes may get washed downstream into the ocean or brackish water habitats during flooding. Reports of Reticulated Pythons, Eastern Diamondback Rattlesnakes, and many other species swimming between islands are documented. They suggest that these species may intentionally enter the oceans (a hypertonic environment) because they will find food, mates, or a new territory.

Figure 1.14 shows a *Thamnophis ordinoides* on the Oregon coast just north of Port Orford in August 2012. The snake traveled a considerable distance to reach the ocean. The motivation was unknown. Was the snake lost or intentionally entering the marine environment? This individual snake was not washed down a stream during a flooding event (the evidence is the long track in the sand). Nor was it transported to the edge of the Pacific Ocean by humans.

Figure 1.14. (A) A photo from the parking lot taken the same day I (SB) saw the snake. (B) The second photo shows the view from the beach towards the ocean. (C) The third photo shows the snake tracts go right into the ocean. (D-E) The snake tracks in more detail. (F) The snake, a *Thamnophis ordinoides.* **Photography by Sabine Baer.**

On the next page. The major lineages containing numerous aquatic species are Homalopsidae, the elapid subfamily Hydrophiinae, some dipsadids, and the natricids. All clades have independently evolved species with a viviparous reproductive mode, and the evolution of viviparity could have occurred multiple times within a clade. The image on the following page illustrates eggs with developing embryos from an *Enhydris enhydris.* **Photography by Daryl Karns**



2. Aquatic Snake Biology

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Marion Segall

Acquiring an aquatic lifestyle is associated with physical and chemical constraints related to the properties of the water bodies used by vertebrates. The physicochemical properties of water affect many aspects of life, from their locomotion to sensory signal propagation and homeostasis (Houssaye & Fish, 2016; Vogel, 1994). These extrinsic constraints are driving the evolution of aquatic snakes and have led to convergences (e.g., (Gazzola et al., 2014; Stayton, 2011; Vincent et al., 2009) and some specific adaptations. As mentioned in this book, acquiring an aquatic lifestyle has evolved multiple times independently in snakes all over the globe, and species use the aquatic medium to different extents. For all these reasons, aquatic snakes are a great model to study evolutionary convergences and adaptations. This chapter aims to overview the convergences and specificities of aquatic snakes, from their anatomy to their behavior.

Feeding and Drinking

Feeding underwater, and especially prey capture behavior, is mainly constrained by the density and viscosity of water; these hydrodynamic forces work to oppose a strike. The head of snakes, and especially its external morphology, is directly affected by those constraints. The head of aquatic-foraging snakes presents convergent features such as dorsally positioned eyes and nostrils, a short, stout, and a dorso-ventrally flattened head (Esquerré & Keogh, 2016; Segall et al., 2016). The dorsally positioned nostril allows aquatic snakes to breathe at the water's surface without exposing their head. Aquatic snakes have evolved cutaneous respiration to some degree. In *Hydrophis,* up to 23% of its oxygen intake is cutaneous. This led to increased vascularization of their head and brain (Palci et al., 2019). However, snakes' primary oxygen intake process remains pulmonary respiration (Heatwole & Seymour, 1975; Pratt & Franklin, 2010; Udyawer et al., 2016). The dorsal position of their eyes allows predator and prey detection from above (Heatwole, 1999; Trapp & Mebert, 2011); it should be most beneficial for bottom-dwelling ambush species. In addition, the dorsal position of the eye may lead to an increase in binocular vision, which produces a better 3D image and more accurately targets prey (see the section on the sensory systems). The short, stout head, with a barely visible head-neck transition, provides aquatic snakes with a more streamlined body and allows them to reduce the forces opposing an open-mouth strike underwater (Segall et al., 2019). However, aquatic adaptation in snakes seems related to the extent to which they use water suggesting potential evolutionary trade-offs between aquatic and terrestrial lifestyles. For instance, the head shape of aquatic snakes is more hydrodynamic and efficient at capturing prey than one of semi-aquatic species (Segall et al., 2020).

The relationship between head shape hydrodynamics and prey capture success has not been established yet as we lack data on most behavioral aquatic snake species, especially in a natural context. Aquatic snakes are elusive, and field observations of their foraging behavior are rare or insufficient to provide quantitative data or comparative analysis. However, the diet of aquatic snakes is well-known for many species. It is diverse, from generalist/opportunistic snakes fishing for any prey (i.e., *Cerberus*) to highly specialized species eating only specific species of eels (i.e., *Laticauda* sp.), fish eggs, or crustaceans.

Dietary specialization in aquatic snakes is associated with morphological adaptations. In homalopsids, crustaceans specialists have broad heads and short jaws, while piscivorous species have longer, slender heads and jaws (Fabre et al., 2016), a pattern that seems to apply

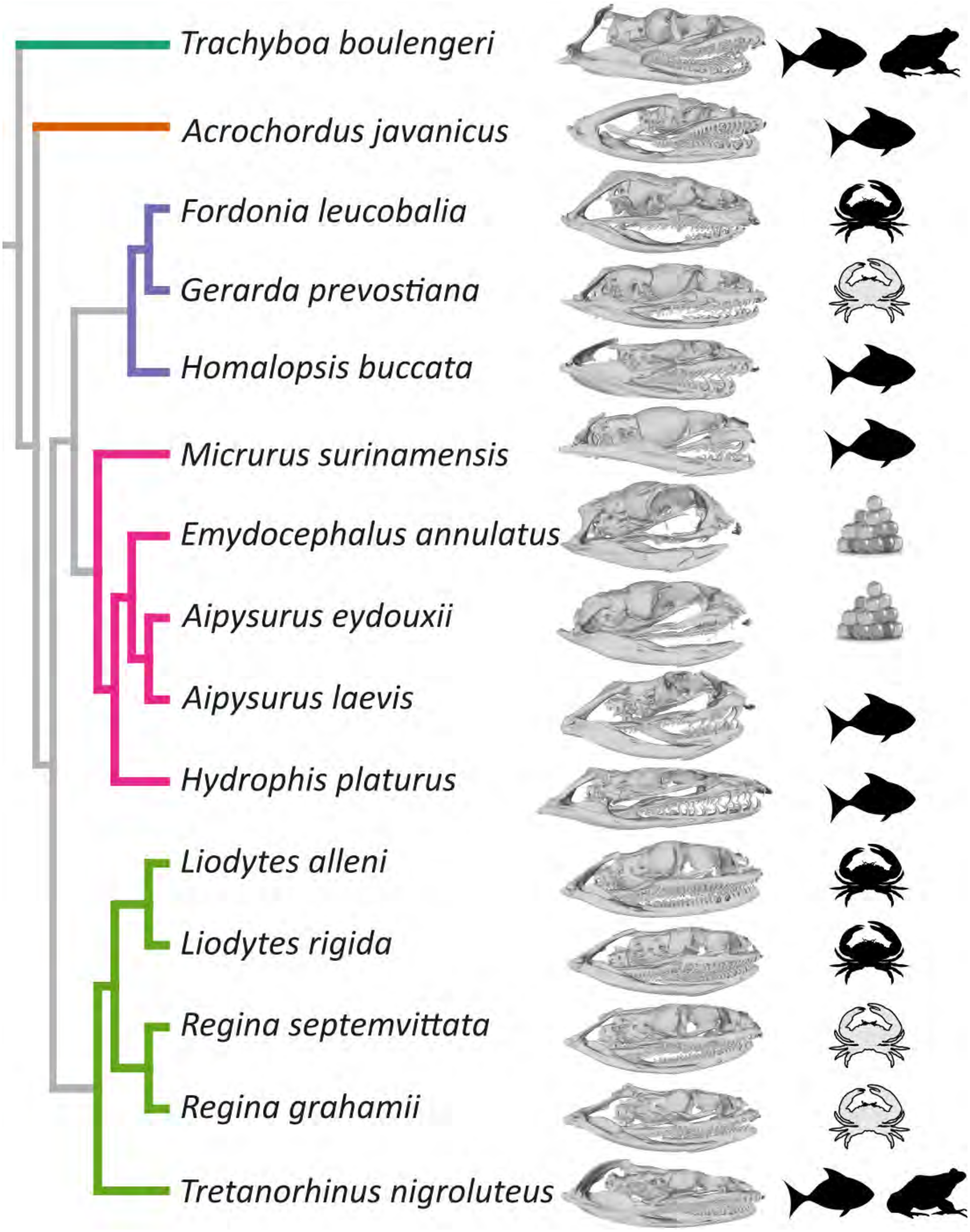


Figure 2.1: Morphological variability in the skull of aquatic snakes. The phylogeny has been adapted from Pyron et al. (2014), color indicates snake families. The silhouettes of the main items in the diet are indicated on the right: fish, anurans, crustaceans, freshly molted crustaceans (black and white), fish-eggs. Skulls from CT scanned specimens (top to bottom) AMNH-R11970, AMNH-R115651, FMNH229747, CAS12391, FMNH229816, AMNH-R152305, AMNH-R161755, AMNH-R14169, AMNH-R161752,AMNH-R19316, AMNH-R159304, AMNH-R160212, AMNH-R101360, AMNH-R162317, AMNH-R103188.

to most aquatic snakes (see below). In hydrophiines, specialization toward burrowing prey has led to the independent evolution of microcephalic species (Sherratt et al., 2018, 2019). Microcephalic sea snakes specializing in eels show convergence and high rates of evolution. However, microcephalic goby-specialists do not. While both are fish, eels and gobies present distinct challenges for snakes: eels are elongated, fierce prey, probably associated with a high manipulation cost, and require an efficient swallowing process.

In contrast, gobies are bulky prey that requires a large gape size through the maintenance of larger head width. This functional hypothesis has been validated on a phylogenetically large sample of aquatic snakes. Yet, the difference in head shape between the two dietary categories (i.e., bulky vs. elongated) is not striking, especially in light of the great head shape variability between all aquatic snakes (Segall et al., 2020). More data on the cost associated with feeding on different prey are needed, such as manipulation time, maximum gape size, or the number of pterygoid walks required to swallow the prey. Such data will establish the contribution of functional constraints related to diet on the head shape of snakes. Unfortunately, for most aquatic species, such behavioral data are lacking.

Morphological adaptations have been found in the skull bones used in aquatic snakes. Most snakes have a hyperkinetic skull composed of over 20 independent bones, and 16 are used in feeding. A study on a phylogenetically large sample of aquatically feeding snakes showed these bones could be divided into functional modules associated with prey capture, restraint, and swallowing (Rhoda et al., 2020). The variation in the shape of each module is related to dietary specialization, either toward durophagy or piscivory. Durophagy in aquatic snakes consists of a dietary specialization toward crustaceans and evolved independently in homalopsids and North American natricids. Anatomically, this specialization is associated with a shorter lower jaw providing a better bite force and a reduction of the number of teeth and smaller and stouter teeth, while piscivorous species have long slender jaws with numerous, long, and sharp teeth that allow them to generate fast prey capture and get a good grip on slippery prey (Figure 2.1)(Rhoda et al., 2020; Savitzky, 1983).

There are two types of crustacean predators in both snake families, the hard-shelled (*Liodytes, Fordonia, Cantoria*) and the soft-shelled (*Regina, Gerarda*) specialists. While the adaptations described above apply to all these species, their "sub-specialization" has led to additional morphological convergences. The hard-shelled specialists have blunter teeth, thickened stomachs, larger gapes, and consume smaller prey (Jayne et al., 2018). Unlike their non-durophagous relatives, crustaceans specialists, except *R. septemvittata*, use their bodies to restrain for capturing and handling their prey, allowing them to reduce their consumption time (Gripshover & Jayne, 2021; Tumlison & Roberts, 2018).

Some crustacean feeders have evolved a unique feeding behavior known as crab-ripping that consists of dismembering the prey's legs and chelipeds. In the case of *Gerarda,* the whole body of large prey, is torn apart, thus circumventing the gape-size limitation (Gripshover & Jayne, 2021; Jayne et al., 2018). Snakes usually swallow their prey whole, limiting the size of the prey they can ingest (Gans, 1974). Besides the crustacean specialists, the only report of food processing in snakes is the evisceration of large toads by the colubrid, *Oligodon fasciolatus* (Bringsøe et al., 2020). Other dietary specializations in aquatic feeding snakes have led to spectacular anatomical adaptations, such as the Hydrophiine snakes that feed on fish eggs such as *Emydocephalus* sp., *Aipysurus eydouxii,* or *Aipysurus mosaicus.* These species have reduced teeth (Fig. 2.1) and derived labial scales for scraping fish eggs from the substrate (Guinea, 1996; Shine, Bonnet, et al., 2004), reduced fangs, atrophied venom glands, and low venom quantity and toxicity (Gopalakrishnakone & Kochva, 1990; Healy et al., 2019; Li et al., 2005).

Among aquatic snake lineages, several species independently invaded saline environments (Murphy, 2012) and hence have to maintain their water balance. Snakes living in marine environments need a source of fresh water. This dependency is reflected in their distribution along coasts or estuaries (Brischoux et al., 2012; Lillywhite & Tu, 2011; Murphy, 2012) and their rainfall-dependent behavior and distributions (Bonnet & Brischoux, 2008; Lillywhite et al., 2008). The few species that live in the open ocean, such as Hydrophis platurus, do not have access to freshwater from land. Still, they drink from rainwater lenses that form at the ocean's surface during the rainy season and suffer severe dehydration during seasonal drought (Lillywhite et al., 2019). Piscivorus snakes suffer further dehydration from a diet of fish that generates an excess of nitrogen that must be excreted through urine, thus increasing the need for freshwater (Lillywhite & Ellis, 1994). When snakes are too dehydrated, they stop eating, probably to avoid additional water loss (Edwards et al., 2021). The dehydration tolerance in marine snakes seems to depend on their access to freshwater and a gradient of habitat specialization.

Estuarine species like *Nerodia* (Edwards et al., 2021), *Acrochordus:* (Lillywhite et al., 2014), *Laticauda*: (Lillywhite et al., 2008), and hydrophiines (Lillywhite et al., 2015) have a lower tolerance than sea snakes. In addition, marine snakes have less permeable skin allowing them to decrease water loss through skin evaporation (Edwards et al., 2021; Lillywhite et al., 2009). To cope with salt and dehydration, sea snakes, acrochordids and at least one homalopsid, *Cerberus rynchops,* have evolved supralabial or sublingual salt glands (Dunson & Dunson, 1973, 1979). Combined with cloacal excretions, they can reduce the excess salt they absorb. However, unlike other marine vertebrates that maintain normal natremia, marine snakes can sustain high salt concentrations (Brischoux et al., 2013) and seem only to use their glands when natremia reaches critical levels. Therefore, osmoreceptors probably alter the snake the snake's condition (Dunson et al., 1971).

Sensory System

Snakes possess an arsenal of senses, from the light and UV spectra, olfaction, and vomerolfaction to mechanoreception and even audio-reception. However, air and water have different physical properties that affect signal propagation, such as refractive index, viscosity, and density. Thus, the sensory system and the preferred sensory modalities used by species depend on the media they use. The sensory system of aquatic snakes presents considerable differences from their terrestrial relatives and some novelties, such as phototactic tails. Among hydrophiines, most of the species of Aipysurus show a behavioral response to light stimulation on their tail, especially in the green and blue spectra, a feature found in other elongated aquatic vertebrates (Crowe-Riddell, Simões, et al., 2019). Other elapid sea snakes show no sensitivity to light along their body, neither does *Aipysurus mosaicus*. The ancestral origin of this different sense remains to be determined. The adaptive value of a photosensitivity body is not well understood, but the tail of sea snakes resembles a paddle and increases their swimming efficiency (see the section on locomotion). Phototaxis could be an adaptive feature if it decreases the risk of tail injuries or predation. However, there is no evidence of how this compares to other sea snakes. The tail of sea snakes also presents scale organs of unknown functions. These may involve mechanoreception (Crowe-Riddell, Williams, et al., 2019). However, compared to the mechanosensitive scale organs found on the head of sea snakes, the ones on the tail have a simpler structure that suggests less sensitivity. Other dermal structures in the tail could be involved in sensory modalities such as phototaxis, but further investigations are needed.

Highly aquatic snakes present various degrees of mechanoreceptor coverage, from the entire body and shark-like skin of acrochordids (Figure 2.2)(Povel & Van Der Kooij, 1997) to the tentacles of

The tentacles of *Erpeton* (Catania et al., 2010) and the scale sensilla on the head of hydrophiines (Crowe-Riddell et al., 2016; Crowe-Riddell, Williams, et al., 2019) detect water movement. These kinds of sensory organs have recently been characterized in Helicops sp. (García-Cobos et al., 2018). Similar mechanosensitive scale organs are present in terrestrial snakes. Still, these scale sensilla are more protruding and more abundant in sea snakes, indicating a better sensitivity than their terrestrial relatives (Crowe-Riddell et al., 2016). However, experiments on *Hydrophis* (*Lapemis*) *curtus* revealed that they can detect a low amplitude pressure variation they might use to detect a nearby swimming fish. However, this might have lower sensitivity than other aquatic animals (Westhoff et al., 2005). Similar results were found with the hearing abilities of sea snakes (Chapuis et al., 2019). Yet, some highly aquatic species rely on mechanosensitive cues to detect and catch their prey. Acrochordids, for instance, catch prey with their whole body, with no visual cues (pers. obs.; Dowling, 1960). *Erpeton tentaculatum* uses its mechanosensitive tentacles to detect prey in the absence of light, yet, this species seems to rely on both visual and mechanical cues for prey detection (Catania et al., 2010). Mechanoreception in other aquatic snakes has not been functionally investigated. Still, *Subsessor bocourti* can strike fish without visual information if the prey touches any part of its body. This suggests that their skin is sensitive to touch and can elicit a prey-capture behavior (MS pers. obs.). Many aquatic snake species use tactile cues, natricids, acrochordids, homalopsids, and even hydrophiines (Drummond, 1979; Heatwole, 1999; Jayne et al., 2018; Rossman et al., 1996; Shine, Brown, et al., 2004; Voris et al., 1978). More controlled experiments to evaluate the sensory modalities aquatic snakes use are needed as mechanoreceptors could be sensitive to water pressure or tactile stimuli (Crowe-Riddell et al., 2016).

Aquatic snakes most likely use several senses to detect and catch their prey, as in *Erpeton.* Previous works demonstrated that the preferred sensory modalities used by aquatic snakes depend on many factors, such as their diet, their prey capture strategy, and the availability of sensory cues (Kutsuma et al., 2018; Vincent et al., 2005; Waters & Burghardt, 2013). Yet, because of the properties of water, the senses of aquatic snakes have functionally diverged from their terrestrial relatives. The most striking –albeit obvious— example of these adaptations is the loss of vomerolfaction and olfaction. Vomerolfaction and olfaction are crucial to trail airborne compounds in terrestrial snakes (Halpern et al., 1997) and to elicit tongue flicks if no other sensory cues are available (Zuri & Halpern, 2003). Because they cannot use their primary olfactory system underwater, aquatic sea snakes have lost most of their olfactory receptor genes (Kishida et al., 2019), while the amphibious Laticaudinae retain most of these genes (Kishida & Hikida, 2010). Despite losing this chemosensory system, most aquatic snake taxa rely on vomerolfaction and olfaction. Its efficiency underwater largely depends on the ecology of species. Although tongue-flicks in some aquatic species, such as acrochordids or hydrophiines, are discrete thanks to an elongation of their long and thin tines (pers. obs., Gove, 1979; Heatwole, 1999), the flicking behavior might warn prey of the predator's presence. This may be a trigger some species have exploited to their advantage by using a "tongue-fishing" technique. Such lingual luring has been reported in semi-aquatic piscivores (Figure 2.3). In North America, natricids, such as *Thamnophis atratus* (Welsh & Lind, 2000), *Nerodia rhombifer* and *Nerodia sipedon* (Czaplicki & Porter, 1974), *Nerodia clarkii compressicauda* (Hansknecht, 2008; Hansknecht & Burghardt, 2010) use lingual luring to attract fish. The behavior was recently reported in *Thamnodynastes strigatus*, a semi-arboreal South American dipsadid that catches fish while hanging on branches (Mario-Da-Rosa et al., 2020).

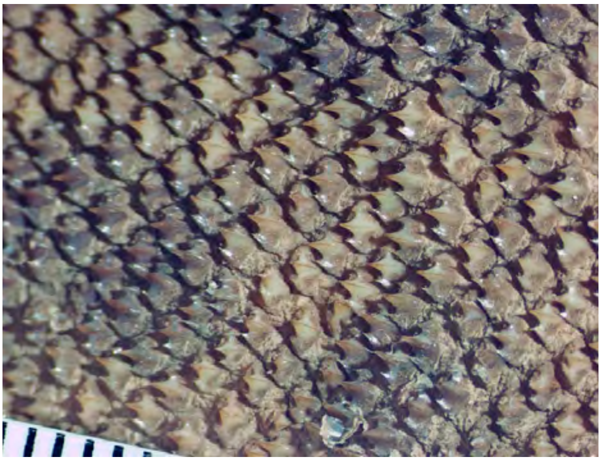


Fig.2.2. The strongly keeled scales of *Acrochordus*. Photography by JCM

This peculiar strategy is used in an ambush context in the presence of visual and chemical cues (Hansknecht & Burghardt, 2010).

The availability and reliability of both chemical and visual cues depend on the environment's properties and the species' ecology. For instance, aquatic ambush predators that need a fast and traceable signal to strike quickly and accurately cannot only rely on chemical cues to detect prey. Because the diffusion of molecules underwater is too slow in lentic environments (e.g., ponds, lakes, swamps) or too fast and untraceable in lotic environments (e.g., streams, rivers). Snakes using ambush strategies might therefore rely more upon visual cues. But active foragers can use chemical signals' excellent persistence and traceability underwater to trail prey over long distances. Such behavior-dependent sensory modalities have been demonstrated in *Acrochordus arafurae;* active-foraging males use chemical cues, while ambush females use vision (Vincent et al., 2005). Generally, piscivores species rely mostly on visual and chemical cues depending on the properties of the environment (Catania et al., 2010; Czaplicki & Porter, 1974; Kutsuma et al., 2018; Shine, Brown, et al., 2004; Udyawer et al., 2020). Crustacean and fish-egg specialists rely on chemical cues (Mark Waters & Burghardt, 2005; Shine, Bonnet, et al., 2004).

Interestingly, some aquatic snakes, such as acrochordids and hydrophiines have a peculiar tongue morphology and flicking behavior that consists of protruding only their long and thin tines. While terrestrial snakes usually extend the fused base of their tongue (MS pers. obs., Gove 1979; Heatwole 1987). Counterintuitively, snakes do not use their forked tongue to stereo-sample chemicals from their environment, and they can trail prey with a single tine (Parker et al., 2008). However, flicking their forked tongue generates a recirculation of the flow to get a better sample of volatile molecules by "mixing" the air (Ryerson & Schwenk, 2014). How the peculiar tongue morphology and flicking behavior of aquatic snakes affect the chemical sampling in these species has yet to be investigated. Unfortunately, we lack comparative data for the tongue morphology and flicking behavior of most aquatic snakes despite the relative ease of access to these data and the recent efforts to maintain aquatic snakes in captivity.

The importance of visual cues in aquatic snakes might have been underestimated. Most snakes respond to visual cues, epecially moving objects (Catania et al., 2010; Drummond, 1985; Shine, 2005), but their acuity is relatively poor (Drummond, 1985; Hart et al., 2012), albeit better than some small mammals (Baker et al., 2007). Using visual cues probably depends on the properties of water, such as turbidity or depth, on the activity period during which species forage, the foraging strategy, and the size of the eyes and their respective position. The size and position of the eyes determine the binocular vision field (i.e., the area where the visual field of each eye overlaps), which allows for depth perception. The dorsally positioned eyes of aquatic snakes might grant them a larger binocular field of vision, thus enhancing their visual-spatial resolution, which would benefit species living in complex habitats. Yet, those have not been measured in most aquatic snakes. Among hydrophiines, species foraging among rocks (i.e., *Aipysurus laevis*) seem to have a visual acuity slightly better than their "bottom cruising" relatives (i.e., *H. curtus, H. major*) (Hart et al., 2012). Despite their limited acuity, aquatic snakes present adaptations of their visual system, such as the accommodation mechanisms in semi-aquatic *Thamnophis, Nerodia*, and *Natrix* (Schaeffel & de Queiroz, 1990; Schaeffel & Mathis, 1991) or the adaptive convergence of the diversification of visual pigments in hydrophiines that provide them with a better vision in the parts of the visible spectrum in their environment (Simões et al., 2020). Similarities have been found in the visual genotypes of *Hydrophis* and *Helicops*, namely a polymorphism in the pigment opsin. At the same site is a unique feature among reptiles that, if the two alleles were expressed, it could provide aquatic snakes with better color vision (Hauzman et al., 2017; Simões et al., 2015; Simões et al., 2020). Still, additional work is needed to validate this functional hypothesis.

The importance of the contribution of vomerolfaction, olfaction, and vision in aquatic snakes is reflected in the endocranial space allocated to both senses. The olfactory and optic tract morphology are related to aquatic species' activity period. Diurnal snakes have an optic area larger than nocturnal species, while the olfactory tract is bulkier in nocturnal snakes. Many species, however, can be active day and night and show an intermediate morphology (Segall et al., 2021). Besides its reflection in the endocranium, the activity period is related to eye size, with diurnal snakes having larger eyes (Da Silva et al., 2017; Liu et al., 2012). However, aquatic snakes also have a relatively thick spectacle (Da Silva et al., 2017) which does not seem to prevent light transmission (Simões et al., 2016) and might protect the eyes from fluid pressure. It would be interesting to test whether the spectacle thickness depends on the maximum pressure experienced by snakes. Or if it depends on the maximum depth encountered during diving. Or, does it depend on the physical properties of the media, such as the viscosity and density of the water used by "mud" snakes. Or the speed of the stream flow for snakes living in rivers.

Finally, while the sense of balance has rarely been functionally investigated in snakes, it is likely to play a crucial role in these limbless tetrapods, especially those moving in a 3D environment that offers no (or negligible) body support, such as water. Balance control is essential in locomotion and is therefore developed in the following section.

Locomotion

All aquatic snakes use undulations to move underwater; they generate a wave that propagates from their head and extends to their tail thus inducing forward motion at a constant frequency. However, the amplitude of the wave increases along the body (Francois Brischoux et al., 2010; Jayne, 1985). Some sea snakes can swim backward by generating reverse undulations (tail-to-head), probably similar to the backward swimming of eels (D'Août & Aerts, 1999). The pelagic sea snake, *Hydrophis platurus,* often uses this behavior to chase fish swimming nearby. The specific eel-like morphology and the paddle-like tail of sea snakes probably facilitate this backward motion. Yet, the homalopsid *Subsessor bocourti*, which does not have a specialized tail seems able to swim backward (MS pers. obs.)

Snakes show various degrees of aquatic adaptation depending on how much time they spend in the water. More aquatic species, such as acrochordids or hydrophiines (Lillywhite, 1996; Shine & Houston, 1993), present a lateral compression of their body that increases their swimming efficiency (Brischoux & Shine, 2011). In addition, most sea snakes can expand their skin ventrally. At the same time, the semi-aquatic natricine, *Nerodia sipedon*, can actively compress its body laterally through rib movements to increase the body surface that is used to generate propulsion during swimming (Pattishall & Cundall, 2008). The skin of aquatic snakes also demonstrates several degrees of adaptations related to locomotion and habitat use (Martínez et al., 2021). Most highly aquatic snakes' bodies are uniformly covered in small, rough scales, even their belly. While the hydrodynamic advantage of such skin roughness has not been characterized in snakes, the ridges in shark skin are associated with drag reduction and thrust enhancement (Oeffner & Lauder, 2012). Another –yet to be functionally tested—morphological characteristic providing aquatic snakes with a hydrodynamic advantage is their almost absent head-neck transition. Unlike most other snakes, except fossorial species (see Discussion), the tips of the mandibles are barely noticeable without palpation, giving aquatic species a streamlined profile, which might prevent the formation of vortices at the rear of the jaw, thus reducing drag.

While snakes' elongated, slender body is hydrodynamically advantageous as it reduces pressure drag, the absence of limbs requires specific adaptations to prevent their body from rolling - absent a hard substrate to stabilize them. To control their buoyancy and balance, aquatic snakes have evolved anatomical specificities, such as an elongated lung,

Figure 2.3. ***Nerodia*** **tongue luring. Photography by Kerry A. Hansknecht**

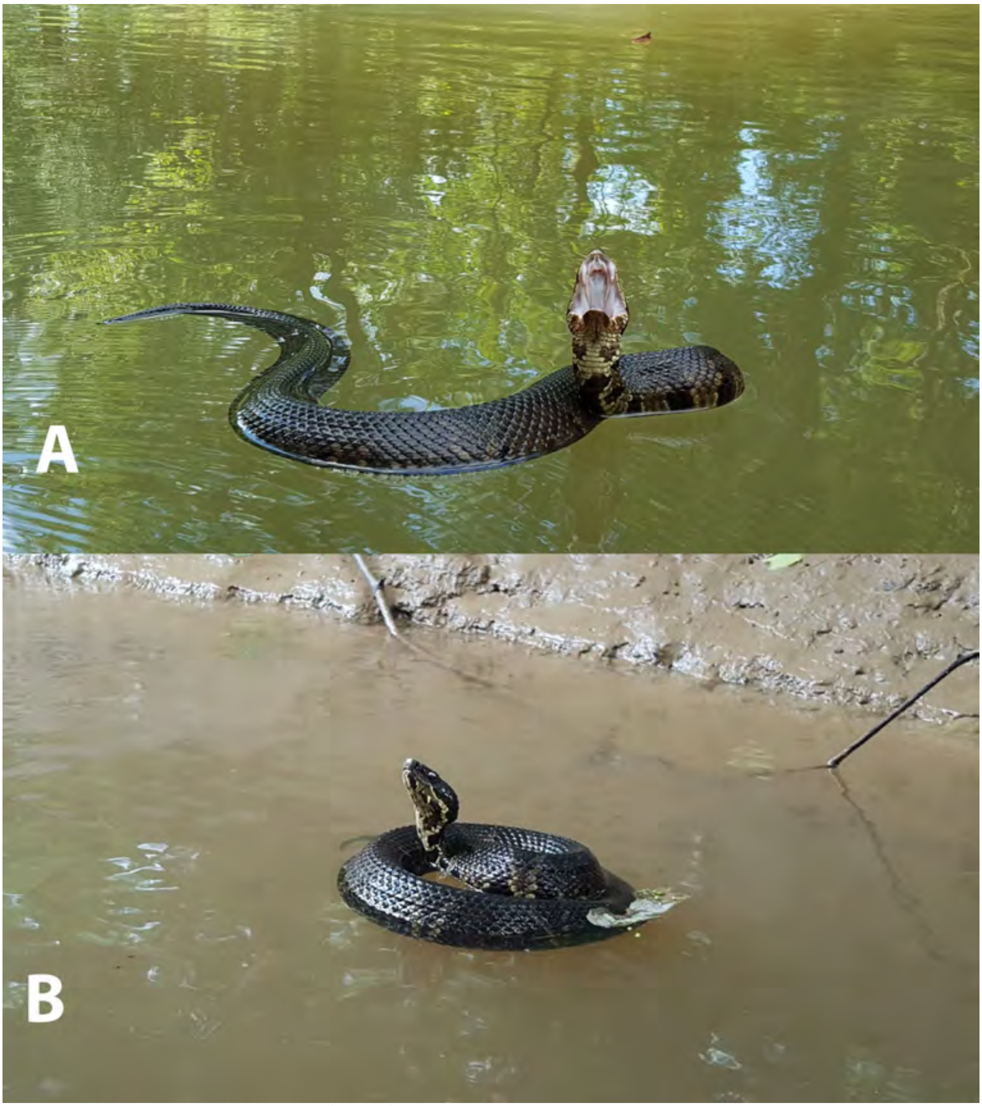


Figure 2.4. Water moccasin, *Agkistrodon piscivorus,* **(A) displaying and (B) coiling at the water's surface. Photography by Seth LaGrange.**

that can extend up to 80% of the total body length of the animal (Cook & Brischoux, 2014; Jayne, 1985; Lillywhite et al., 2012). Some semi-aquatic species, like the heavy-bodied water moccasin *Agkistrodon piscivorus*, demonstrate remarkable buoyancy and balance control while swimming and resting at the surface (Herault et al., 2021) (Fig. 2.x). However, more aquatic species, such as *Nerodia,* sink when they stop swimming (Jayne, 1985). Such impressive stability without a solid substrate requires fine sensorimotor control of balance.

Several sensory organs achieve balance in snakes—the inner ear, sense linear and rotational accelerations of the head. The somatosensory system comprises mechanoreceptors on the joints, muscles, and tendons. And, along the spinal cord, which is sensitive to stretching, generates a proportional reflex response (Crowe, 1992). In addition, the proprioceptive system and the mechanoreceptors in the skin may provide information on pressure. Some studies have demonstrated a relationship between the different structures involved in balance: the inner ear (Palci et al., 2017; Yi & Norell, 2015), skin mechanoreceptors (Crowe-Riddell et al., 2016), the cerebellum (Macrì et al., 2019; Segall et al., 2021) and visual system (Simões et al., 2020) vary with the ecology and behavior of aquatic species. However, we know little about the functional relevance of those anatomical variations, nor do we see the contribution of the different systems in maintaining balance and their available integration.

Discussion

Aquatic snakes are a fantastic study system for many reasons. First, independently acquiring an aquatic lifestyle during the evolutionary history of snakes and their wide geographic distribution make them a fertile ground for studying morphological and functional convergences and, more generally, in our understanding of the evolutionary success of snakes through exceptional adaptability. Second, their ecological and behavioral richness, from semi-aquatic and semi-arboreal species such as *Psammodynastes* or *Grayia*, that catch fish from branches to the aquatic sea snakes that scrape fish-egg, *Aipysurus eydouxii* or *Emydocephalus* sp., or the semi-fossorial homalopsids *Brachyorhos, Calamophis,* and *Hypsicopsis* or the natricids *Regina* and *Liodytes* that exploit burrow systems, provide an opportunity for the study of niche invasion or habitat adaptation. Finally, despite a growing scientific interest, there is much to discover about aquatic snakes' ecology, behavior and evolution.

Among these various topics, attention should be drawn to the natural history of these snakes as these data are the base for most evolutionary studies and could help us unravel the ecological origins of snakes. This debate is fueled by the many convergences –or at least resemblances—between fossorial and aquatic species. For example, fossorial snakes also bear sensilla on the head. However, flatter than those of aquatic species (Povel & Van Der Kooij, 1997), they have thick spectacles (Da Silva et al., 2017) and small eyes (Liu et al., 2012), no noticeable head-neck transition, dorsally positioned eyes and a short, stout and flat head (Esquerré & Keogh, 2016). Besides these resemblances, some aquatic species use burrows from crustaceans or coral reefs to forage or hide, which might have led to selective pressure toward more streamlined (or smaller) heads (Fabre et al., 2016; Sherratt et al., 2018). Therefore, classifying these species as aquatic might result in biased conclusions regarding the ecological origin of snakes.

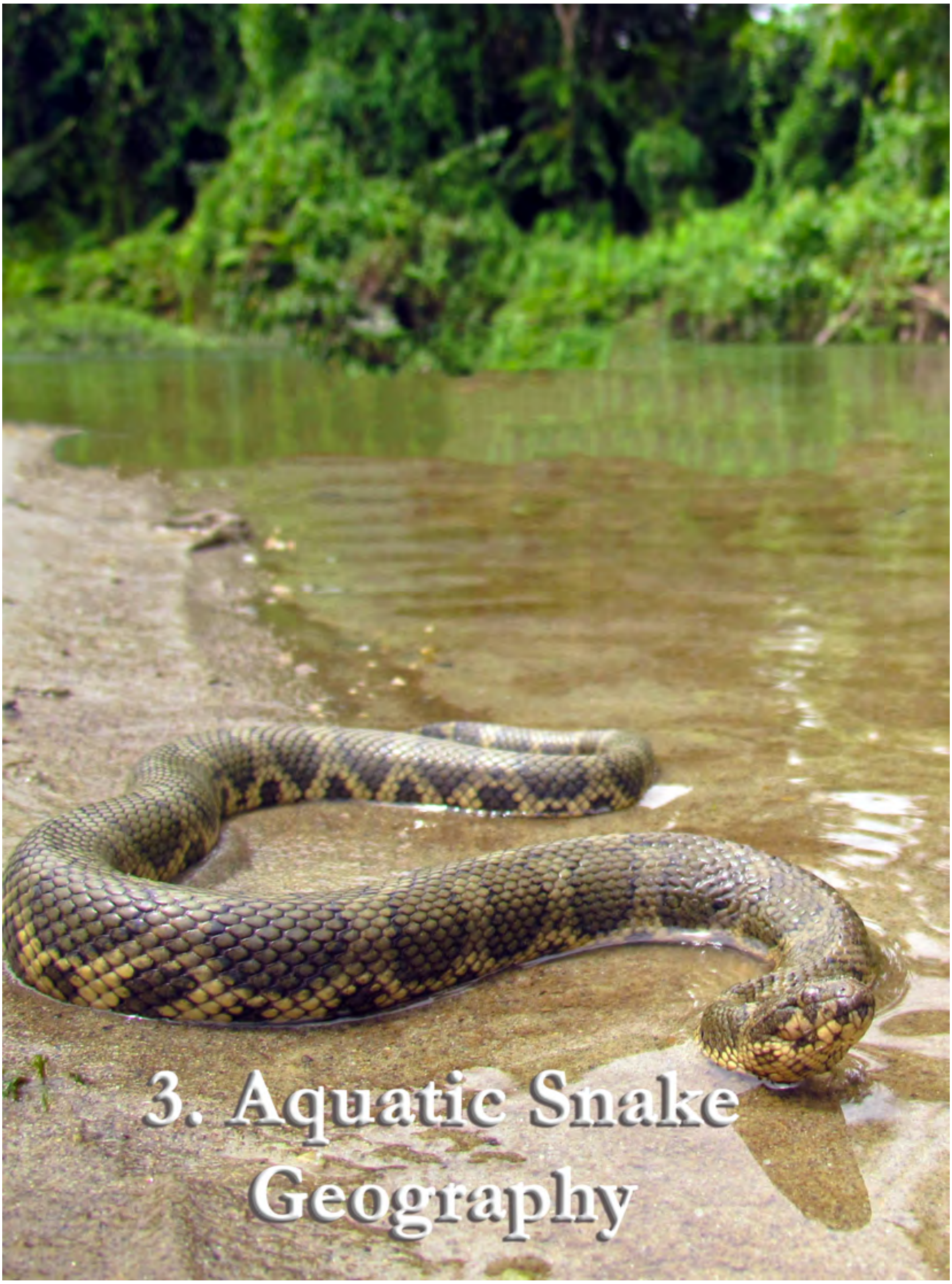
Similarly, fossorial habits are attributed to species with distinct ecologies, from leaf-litter snakes, burrow-users, and active burrowers. In contrast, each ecology is probably associated with different mechanical constraints, resulting in various degrees of selective pressure. Palci and colleagues emphasized this issue in their study on the inner ear of snakes (Palci et al., 2017).

We need a better understanding of the ecology of extant snakes and how they interact with their environment to understand what drives their evolution. For instance, one might consider that aquatic snakes roughly share the same ecology as they use water as a medium. Yet, each aquatic environment has its constraints, from quiet ponds to streams, brackish water to the deep ocean. Each habitat impacts the biology of snakes and should be differentiated while investigating the evolution of aquatic organisms. Drawing a more accurate description of the body of water they inhabit, along with their habitat use (i.e., to what extent the animals use water as a resource) would allow us to understand the evolution of aquatic snakes better. Knowledge of habitat use and the quantifiable aspects of ecology would increase our understanding of snakes' evolution and ecological origins.

To conclude this chapter with a thought, or more precisely, a lead that might deserve attention to shed light on the origin of snakes. The key might lie in semi-fossorial/

semi-aquatic species such as *Cylindrophis ruffus,* homalopsids such as *Fordonia, Gerarda, Cantoria, Myron*, and the natricid *Liodytes,* as well as other aquatic species that use burrows or actively burrow in the mud. These species' inner ear and endocranium demonstrate similarities (Allemand et al., 2017; Palci et al., 2017) and an intriguing convergence with the fossil species *Dinilysia patagonica* (Palci et al., 2017).

On the next page. The homalopsid *Ferania sieboldi* inhabits the large rivers that drain the Himalayas. Photography by Avrajjal Ghosh.



3. Aquatic Snake Geography

3. Aquatic Snake Geography

Lakes, rivers, swamps, marshes, peatlands, mangroves, estuaries, and oceans provide habitats for much of Earth's biodiversity. Marine, brackish, and saline ground water compose 97% of all the water on Earth. Freshwater is only 2.5% of the planet's water. Most freshwater is in the polar ice caps, groundwater, and soil moisture. Liquid freshwater at the surface is 0.01% of Earth's total water in lakes, swamps, and rivers. Lakes contain about 87% of fresh surface water, including 29% in the African Great Lakes, 22% in Lake Baikal in Russia, 21% in the North American Great Lakes, and 14% in other lakes. Swamps have most of the remaining freshwater, followed by rivers, most notably the Amazon River. The atmosphere contains a mere 0.04% water (USGS, WWW).

The areas of the globe and the aquatic snakes they support are summarized here by continents, island groups, and oceans. Maps in this chapter were made using ESRI and the World Surface Water Layer.

North America and the Caribbean

Aquatic North American snakes represent three family/subfamily level clades, Dipsadidae, Natricidae, and Viperidae.

Dipsadidae snakes are diverse in Central and South America. But relatively few species occur in North America, and only Farancia is aquatic. Grazziotin et al. (2012) found the phylogenetic placement of North American dipsadids unstable and controversial.

There are three semi-aquatic vipers in North America. First, the Massasauga Rattlesnake, *Sistrurus cantenatus,* uses an unconventional aquatic habitat – flooded crayfish burrows for over-wintering. But they also use mammal burrows and logs for over-wintering. Secondly, the two semi-aquatic viper species are the Northern Cottonmouth, *Agkistrodon piscivorus*, and the Southern Cottonmouth, *A. conanti*. These snakes spend much of their time in shallow water swamps, catching fish, frogs, and other prey. Wüster et al. (2008) found the New World pitvipers diverged from their Asiatic sister group at approximately 24 MYA, and the first radiation of the New World clade occurred at about 22 MYA.

Most North American aquatic snakes are in the family Natricidae, and aquatic and semi-aquatic taxa occur in five genera forming the clade Thamnophiini. *Clonophis, Nerodia, Liodytes, Regina,* and *Thamnophis.* These species shared an ancestor with the Eurasian genus *Natrix* about 29 MYA, and radiated about 12 MYA in North America (Depaak et al. 2022).

The Thamnophiini inhabit the most extensive wetlands in North America, the western US, and Mexico. All of these species are viviparous

The Gulf Coastal Plain extends from the southeast coast of the US to southern Texas and into Mexico and expands inland at some locations for hundred miles. The region covers over 250 million square kilometers. The area has high biodiversity and was long overlooked as a global biodiversity hotspot. Noss et al. (2015) showed the Gulf Coastal Plain is older, more climatically stable than usually assumed, and rich in species, some of which are endemics. They consider the region a biodiversity hotspot. The Lower Mississippi Valley (including the delta) was North America's largest forested wetland ecosystem. The floodplain extends from the confluence of the Mississippi and Ohio rivers at Cairo, Illinois, to the Gulf of Mexico. The drainage basin encompasses 41% of the continental United States. The floodplain is a mosaic of ridges, swales, meander belts, and swamps that support a diverse and ecologically rich forested wetland ecosystem.

Figure 3.1. Wetlands and rivers in Canada and the USA.

The area also includes the Everglades of southern Florida – a shallow, slow-moving river from Lake Okeechobee to Florida Bay dominated by grass. Water levels drop during the dry season except for the deeper locations. As a result, the region supports rich biodiversity and many invasive species that arrived via the pet trade, including the highly publicized invasive Burmese Python.

The Cuatro Ciénegas Basin is a Chihuahuan Desert wetland in Coahuila, Mexico. It includes several natural springs that supply over 200 small ponds and wetlands, covering 1500 square kilometers. The wetlands are part of the UNESCO-designated Cuatro Ciénegas biosphere reserve. The basin has long been known for its exceptional biodiversity, including North America's most significant number of endemic species (Stein et al., 2000). The region is a biological island on the Sierra Madre Oriental's northern extension and ranges in elevation from about 740 m on the grassy basin floor to above 3,000 m in the surrounding mountains. Abundant freshwater originates in springs that emerge from hundreds of interconnected, spring-fed pools and spring-fed lakes with endemic fish, aquatic snails, and crustaceans. Semi-aquatic snakes found here are in the genera *Thamnophis* and *Nerodia*.

To the south, the trans-volcanic belt in southern Mexico supports seven endemic semi-aquatic *Thamnophis eques* populations that have been recognized as subspecies.

The Gulf of California has about 300 estuaries and other wetlands and is the northern-

Figure 3.2. The wetlands and rivers of Middle America.

most limit for the distribution of mangroves in the Eastern Pacific. On the west coast of the Gulf of California, mangroves are distributed from the Cape region to the center of the Baja California peninsula. These are primarily in small bays, estuaries, and isolated pockets. On the Gulf's eastern side, mangrove forests are distributed southward from Tiburon Island in Sonora to Sinaloa and Nayarit in large coastal lagoons with extensive mangroves. On the Pacific side, the largest mangrove forests occur inside the coastal lagoons of Magdalena Bay. (Aburto-Oropeza et al. 2008).

The region contains the endemic semi-aquatic garter snake, *Thamnophis validus,* a polytypic species that use mangroves and freshwater habitats. The area also supports the Yellow-bellied Sea Snake, *Hydrophis platurus*, an elapid. It is unclear if *Hydrophis platurus* is a resident population that migrates in and out of the area or is composed of waifs.

Relatively few semi-aquatic and aquatic snakes occur in Central America. The snake genera containing aquatic species are the tropidophiid genus *Trachyboa* is represented in Panama; the dipsadid genera: *Hydromorphus, Tretanorhinus,* and *Erythrolamprus,* and the natricid genera *Nerodia*, and *Thamnophis*. Central America covers about half a million km2 with steep topography concentrating wetlands in lowland and coastal areas. Lake Nicaragua is the largest body of fresh water in Central America. The limestone plain of the Peten in northern Guatemala has a mosaic of lakes, rivers, and wetlands, including the Laguna del Tigre, a vast expanse of palm forests, flooded forests, grasslands, and mudflats, which together form the largest Central American wetland. Coastal Belize has a chain of saltwater and freshwater lagoons surrounded by flooded forests, mangroves, and swamp forests, along much of its coastline. The Caribbean coasts of Honduras, Nicaragua, and Costa Rica have tidal lagoons with mangroves, swamp forests, and palm swamps that stretch inland and cover much of the landscape. Mangroves occur on the Atlantic and Pacific coasts, and the largest concentrations occur in the Gulf of Fonseca, Nicoya, and the Gulf of Panama, *Hydrophis platura* is a likely resident. Unconfirmed records of the sea krait *Laticauda colubrina* from the Pacific coasts of several Central American countries: Nicaragua (Villa, 1962), Mexico (Alvarez de Toro, 1982), and El Salvador are also noted by Cogger and Heatwole (2006).

There are no sea snakes in the Caribbean (but see Shuntov 1965; Hernández- Camacho et al. 2006) or Atlantic, and very few aquatic snakes on Caribbean islands. However, the Mangrove Water Snake, Nerodia clarki (a natricid), is in the Bahamas, and the tropical water snake, *Tretanorhinus variabilis* (a dipsadid), is present in the Cayman Islands, Cuba, and on some islands off the coast of Central America. Trinidad's continental fauna has six aquatic species, the booid *Eunectes murinus*, the dipsadids *Hydrops triangularis, Helicops angulatus*, two species of *Erythrolamprus* (one of these is found on Tobago), and one species of *Thamnodynastes.*

South America

South America has a rich aquatic snake fauna, undoubtedly due to the large river basins of the Orinoco and Amazon and many smaller rivers, and the ancient Pebas Wetlands.

The Orinoco River Delta of Venezuela and Colombia covers 36,000 square kilometers and is dominated by a brackish shoreline of mangrove forests. The Llanos are on the western side of the Orinoco River in western Venezuela and northern Colombia. It covers 450,000 square kilometers and is one of South America's most extensive inland wetlands. The llanos have a winter dry season with a summer wet season that produces annual flooding. Savannas dominate the region.

Aquatic snakes in the region are numerous and include members of the genus Anilius and aquatic burrowing species estimated to have a minimum age of 72.1 Ma (Head 2015). booid genus *Eunectes,* and the dipsadid genera *Erythrolamprus, Hydrops, Helicops, Hydrodynastes, Pseudoeryx*, *Tretanorhinus* and the elapid genus *Micrurus.*

Reynolds et al. (2013, 2014) found the anacondas of the genus Eunectes to be the sister of *Epicrates*. *Eunectes* appear to have evolved by the middle Miocene (Hoffstetter and Rage, 1977; Hsiou and Albino, 2009) based on the fossil remains of *Eunectes stirtoni. Epicrates* and *Eunectes* diverged about 25.3 Ma (19.2–32.5 Ma). Thus, *Eunectes* appears to have separated from South American *Epicrates* in the Oligocene (19.2–32.5 Ma), followed by subsequent diversification into the four extant species.

There are two species of aquatic coral snakes (Elapidae), *Micrurus surinamensis* in the Amazon basin and *M. natteri* in the Orinoco basin.

The aquatic dipsadid genera include *Erythrolamprus, Hydrops, Helicops, Pseudoeryx,* and *Hydrodynastes.* The genus *Erythrolamprus* contains 55 species, of which 48 occur in South America. While most are terrestrial, at least a few are semi-aquatic. They tend to feed on fish, frogs, and lizards. They are oviparous and tend to be less than a meter in length. The genus is in the clade Xenodontini.

The clade Hydropsini includes three aquatic genera H*ydrops, Helicops,* and *Pseudoeryx*. *Hydrops* contains three species restricted to South America east of the Andes and the continental island of Trinidad.

Hydrops martii and *H. triangularis* have overlapping distributions and occur in syntopy, especially along the central Amazon basin and the Iquitos region. *Hydrops caesurus* has a distribution outside of the Amazon basin. *Hydrops martii* is restricted to tropical and subtropical moist broadleaf forests. The distribution of *H. triangularis* is associated with tropical and subtropical moist broadleaf forests, and it is present in tropical and subtropical grasslands, savannas, and shrublands in Venezuela and Bolivia. The distribution of *H. caesurus* is associated with flooded grasslands and savannas, in Brazil, Paraguay, and Argentina. The distribution does not overlap with the other two species. Ecological barriers of river basins likely drive the distributions of these species. One biome, tropical and subtropical dry broadleaf forest, is between the northernmost localities of *H. caesurus* and the southernmost localities of *H. triangularis.* Neither species has been recorded in this biome (von May et al. 2019).

Helicops contains 20 species with distributions in South America, mostly east of the Andes. The genus is poorly studied but interesting because some populations have been

Figure 3.3. The wetlands and rivers of South America.

suggested to have facultative viviparity and cryptic diversity (Murphy et al. 2020; Schöneberg and Köhler 2022).

The genus *Pseudoeryx* occurs in Amazon lowland rainforests and the Chaco of northern Argentina and Paraguay (Giraudo and Scrocchi 2002) it is poorly known. However, the discovery of a second species of *Pseudoeryx,* in the Lake Maracaibo Basin supports previously hypothesized paleogeographic reconstructions of the changing course of the Orinoco River (Schargel et al. 2007).

The two species of *Hydrodynastes* are large (approach or exceed three meters) and widespread. Zaher et al. (2019) found Hydrodynastes to be the sister to the terrestrial and arboreal *Oxyrhopus* and *Siphlophis*. In addition, the highly aquatic *Tretanorhinus* was found to be paraphyletic by Zaher et al. (2019). The genus also occurs in Cuba, and Central America.

Gomesophis the Brazilian endemic is the sister to *Thamnodynastes* (Zaher et al. 2019). The 21 species in the genus *Thamnodynastes* are not monophyletic (Zaher et al. 2019) and it has and has many semi-aquatic-arboreal species specialized to feed on frogs.

The Amazon River Basin covers 300,000 square kilometers, is 3,000 km long, and floods 5-15 meters annually. It is the world's largest river, with a flow that results in about one-sixth to one-fifth of all the world's fresh water. It is so large that it creates its own weather patterns.

The Ancient Pebas Wetland

In what is now the Western Amazonia, an ancient wetland was likely the incubator for aquatic snake evolution on the South American continent. Hoorn et al. (2010) reviewed the characteristics of this mega-wetland and its phases of development. The region consisted of fluvial systems that originated on the Amazonian Craton and were directed towards the sub-Andean zone and the Caribbean. In the Early Miocene, the fluvial systems were primarily replaced by lakes, swamps, tidal channels, and marginal marine embayments, forming a mega-wetland.

At its maximum extent, the wetland covered over 1.5 million square kilometers comprising much of the present western Amazonian lowlands. Descriptions of the snake fossils from the Pebas system have not yet been published. Salas-Gismondi et al. (2015) report on the crocodilians from two species-rich bonebeds from late Middle Miocene proto-Amazonian deposits of northeastern Peru and some highly aquatic snakes throughout the Neogene.

In Amazonia, marine incursions are recorded as thin beds in the Middle to Upper Miocene fluvial strata and contain evidence of marine and coastal taxa (foraminifera, mangrove pollen).

The Pantanal

The Pantanal is the largest tropical wetland and the world's most extensive flooded grasslands. The region is a vast alluvial floodplain in southwestern Brazil's upper Paraguay River basin. The subsidence that created the basin probably occurred about 2.5 Ma and was subject to severe climatic changes during the Quaternary. It was a sandy desert during the last glacial period 13,000 years ago. About 80% of the Pantanal floodplains are submerged during the rainy seasons, supporting a diverse collection of aquatic plants and animals.

The gradual slope of the basin receives runoff from the upland Planalto highlands and slowly releases the water through the Paraguay River and its tributaries. The concave formation resulted from a pre-Andean depression of the earth's crust, related to the Tertiary

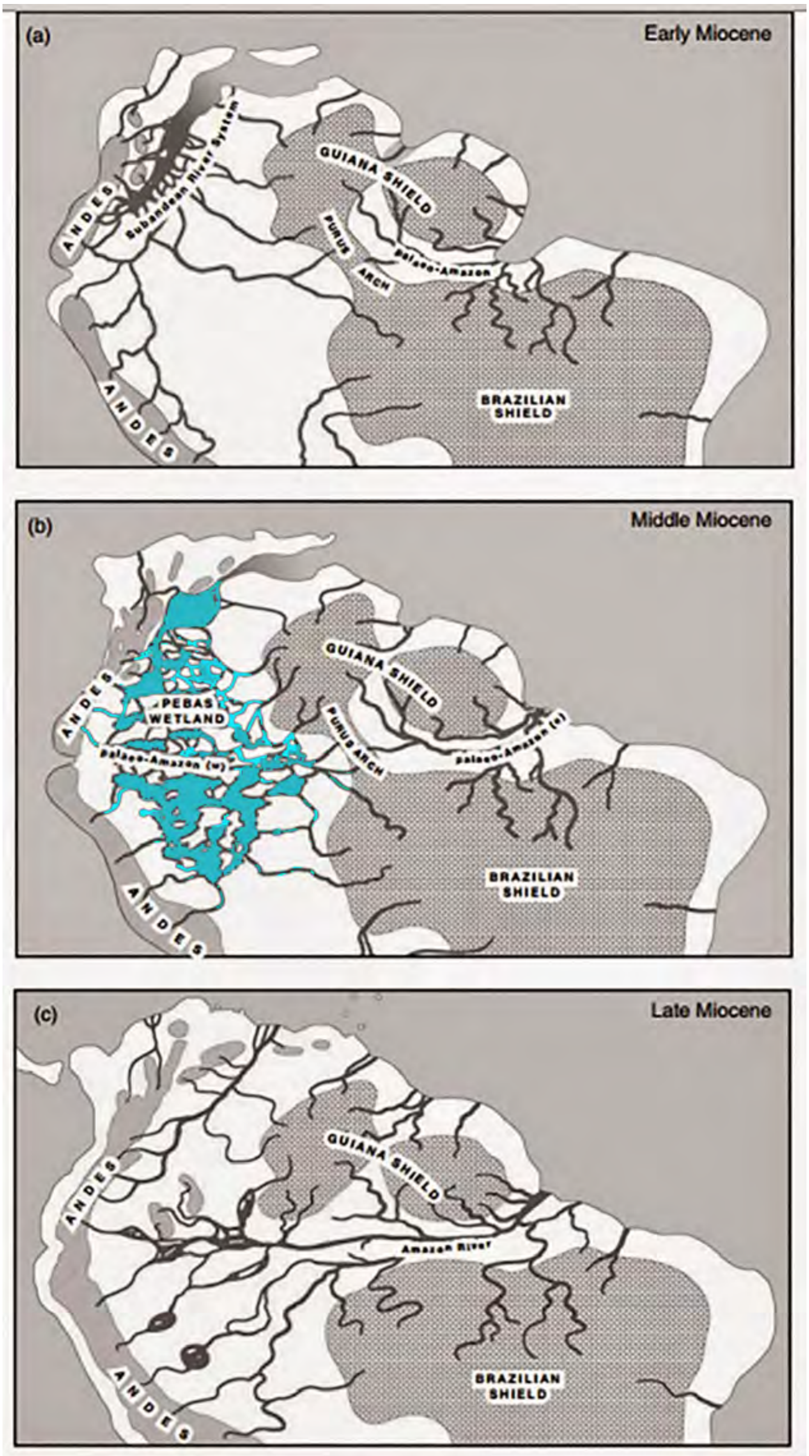


Figure 3.4. The development and reduction of the Pebas Wetland. From Hoorn and Wesselingh, 2010.

Andean orogeny. It constitutes a huge inland delta, in which several rivers flowing from the surrounding plateau merge, depositing their sediments and erosion residues.

The Pantanal is bounded by mostly arid habitats - the Chiquitano dry forests to the west and northwest, the arid Chaco dry forests to the southwest, and the humid Chaco to the south. The Cerrado savannas lie to the north, east, and southeast. Throughout the year, temperature varies about 6.0 °C, with the warmest month being November (with an average temperature of 26 °C) and the coldest month being June (with an average temperature of 20 °C).

Europe

Europe has few aquatic snake species, all in the natricid genus Natrix. However, Zaher et al. (2019) found Natrix to be the sister to all New World natricids. Mediterranean Sea Deltas. The Rhone River Delta forms France's most important wetland, the Camargue, covering about 9,000 square kilometers. The dealt has a hot, dry summer and cool, wet winters. About a third of the Camargue comprises lakes or marshland. Its brine ponds provide one of the few European habitats for the greater flamingo.

Po River Delta – Venice. The Regional Park of the Po River Delta is in the provinces of Ravenna and Ferrara, in the Emilia-Romagna region, was established in 1988 to safeguard the native flora and fauna of this area. It is a unique environment and was declared a human heritage site by UNESCO in 1999.

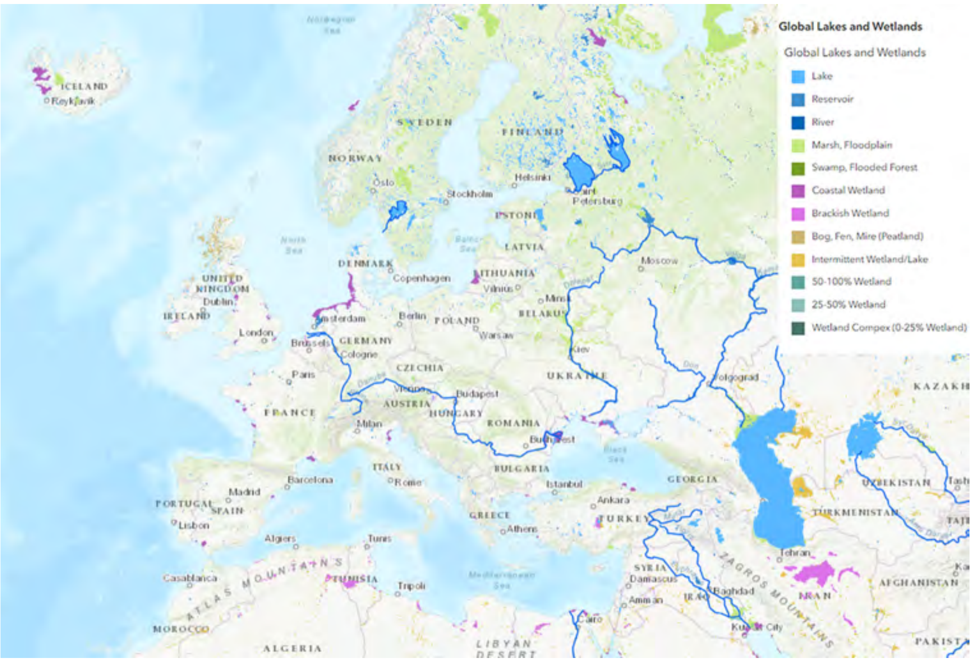


Figure 3.5. The wetlands and rivers of Europe.

Coastal Salt Marshes in northern Europe are extensive, and mudflats occur along the Atlantic Ocean and Europe's North Sea coastlines.

Northern boreal and subarctic peatlands compose more than half of the world's wetlands. Unfortunately, much of this is at latitudes well above where most snakes can survive. However, there are records of *Natrix* close to the Arctic Circle.

A collision of continental plates about 12 MYA raised new mountains in central Europe and created the most extensive lake ever known, the Paratethys Sea. This inland sea's fauna included the smallest known whales. Palcu et al. (2021) estimate the lake once contained over 1.77 million cubic kilometers of water (more than ten times the volume found in all of today's fresh- and saltwater lakes combined). However, a changing climate caused the lake to shrink at least four times dramatically in its five-million-year life. Water levels and salinity fluctuation resulted in aquatic species passing into extinction. Species that could survive changing salinities repopulated the lake when it expanded. The Paratethys ceased to exist 6.7 -6.9 Ma when erosion formed an outlet.

Africa & Madagascar

Wetlands are abundant in sub-Saharan Africa, including the Congo River Swamps, the Inner Niger Delta, the Sudd of the Upper Nile, and the Okavango Delta. Six snake families contain aquatic species. The Pythonidae has two species of giant python that are semi-aquatic (*P. natalensis* and *P. sebae*). A lineage within the elapid genus *Naja* has at least four semi-aquatic species. The family Lamprophidae has aquatic snakes in two lineages *Lycodonomorphus* (about eight species) and one species of *Boaedon.* Africa has a radiation of natricids composed of six genera, five of which are endemic *Afronatrix, Limnophis, Helophis, Hydraethiops, Natriciteres,* and *Natrix*. The family Colubridae has one semi-aquatic genus with several species in the endemic *Crotaphopeltis*. For many years snakes in the endemic African genus *Grayia* were considered natricids. The four species are now placed in their own family Grayidae.

Madagascar has two genera of semi-aquatic snakes that are poorly known, *Liopholidophis* and *Thamnosophis.* Both are in the sub-family level clade Pseudoxyrhophiinae.

The Nile Delta is (or was) one of the largest river deltas, but much of the area is now farmland and no longer floods due to the Aswan Dam. The Nile Crocodile and hippopotamus are two aquatic vertebrates once widespread in the delta during antiquity. They have been replaced by 39 million people living on the delta.

The Congo River Basin is in west equatorial Africa and is sometimes known as the Congo. The drainage basin originates in the highlands of the East African Rift system with input from many rivers. The young age (1.5 to 2 MYA) and active uplift of the East African Rift at the headlands results in the river's huge annual sediment load (Beadle 1981). The basin is 3.7 million square kilometers and has extensive, undisturbed tropical rainforests and significant wetlands. The drainage basin empties into the Gulf of Guinea on the Atlantic Ocean. The climate is equatorial tropical, with two rainy seasons and high temperatures all year. The Congo River is the second longest river in Africa, shorter only than the Nile, and it is the second largest river in the world in discharge volume, following the Amazon. It is also the world's deepest river, with depths of over 220 m (Oberg et al. 2009).

The genus *Crotaphopeltis* reaches its highest diversity with many sympatric species in the Congo River Basin. These snakes are considered primarily mesic savanna dwellers. However, some, such as *C. hotamboeia* have been found in coastal fynbos (areas with sclerophyllous vegetation) less than 200 m from the Indian Ocean in South Africa. Aquatic snake genera of the Congo Basin include *Afronatrix, Crotaphopeltis, Grayia, Helophis, Hydraethiops, Limnophis, Lycodonomorphus, Natriciteres,* and *Naja*.

The Blue and White Nile confluence forms the Sudd in southern Sudan. The Sudd created a mosaic of wetlands, and at one time, it was an impenetrable barrier to navigation on the Nile. The shallow, flat inland delta covers an area of about 30,000 square kilometers but can

Figure 3.6. The wetlands and rivers of Africa.

be as large as 130,000 km2 depending on the inflowing waters. The Sudd consists of meandering channels, lagoons, reeds, and papyrus marshes. Aquatic snakes inhabiting the Sudd include *Natriciteres and Grayia.*

The Okavango River empties into a basin in the Kalahari Desert and forms an inland delta. The Okavango Delta is famous for its wildlife. However, despite the high diversity, the delta supports few aquatic or semi-aquatic snake species. Six species of snakes representing the genera *Crotaphopeltis, Limnophis, and Natrici*teres approach the northern edges of the delta. The Okavango River system remains under studied in Zambia, central Angola, and Botswana.

The Nile Delta covers about 25000 km2, but the outer edges have been eroded, and some coastal lagoons have increasing salinity levels because of their connection to the Mediterranean Sea. Since the Delta no longer receives an annual supply of nutrients and sediments from upstream due to the construction of the Aswan Dam, the soils of the floodplains have lost the yearly input of nutrients. The Suez Canal is east of the Delta and enters the coastal Lake Manzala northeast of the Delta. To the northwest are three other coastal lakes or lagoons: Lake Burullus, Lake Idku, and Lake Mariout. The Delta has a hot desert climate, as does the rest of Egypt. Still, its northern portion is the wettest region in the country and has relatively moderate temperatures, with highs rarely surpassing 31°C in the summer. There appear to be only one aquatic snake species in the Nile Delta, Natrix tessellata (El Din 2006).

Australasia

Semi-aquatic and aquatic snakes in Australasia include the genera Liasis (Pythonidae), *Acrochordus* (Acrochoridae), *Cerberus Djokoiskandarus, Pseudoferrania, Myron, Fordonia, Heurnia* (Homalopsidae), *Tropidonophis* (Natricidae), *Hemiaspis, Laticauda, Aipysurus, Emydocephalus, Hydrophis, Ephalophis,* and *Hydrelaps* (Elapidae).

Australian wetlands are distinctive due to seasonal dry periods with high evaporation rates and low rainfall. Thus, saline wetlands and lakes are common due to the high evaporation rates.

Kakadu National Park is about 20,000 km2 in the Northern Territory of Australia. One of Kakadu's best-known landmarks is the Yellow Water billabong. A wetland near the small settlement of Cooinda. The billabong, which floods and connects other waterways during the wet season, attracts millions of migratory birds yearly. In addition, aquatic snakes in the genera *Liasis, Acrochordus, Cerberus, Fordonia, Myron, Pseudoferrania,* and *Tropidonophis* inhabit the area.

The Coorong, Alexandrina Lake, and Albert Lake in South Australia support a diverse waterbird assemblage that visits the 1405 square kilometers of wetland. The area comprises 23 individ*ual wetlands. Semi-aquatic snakes present includes Notechis and Pseudechis*.

Barmah Forest, Victoria, is a 285-square-kilometer forest wetland that provides natural flood control for the Murray River. The wetlands support 13 vegetation communities– including the greatest extent of river red gum in Victoria – which provides vital habitats for native bats, parrots, possums, and the Red-bellied Black Snake *Pseudechis porphyriacus*.

Macquarie Marshes, in northwestern NSW, have swamps, lagoons, and channels on the floodplains of the Macquarie River. Semi-aquatic snakes present include *Austrelaps* and *Hemiaspis*.

Mareeba Tropical Savanna and Wetland Reserve, Queensland, also known as the Mareeba Wetlands, comprises 12 interconnecting lagoons, creeks, and channels across 20.25 ha reserve.

Aquatic snake genera include *Liasis, Pseudoferrania, Tropidonophis,* and possibly *Hemiaspis.* Many of Australia's wetlands are coastal and essential to this work because they support a significant diversity (about 38 species) of sea snakes and several homalopsids. Coral reefs in Australian waters are also crucial to marine snake communities.

Ashmore Reef National Nature Reserve and Cartier Island Marine Reserve (the Reserves) are two discontinuous exposed open ocean platform reefs on the northwestern edge of the Sahul Shelf in northwest Australia, in the Timor Sea. Ashmore Reef comprises an area of approximately 583 km2 and includes three small, vegetated islands, several sand cays, two lagoons, and an extensive reef. Cartier Island covers about 167 square kilometers and is about 25 nautical miles southeast of Ashmore Reef. Cartier Island is an unvegetated sand cay sur-

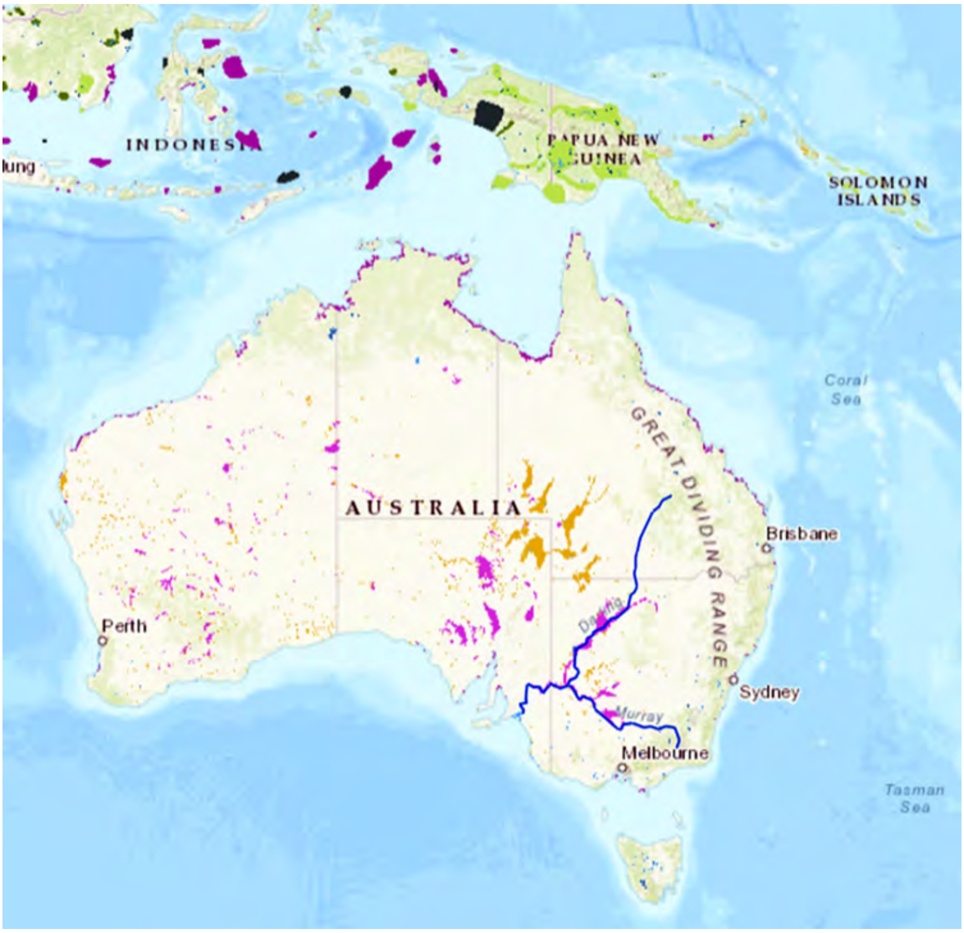


Figure 3.7. Wetlands of Australiasia.

rounded by a coral reef with an extensive reef flat and no lagoon. The Reserve includes the seabed and substrata to 1000 meters depth. The Reserves are protected for their high biodiversity, including sea snakes. The Reserves are in an isolated oceanic location and thus undisturbed; they have extraordinary cultural value. Declines in biodiversity are especially troublesome when they occur in isolated locations relatively protected from most major anthropogenic disturbances.

Lukoschek et al. (2013) examined declines in sea snakes at Ashmore Reef based on surveys conducted between 1973 and 010 recorded the highest abundances (average of 42–46 snakes per day) and species richness (nine species) in 1973 and 1994. In 2002 abundance had declined by over 50% (21 snakes per day representing five). Since 2005 abundances have been consistently low (1–7 snakes per day), with just two species, *Aipysurus laevis,* and *Emydocephalus annulatus,* recorded in significant numbers. Despite extensive searches since 2005 (especially in 2010), five species of sea snake historically abundant at Ashmore Reef have not been sighted and are presumed locally extinct. These species include three Timor Sea endemics *Aipysurus apraefrontalis, Aipysurus foliosquama, Aipysurus fuscus*, and one Australasian endemic *Aipysurus duboisii*. Declines in the abundance and diversity of sea snakes at Ashmore Reef cannot be attributed to differences in survey methods over the years.

In New Guinea, the Wasur National Park is a massive wetland region in the Indonesian province of Papua. It was dubbed the Serengeti of Papua owing to its incredible biodiversity. The area supports many waterfowl species and migrant birds. However, the invasion of alien species such as water hyacinth and the Giant Sensitive Tree threatens the park's naturally flooded grassland systems.

Asia

Asia, the largest continent, has diverse climates and landscapes ranging from the arctic to tropical, tundra to rainforest. Southeast Asia is wet, while western Asia is dry. The Himalayas influence the monsoon by forcing a thermal low to form and draw moisture into the atmosphere during the summer. The dynamic range of the climates and landscapes has created numerous and often extensive wetlands where biodiversity can thrive and evolve.

China

The Pearl and Yangtze River Deltas have approximately 650,000 km2 of wetlands. Of that, 250,000 km2 have been reserved, and 400,000 km2 are used for rice paddies and fishponds. The great plains of the Yellow and Yangtze River basins in eastern China contain some of the most extensive wetlands in the country and the greatest concentration of large freshwater lakes. The total area of lakes is over 0.22 million square kilometers. The Yangtze basin is noteworthy for its lakes, including the Dongting lakes in Hunan Province, the Wuhan lakes in Hubei Province, Poyang Lake in Jiangxi Province, a chain of large lakes including Shengjin in southwestern Anhui Province, Cao Hu in central Anhui Province, and Tai Hu, Hongze Hu and Gaoyou Hu in Jiangsu Province. Many lakes are fringed with marshes. Extensive marshes occur in ancient lakes' dried-out beds, old river channels (along the Yellow River), and seasonally flooded areas (An et al. 2007). Aquatic and semi-aquatic snakes include: *Acrochordus, Thermophis, Hypsiscopus, Myrrophis, ?Subsessor, Enhydris, Amphiesma, Amphiesmoides, Atretium, Fowlea, Hebius, Herpetoreas, Natrix, Opisthotropis, Rhabdophis, Rhabdops, Trimerodytes,* and *Xenochrophis*.

South Asia

The South Asian (Fig.3.17) region includes Bangladesh, India, Nepal, Myanmar, Pakistan, and Sri Lanka. The region is rich in aquatic snake diversity *Acrochordus, Python, Cerberus, Enhydris, Dieurostus, Ferania, Fordonia, Gerarda, Gyiophis, Homalopsis, Mintonophis, Myanophis. Hydrophis, Amphiesma, Hebius, Fowlea, Rhabdophis, Xenochrophis* are all represented.

Bangladesh

Much of Bangladesh is low-elevation terrain with many riparian systems. It has a 580 km coastline on the Bay of Bengal. The delta plain of the Ganges (Padma), Brahmaputra (Jamuna), and Meghna Rivers and their tributaries occupy 79% of the country. The Hill Ranges make up only nine percent of the country. Thus, the country is characterized by a broad deltaic plain subject to frequent flooding and a small hilly region crossed by swiftly flowing rivers.

Roughly 80% of the landmass is the alluvial lowland. The Bangladesh Plain, with altitudes up to 105 meters above sea level, occurs in the plain's northern part, but most are less than 10 m above sea level. The south coastal region is at sea level. With such low elevations and numerous rivers, water—and concomitant flooding—is a predominant physical feature. About 10,000 square kilometers of Bangladesh are covered with water and are routinely flooded during the monsoon season. The alluvial soils in the Bangladesh Plain are nutrient-rich due to heavy silt deposits carried downstream during the rainy season. The rivers of Bangladesh mark both the nation's physiography and the people's life. About 700 in number, these rivers generally flow south. The rivers also drain excess monsoon rainfall into the Bay of Bengal. Thus, the great river system is simultaneously

the country's principal resource and its most significant hazard. The network of four river systems flowing through the Bangladesh Plain drains 1.5 million square kilometers. The numerous channels of the Padma-Meghna, its tributaries, and smaller parallel rivers that flow into the Bay of Bengal are called the Mouths of the Ganges. During the annual monsoon, the rivers of Bangladesh flow at about 140,000 cubic meters per second, but during the dry season, the water flow is reduced to 7,000 cubic meters per second (Islam 2014).

India

India has about 14,500 km of inland navigable waterways with twelve significant rivers and a total catchment area exceeding 2,528,000 square kilometers. All major rivers of India originate from one of the three main watersheds: The Himalaya and the Karakoram ranges; Vindhya and Satpura ranges in central India; and the Sahyadri or Western Ghats in west-

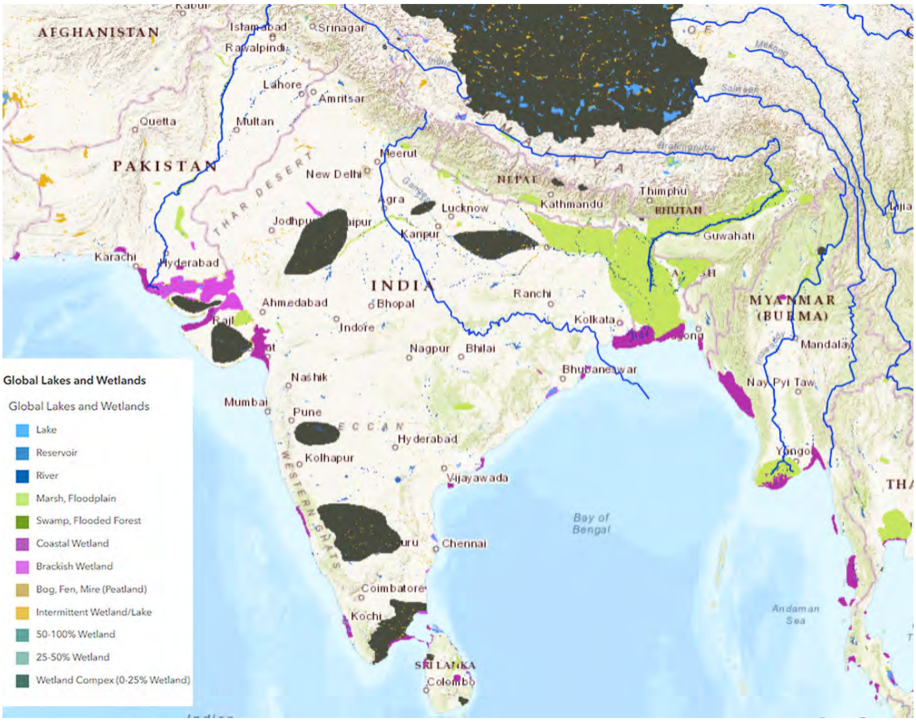


Figure 3.8. South Asian wetlands.

ern India. The Himalayan river networks are snow-fed and have a perennial water supply throughout the year. The other two river systems depend on the monsoons and shrink into creeks during the dry season. The Himalayan rivers that flow westward into Punjab are the Indus, Jhelum, Chenab, Ravi, Beas, and Sutlej.

The Ganges-Brahmaputra-Meghana system has the largest catchment area of about 1,600,000 square kilometers. The Ganges Basin has a catchment of approximately 1,100,000 square kilometers. The Ganges originates from the Gangotri Glacier in Uttarakhand. It flows southeast, draining into the Bay of Bengal. The Brahmaputra originates in Tibet, China, and enters India in Arunachal Pradesh, then flows west through Assam. The Brahmaputra merges with the Ganges in Bangladesh, where it is known as the Jamuna River. The Chambal, another tributary of the Ganges, via the Yamuna, originates from the Vindhya-Satpura watershed. The river flows eastward. Westward-flowing rivers from this watershed are the Narmada and Tapi, which drain into the Arabian Sea in Gujarat.

The Western Ghats are the source of all Deccan rivers, including the Godavari River, Krishna River and Kaveri River, draining into the Bay of Bengal. These rivers constitute 20% of India's total outflow. However, the heavy southwest monsoon rains cause the Brahmaputra and other rivers to distend their banks, often flooding surrounding areas.

The Pichavaram Mangroves. Tamil Nadu India's wetland ecosystem is widely distributed from the cold and arid in the Ladakh region of Jammu and Kashmir and those with the wet and humid climate of peninsular India. Most wetlands are directly or indirectly linked to river networks. Mangrove forests border the Indian coastline in sheltered estuaries, creeks, backwaters, salt marshes, and mudflats. Mangroves cover 4,461 square kilometers or about 7% of the world's mangrove forests. Prominent mangroves are in the Andaman and Nicobar Islands, the Sundarbans delta, the Gulf of Kutch, and the deltas of the Mahanadi, Godavari, and Krishna rivers. Parts of Maharashtra, Karnataka, and Kerala also have extensive mangrove forests. The Sundarbans delta is home to the largest mangrove forest. It lies at the mouth of the Ganges and spreads across areas of Bangladesh and West Bengal. The Sundar-

Figure 3.9. The mangrove dwelling homalopsid *Gerarada prevostiana.*
Photography by Avrajjal Ghosh.

bans is a UNESCO World Heritage Site but is identified separately as the Sundarbans (Bangladesh) and the Sundarbans National Park (India). A complex network of tidal waterways, mudflats, and small islands of salt-tolerant mangrove forests intersects the Sundarbans. The Rann of Kutch is a marshy region in northwestern Gujarat and the bordering Sindh province of Pakistan. It occupies a total area of 27,900 square kilometers.

The Kerala Backwaters are a chain of lagoons and lakes lying parallel to the Arabian Sea coast in the state of Kerala in southern India. The network includes five large lakes linked by canals; some constructed, others natural, and the area is fed by 38 rivers (Bassi et al. 2014).

Myanmar

The Irrawaddy River is the country's largest river originating from the N'mai and Mali rivers; it flows relatively straight from north to south before emptying into the Andaman Sea at the Irrawaddy delta. Its drainage basin covers about 404,200 square kilometers. The delta is the lowest expanse of land in Myanmar; it spreads out from the limit of tidal influence at Myan Aung to the Bay of Bengal and the Andaman Sea, about 290 km from the south end of the Ayeyarwady River. The region consists of mangroves and freshwater swamp forests. The Irrawaddy Delta holds Myanmar's largest remaining area of mangrove forest. However, over the past thirty years, an estimated 75-83 percent of mangroves have been lost.

Nepal

Nepal is about 800 kilometers along its Himalayan axis and 150 to 250 kilometers across. Nepal can be divided into three belts on the south-to-north axis: Terai, Pahad, and Himal. It is divided into three major river systems from east to west: the Koshi, the Gandaki/Narayani, and the Karnali - all are the Ganges' tributaries. The Ganges-Yarlung Zangbo/Brahmaputra watershed coincides with the Nepal-Tibet border; however, several Ganges tributaries form in Tibet. These tributaries have cut through the highest mountains in deep gorges. They flow south through the Middle Hills, then join in a parallel configuration before crossing the Mahabharat Range and emerging onto the plains where they deposited alluvial fans exceeding 10,000 square kilometers (Jha 2006).

Sri Lanka

The Kirila Kelle wetlands are found a short distance inland from the southern Sri Lankan city of Matara. The wetlands are a part of the Nilwala River basin and comprise some 3.0 km2 of wetlands. Portuguese colonialists built canals to mitigate flooding of the Nilwala river into Matara township and aid in the cropping of a further surrounding 24 square kilometers of rice and other farming. The Kirila Kelle Wetlands are the focus of a sustainable Environmental Conservation Community Development program. The program is being developed through Ecotourism and community development through a provincial integrated development strategy managed and implemented by the community for the community.

The Muthurajawela is a marsh complex in the southern region of the Negombo lagoon, 30 km north of Colombo. The Muthurajawela is 30.68 square kilometers and is the country's largest saline coastal peat bog. The marsh is notable for its unique and highly diverse ecosystem and is listed as one of the 12 priority wetlands in Sri Lanka. "Muthurajawela" translates to "Swamp of Royal Treasure" (Kotagama and Bambaradeniya, 2006).

Figure 3.10. The Crab-eating Snake *Fordonia leucobalia* is the only species that has a distribution extending from peninsular India to Australia and New Guinea. Today it is considered one species. That may change in the future. Photography by Harry Ward-Smith.

Pakistan

The Indus River is one of Asia's longest rivers. The headwaters, fed by glacier meltwater and rivers in the Himalayan, Karakoram, and Hindu Kush ranges, originate in the mountains of the Tibetan Plateau near Lake Manasarovar. The river supports ecosystems with temperate forests, plains, and arid landscapes.

The Indus runs through the Ladakh region of Jammu and Kashmir, India, towards the Gilgit-Baltistan region of Pakistan and the Hindukush ranges. It then flows in a southerly direction along the entire length of Pakistan to merge into the Arabian Sea near the port city of Karachi in Sindh. The drainage area exceeds 1,165,000 square kilometers and is one of the largest rivers in the world in terms of annual flow. The northern part of the Indus Valley, with its tributaries, forms the Punjab region, while the lower course of the Indus is known as Sindh and ends in a large delta (Kahn and Arshad 2014).

Southeast Asia

Southeast Asia has the most extraordinary diversity of aquatic snakes. Seven families contain 44 genera. Aquatic and semi-aquatic snakes found in this region include the acrochordid genus *Acrochordus*; pythonid genera *Liasis, Malayopython, Python;* the xenopeltid genus *Xenopeltis*; the cylindrophid genus *Cylindrophis;* the homalopsid genera: *Bitia, Cantoria, Cerberus, Enhydris, Erpeton, Fordonia, Gerarda, Homalophis, Homalopsis, Hypsiscopus, Karnsophis, Kualatahan, Miralia, Myrrophis, Phytolopsis, Raclitia, Subsessor, Sumatranus;* the elapid genera: *Aipysurus, Hydrophis, Laticauda;* the natricid genera *Amphiesma, Amphiesmoides, Anoplohydrus, Atretium, Fowlea, Hebius, Herpetoreas, Hydrablabes, Isanophis, Opisth-*

Figure 3. 11. Southeast Asia has many rivers and wetlands as well as a diverse aquatic snake fauna. Historically the wetlands have expaded and contracted . It also has the most family level clades, genera, and species of aquatic snakes than another region of the planet.

otropis, Pseudagkistrodon, Rhabdophis, Rhabdops, Smithophis, Trimerodytes, Tropidonophis, Xenochrophis.

The Mekong begins at the Tibet Plateau and runs through China, Laos, Cambodia, and Vietnam, draining 625,000 square kilometers. The Mekong Delta is in southern Vietnam.

Sundaland (Fig.3.22) is a biogeographical region of Southeastern Asia corresponding to a landmass exposed during the last 2.6 Ma when sea levels were lower than today. It includes the Malay Peninsula on the Asian mainland, the large islands of Borneo, Java, Sumatra, and their small islands.

The area covered by Sundaland is about 1.8 million square kilometers. The land area of Sundaland has expanded, and the contracted considerably during the past two million years, and the exposed land area is approximately half of the maximum historic area.

Sundaland's western and southern borders are marked by deep water and the Indian Ocean. The eastern boundary of Sundaland is Wallace's Line, the east boundary of Asia's terrestrial mammal fauna, and the western edge of the Indomalaya and Australasia biogeo-

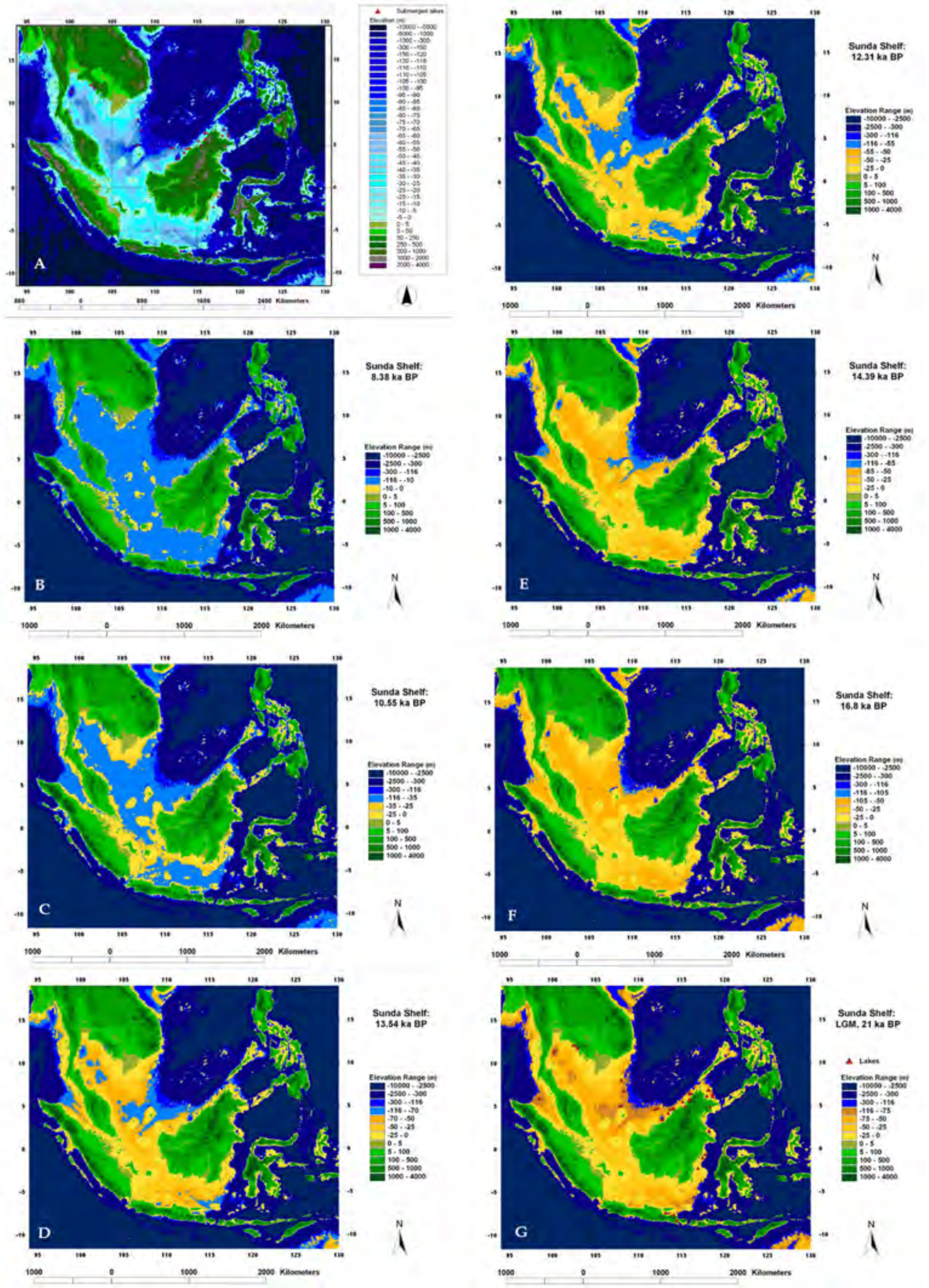


Figure 3.12. The expansion and contractions of the Sunda Shelf wetlands. Map A shows the Sunda Shelf in the present, figure G shows the Sunda Shelf 21,000 YBP. The other maps show views of the region in between the present and 21,000 YBP. From Voris (2000).

Figure 3.13. The distribution of terrestrial, fossorial arboreal, and freshwater snakes is shown in brown , the distribution of marine snakes is shown in blue.

graphic provinces. The islands east of Wallace's Line are Wallacea, a separate biogeographical region considered part of Australasia. Wallace's Line is a deep-water channel never crossed by any land bridges (Bird et al. 2005).

Large portions of Sundaland were most recently exposed from approximately 110,000 to 12,000 YBP during the last glacial period. When the sea level was decreased by 30–40 meters or more, land bridges connected the islands of Borneo, Java, and Sumatra to the Malay Peninsula and mainland Asia. Because the sea level has been 30 meters or lower throughout much of the last 800,000 years, the isolation of Borneo, Java, and Sumatra as islands have been uncommon throughout the Pleistocene. In the late Pliocene, the exposed area of Sundaland was reduced compared to the present. At the Last Glacial Maximum, the sea level fell by approximately 120 meters, and the entire Sunda Shelf was exposed (Bird et al. 2005).

Figure 3.14. The homalopsid *Cantoria violacea* is an example of a snake that occurs in freshwater, brackish water, and marine habitats, Photography by Harry Ward Smith.

The equator runs through central Sumatra and Borneo. Thus, Sundaland is in the tropics. Consequently, rainfall is the primary determinant of regional variation. Most Sundaland receives over 2,000 millimeters of rain annually, and rainfall exceeds evapotranspiration throughout the year. Thus, there are no predictable dry seasons like elsewhere in

Southeast Asia.

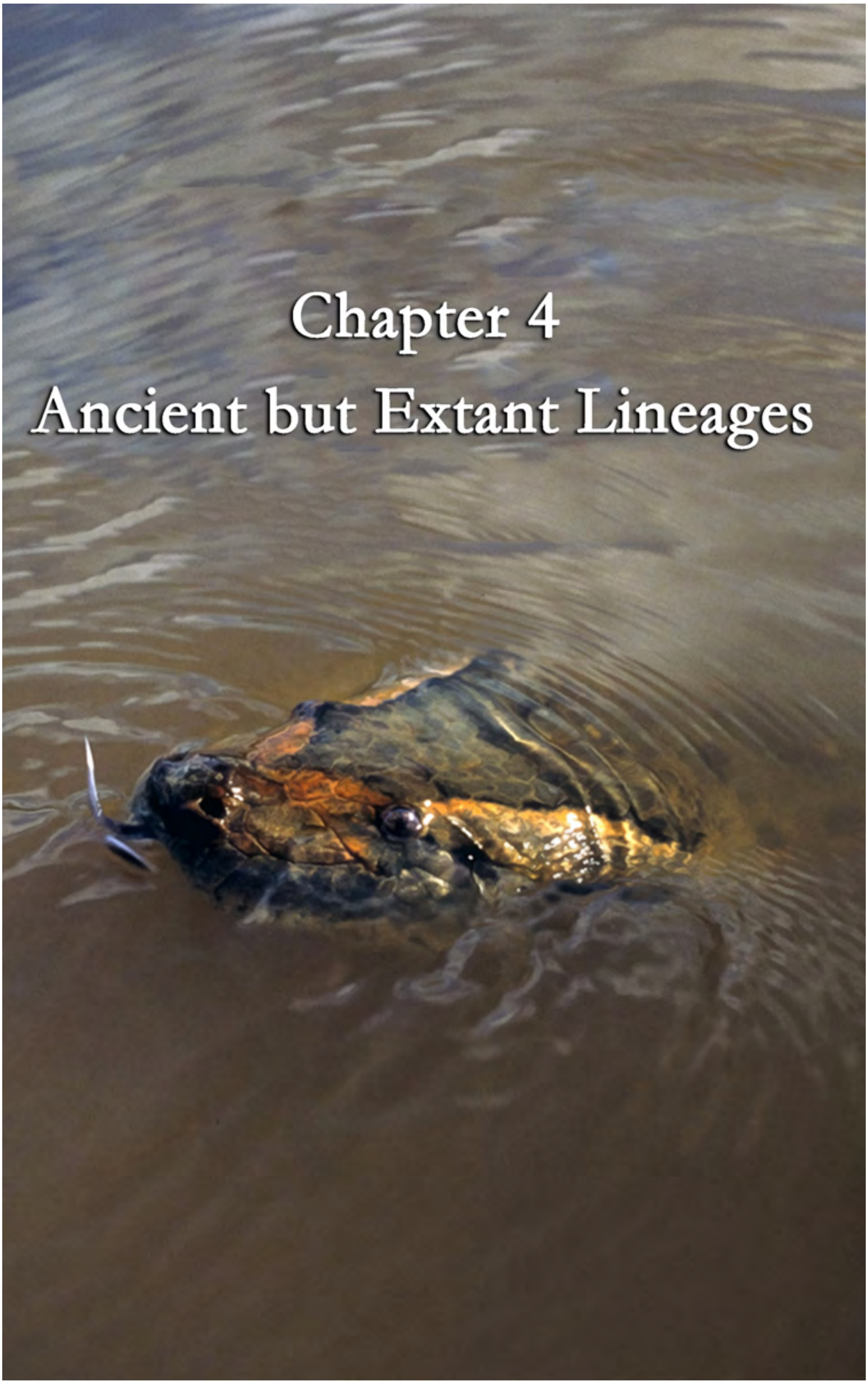
In summary, aquatic snakes are found throughout the distribution of snakes (Figure 13.23), but they have evolved multiple times in multiple lineages. Some have recent origins, while others are more ancient. In addition, they have adapted to numerous aquatic microhabitats that differ in water chemistry, temperature, substrate, flow rate, and prey availability. However, Southeast Asia's Sunda Shelf, the Amazon Basin, the Pantanal, the Congo Basin, North America's Gulf Coastal Plain, and the coastal waters of Australasia stand out in supporting the rich diversity of aquatic species.

Figure 3.15. The Banded Water Cobra *Naja annulata.* **Photography by Vaclav Gvozdik**

On the next page. A Green Anaconda surfaces in a Venezuela River. *Eunectes murinus* **is the largest snake and inhabits the rivers of the Amazon and Orinoc basins of South America. Photography by William W. Lamar.**

Chapter 4

Ancient but Extant Lineages



4. Ancient but Extant Lineages

The Henophidia was established by Hoffstetter (1939) for a group of snakes that included boas, pythons, and "anilioids." Various studies added or subtracted groups of snakes to this superfamily in the 21st century. However, the Henophidia is no longer considered monophyletic (Reynolds et al., 2014). These families may be best thought of as a collection of ancient lineages that have survived to the present day.

Eyelash Boas – Tropidophiidae

The family contains two genera of ancient Neotropical snakes, Trachyboa and Tropidophis. Both have been considered booids but form an independent clade that diverged relatively early in snake radiation (Wilcox et al. 2002). The left lung is absent, and the tracheal lung is well-developed. Males have cloacal spurs, and pelvic elements are present. *Tropidophis* are terrestrial-arboreal snakes that are sometimes called wood snakes or tropes. However, there is evidence that the two species of *Trachyboa* are semi-aquatic.

Trachyboa contains two poorly known species: *Trachyboa boulengeri* inhabits the Choco forests of Panama, Colombia, and Ecuador, and *Trachyboa gularis* occurs in the dryer coastal areas of Ecuador. Both species are terrestrial, sedentary snakes with the peculiar defensive behavior of coiling into a flattened disk or forming a rigid stick-like posture when disturbed (Arnett et al. 1992). Much of what we know about these snakes come from captive animals. Successful captive maintenance requires cool ambient temperatures. Both species prey on frogs and toads but thrive on live fish in captivity. Litters average 5–6 young.

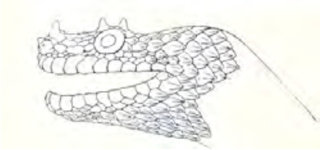


Figure 4.2. *Trachyboa boulengeri.* **From Peracca 1910.**

They are unusual in appearance because of their very rugose scales and the projecting scales from above the eye. Both species will eat anurans but prefer fish; they seem to do well at temperatures between 18–26C. At temperatures above 21C, they stop feeding (Arnett et al. 1992). *Trachyboa* have a hypapophysis (small projections) coming from the ventral side of each vertebra; these are frequently found in aquatic snakes.

Northern Eyelash Boa

Trachyboa boulengeri Peracca, 1910

Distribution and Habitat. Streams with gravel substrates and swamps in Panama, Ecuador, and Colombia (Valle del Cauca) (Figure 4.1) (Ortega-Andrade et al. 2010). Type locality: none given.

Figure 4.1. The distribution of *Trachyboa boulengeri*

Natural History. The literature on this species' food habits is mainly based on captivity specimens. The diet is composed of frogs and tadpoles (*Pristimantis, Rhinella*, and *Gastrotheca*), as well as fish Dwyer et al. (2018) observed a sub-adult in a temporary pond along a small stream in Esmeraldas Province, Ecuador. The snake had its head and about four centimeters of its body underwater. A catfish

Figure 4.2. A *Trachyboa boulengeri f*rom Esmeralda, Ecuador. Photography by Ross J. Maynard.

(family Astroblebidae) in the same pool was coaxed to swim close to the snake. The snake immediately seized and constricted the fish. After 30 minutes, the snake released the fish without having killed it. Thus, coiling is for control rather than killing it. At the same locality, at 2130 h, a subadult *T. boulengeri* in damp leaf litter next to a permanent pond in the primary forest was feeding on a juvenile leptodactylid frog, *Leptodactylus melanonotus*. The authors report observing 23 individuals of *T. boulengeri,* of which eight were displaying "fishing" behavior. Shawn Harrison (personal communication) found these snakes in a similar situation - submerged in a small stream with gravel and rock substrate (Figure 4.3).

Figure 4.3. The microhabitat of *Trachyboa boulengeri.* The snake in the insert was collected in the stream shown in the larger photograph. Photography by Sean Harrison.

Southern Eyelash Boa

Trachyboa gularis Peters, 1860

Figure 4.4 The distribution of *Trachyboa gularis*

Distribution and Habitat**.** Dry, coastal Ecuador. Type locality: Guayaquil, Ecuador (Figure 4.4).

Natural History**.** A poorly known species. Its habits are assumed to be similar to *Trachyboa boulengeri*. The species is probably extinct due to the the descruction of its habitat. The savanna habitat for this species is "almost entirely gone." It has become cattle pasture and banana plantations. All known localities are in the vicinity of human settlements (Arteaga-Navarro and Cisneros-Heredia 2021).

Neotropical Pipe Snakes

The family Aniliidae is often considered monotypic with a single species, *Anilius scytale.* However, a second species, Anilius phelpsorum Roze, is likely valid. The Neotropical Pipe Snakes have a small gape and form the sister to the large gape wood snakes of the family Tropidophiidae. As unlikely as this may seem, the relationship has been demonstrated in multiple molecular investigations, given the morphological and ecological differences. They form the Amerophida clade composed, and members share constriction to subdue prey and viviparity. The molecular work suggests the two families shared an ancestor in the Cretaceous about 89.1 Ma (Burbrink et al. 2020). Like many other ancient snake clades, the species in this family have a remnant pelvic girdle and hind limbs.

The South American Pipe snakes are found in the tropics of northern South America from southern and eastern Venezuela, Guyana, Suriname, and French Guiana south through the Amazon Basin of Colombia, Ecuador, Peru, Bolivia, and Brazil. Despite the fact it has been called the "Trinidad Pipe Snake," its presence in Trinidad is problematic.

These snakes may be active at any time of day but are often found at night. It uses forests and open areas and is usually associated with aquatic situations. Prey handling, described by Marques and Sazima (2008), included seizing and coiling around small, elongated fish. Wanting to see how the snake would deal with larger prey, they fed the snake an amphisbaenian. The lizard was bitten on the anterior body; the snake held its grip for 25 seconds. Horizontal coils contacted the lizard's body as the prey twisted around its long axis in a defensive move. The snake loosened its hold and constricted the prey again. The pipe snake continued to bite and constrict the lizard for about 30 minutes until the lizard died. The snake released its bite hold and coils, swallowing the lizard headfirst.

Martins and Oliveira (1998) reported the fish *Synbranchus marmoratus,* the lizard *Amphisbaena vanzolinii*, and the snake Atractus torquatus in the diet of this species. The diet of *Anilius* in the Brazilian Amazonia basin is based on the analysis of 162 specimens, including Amphisbaenians (81.25%), *Tantilla melanocephala* (12.5%), and caecilians (6.25%). *Anilius scytale* forages at night on the ground and in aquatic environments. Swallowing prey headfirst may minimize the risk of injury to the predator

(Maschio et al. 2010). It seems likely that this species is fossorial and may be semiaquatic. The pipe snakes reach a length of about one meter. The body is cylindrical, hence the name pipe snake. The tail is short, flatted, and raised in a defense display to draw attention away from the head. Ventral (208-254) and subcaudal (10-15) scales are relatively small - about twice the size of dorsal scales. The body is bright red with black transverse bars on the dorsal and ventral surfaces.

Neotropical Pipe Snake

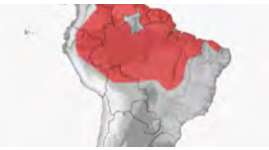


Figure 4.5. The distribution of *Anilius scytale.*

Anilius scytale **(Linnaeus, 1758)**

Distribution and Habitat. Forest leaf litter, swamps, and streams in Amazonian Brazil, Venezuela? Trinidad?, Colombia, Bolivia, Ecuador, French Guiana, Guyana, and Peru. In Venezuela is known to reach 700 m in elevation. Type locality: "Indiis."

Natural History. The diet consists of elongated amphibians and reptiles. Ferreira et al. (2020) report litters of 4-15 young 150-180 mm in total length.

Orinoco Pipe Snake

Anilius phelpsorum **Roze, 1958**

Distribution and Habitat. Uncertain, likely restricted to the Orinoco Basin, including the Delta Amacuro and maybe Trinidad. Type locality: "La base del Auyantepui, Estado Bolívar, Venezuela. This species has been neglected and little is known about it. Many authors have synonomized it with *Anilius scytale*

Figure 4.6. An *Anilius scytale* **from the Napo region of Ecuador. Photography by JCM**

Sunbeam Snakes

Two species compose the Asian Sunbeam Snake family Xenopeltidae. *Xenopeltis unicolor* is widespread, ranging from India to the Philippines. The other *X. hainanensis* is restricted to the Chinese island of Hainan. Most authors (e.g., Orlov et al. 2000) regard these snakes as fossorial. However, they are also semi-aquatic and are sometimes collected in gill nets by fishers (Karns et al. 2020); Stuart (2004) found *Xenopeltis unicolor* to be the most traded snake at U Minh Thuong National Park in southern Viet Nam. Asian Sunbeam snakes slightly exceed a meter in length and feed on other snakes and many other vertebrates. Gilbert and Goodyear (2019) report an adult *X. unicolor* preying on an adult Asian Bullfrog, *Kaloula pulchra,* in Bangkok, Thailand. The extent to which these snakes are aquatic needs further investigation.

The Mexican Burrowing Boa family Loxocemidae is monotypic. *Loxocemis bicolor* is considered a member of the Constrictores clade resurrected by Georgalis et al. (2020) and occurs in Mexico and Central America. Molecular studies suggest *Loxocemus* is related to the Asian sunbeam snake. However, it is not known to be aquatic.

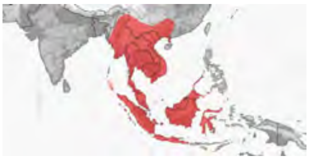


Figure 4.7. The distribution of *Xenopeltis unicolor.*

Figure 4.8. The Sunbeam Snake, *Xenopeltis unicolor.* **(A-B) photographs were taken in Borneo, and Thailand. Photography for A and B by Harry Ward-Smith (C) a juvenile feeding on an** *Enhydris enhydris* **in Thailand. Photography by JCM**

Sunbeam Snake

Xenopeltis unicolor Reinwardt, 1827

Distribution and Habitat. South and Southeast Asia from India to the Philippines and throughout the Indo-Chinese Peninsula and Indonesia. Type locality: Java. While this snake is terrestrial and inhabits lowland and lower montane forest, scrub, and disturbed habitats, it prefers wet ground and burrows and enters bodies of water (Figure 4.7).

Natural History. A nocturnal, fossorial, and semi-aquatic snake typically encountered on land near water. It feeds on various prey, including frogs, snakes, lizards, and small mammals. Its detention is specialized for grasping and swallowing hard-bodied prey, such as skinks. Larger prey is constricted smaller prey is eaten alive. Male combat has been reported on a roadside verge consisting mainly of tall grass. The snakes displayed body-bridging behavior, twisting continuously while moving forward. After approximately 10 minutes, they coiled around each other and bit each other for about one minute. Then, they continued body bridging behavior and, once aligned, simultaneously pushed their anterior downwards onto each other. Clutches of up to 17 eggs have been reported. Of 26 females, five ranging from 653 to 1020 mm in body length contained eggs from 8 to 20 mm. The smallest gravid female was 653 mm, was caught in January, and had eggs of 12 mm. The individual with the largest ovarian eggs was seen at the end of July.

The Pythons

There are no highly specialized aquatic pythons that converge with the anacondas – the highly aquatic boas. However, some python species are best considered semi-aquatic. The largest pythons (*Malayopython reticulatus, Python sebae, Python natalensis*, *Python bivittatus*) use aquatic situations to hunt and thermoregulate (Murphy and Henderson 1997, Walters et al. 2016, Murphy and Crutchfield 2019). The largest pythons are habitat generalists, but they are also frequently associated with water. The large body size may be possible because of their buoyance in water makingmoving more efficient. The four species of short-tailed pythons (*Python curtus* Group) are also frequently associated with water, and the question of whether they are semi-aquatic is controversial even though they are often associated with streams, stream banks,and poorly drained soils, some have specifically stated that they are not aquatic, but see Figure 4.9b.

Figure 4.9. Brongersma's Short-tailed Python, *Python brongersmai,* **from Kaeng Krachan National Park, Thailand. (A) an adult, (B) an adult in water. Photography by Rushen Bilgin**

Australian Water Python,
Liasis fuscus, Peters 1873

Distribution and Habitat. *Liasis fuscus* is distributed acrosstropical north Australia, from Broome in Western Australia to thecoast of central Queensland in the east. It also occurs in southernNew Guinea, from Merauke, Irian Jaya eastward through the lowlands of Western Province, Papua. Type locality: Port Bowen (=Port Clinton), Queensland, Australia (Figure 4.10).

Natural History. It is associated with seasonal bodies of water (floodplains, billabongs) as well as permanent water (lakes and rivers).Northern Australia is highly season with a very pronouncedwet season that expands water python's habitat, and the aquatic habitats are very productive resulting in high population densities, like Fogg Dam Northern Territory At this locality *fuscus* reaches one of the highest concentrations of any vertebrate predators.

The Australian Water Python, *Liasis fuscus,* hunts in and out of the water and is probably the most aquatic species in the clade. Its relative, the Olive Python, *Liasis olivaceus*, also uses streams and associated flood plains. However, it does wander far from water and frequents rock outcrops (Auliya 2006, Madsen et al. 2006, Walters et al. 2016, Ujvari et al. 2918).

The Australian Water Python can maintain a high body temperature throughout the

Figure 4.11. Australian Water Python, *Liasis fuscus*. From the Tully area. Photography by Scott Eipper.

year without showing visible basking behavior. However, cool nights during the dry season depress snake activity (Shine and Madsen 1995)

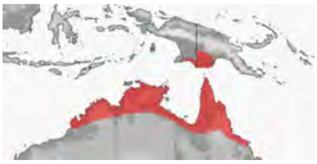


Figure 4.10. The distribuition of *Liasis fuscus*.

A five-year field study by Shine and Madsen (1997) focused on ways the Dusky Rat's (*Rattus colletti*) abundance can influence the reproductive rates of its predator, the Water Pythons (*Liasis fuscus*), on the Adelaide River floodplain in tropical Australia. The python preys almost exclusively on the Dusky Rat. Rat numbers varied dramatically over the five years of the study. Feeding rates of pythons were highest when rats were abundant and the snakes were in good condition; that is, they had a good mass relative to body length. The proportion of adult female pythons reproduced each year was closely tied to rat abundance. However, reproductive output per litter, that is, offspring size and fecundity relative to maternal body size, was unaffected by prey availability. Female pythons reproducing in years with abundant rats were in better condition after oviposition.

Water Pythons use facultative maternal brooding with shivering thermogenesis to warm their eggs. Shine et al. (1997) found that both nest-site selection and maternal care influence incubation temperatures. They experimentally simulated three thermal regimes typical of different natural nests in their study population. These were (1) hot, stable temperatures typical of nests laid in the burrows of varanid lizards -a constant 32°C; (2) lower and more variable temperatures typical of nests laid inside tree root boles, either with maternal attendance, diel range 27.1°–32.9°C; or (3) in root boles but without the maternal presence (24.3°–32.9°C). The authors incubated 187 eggs from 15 clutches obtained from field- caught gravid pythons. The temperature treatment during incubation strongly affected incubation periods, body sizes, body shapes (mass and tail length relative to snout-vent length), initial growth rates, escape behavior, and willingness to feed. In addition, the authors detected strong maternal effects on all these traits and interactions between maternal outcomes and incubation regimes. Thus, a female python's decisions about where she lays her eggs and whether she remains and broods them through development have significant consequences for the phenotypes of her offspring.

Olive Python

Liasis olivaceus Gray, 1842

Figure 4.12. The distribution of the Olive Python, *Liasis olivaceus.*

Distribution and Habitat. Endemic to northern Australia, it is polytypic. Two subspecies are recognized: *Liasis o. olivaceus* in Queensland and the Northern Territory and *Liasis o. barroni* Smith, 1981 in Western Australia (Type locality Pindrunna, 32 km north-west of Tambrey, WA. The Western Australian subspecies is the second-longest snake in Australia and is likely a valid species. Habitat includes rocky terrain, including gorges and rocky areas near water. It shelters in caves and rock crevices but uses hollow logs and burrows under rocks. Type locality: Port Essington, Northern Territory (*L. o. olivacea*), Australia (Figure 14.12).

Natural History. Prey includes most vertebrates. It hunts from ambush and actively forages in the water in search of prey. In waterholes, it will submerge and capture prey while concealed by the water. Mating occurs from May to mid-July. Eggs require a gestation period of 81–85 days, and the female lays 12–40 eggs in late spring. The average clutch size is about 19 eggs. Incubation is about 50 days. Hatchlings are approximately 35 cm in length. (Smith 1981).

Figure 4.13. The Olive Python, *Liasis olivaceus* **from Sybella Creek. Photography by Scott Eipper.**

Reticulated Python

Malayopython reticulatus Schneider, 1801

Distribution and Habitat. The species is native to Southeast Asia and occurs primarily in the Indonesian Archipelago. It has been reported from northeast India, but its presence is poorly documented. Its distribution includes many islands reinforcing its aquatic behavior. It uses both primary forests, secondary forests, and human-modified environments. Forest swamp habitats are used, as well as riparian environments that transect more open agricultural landscapes (Auliya 2003). Type locality: None given by Schneider (Fig. 4.14).

Three subspecies are recognized. *Malayopython reticulatus saputrai*: Selayar Island, Indonesia. *Malayopython reticulatus jampeanus*, and *Malayopython r. reticulatus.* The first two are from very restricted ranges in the eastern Indonesian Archipelago.

Natural History. This is likely the longest extant species of snake. *Malayopython* is highly adaptable, occupying a wide range of habitats from lower montane forests (up to elevations of at least 1500 meters), agricultural areas, scrubland, mangroves, and cities. Prey is generally small to medium mammals (small deer, wild pigs, rats, cats, dogs, goats, and other domestic species). Prey is killed by constricting. And there are well-documented cases of large specimens killing and consuming humans.

It is an excellent swimmer and has been reported at sea far from land. It has also colonized many small islands. For example, it was the first snake species to reach the island of Krakatoa after its eruption.

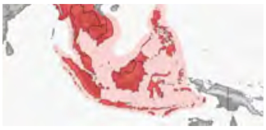


Figure 4.14. The distribution of the Reticulated Python, *Malayopython reticulatus.*

Reproduction. Much of what we know about *Malayopython* reproduction in nature comes from the Sumatra population (Shine et al. 1999). Testes are enlarged in October compared to April. Males engage in combat over females (Murphy and Crutchfield, 2018). Females lay their eggs from March through May. According to Ross and Marzec (1990) and Malkmus et al. (2002), egg-laying occurs from February to March in Sabah, East Malaysia. Auylia's (2006) reproduction schedule for West Kalimantan reticulatus seems to be correlated with wet and dry seasons. Mating occurs from October to December. Egg laying starts at the end of the wet season and lasts from January to March-April, so the eggs are incubated during the dry season. Hatchlings are present at the beginning of the wet season in August-October. Various authors estimate the incubation time at 55–105 days, suggesting that females in some populations may retain eggs during development.

Figure 4.15. The Reticulated Python, *Malayopython reticulatus*.
Photography by Kenneth Chin.

Females in the Sumatra population may not reproduce every year and may hold for other localities. Reproduction depends on the available food supply and the hunting success of individual females. Clutch sizes reported in the literature range from 8–124, with many clutches in the 20–40 range. Maturation may occur in two-year-old males and three-year-old females that are captives. Age to maturity in the wild is undoubtedly longer. Cox (1991) suggests five years.

Burmese Python

Python bivittatus Kuhl, 1820

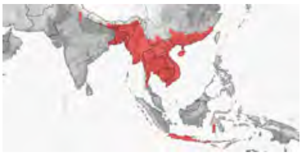


Figure 4.16. The distribution of P*ython bivittatus.*

Distribution and Habitat. Eastern Nepal, India (Arunachal Pradesh, S Bhutan, Bangladesh, Myanmar, Thailand, Laos, Cambodia, Vietnam, S China including Hainan and Hong Kong; Sichuan, Guangxi, Guangdong; Indonesia (Java, Bali, Sulawesi). Type Locality Java (Mertens 1930). Introduced into southern Florida (Figure 4.16).

Natural History. Prey taken by *Python bivittatus* is diverse. Stomach contents within its natural distribution are almost always terrestrial or semi-aquatic vertebrates. They include frogs, monitor lizards, birds, bats, rodents, pangolins, porcupines, langurs, jackals, mousedeer, hog deer, chital, barking deer, pigs, chinkara, civets, and leopards.

Figure 4.17. The Burmese Python, *Python bivittatus.* Photography by Artur Tomaszek.

Reproduction occurs in the early spring, with females producing 12–36 eggs in March or April. Females attend to the eggs, usually until they hatch, wrapping around them and rapidly contracting their muscles to raise the temperature of the eggs by several degrees. However, their muscle twitch and metabolic rate were negatively correlated with nest temperature after hatchling maternal care ceased.

Hatchlings are 480 to 790 mm and weigh 75 to 165 g. Sexual maturity is probably reached at about 2 m in males and 2.6 m in females, although maturity at smaller sizes has been reported. It seems likely that reaching maturity in less than two or three years is an artifact of captivity. Willson et al. (2014) said a female, 2.1 m in total length with a 1.85 m SVL with 11 viable eggs in the Florida population.

Molecular evidence for facultative parthenogenesis in this species was provided by Groot et al. (2003). In addition, a female *Python bivittatus* from the Artis Royal Zoo in Amsterdam produced eggs for five consecutive years that contained embryos while she was isolated from males.

The aquatic nature of *bivittatus* may be best demonstrated by its successful colonization of the Florida Everglades, a riparian environment dominated by grass and canals. Smith et al. (2021) found this python uses aquatic habitats within its native range. Movements were positively associated with aquatic habitat features such as water bodies (i.e., ponds, irrigation canals) and agriculture (i.e., rice paddy), suggesting that aquatic elements are essential in habitat selection. Smith et al. (2021) suspect that the Burmese Python's use of connected systems of aquatic agriculture in their native range may help explain their success in the Everglade wetlands of Florida. Rice paddies are often wetland-like habitats and support diverse wading bird communities. In addition, the vegetation that typically grows at the edges of ponds and irrigation canals may serve as refugia in areas highly modified by humans.

The Burmese Python has been reported swimming in the ocean. Li-Wei Chung et al. (2016) observed this snake swimming between two islands near the China coastline. It was about 2 km from its origin of, Lesser Kinmen Island, and about 1 km from its destination (Major Kinmen Island).

Indian Python

Python molurus (Linnaeus, 1758)

Figure 4.18. The distribution of the Indian Python, *Python molurus.*

Distribution and Habitat. The Indian Python tends to follow rivers into dry and upper-elevation habitats that it would otherwise not be able to colonize. They are present from Pakistan's Indus Valley eastward into India, Nepal, Bhutan, and western Bangladesh, then southward into peninsular India (O'Shea 1998; Barker and Barker 2008). Schleich and Kastle (2002) suggest that *P. molurus* and *P. bivittatus* may be sympatric in the Terai of Nepal. Shaw et al. (1942), writing about the snakes of Sikkim and Bengal, recognized a light and dark phase of this snake but suggested the dark phase was from northeast India and the lighter phase from southwest India. They considered it common up to about 1,219 m and noted that Wall reported it from 1,828 m. Pope (1935, 1961) says it from 1,500 m and 1,650 m, and it has been reported from 2,000 to 2,500 m (Whitaker 1978; Ernst and Zug 1996; Kabish in Schleich and Kastle 2002; Whitaker and Captain 2004). Type locality: Java (Mertens 1930) (Figure 4.18). The Java holotype may be based on a feral specimen or population.

Its northern and eastern borders are poorly understood. In part, this is due to the long-standing confusion with *bivittatus*. It is possible, even probable, that the current distribution of this species represents a combination of its natural distribution and human introductions. People have been moving this snake around for centuries. See Stothers (2004) for evidence that humans transported it in ancient times. Vyas (2011, 2013) describes moving rescued specimens of *molurus* from urban areas to agricultural lands and forest reserves.

Natural History. A habitat generalist uses open rocky habitats, deserts, cultivated lands, grasslands, marshes, scrub forests, mangrove forests, deciduous forests, wet tropical forests, and urbanized areas. The variety of habitats and its ability to survive in agricultural and urbanized lands suggests this is a highly adaptable snake. Despite its plasticity, *P. molurus* is the only large constricting snake considered threatened. This is probably justified since much of its distribution coincides with a human population that exceeds one billion humans. The snake could be easily extirpated through overhunting, habitat destruction, and pollution. In

Figure 4.19. *Python molurus*. **Photography by JCM.**

India, it occurs throughout the country, avoiding the extreme elevations and xeric desert areas. Perhaps the most prominent and best-studied population of *P. molurus* can be found in Keoladeo National Park, near Agra in Rajasthan. Whitaker (1993) suggests that the population consisted of 100 adults. Keoladeo is a temporary monsoonal wetland and remains dry from April–July. Colder months (December–February) corresponded to the mating season (Bhupathy and Ramesh 2010) when snakes were found near burrows and basking. Pythons were active during the day (0600 to 1800 h) in winter and summer. Winter activity was diurnal and was throughout the day in the spring, becoming crepuscular in summer. The burrow temperatures correlated with the ambient temperature during the day, but nighttime burrow temperatures were warmer than the ambient temperature. Prey activity peaked in the morning and evening hours throughout the study. The decline in sightings towards the summer may be due to the emigration of pythons or a decrease in conspicuous basking activity (Krishnan et al. 2009).

South African Python

Python natalensis Smith, 1840

Figure 4.20. The distribution of *Python natalensis.*

Distribution and Habitat. It ranges from the equator in Kenya and the Central Congo DRC southward through Angola, Zambia, Tanzania, Malawi, Mozambique, Zimbabwe, Botswana, Namibia, and South Africa. Type locality: Port Natal = Durban, Natal, South Africa. Broadley (1984) suggests *natalensis* favors moist, rocky, well-watered wooded valleys, plantations, and bush country and observed that they are rarely far from water. In Kruger National Park, Piennar (1966) describes its habitat as moist, rocky, well-wooded valleys, reed beds, and bush country

Figure 4.21. Southern African Rock Python, *Python natalensis,* **at the edge of the Cuando River in Botswana, Kwando Lagoon Camp, north of Moremi Wildlife Reserve and to the west of Chobe National Park. Photography by Martha de Jong-Lantink.**

but notes that it seldom ventures far from permanent water (Figure 4.20).

Natural History. Hatchling snakes feed on mice, rats, birds, lizards, and frogs. Adult South African Pythons sometimes hunt from ambush, including from a submerged position. Fitzsimons (1930) describes a python striking and overpowering a duiker buck when it stepped into a shallow pool. He also reports this species lying along a tree branch waiting for prey. Thomas (1985) says a *natalensis* captured a dove from an arboreal ambush as the bird flew into a water hole to get a drink.

Males may follow receptive females for as long as two months—*Python natalensis* mates in the autumn. The number of eggs laid is correlated to the female body size and clutches of 23–69 eggs (Alexander 2018). The eggs are 142–156 g, and no visible embryo is present when the eggs are laid. Females lay their eggs in anteater or aardvark burrows, cavities in rocks, cavities among tree roots, and accumulations of vegetation such as leaf litter, grass clumps, and sugar cane. Eggs are deposited in December and January, but egg laying in October and November did occur. The female coils around the eggs and produces body heat (thermogenesis) to raise the temperature of the developing embryos to about 38–40°C. Captive snakes were less likely to attend to their eggs. Additionally, the captive females paid little attention to the young after hatching.

Monitor lizards, mongooses, rats, and jackals are egg predators, and their presence may encourage the female to stay with their eggs. Incubation is about 60 days. Hatchlings are 450–600 mm long. Female *Python natalensis* do not eat while attending eggs and may lose 40% of their body mass during the attending period. Alexander (2018) saw that females continue to care for neonates after the eggs hatch. Female pythons would transmit heat to the eggs but also to the hatchlings. The female's skin turns dark, almost black, when basking outside the burrow. Females may only reproduce once every two or three years.

North African Python

Python sebae Gmelin in Linnaeus, 1789

Figure 4.22. The distribution of *Python sebae.*

Figure 4.23. The North African Python, *Python sebae*.. **Photography by JCM**

Distribution and Habitat. It inhabits the dense semi-evergreen and semi-deciduous forest and more open savanna environments, marshland, and gallery forest. Often it occurs close to water. It has been found in swamps, trees, and shrub savanna in the Gambia (Starin and Burghardt 1992). It occurs in the lower Tana River basin, at low elevations in the Lake Victoria Basin, and in the coastal lowlands of Kenya (Broadley 1990). In southeastern Nigeria, Luiselli and colleagues (2001, 2007) report that it uses a variety of habitats, noting that it is most abundant in coastal mangroves and spends considerable time in the water. In Somalia, it has been found in xerophilic open woodland, lowland evergreen thicket and scrub, lowland dry evergreen forest, lowland moist evergreen forest, and riparian formations. Pakenham (1983) discussed a possible waif in the Pemba Islands off the coast of Tanzania, confirming its tolerance to salt water (Figure 4.22).

Ranges south of the Sahara from Senegal eastward to Ethiopia, extending southward into northern Angola as far south as Ambriz on the coast, the Shaba Province of Zaire, Kenya, and Tanzania. Type locality: Guaira dans le Bresil (in error). Guaira may refer to Guayrá in present-day Paraguay and under the control of Spanish conquistadors in the 1550s. Or it may also refer to a locality in the former Dutch Brazil. The specimen was most likely collected in West Africa on a return trip from the New World. The type locality is thus in West Africa (Åhlander in Uetz 2020). Rarely does it go above 2,250 m in elevation?

Natural History. The diet in natural and urbanized habitats in southern Nigeria was studied by Luiselli et al. (2001). They found it fed mostly between 4:00 PM and 12:00 AM in the suburban areas, whereas, in the natural habitat, it feeds mainly during the day (7:00 AM to 7:00 PM). The urbanized population preys primarily on human commensals such as poultry, rats, goats, and dogs. It fed on rodents, fruit bats, and crocodiles and monitor lizards in more natural habitats. Predation in suburban areas often occurs near rivers because the snakes hide in riparian vegetation and riverbanks and uses the waterways as dispersion routes through heavily populated areas. Comparing the body size of snakes in natural habitats versus urbanized areas, they found smaller body sizes, averaging 2.9 m (1–4.5 m), than those from forested regions, which averaged 3.4 m (1–5.5 m). Python predation on large prey (dogs) was unusual in urban areas, possibly because of the relatively smaller body size. The hatchlings and young pythons fed on the giant rats of the genus *Cricetomys*, among the largest West African rodents. Adults take much larger prey, including antelope that may weigh more than the snake.

Hatchlings captured in the wild and raised at the London Zoo included a female that grew to 8 or 9 feet [2.4–2.7 m] in five years and mated when she was five years and ten months old (Flower, 1925). Lederer (1956) had two females, one 11 feet (3.35 m) and another 11 feet 9 inches (3.58 m), that laid eggs; both were five years of age.

Size. Hatchlings are 570-710 mm. Hatchlings captured in the wild and raised at the London Zoo included a female that grew to 8 or 9 feet [2.4–2.7 m] in five years and mated when she was five years and ten months old (Flower, 1925). Lederer (1956) had two females, one 11 feet (3.35 m) and another 11 feet 9 inches (3.58 m), that laid eggs at five years of age.

Aquatic Boas

Booid taxonomy and systematics have changed radically over the past several decades, while knowledge of the natural history of many booid snakes remains poorly known. However, the largest boas, the highly aquatic anacondas (*Eunectes*), are relatively well known. The oldest and largest member of the clade (*Titanoboa*) was aquatic, and today, the most aquatic members of the family are the anacondas of the genus *Eunectes*.

Anacondas, *Eunectes*

The Anacondas are Neotropical snakes found east of the Andes. Four extant species and one fossil species compose the genus. The clade includes the largest snake, the Green Anaconda, *Eunectes murinus,* which reaches at least 8 m and has the greatest mass (in females) of any extant snake (250 kg). *Eunectes* is derived from a Greek word that means "good swimmer." The aquatic habitats of these snakes are well documented. Pizzatto et al. (2007) found an aquatic habitat to be a synapomorphy for this genus. The large body size, a relatively long tail, and the dorsal positioning of the eyes and nares are all traits associated with life in water.

Anacondas are not the longest snakes but the most massive (a high mass/length ratio). The giant snakes have the most specialized habitat requirements—they are almost entirely aquatic. The Green Anaconda is the species that receive the most attention, but three other species are smaller, and they remain poorly studied. Hard evidence for a Green Anaconda exceeding nine meters is elusive. However, the Green Anaconda is an apex predator in the Amazonia's aquatic and terrestrial ecosystems, thus of considerable ecological importance.

The timing of reproduction varies with the species and location but tends to be associated with the dry season. Females attract males with a pheromone, resulting in polyandrous breeding aggregations with multiple males coiling around a female, forming breeding balls. This mating system has been observed in three of the four species in the genus.

Sexual cannibalism has been reported in *Eunectes* and its sister clade, *Epicrates.* Females benefit from the post-copulatory meal through the additional nutrients and energy that can be given to their offspring. Facultative parthenogenesis in captive females that were not in contact with males for more than eight years was documented by Shibata et al. (2017).

Beni Anaconda
Eunectes beniensis Dirksen, 2002

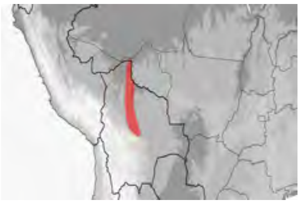


Figure 4.24. The distribution of the Beni Anaconda, *Eunectes beniensis.*

Distribution and Habitat. Known only from the vicinity of the Type locality: Type locality: Bolivia (Beni: Trinidad) (Figure 4.24).

Natural History. Poorly known. In one of the few studies on this snake, De la Quintana et al. (2017) used radiotelemetry to study the home range and habitat use of nine adult Beni Anacondas. The authors located the snakes 242 times in the wet and 255 in the dry seasons. The mean wet season home range was 25.81 ha (6.7 to 39.4 ha), while the mean dry season home range was 0.29 ha (0.13 – 0.42 ha). Beni Anacondas seem to prefer swamps while avoiding forest and rice fields. However, individual snakes' habitat use appears to vary based on the habitats available within their home range. Notably, rice fields were avoided by most individuals.

Figure 4.25. The Beni Anaconda, *Eunectes beniensis*.
Photography by Myke Clarkson.

DeSchauensee's Anaconda
Eunectes deschauenseei Dunn and Conant, 1936

Figure 4.26. The distribution of the DeSchauensee's Anaconda, *Eunectes deschauenseei*

Distribution and Habitat**.** Wetlands, swamps, and seasonally flooded areas of the Amazonian savanna in the Brazilian states of Pará and Amapá and in French Guiana (Dirksen and Henderson 2002). Including Marajó Island and the adjacent regions at the mouth of the Amazon River and several drainages French Guiana. It may also be found in adjacent Suriname, and the range may be disjunct. DeSchauensee's Anaconda is a lowland species occurring between sea level and 300 m above sea level. Type locality: Marajo I; Pará, Northeast Brazil. Habitat loss and degradation may be a problem for this species (Figure 4.25).

Green Anaconda

Eunectes murinus (Linnaeus, 1758)

Figure 4.27. The distribution of the Green Anaconda, ***Eunectes murinus.***

Distribution and Habitat. The Green Anaconda uses aquatic habitats in tropical wet forests, tropical dry forests, and savanna Distribution and Habitat. The Green Anaconda uses aquatic habitats in tropical wet forests, tropical dry forests, and savanna at elevations below 240 m. In Venezuela, it is widespread in the Orinoco drainage system and is most likely found throughout the country; there is the possibility of an isolated population in the Maracaibo Basin (Barrio-Amorós and Manrique 2007). It is endemic to the Amazon Basin and peripheral drainage systems and is restricted to rivers and wetlands. Populations are known in Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia, and probably Paraguay. A population also exists on the continental island of Trinidad, near the mouth of the Orinoco River and the northern edge of the range (Figure 4.27). Type locality: "America."

Natural History. Monitored neonates were always in shallow water (less than 20 cm deep). Their cryptic coloration made them difficult to see in water with hyacinths and grasses (Rivas et al. 2016). The only well-studied population of Green Anacondas is in the Venezuelan Llanos. The Llanos is a mosaic of savannas, rivers, flood plains, lagoons, palm, and gallery forests. Radio-tracked snakes were

Figure 4.28. The Green Anaconda, ***Eunectes murinus.*** **Photography by William W. Lamar.**

found in the water 86% of the time and at the water's edge the other 14% of the time they were located (Rivas, 1999). Rivas (2000) found that anacondas have relatively distinct home ranges. During the dry season, they have a mean home range of about 25 ha. Wet season home ranges are more extensive and average 37.4 ha. They are active during the day, with activity peaking in the evening. Late-night activity was expected.

The Green Anaconda is an ambush predator (Rivas, 2000) but may also actively forage for food (Allen, 1963). Müllner and Linsemair (2007) observed an individual that had fed on a nest of fledgling Hotzans, a bird known for over-water nesting. Populations living in wetlands with a dry season, like the llanos, may experience increased prey densities as wetlands reduce their size in the dry season, and fish and other aquatic animals are concentrated in small areas. Rivas (2000) reports that some individuals move to rivers in the dry season, while others remain in drying pools and estivate as the water evaporates.

Gravid females are relatively sedentary and probably do not forage. Parturition occurs at the end of the wet season between October and late December, with a gestation of 202.6 days. Most births occur in the evening after the peak heat has passed, and birthing lasts between 20 to 40 minutes, but some females take up to 145 minutes. Litter size was correlated with the mass of the female and averaged 29.4. The neonates average about one percent of the mass of the female. The sex ratio at birth, calculated from all the newborns obtained in the study, was even. Neonate anacondas did not show any sexual size dimorphism. Neonates in captivity have been reported to grow at 2.13 mm/day (Lamonica, 2007), while wild individuals grow much slower (0.068–0.074 mm/day) (Rivas et al. 2016).

Neill and Allen (1962) observed a captive female *E. murinus* give birth to four young and 19 undeveloped eggs. After parturition, the female ingested the undeveloped eggs. Rivas (2000) found relatively large numbers of stillborn young and attributed it to the stress of handling during the study. Still, this seems true for captive animals that should be acclimated to captivity and handling.

Neonates have a diet composed of birds, the same prey as young adult snakes. The absence of small caiman, hatchling turtles, fish, and frogs in the diet was unexpected, although adult anacondas rarely eat fish and amphibians. The small relative prey size, their low feeding frequency, and their lack of mobility suggest a low metabolism. The young prefer stagnant, shallow water covered by aquatic vegetation, essentially the same habitat used by the adults (Rivas et al. 2016). Adults capture prey as large as adult capybaras (40–55 kg), adult white-tailed deer (55–70 kg), and full-grown spectacled caimans (35–55 kg). Anacondas are dietary generalists who take any prey they can subdue and swallow. Anacondas hunt almost exclusively from the water.

Yellow Anaconda

Eunectes notaeus Cope, 1862

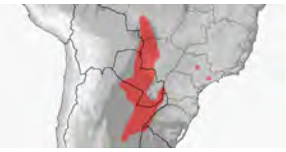


Figure 4.29. The distribution of the Yellow Anaconda, *Eunectes notateus.*

Distribution and Habitat**.** Distributed from about 15°S in Bolivia and Brazil to 32°S in Argentina. It inhabits wetlands, including swamps, seasonal floodplains, palm savanna, marshes, gallery forests, and oxbow lakes. In Argentina, it is restricted to the northeast portion of the country in the states of Corrientes, Chaco, Entre Rios, Formosa, Misiones, and Santa Fe. In Bolivia, it occurs in the northeast border region with Brazil. Here it is sympatric with the Green Anaconda. In Brazil, the Yellow Anaconda inhabits the western Pantanal in Mato Grosso, and Mato

Figure 4.30. The Yellow Anaconda, ***Euneces notateus*****. Photography by JCM.**

Grosso do Sul. In addition, there is an outlying, isolated population in São Paulo Province. In Paraguay, the species is widespread, inhabiting the Paraguay, Parana, and Pilcomayo River Basins. In Uruguay, it is known from only one specimen from Achaval Province (Figure 4.29). The type locality is the Paraguay River and its tributaries.

Natural History**.** Prey items were collected from 49 males and 37 females by Waller et al. (2007). They found all vertebrate classes represented. Rodents were eaten most often (67%) by both sexes. The largest female examined was 3.1 m and contained hairs from a Capybara. The most common prey was the Water Rat (*Holochilus chacarius*). Birds found in nine snakes included cormorants, limpkins, and wading species. Three individuals had eaten the semi-aquatic dipsadid snake *Hydrodynastes gigas*.

Reproduction. Waller et al. (2007) found sexual maturity is reached in males at a body length of 1.28–1.43 m. The smallest reproductive female was 1.47 m in body length. Mating occurs in September and October. Females showed synchronous reproductive cycles. Oviducal eggs were found in October and November. Neonates are born in April. The average litter size for wild-caught snakes is 11, and the size of the litter is positively correlated with the size of the female.

Malagasy Booids, Family Sanziniidae

Habitat use and foraging habits of the Malagasy Ground Boa genus *Acrantophis* are poorly known. However, Gardner et al. (2017) observed *Acrantophis dumerili* in a pond (in a cave) with most of its body submerged. They also reported *A. madagascariensis* submerged in a pond at a different location. In both instances, they suggest the snakes were foraging from ambush. Both observations occurred in semi-arid areas lacking abundant surface water. In such contexts, diverse species may visit water to drink and thus occur at higher densities than in the surrounding landscape, increasing the probability of encountering prey. These snakes may not be using aquatic habitats regularly.

Figure 4.31. The Malagasy Ground Boa, *Acrantophis dumerili.* **Photography by JCM.**

Asian Pipe Snakes, Family Cylindrophiidae

The thirteen species of *Cylindrophis* are considered fossorial in much of the literature. However, *Cylindrophis ruffus* composes part of the Tonlé Sap snake harvest, which is collected using gill nets. A telemetered individual in southern Thailand stayed at the exact underwater location for several weeks, not moving more than a few meters (Murphy et al. 1999, Karns et al. 2005, Brooks et al. 2009). *Cylindrophis* is superficially similar in its ecology to the

Western Hemisphere *Anilius scytale*. The two families share similar, superficial appearances, ecology, and defense behaviors. These snakes are likely adapted to inhabit flooded burrows.

Cylindrophis is widespread in southeastern Asia, ranging from Myanmar, Laos, Vietnam, Cambodia, Thailand, and the Malay Archipelago, including Singapore, both peninsular Malaysia and eastern Malaysia (Borneo); in the Indonesian Archipelago, they occur in the Greater Sunda Islands (Borneo, Sumatra, and Java, as well as some of their offshore islands), Sulawesi, the Lesser Sunda Islands (Lombok, Komodo, Flores, Sumbawa, Timor including Timor-Leste, and east to the Maluku Islands (Halmahera, Wetar, Damar, Babar, and into the Tanimbar Archipelago). The eastern distributional limit, sometimes given as the Aru Islands off the southwestern coast of New Guinea, is questionable. They are known from Sri Lanka but are not known from India. They are present in southeastern China (Fujian, Hong Kong, and Hainan Island).

Pipe snakes of the genus *Cylindrophis* have a relatively blunt rounded head with large plates, not distinct from the anterior body, the eyes are small, and a mental groove is present. The body is uniformly cylindrical; the ventral scales are narrow and barely wider than the dorsal scales; they have a pair of pelvic spurs in both sexes; the tail is exceptionally short tail, often with aposematic ventral coloration. The body is cylindrical, with a nearly uniform diameter, thus the name pipe snakes. The eyes have round or vertically subelliptic pupils. The head has large plate-like shields, with the nostrils in a single nasal scale; a loreal scale is present; the postocular scale is small. The dorsal scales are smooth, in 17 to 23 rows depending on the species. They range in size from small (120 mm) to medium sized snakes (1000 mm). The life history and habits of these snakes need more documentation (Figure 4.34). Some *Cylindrophis* have a coloration and pattern that makes them appear very similar to North American *Farancia*.

Figure 4.32. The Oriental Pipe Snake, ***Cylindrophis ruffus.***
Photography by Kenneth Chin.

On the next page. A Little File Snake, *Acrochordus granulatus,* **is in a puddle. Photography by Kenneth Chin.**

5. File Snakes

5. File Snakes

Myke Clarkson and John C Murphy

The family Acrochordidae is a fully aquatic snake lineage comprised of three extant species (*Acrochordus javanicus, Acrochordus granulatus, and Acrochordus arafurae*) and one extinct species (*Acrochordus dehlmi*). The extant species are found throughout the Indo-Australian region, ranging as far west as three file snake species range from the North West coast of India and as far East as the Philippines Sea and the Solomon Islands, with *Acrochordus granulatus* occupying the most extensive range of the three (McDowell 1979).

Fossil records from the Miocene of the extinct *Acrochordus dehmi* indicate this species had a more inland distribution earlier in its history, with fossil evidence found in Siwalik, Pakistan, Nepal, northern India, and Thailand. Only a single fossil in Thailand has been found within the group's extant range, suggesting an Asian origin with later dispersal to Indonesia and Australia. Australian fossil records only date to the Pliocene, indicating Australia as a more recent range for the group. In addition to a more inland range, *Acrochordus dehmi* was the largest of the known *Acrochordus*, with an approximate size of ~3 meters (Head et al. 2007 and Sanders et al. 2010).

The highly aquatic and unique file snakes have loose, baggy skin and minor, rough scales, each with sensory organs. Their short tails are round, prehensile, flat, and sword-like; the eyes and valvular nostrils are dorsally or dorsolateral. Their lack of muscle tone is spectacular and can only be fully appreciated by handling one; a physiological feature restricting them to an entirely aquatic lifestyle. The rough, file-like surface of the skin and its loose folds are used in catching and holding slippery, mucus-covered fish. Their maxillary teeth are similar in size, long, and fluted on the sides and posterior surfaces. The fluted condition is found in many fish-eating snakes. File snakes usually have more than 100 teeth. Their thick bodies, slow movements, sluggish metabolism, and complete reluctance to leave the water render them helpless out of the water (McDowell 1979).

Figure 5.1. *Acrochordus javanicus* **15 kg, 1.95 cm from Bangkok, Thailand. Mr. Eakasak Kanjaruke is the person in the photo. Photography by Kittipong Jarutani.**

Figure 5.2. A dorsal view of the head of *A. javanicus* that is covered with algae. Photography JCM

Figure 5.3. Note that acrochordid lack plate-like scales on the top of the head. Photography JCM

The extant file snakes range in size from the 1.1 m *Acrochordus granulatus* to the 2.9-meter *A. javanicus,* though fossil evidence of *Acrochordus dehmi* suggests a much larger size earlier in their evolution, with specimens. Although the *A. javanicus* size record has been questioned because it is old and may be an error, most large specimens reach about 2 m. File snakes tolerate various salinity levels and inhabit fresh, brackish, and marine environments.

The Little File Snake (*Acrochordus granulatus*) is the most marine of the three species and has been found 15–20 km offshore. It has the highest blood volume of any snake (13% of its body weight, most snakes are in the 5–6% range), and red blood cells compose 50% of its blood volume (most snakes are in the 25–30% range). Thus, it has the largest oxygen-carrying capacity of any snake. Underwater the file snake's heartbeat is slow, but in anticipation of taking a breath as the snake surfaces, the heartbeat increases so that more oxygen can be taken up by the blood flowing through the lungs. Like other aquatic snakes, file snakes exchange blood gases through their skin, increasing their dive time. File Snakes living in freshwater do not have the high blood volume or the oxygen-carrying capacity found in marine species.

Ecological studies on the Arafura File Snake suggest that it may not have a specific home range; instead, they wander through the murky water. Some individual file snakes stay at one location for a day or more, while others may move almost a kilometer. The freshwater Arafura file snake lives in a seasonally wet climate, and their wetland habitat expands and contracts with the rains as they follow the water. During the dry season, populations may be highly concentrated in small areas, which offers an opportunity for mating. Multiple males compete for females in these situations, and it seems likely that sperm competition is present in this species, as it is in most snakes. With the rain, the area covered by water expands, and the snakes disperse to distant locations, lowering the density of the snakes. Like all animals, file snakes are significantly impacted by climatic events. Madsen and Shine found high rainfall late in the wet season resulted in abundant fish populations and fat file snakes the following year.

Like many aquatic snakes, acrochordids laterally compress their body when swimming. The compression produces a keel on the belly and increases the body's surface area, making the snake a more efficient swimmer.

Questions about file snake relationships were largely unresolved until DNA sequencing and genetic comparisons became possible. While some authors hypothesized that acrochordids were related to boas and pythons, others considered them colubrids. DNA sequences suggest that file snakes are the sister species to all the advanced snakes, the Caenophidia, and last shared an ancestor with them at about 90.7 Ma (Vidal et al. 2009). Sanders et al. (2010) examined relationships within the genus using mitochondrial and two nuclear gene sequences. *Acrochordus javanicus* is the sister to *A. arafurae* + *A. granulatus*, counter to expectations from superficial ecology, external phenotype, and former taxonomy. They reviewed and revised fossil calibrations for dating snake divergences. A Bayesian relaxed-clock analysis of the two nuclear loci found interspecific variations among extant species during the Miocene about 16 and 20 MYA, making this group one of the oldest extant marine snake lineages predating actual sea snakes (Hydrophiinae), which diverged ~7 MYA, and sea kraits (Laticaudinae) which first appeared ~13 MYA (Sanders et al. 2010).

New morphological data for *A. arafurae*, and their molecular timescale supported the placement of the fossil taxon *A. dehmi* within the *Acrochordus* crown group as the sister to *A. javanicus* among nominate species. The study highlights the three *Acrochordus* species as old and highly distinct lineages.

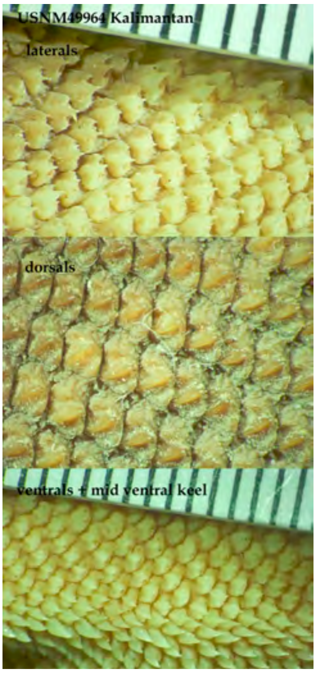


Figure 5.4 Scales on *Acrochordus javanicus* **are differentiated on various regions of the body. Note the lateral scales in the top photo show three cusps. Scales on the dorsum have strong keels but no cusps, and the midventral scales are spine-like. Photography by JCM.**

File Snakes share unspecialized head scales with the boas and pythons, but they are united with colubroids in that they lack vestigial limbs; males have spines on their hemipenes, and they have a well-developed vomeronasal system. Traits unique to acrochordids include skin sense organs, a passive joint between the frontal and parietal skull bones, and the shape of the head on the ribs. Acrochordids also have an unusual lung morphology, with a double row of small lung pouches on the trachea and a more folded intestinal tract than seen in other snakes. Acrochordids can remain submerged for as long as 2.3 hours. When they surface, they take about five breaths per minute. The first several breaths oxygenate the blood, and the last fills the multi-chambered lung.

All three species show sexual dimorphism in body and tail sizes. Reproduction is seasonal in all three species. Ovulation occurs about July, and parturition follows five or six months later.

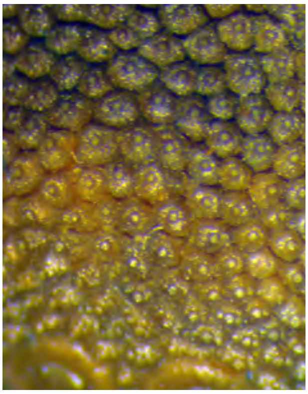


Figure 5.5,. Scales on the snout have a sense organ. Photography by JCM.

Male file snakes mature at about six years of age; females mature at about nine years. Only a small proportion of females are reproductive in any given year, and only the most prominent females reproduce frequently. *Acrochordus arafurae* average about 16 young (with a range of 9–25). One captive *Acrochordus arafurae* gave birth to a single young after seven years of isolation, suggesting file snakes can use facultative parthenogenesis to reproduce.

The three extant species of these aquatic snakes compose this ancient Asian – Australasian family. One species is mostly freshwater (*Acrochordus arafurae*), one is primarily marine (*Acrochordus granulatus*), and one (*Acrochordus javanicus*) is a habitat specialist. It uses streams running through river deltas and it is likely exposed to brackish water. Some authors suggest file snakes are constrictors; however, how they restrain prey with folds of skin covered with scales with keels and cusps. This is not the same as constriction in other snake lineages. Sensory organs occur on tubercles on the interstitial skin between their scales and each scale. These likely provide information about the presence and position of prey. Like many snakes, acrochordids use both ambush and active foraging hunting strategies. Most hunting behavior occurs at night.

During the day, file snakes take refuge by staying in the shadows created by vegetation overhanging the water. They may even move with the clouds to confuse predatory birds (Shine 1985).

Arafura File Snake

Acrochordus arafurae McDowell, 1979

Figure 5.6. The distribution of the Arafurae File Snake, *Acrochordus arafurae.*

Distribution and Habitat. This species is restricted to the freshwater drainages of New Guinea, and Australia connected to the Arafura Sea (including the Gulf of Carpentaria). Shine (1986) found this snake in Northern Territory billabongs during the dry season, expanding their range into inundated grassland with the onset of wet-season flooding. In New Guinea, known from the Mimika and Lorentz Rivers (Irian Jaya), the Fly-Strickland River system, including Lake Daviumbo and Lake Murray, the smaller rivers (Bensbach, Binaturi, Oriomo, Pahoturi) of southwestern Western Province, Papua New Guinea, and the Aramia River drainage. In Australia, they are present in the Daly, Alligator, Koolatong, and McArthur River systems, Northern Territory, and the Leichardt, Gilbert, Mitchell, Lukin, Edward, and Archer River systems of Queensland. The Australian distribution is along the coast from the Kimberly region of Western Australia to the eastern (Coral Sea) coast of the Queensland Peninsula. Although the Fly and Aramia Rivers of New Guinea open into the western end of the Coral Sea, they are connected by swampy lowlands to the rivers draining into the Arafura Sea. Type locality: Lake Daviumbo, western Province, New Guinea (Figure 5.6).

Natural History. Telemetered file snakes were sedentary during daylight hours but moved extensively at night (Shine and Lambeck 1985). Sex differences in habitat use during the wet season were evident. Females were often collected in deep-water (more than one meter) nets, and males were collected in shallow-water nets (less than one meter deep). Most (88%) of the females from deep water were adults, while many females from shallow water were juveniles. Most males (87%) and immature females (69%) were in shallow water. Adult females occur in both habitat types (54% in deep water). During the dry season, a female sex bias related to water depth or maturity was found. The proportions of juvenile to adult males did not differ between deep and shallow water in either comparison.

Shine (1986) found sexual dimorphism in *A. arafurae* is consistent with the hypothesis that sexual selection is responsible for body length sexual dimorphism. Female reproductive success depended on body size—larger females produce larger and more frequent litters. In contrast, the reproductive success of males probably does not rely so much on body size—

multiple males in shallow water court females. The observations of several males around one female suggest that male-male aggression may not occur.

However, sexual dimorphism in *A. arafurae* involves more than body length. The longer tails of males presumably reflect the need to fit the hemipenes into the base of the tail: this tail-length dimorphism is widespread in reptiles. Sexual differences were also apparent in the prey taken by each sex, and adult females ate much larger prey than did adult males (mean prey masses 291 g in females as opposed to 24 g in males). Prey-size differences were evident even in males and females of the same body size.

Figure 5.7. The skull of an *Acrochordus javanicus.* **Photography by JCM**

A four-year mark-recapture study of the Arafura File-snake in the "wet-dry" Australian tropics of Kakadu National Park by Houston and Shine (1994a) showed less movement on moonlit nights. Trap sites under overhanging vegetation consistently caught more snakes than trap sites in open water, and juvenile snakes were mainly caught in areas covered in floating vegetation. The authors suggest that the preference for nights, traveling primarily through heavily vegetated areas, is adaptive in reducing their vulnerability to predators (especially visually hunting birds). The movements of marked filesnakes suggest they are nomadic instead of having fixed home ranges. Larger snakes moved greater distances; males were more likely to remain at their initial capture site than females, but dispersal patterns of males and females were similar in most respects. Filesnakes sometimes move between billabongs during the wet season when large expanses of shallow water connect the billabongs.

Some individual file snakes stay at one location for a day or more, while others may move almost a kilometer. The freshwater Arafura File Snake lives in a seasonally wet climate, and its wetland habitat expands and contracts with the rains as they follow the water. Population dynamics in these snakes are driven by rainfall in northern Australia. During the dry season, populations may be highly concentrated in small areas that offer mating opportunities. Multiple males compete for females in these situations, and it seems likely that sperm competition is present in this species, as it is in most snakes. With the rains, the area covered by water expands, and the snakes disperse to distant locations, lowering the density of the snakes. Like all animals, file snakes are impacted by climatic events, and Madsen and Shine (2000) found high rainfall late in the wet season resulted in abundant fish populations and fat file snakes the following year.

The following description of *A. arafurae* dive physiology and behavior is from Pratt (2009). File snakes respire bimodally, using both atmospheric and aquatic (cutaneous) gas exchange. Pratt (2009) investigated its ability to up-regulate cutaneous oxygen uptake to compensate for the temperature-induced increases in metabolic rate. She found cutaneous oxygen uptake was independent of temperature, and the snake met all elevated metabolic demands by increasing atmospheric oxygen uptake. Consequently, the maximum dive duration was reduced by 70%, from 77 minutes at 20°C to 28 minutes at 32°C. Cutaneous oxygen uptake significantly contributes to dive duration. When the ability to respire aquatically was removed (severe hypoxia), dive duration was reduced by up to 30%.

Figure 5.8. The Arafurae File Snake, *Acrochordus arafurae.*
Photography by Scott Eipper

Acrochordus arafurae infrequently feeds on large meals; thus, the post-eating metabolic response requires more energy. After fasting for one month, peak oxygen consumption was up to 12 times the standard metabolic rate. The substantial reductions in dive duration following feeding may reduce the snake's vulnerability to predators. *Acrochordus arafurae* is prone to predation bybirds of prey and aquatic predators such as crocodiles and large fish. Simulated avian predation did not change dive or surface duration or proportion of time at the surface or spent active. However, a larger number of longer dives were observed with fewer long surface intervals suggesting an increase in cutaneous oxygen uptake.

At night, *A. arafurae* became more active; its reduced dive duration and increased surface-active suggest it is foraging. The mean dive time was 6.6 minutes, with 85% of dives less than 10 minutes. The maximum dive duration was 153 min. Snakes were located at a mean depth of 0.62 m; however, they occasionally dove to 6 m, but very infrequently.

Pratt et al. (2010) remotely monitored diving in free-ranging A. arafurae. The average dive depth was 0.62 m, and 95% of dives had an average depth of one meter or less. The average dive duration was 6.6 min, and 84% of dives were terminated within 10 min, but all snakes performed dives 450 min during the 14-day observation period. The authors hypothesized that dive behavior was strongly influenced by predation pressure. The short dives within the aerobic dive limits reduced the time they needed to spend at the surface on each breathing bout, reducing the risk of bird predation. Predation is a strong selective force that might alter the time allocation during dive cycles.

Growth increments of snakes (71 males, 77 females) recaptured after periods of more than six months were used to estimate growth curves. The low metabolic rates, and slow growth rates suggest these snakes mature at ages older than most other snakes. Male file-snakes mature at about five years, and females mature at about seven. Male grew more slowly than females as juveniles and matured at smaller body sizes (87 cm in males vs. 117 cm SVL in females) (Houston and Shine 1994b).

Little File Snake

Acrochordus granulatus Schneider, 1799

Figure 5.10. The distribution of the Little File Snake, *Acrochordus granulatus.*

Distribution and Habitat. It occurs on both coasts of the Indian Peninsula, Sri Lanka, and is widespread in the Indo-Chinese and Malayan regions; it is also present in the Philippine Islands; the Greater Sunda Islands, Sulawesi, and Flores and Timor in Lesser Sundas; the coasts of New Guinea and is present in the Lorentz, Sepik, and Fly-Strickland river systems. In addition, it occurs on the islands of Biak and Japen Islands in Geelvink Bay; Kiriwina Island, Trobriands, Mussau Island and the Willaumez Peninsula of New Britain in the Bismarck Archipelago, Bougainville Island, and at least Morgusaia (Shortland Group), Santa Isabel, Malaita, and Guadalcanal Islands in the Solomon Islands. It inhabits coastal marine waters and some freshwater lakes and rivers. Type locality: None given (Figure 5.10).

Natural History. The habitats of *A. granulatus* reported in the literature (Cantor, 1847; Flower, 1899; and Boulenger, 1912) include marine and freshwater environments in coastal rivers of south and southeastern Asia. Dunson and Dunson (1973) found this species in full seawater and fresh water. They also reported on snakes collected over a shallow reef flat exposed at low tide near Townsville, Queensland.

The diet includes gobies and goby-like fish that are small and demersal, often in caves, under rocks, and crevices. These fish reproduce and care for their young in burrows, suggesting that *A. granulatus* feeds by exploring crevices and burrows along the bottom. Four of the fish species eaten by *A. granulatus* are also preyed upon by the venomous sea snake, *Hydrophis* (*Lapemis) hardwickii* (Voris and Glodek 1980)

Figure 5.12. (A) The Little File Snake, *Acrochordus granulatus.* **(A-B) Photography by Harry Ward-Smith. (C). Photography by Law Ing Sid.**

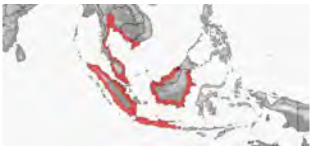
The Little File Snake produces small litters of 6–12 (mean = 4.8 offspring) and they have a relative clutch mass (RCM) that is lower than in its larger relatives.

Like other marine-dwelling species, it drinks freshwater and has a dehydration threshold for the first drinking response. A deficit of 7.4% of the original body mass will trigger it to drink from the freshwater lens on the ocean's surface. The thirst mechanism in this species is more sensitive than that of sea snakes. The volume of water ingested increases with increasing dehydration. In marine environments, freshwater is obtained at the water's surface, and *A. granulatus* tests the water with tongue flicks between swallows of water. Large volumes of freshwater may be consumed, and approach 50% of the snake's body mass (Lillywhite et al. 2014).

The Tiger Shark is a known predator of this snake in Northern Australia (Lyle and Timms, 1987).

Karung

Acrochordus javanicus Hornstedt, 1787



Distribution and Habitat**.** Southeast Asia - a Sundaland-Indochinese species. Indonesia (Borneo, Java, Kalimantan, Sumatra; the range in eastern Indonesia is unknown); Cambodia; Malaysia (Malayan Peninsula and East Malaysia); Singapore; Thailand; and Vietnam.

The Type Locality of *Acrochordus javanicus* Hornstead

There is some confusion in the literature concerning the type locality of *A. javanicus.* Shaw (1802:573) suggests the type specimen came from a "large pepper-ground near Sangasan" Java. Smith (1943: 132) reports the type locality as Java. Steubing (1991:329) reports the type locality as Bantam (also spelled Bantem), W. Java. And McDiarmid et al. 1999:229 reports both of these literature accounts and make no judgment as to the actual type locality.

My translation of Hornstead follows, parentheses with italics are Hornstead's words, and parentheses with bold are my interpretation. He wrote,

> During my stay on the island of Java, in the years 1783 and 1784, I had the pleasure, during a journey from Bantam, of discovering one of the largest snakes there are in the Indies, and one that until this time has evaded discovery and thus the scrutiny of natural scientists. The snake was found inside a big pepper forest at Tangaran. A Chinese in our travel party brought him (**the snake**) alive to Batavia, using a forked bamboo stick to fix/hold the head. As the snake was too big to be stored in alcohol, I had it skinned, and the Chinese chopped up the meat, which they fried and boiled and used for delicious courses/dishes. I stored the skin in arrak and it is now part of His Majesty the King´s priceless collection. When the snake was opened we found, beside an abundance of semi-digested fruits, five young of (*halfannat kvarters)* **(20-25 cm)** length, which probably were the reason for the bulky/bulging belly/stomach of the female snake.
>
> Although this snake had all the characters other snakes possess, it struck me as peculiar that it lacked, not only the scales under the belly and tail (= ventral and subcaudal scales), which are the only the holy Creator have bestowed upon

> this naked genus so that they may move with speed from one place to the next, and which are also a common feature for all snake types known to date; (**but also lacked**) the rings and wrinkles (*annuli et rugae*) characterizing the two latter genera of snakes in von Linnaeus' system. In contrast to other snakes, which possess smooth and shiny skin, this snake was instead covered by warts all over, warts which were rough and covered the upper as well as the lower side (of the snake). Thus, in this respect it could not be placed in any genus of hitherto known snakes, why I call it *Acrochordus,* and whose description I here have the honor of submitting to the Royal Academy of Science.

Thus, Hornstead (1787) described *Acrochordus javanicus* from a specimen (Figure 5.15) collected in a pepper forest at "Tangaran," Java. I have not found any localities on Java with this spelling; however, about 68 km northwest of Bantem in West Java is Tangerang, now a suburb of Jakarta located on the Cisadane River. The 18th-century Cisadane drainage undoubtedly supported swamp forests with large stands of the tree *Elaeocarpus macrocerus* (family Elaeocarpaceae), a tree with a fruit that looks remarkably like a pepper (Whitten et al. 1996; Wiart 2006). Thus, I am restricting the type locality of *A. javanicus* to Tangerang, Java, Indonesia (~ 6°10'50"S 106°37'55"E).

Natural History. Only three of 100 hundred dissected *A. javanicus* examined by Shine et al. (1995) contained identifiable prey remains. Two contained fish, and one contained a large aquatic snail that may have been a secondary prey item. Most of the snakes also included fishhooks embedded in their stomach walls.

Males mature at about 1.0 m, and females mature at about 1.14 meters. About 64% of adult females were reproductive. Litter sizes ranged from 13–52 offspring (mean = 29.3) and were significantly correlated with maternal snout-vent length. The relative clutch mass (RCM) ranged from 0.15 to 0.47 (mean = 0.29). However, this estimate of RCM will be much lower than the RCM at parturition, because of the increase in embryonic mass through gestation (Shine, 1986).

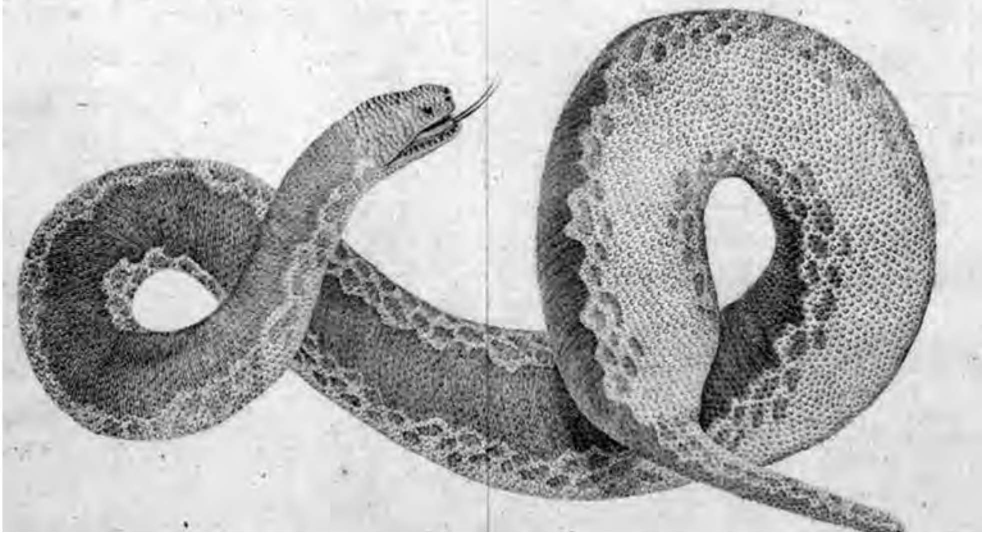


Figure 5.15 The plate from Hornstead (1787) is the type of of *A. javanicus.*

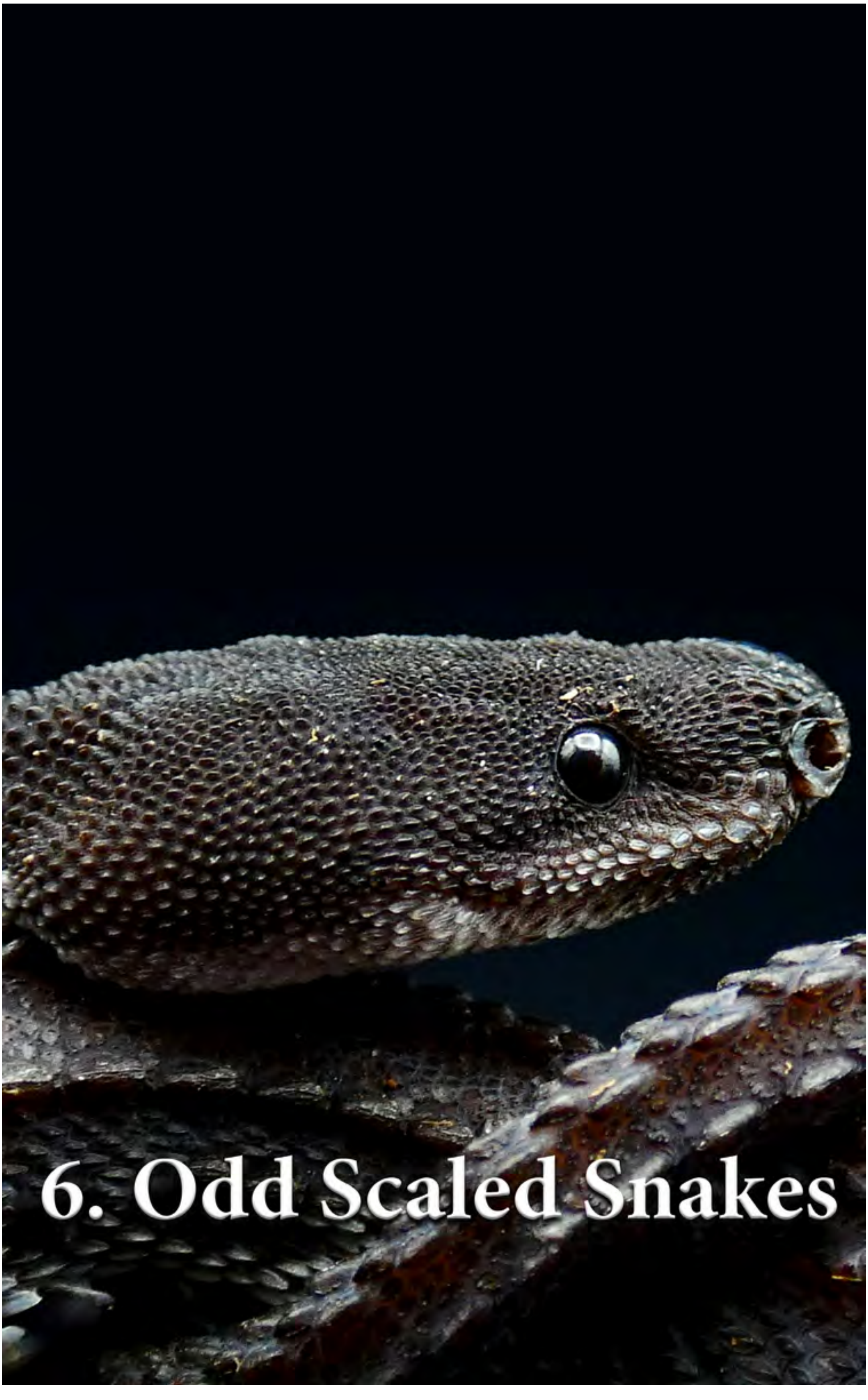
Acrochordus is capable of sustaining breath holding due to its effective elimination of CO2 through its skin. The snake has a regulated mode of breathing that maximizes its oxygen usage and allows it to stay submerged for up to 90% of the time. The control system governing its breathing is sensitive to hypoxia and ends breath holds when oxygen stores are almost depleted. Despite having a relatively small lung volume, *Acrochordus* has a well-vascularized lung that enables it to breathe without conflicting with the buoyancy requirements of a bottom-living lifestyle (Glass and Johansen 1976).

Shedding skin can be problematic for file snakes since they live in a low-friction environment. According to Lillywhite (1989), the keratin layer comes loose from the body, and the snake crawls out of it. Occasionally, however, the skin being shed can tighten around the snake's body and form a knot. In this case, the snake moves the knot towards its tail to push the skin off.

Based on the biology of *A. javanicus,* it is unlikely that the current harvest will significantly reduce wild populations (Shine et al. 1995). Factors such as the precipitation regime, extensive and inaccessible habitat, lack of efficient capture techniques, high reproductive output, and low economic value of the skins contribute to a sustainable harvest.

Figure 5.16. The Krung, *Acrochordus javanicus* from Borneo.
Photography by Rob Steubing

On the next page. The odd-scaled snake, *Xenodermus javanicus* shows off its unusual head and tail scalation . Photography credit Herpetoeditor CC-BY-SA-4.0 and Wikapedia. The original image was cropped and the resolution increased to 300 dpi.



6. Odd Scaled Snakes

6. Odd Scaled Snakes

Jason A. Fantuzzi

While the Xenodermidae live only a marginally semi-aquatic lifestyle, they are here included given their close phylogenic relations with the fully aquatic Acrochordoidea, and to their extremely unusual ecomorphologies which may lend to at least a semi-aquatic existence. One of the most basal clades of the Caenophidia, the Xenodermidae are distributed from the Greater Sunda islands of Indonesia northward through southeastern and eastern Asia. The family reaches its highest diversity in Vietnam, which is home to seven *Achalinus*, four of which are endemic (Zeigler, et.al. 2020), and all species of the *Fimbrios*/ *Parafimbrios* group. Several recent phylogenies have recovered an origination timeline for this unusual group of snakes dating back to at least 45 mya and as early as 80 mya, at the end of the Cretaceous period (Burbrink & Pyron, 2011; Pyron, et.al. 2014). While the timeline of origin for these taxa is well realized, the relationships of the family within the Caenophidia is still a matter of uncertainty, and even the most recent publications position them as incertae sedis, a most unresolved placement. The relationships between the Xenodermidae and Acrochordidae were recognized as early as 1893 when the great taxonomist George Albert Boulenger placed them within the same clade, the Acrochordinae based solely on morphology and anatomy. Phylogenies more than 100 years afterward have solidified that relationship, however the exact placement of the two regarding the rest of Colubroidea has flipped back and forth more than five times since 1998 (Durso, online. 2016). Notwithstanding, most studies recover an earlier occurrence and more distant relation of the Acrochordids to the Colubroidea. Current investigators (Kraus & Brown, 1998; Kelly, et.al. 2003; Oguiura, et.al. 2010; Pyron, et.al. 2013, 2014; Figueroa, et.al. 2016) have recovered the xenodermids (sometimes coined Xenodermatoidea) as sister to the Colubroidea, together with Acrochordoidea, whereas both previous and later phylogenies placed them as basal within the superfamily, with a caveat of varying degrees of support. Recent phylogenies (Pyron, et.al. 2013; Figueroa, et.al. 2016; Zaher, et.al. 2019) found high support for a sister relationship between *Stolizckia* and *Xenodermus*, with the former occurring earlier. These and other current studies have also found high support for two distinct groups of *Achalinus*, though no further recognitions have been suggested at the present. Once included in this group were the "wood snakes" (*Xylophis* spp.), now nested within the Pareidae (V. Deepak, et.al. 2019). The Xenodermidae are represented by 6 genera comprising 28 species, all of which possess odd scalation, hence the family name, Xenos (Greek for "strange" or "odd" and dermus, "skin"). Typically characterized by undivided subcaudals, juxtaposed (and often keeled) dorsolateral scales, and perhaps most intriguingly, by pronounced discoid nasal scales. The arrangement, size, and structure of this bizarre scalation is perhaps most pronounced in the type genus and monotypic, *Xenodermus javanicus*. As its species epithet "javanicus" implies, populations of this species are unequivocally more abundant on the Greater Sunda island of Java, the species' type locality, than anywhere else within its highly disjunct range. Despite an apparently widespread geographic distribution according to historic records from the Isthmus of Kra border areas of Burma (Robinson & Kloss, 1920), Thailand, and Peninsular Malaysia, although the latter two countries continue to produce much more recent observations than the former. The bizarre scalation of this species begins at the glossy and contrastingly pearly and black ventral scales and undivided subcaudals, then upward to the matte grey dorso-lateral scales which are somewhat obliquely arranged and largely juxtaposed to one another, finally followed by three ridges of osteoderm-like vertebral scales.

The cephalic scalation is no less unusual than the body, appearing mostly granulated throughout the head with undifferentiated labial and gular scales. Within the Xenodermidae, this species is the only taxon which lacks any large, colubroid cephalic scales save for the enlarged nasals and internasals. Dorsal scales number 40-50 at midbody (DeLang, 2017). Ventrals of males range from 171-177, with 147-165 subcaudals. Ventrals and subcaudals of females, 176-186, and 133-150, respectively. Labial scales while slightly enlarged, remain small enough to number up to 20 and 25 upper and lower, respectively: truly a non-colubroid trait. The peculiarity of *X. javanicus* does not end with its strange scalation. With a tail to body length percentage of up to 42% (50.3% according to De Rooij, 1917), these snakes might possess the longest tails of any serpents, alongside *Scaphiodontophis* and *Urotheca* spp. of Central America. Males possess longer tails (38-44%) than females (34-38%). Given a relatively high degree of prehensility, the tails of *X. javanicus* may be used to traverse low streamside vegetation while seeking semi-arboreal anuran prey, and it has been suggested to re-consider a solely burrowing or fossorial natural history of these snakes. While we do not doubt the observations of authors involving the observed burrowing habits of *Xenodermus*, those specimens found commonly occupying rice paddy fields may have simply adapted to these anthropogenic alterations as secondary habitat due to an abundance of anuran prey sources. Most primary habitat harboring these snakes occurs as low to mid-elevation rainforest in hilly country offering plentiful streams, swamps, and other forested wetlands. While *Xenodermus* can hardly be considered the strongest swimmers, observations have been made of *javanicus* swimming or rather “floating” (T. Charlton, personal communication) in pursuit of anuran larvae and small fish prey.

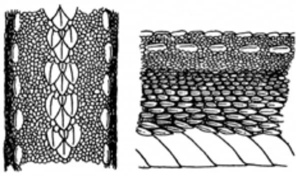


Figure 6.1. The unusual scale arrangements of the Odd Scaled Snake, *Xenodermus javanicus*. **From M. Smith, 1943.**

Most morphologically like *Xenodermus* are three species of equally rarely known and possibly anuran and fish-eating snakes from the northeastern Indian states of Meghalaya, Assam, Mizoram, and the Indo-Malayan Island of Borneo. Until very recently, these three species (including the newly discovered *S. vanhnuailianai*) com-

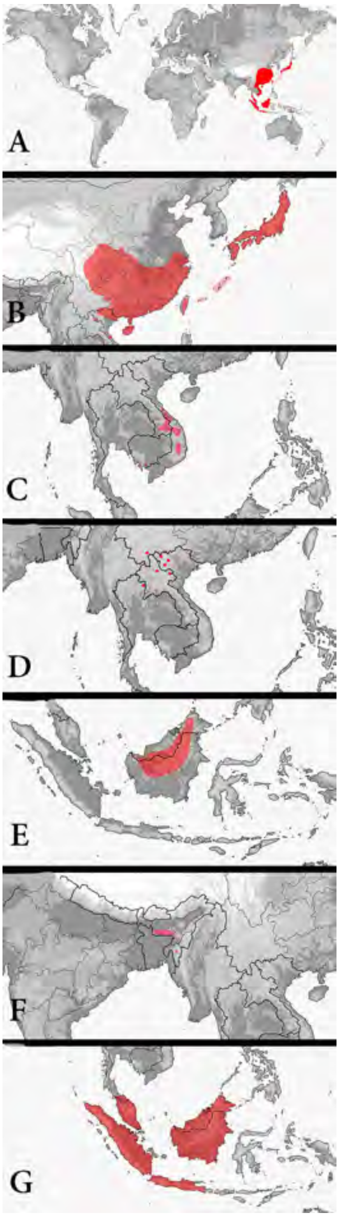


Figure 6.2.A. Distributioon of the family Xenodermatidae. B. Distribution of the genus *Achalinus*. C. The distribution of *Fimbros*. D The distribution of *Parafimbrios*. E. The distribution of *Paraxenodermus*. F. The distribution of *Stoliczkia*. G. The distribution of *Xenodermus*.

Figure 6.3. The Odd Scaled Snake, *Xenodermus javanicus.* PT Karyanusa Eka Daya (Oil Palm Plantation) in Muara Wahau Sub-district, Kutai Timur District, Kalimantan Timur Province - Indonesia Photography by Mediyansyah.

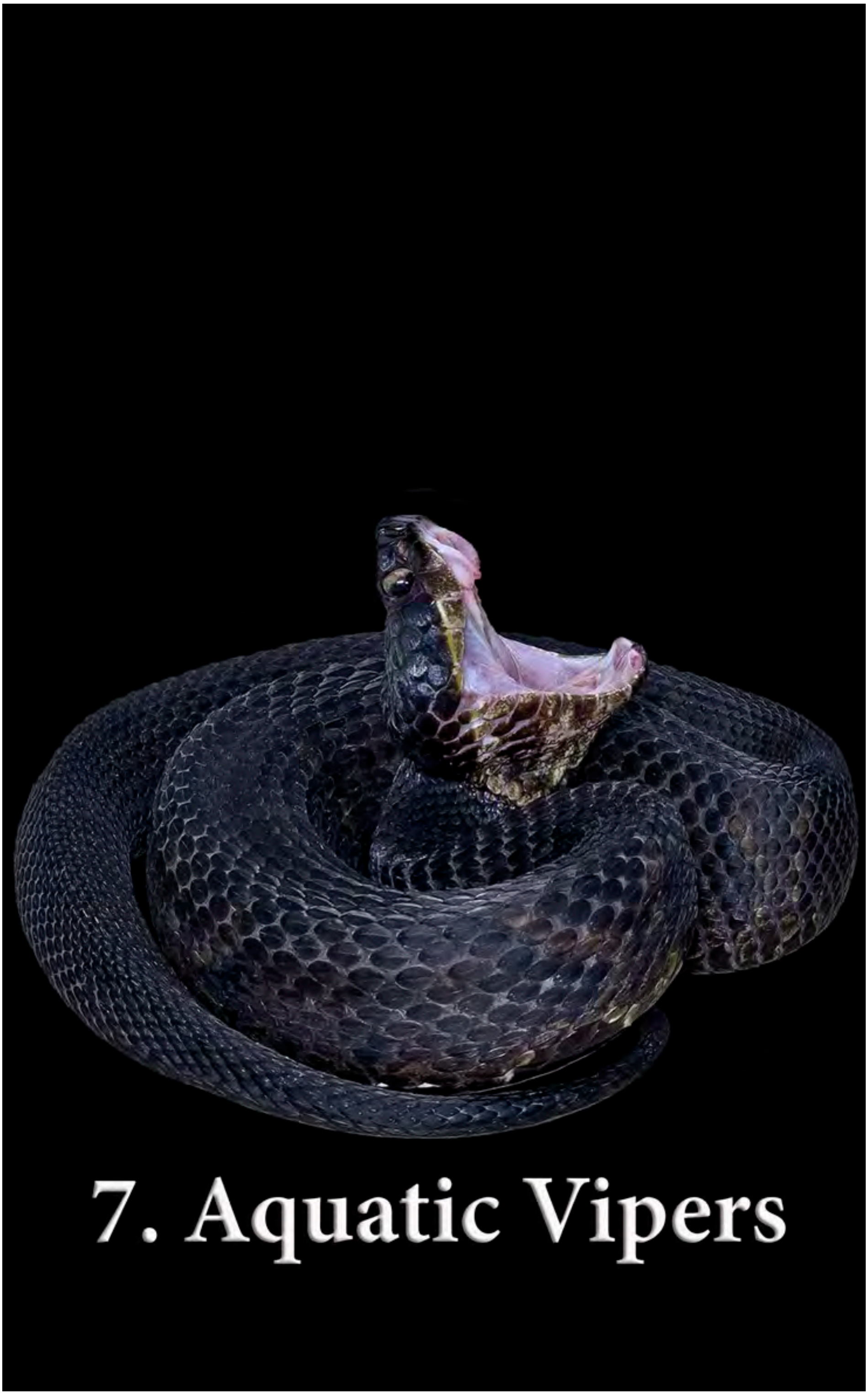
prised the genus *Stoliczkia*. The genus name was erected for these unusual snakes by Dr. Thomas Caverhill Jerdon honoring Dr. Ferdinand Stoliczka, an early Moravian (now Czech Republic) zoologist who performed extensive surveys in India including the Himalayas, where he met an untimely fate, dying of spinal meningitis triggered by Acute Mountain Sickness, or AMS (Boelens e.al. 2011). A recent updated phylogeny of the group found *borneensis* as sister taxon to *X. javanicus* (Deepak, et.al. 2021). Applying a multilocus dataset including new mitochondrial and nucle ar gene sequence data as well as several morphological character differences of the cephalic scutellation resulted in the authors' creation of the genus name *Paraxenodermus* (gen. nov.) to represent "*Stoliczkia*" *borneensis*. As earlier stated, *Stoliczkia* share a slim, laterally compressed body form with *Xenodermus javanicus* including similarly long, flagellate tails comprising about a third or more of the total body length. However, unlike the latter, the former possesses distinctly keeled lateral scales and contrastingly enlarged cephalic scutation particularly from the parietals to the internasals. Dorsal scales of *S. borneensis* number 30 at mid-body, with 210 ventrals and 124 subcaudals (De Rooij, 1917). Steubing, et.al. 2014 report scale counts of 31-35 at mid-body, with ventral scales of females ranging from 205-210 with 117-124 undivided subcaudals. Upper labials number 10 or 11 with the sixth and seventh touching the eye, though these may be separated from the eye by a row of subocular scales (Steubing, et.al. 2014).

Of *Stoliczkia* and *Paraxenodermus*, perhaps the latter is the best known ecologically, with a handful of observations and several photographs circulating online or published in regional guides. One of these images portrays the species traversing rainforest dipterocarp fronds within proximity of a forested stream. Indeed, it has been suggested that the elongated tails of this group (including *Xenodermus*) atypical to this family of serpents facilitate life ecologies amongst a three-dimensional environment at least to some extent above the forest floor, possibly in search of arboreal anuran prey. Besides these random, extremely sporadic observations, this genus is represented by six specimens, of which four are accompanied by legitimate institutional and cataloguing records. Even less is known about their behavioral ecology.

The genus *Achalinus* is unquestionably the most speciose of the group with 26 species currently recognized (Uetz, et.al. 2023). Achalinus are small (60cm-75cm) burrowing forms indigenous to the eastern aspect of Asia, from southern Japan's Ryukyu Archipelago and thenceforth southward through China including Taiwan, and into the hills and valleys of northern Vietnam. The stomach of a specimen (USNM 81513) contains earthworm remains (Pope, 1935). Yamasaki and Mori, 2017 reported bimodal seasonal activity peaking in early summer and then again in autumn, often coinciding with the appearance of earthworms on the ground surface. They reported annual activity patterns that agreed with most snakes of temperate regions, however unlike most of those examples, the hatchlings of A. spinalis remained underground in cavities until the following spring/early summer. A female from Chungan Hsien contains seven well-developed eggs, one of which measures 19x7mm (Pope, 1929). Pope opined on the fragile nature of collected *Achalinus*: "It is extremely delicate and dies more readily than almost any other snake. Soon after death it dries and hardens in a most unusual way. This drying up might lead one to conclude that it is a secretive burrower but the greatly reduced rostral is anything but a characteristic of burrowing species. It shows not the slightest signs of defensive behavior when handled."

The "bearded" burrowing odd-scaled snakes: *Fimbrios* and *Parafimbrios* represented by two species apiece. The generic names are from fimbria, Latin for "a fringe", an allusion to the strangely enlarged labial scales of these taxa, unique to the genera. It is highly possible that these fringes contain sensory epithelia (akin to the rostral appendages of *Erpeton*, a homalopsid also from Indochina) which enable these burrowing and small-eyed snakes to seek out annelid worms in complete darkness and largely incapable of tongue-flicking while tunneling through porous substrate for prey. While recent phylogenies (Ziegler, et.al. 2018, Zaher, et.al. 2019) place these two genera at a later node within the family, morphologically, this group appears to fall somewhat intermediately between *Achalinus* and the *Xenodermus/ Stoliczkia* group, featuring the stouter bodies of the former with the oddly juxtaposed dorsolateral scales and fragmented cephalic scales of the latter. Ecologically, they are typical of all xenodermids in sharing a secretive lifestyle not far from wet habitats such as streams and swamps, often sheltering beneath stones and decomposing logs.

On the next page. A Northern Cottonmouth, *Agkistrodon piscivorus* **threatens the photographer with envenomation by opening its mouth and exposing the white lining. Photography by William W. Lamar**



7. Aquatic Vipers

7. Aquatic Vipers

Very few vipers are considered aquatic or semi-aquatic. The reason for this is open to speculation.

Copperheads and Cottonmouths of the genus *Agkistrodon* are distributed in North America from the northeastern and central United States southward through peninsular Florida and southwestern Texas, and in Central America on the Atlantic versant from Tamaulipas and Nuevo León southward to the Yucatan Peninsula, Belize, and Guatemala. In addition, they occur along the Pacific coastal plain and lower foothills from Sonora south through Guatemala, El Salvador, Honduras, and Nicaragua to northwestern Costa Rica. There are eight extant species of *Agkistrodon*. They are semiaquatic to terrestrial and are often found near water. Two species, *A. contortrix,* and *A. bilineatus* are also found in dry habitats, often far from permanent streams or ponds.

Underwater hibernation by the Eastern Massasauga, *Sistrurus catentatus,* has been documented but poorly studied. While this is a mostly terrestrial species, it may spend the winter submerged in a crayfish burrow (Yagi et al. 2020). *Sistrurus* are known to swim across relatively larges bodies of water. Hullinger et al. (2018) reported a Western Massasauga, *Sistrurus tergeminus,* removed from the percid fish, *Sander vitreus,* at Wilson Reservoir Russel Co., Kansas.

Submerged hibernation has also been reported in *Vipera berus* (Viitanen 1967). While the risk of drowning remains a problem for these snakes, spending the winter underwater may increase the survival rate in some situations.

Figure 7.1. The distribution of the Florida Cottonmouth, *Agkistrodon conanti.*

Florida Cottonmouth

Agkistrodon conanti (Gloyd, 1969)

Distribution and Habitat. Marshes, lakes, ponds, streams, roadside ponds, drainage ditches, coastal islands, mangrove swamps, and rice fields from southern Florida to Savannah, Georgia, and west to southeastern Alabama.

A medium- to large-bodied semi-aquatic pit viper with an average adult size of 76–122 cm. Maximum size 189.2 cm (Gloyd and Conant, 1990; Conant and Collins, 1991), with a tail/total length ratio of 0.15–0.19 in males and 0.13–0.18 in females.

Geography and color patterns distinguish the Florida Cottonmouth from related species. The head is typically brown with vertical stripes along the snout on the rostrals, prenasals, and first upper labials (Gloyd and Conant, 1990). Dark stripes appear on the lower jaw extending from the mental to the first four or five infralabials (Gloyd and Conant, 1990). A dark cheek stripe is bordered above and below by pale stripes and is often present in adults, although it may be indistinguishable from the ground color in adult *A. piscivorus* (Gloyd and Conant, 1990; Conant and Collins, 1991).

Natural History. *Agkistrodon conanti* is a generalist predator with a diet composed of invertebrates, fish, amphibians, reptiles, birds, and mammals. They will also feed on carrion (Gloyd and Conant 1990).

A heron rookery on Seahorse Key, (a small island adjacent to the northern Florida peninsula in the Gulf of Mexico) contains a population of cottonmouths that feed on the fish dropped by the birds. Young et al. (2008) report that a fish-based olfactory stimulus, without associated ground-borne vibration or motion, triggered a foraging response in the Seahorse Key cottonmouths. Snakes from the two study sites reacted differently to the olfactory stim-

Figure 7.2. The Florida Cottonmouth, *Agkistrodon conanti.*
Photography by Kaylyn Cullen.

ulus; those with less ground cover, more rats, and fewer snakes exhibited a weaker foraging response. Sandfoss et al. (2018) reported that cottonmouths unexpectedly abandoned the Seahorse Key rookery in April 2015 and did not return.

Males are larger than females and compete for females using combat behavior. The litter size ranges from 1-15; the neonates are 21-27 cm in total length. Parturition occurs in August and September.

Northern Cottonmouth

Agkistrodon piscivorus (Lacépède, 1789)

Distribution and Habitat. Found throughout the southeastern USA from southeastern Virginia to central Georgia, east of the Appalachian Mountains, north to southern Illinois and eastern Kansas, and southward into central Texas in the west (Fig. 7.3).

Hybridization with the Florida Cottonmouth occurs in the mid-Atlantic coastal plains in southern North Carolina to the coastal plains in southeastern Louisiana. Diagnosis may be difficult for some individuals in this area without additional morphological and molecular data.

Natural History. Males consume significantly more fish, amphibians, and arthropods than females, whereas females consume significantly more reptiles and mollusks than males. Therefore, when expressing dietary preferences using the relative mass of the prey, arthropods, mollusks, and mammals are no longer essential prey sources for either males or females relative to the overall mass of prey consumed (Vincent et al. 2004).

Delisle et al. (2019) conducted a year-long telemetric habitat selection study on two Northern Cottonmouth populations in northeast Texas. The home range selection of both males and females exhibited a preference for edges and avoidance of pasture. In addition,

Figure 7.3. The distribution of *Agkistrodon piscivorus*.

both sexes selected microhabitats with thick vegetation in the spring and summer. However, in the fall, male microhabitat selection was influenced by lower temperatures and female microhabitat use appeared to be driven by parturition.

Life history data for the Cottonmouth was described by Hill and Beaupre (2008) for a population inhabiting a "riffle–pool" creek system (Rocky Grove) located in the Ozark Mountains in northwest Arkansas. One hundred and forty-two individual snakes were captured 283 times from August 1996 through September 2003. Mean snout–vent length (SVL) of adult Rocky Grove *A. piscivorus* (males 60.8, females 54.9 cm) was among the smallest reported for any population of *A. piscivorus.* Rocky Grove *A. piscivorus* also exhibited a low degree of sexual size dimorphism (SSD) compared to other localities, and mean female SVL was 90.3% that of males. Growth rates were the slowest reported for any temperate zone pitviper (males 0.151, females 0.178 cm/month). Limited data also indicate low reproductive

Figure 7.4. Northern Cottonmouth, ***Agkistrodon piscivorus,*** **(A) profile of an adult. (B) a juvenile from Union Co., Illinois, (C) an adult from North Carolina (D) an adult from Union Co., Illinois, (E) a juvenile in a defense posture. Photography by (A-B, D-E) JCM. (C) Jason Fantuzzi.**

output for this population in terms of frequency of reproduction and litter size. Female reproduction averaged less than biennial, as evidenced by the consistently low proportion of pregnant to non-pregnant females (18.4%) and the reproductive histories of individual female snakes. Litter size averaged 4.1. Mating at Rocky Grove may occur in late summer and spring. *Agkistrodon piscivorus* at this study site may be limited in energy acquisition rates relative to the conspecifics in other parts of the range.

Eskew et al. (2009) characterized the foraging strategy and microhabitat use of cottonmouths at Ellenton Bay, an isolated Carolina Bay freshwater wetland on the Savannah River site in South Carolina. They measured the habitat characteristics of 55 ambush sites used by 51 individual cottonmouths located visually at night and compared them to 225 randomly selected locations. They found Northern Cottonmouths exhibited an ontogenetic shift in foraging strategy, with juveniles using predominately ambush foraging around the edge of the wetland. At the same time, adults were most often encountered actively moving within the wetland. Juveniles selected foraging microhabitats that differed from random and consisted of mud substrate with sparse vegetation. Adults occupied a greater variety of microhabitats that did not differ from random sites. In addition, free-ranging cottonmouths exhibited ontogenetic shifts in diet: juveniles consumed mostly salamanders, while adults ate a greater variety of prey, including other snakes and birds.

Survivorship was estimated by Rose et al. (2010) for the Northern Cottonmouths in central Texas. The annual probability of survival at Honey Creek, Comal County, Texas, a spring-fed stream flowing 3.2 km to its confluence with the Guadalupe River, was 0.81 and was consistent with estimates for similar species of snakes.

Siegel et al. (2009) found that males and females store sperm, allowing for the dissociation of reproductive event timing between the sexes. Thus, the only reproductive event coordinated between the sexes is copulation, which is likely to occur in the fall and the spring. In females, the atrophy and activity of the reproductive organs vary concurrently with vitellogenesis and the mating seasons. In males, spermatogenesis peaks in the summer, independent of the mating season.

Asian Bamboo Vipers

Craspedocephalus occurs in Asia from the Indian Subcontinent Sri Lanka, Thailand, and the Sunda Shelf. About 14 species are recognized. Most species in the genus are relatively small and arboreal, with prehensile tails. Often they are green in color, but some species also have yellow, black, orange, red, or gold markings. One species shows unexpected aquatic foraging behavior and is highly polymorphic in coloration.

Figure 7.5. The distribution of *Craspedocephalus malabaricus.*

Malabar Bamboo Pit Viper

Craspedocephalus malabaricus (Jerdon, 1854)

Distribution and Habitat. Endemic to the Western Ghats along southern and western India at 600–2,000 m ASL in elevation. The type locality is the Western Ghats of southwestern India. It inhabits riparian forests and is very partial to hill streams and torrents. It is situated within dense wet rainforests and evergreen and deciduous forests, where it may be found on the ground, on rocks in stream beds, on

Figure 7.6 *Craspedocephalus malabaricus.*
Photography by (A) Vaclav Gvozdik; (B,D) © B R. Ansil. (C) Dilshad Kanniyan.

low vegetation, or in shrubs. Recently it was found in the Korba District of Chhattisgarh. *Craspedocephalus malabaricus* prefer semi-arboreal and arboreal habitats facilitated by their prehensile tail but sometimes exploit the habitats on the ground (Fig. 7.5). Note that this snake was long placed in the genus *Trimeresurus.*

Natural History. Riparian habitats are frequently used by the Malabar Bamboo Pit Vipers (Whitaker and Captain 2002; Ganesh et al. 2010). This is a nocturnal species. During the day, they are sometimes observed basking. They forage for food in the evening, possibly to avoid predators. *Craspedocephalus malabaricus* are semi-arboreal and are often detected in the lower canopy, shrub layer, and ground level. Prey includes small mammals, lizards, frogs, toads, birds, and their eggs. Adults prefer rodents, whereas juveniles feed on small frogs and lizards. The tail's white tip and prey choice suggest the young and juveniles use caudal luring. Reproductive data for this species is lacking. Wall (1919) reported that the breeding occurs from February to October. Sagar (2016) said the presence of six juveniles in August and September, indicate that breeding at Agumbe is well within the season.

Diving behavior was reported by Bhasare and Pelling (2015). They observed the tropical moist evergreen forest of Agumbe, which is in the central Western Ghats of Karnataka State, India. The region receives heavy annual rainfall (7,500 to 10,000 mm) during the monsoon from June to September.

Swimming at a slow pace, the snake was observed to halt in mid-stream (approximate depth 35–45 cm) and was followed by a short backward jolt of the leading half of the body, causing the snake to completely submerge 8–10 cm below the surface. After the backward jolt, the snake remained underwater for 5-6 seconds, of which, for approximately 3-4 seconds, it was completely motionless. Resurfacing involved a slight forward progression during which only the head broke the surface for about 1-2 seconds before repeating the backward jolt action. The snake repeated this action three more times, remaining submerged for 5-6 seconds each time. After surfacing for a fourth time, the snake swam a further three meters downstream to a submerged horizontal branch. It then wrapped its tail around the stem and coiled its body in a typical ambush position, fully submerged approximately 5 cm under the surface, with its head facing upwards. Underwater tongue flicks with the occasional slow sideward movement of the head were observed. The snake remained in this position without any attempt of surfacing to breathe for approximately 20 minutes and then emerged in a slow and controlled manner with tongue flicking, leaving the body submerged and coiled. The snake was not visibly gasping or heavily breathing on surfacing.

Another adult observed by the same authors had a total length of approximately 35 – 40 cm. It was in an open concrete tank (80 cm wide, 250 cm long, and 45 cm deep) at Agumbe Rainforest Research Station. During the monsoon season, the tank is a breeding site for the Malabar Gliding Frogs, *Rhacophorus malabaricus,* prey for *C malabaricus.* Initially, the snake was observed floating, partially submerged, at the surface of the 30 cm deep water. The snake remained motionless with its head under the surface, pointing downwards and floating in an unusual sideward position due to an inflated body. After one minute, the snake surfaced and swam a little distance. Once stopped, the snake retracted its head and anterior body and submerged again. The snake repeated the action of partial submergence four more times for approximately one minute during each submergence event within a 15-minute observation period before it ceased due to heavy rain.

The drag created by the large head of a viper was proposed by Young (1990) as the reason why there are no aquatic vipers. However, at least two of the three aquatic vipers discussed here do fine catching prey in the water.

8. The Homalopsidae

8. The Homalopsidae

Justin M. Bernstein & John C. Murphy

The snakes of the family Homalopsidae (mud snakes) are indeed a diverse (and often odd-looking) group of primarily aquatic snakes. Perhaps one of the most poorly known, aquatic, caenophidian groups regarding their evolution and natural history, many of the species in this family remain to be investigated, and speculations of their diets, behavior, reproduction, physiology, and biogeography are inferred from what is known about congeners or other homalopsids. With advances in DNA acquisition methods/technologies (i.e., high-throughput sequencing) and software aimed at biological inference, many answers to the questions we have about homalopsid evolution and diversity will likely come to light soon.

Homalopsid snakes have a family-wide distribution throughout the Old World (Figure 8.1). The Indus River Delta in Pakistan represents the westernmost range limit for Homalopsidae. Eastward, they are distributed throughout much of South Asia, throughout mainland and maritime Southeast Asia, and reaching New Guinea and northern Australia at the eastern margin of their range. Their widespread distribution and the fact that they comprise a large part of the biomass in aquatic ecosystems of Southeast Asia (Murphy, 2007a) are evidence of their evolutionary success. There are currently 56 described species of homalopsids, distributed across 29 genera, with new species continuously and recently being described from underexplored regions (e.g., Quah et al., 2017; Kohler et al., 2021, Murphy and Voris, 2020). The greatest species richness of homalopsids are found in mainland Southeast Asia (excluding the totality of Indonesian islands throughout the Indonesian Archipelago). While there has yet to be any synapomorphies discovered for Homalopsidae, a suite of morphological characters is found amongst most representatives of the family, many of which are characteristic of aquatic lifestyles: hypapophyses present along the length of the vertebral column; hemipenes forked with distal end finely calyculate, with shallow cups (spines present and variable); tracheal lung; crescent-shaped valvular nostrils; shallow rostral notch; elliptical pupils; subcaudals and cloacal plate divided; and viviparous with a placenta-like connection to the female's circulatory system (Murphy and Voris, 2014). Although these characters are not confirmed for all species (as many are known from one or few specimens), the family has been consistently recovered as monophyletic in studies utilizing molecular datasets, with fanged and fangless homalopsids as sister groups (Alfaro et al., 2008; Murphy et al., 2011; Burbrink et al., 2020; Bernstein et al., 2021).

Natural History and Diversity

The diversity of homalopsid snakes is emphasized by their disparate ecologies, diets, morphologies, behaviors, and habitat preferences. The current species richness of Homalopsidae is 56 species, amongst 29 genera. The morphological disparity of homalopsids is seen in their color patterns, body sizes, and head morphology. Species range from stout, heavy-bod-

Previous page. The Puff-faced Watersnake, *Homalopsis buccata* (Homalopsidae) traverses a shallow water habitat. The snake was photographed at Langkawi, Malaysia, Photography by Kai Kolodziej.

ied snakes (e.g., *Subsessor bocourti*) to slender-bodied *Enhydris enyhydris*. The differences in body forms are accompanied by different head shapes that contribute to dietary specialization (Jayne et al., 2018). The most drastic example of morphological disparity in this family is *Erpeton tentaculatum,* the tentacled snake, named after its rostral appendages, that are unique to this taxon. Intraspecific variation is also prevalent in many species, particularly notable in *Fordonia leucobalia*, which contains forms that are only black and white, as well as morphs that contain any combination of rust, red, and orange, or any combination of these. The greatest morphological dichotomy of homalopsids, though, is their dentition. Mud snakes are split into two groups: fangless homalopsids (aglyphous; three genera: *Brachyorrhos, Calamophis, Karnsophis*), and the rear-fanged group (opisthoglyphous; all other genera [Taub, 1967; Gyi, 1970]). It is likely that all the rear-fanged members use venom that help subdue their prey (Mori, 1998). While bites by rear-fanged homalopsids may produce localized effects (e.g., swelling, burning), reports are seldomly medically significant (Murphy, 2007a). It is worth nothing that bites from most species have never been documented; some reports with locals of the Andaman Islands state that bites inflicted by *Cantoria violacea* have resulted in death or unconsciousness (though, these reports may have confused *C. violacea* with the venomous elapid *Bungarus andamanensis*; (Ghodke and Andrews, 2000). Interestingly, the venom of *Cerberus* contains a family of venom proteins that have yet to be discovered in other venomous snakes (OmPraba et al., 2010), and rear-fanged homalopsids may possess a venom protein family (veficolins) that is unique to Homalopsidae. More studies are needed to identify the extent of variation in this group's venom, and the respective physiological effects from bites from each species. As with all snakes, handling species without knowing their exact identity and the potency of their venom is advised against.


Figure 8.1. The distribution of the Homalopsidae

Mud snakes have successfully adapted to an aquatic lifestyle and are well known for dominating the aquatic habitats they are a part of. Unlike most of the species in this family, the fangless homalopsids have adapted to a terrestrial/semi-fossorial lifestyle (reports are mostly limited to *Brachyorrhos*; Murphy et al., 2012a). The rear-fanged clade inhabits a variety of aquatic habitats. Some species are found primarily in freshwater systems such as rivers, estuaries, lakes (*Cerberus, Homalopsis, Enhydris*) and freshwater swamps (*Gyiophis, Heurnia, Raclitia*). Peat swamps are inhabited by *Homalopsis buccata, Phytolopsis punctata, Homalophis doriae,* and *Enhydris innominata,* suggesting that these species may be able to tolerate the high acidity of the substrate. Several genera and species are well-adapted to the brackish waters of coastal mangrove systems and tidal flats (e.g., *Cerberus schneiderii, Bitia hydroides*, *Cantoria violacea, Gerarda prevostiana*). Many closely related species have partitioned into different habitats, such as the freshwater *Myrrophis chinensis* and saltwater tolerant *Myrrophis bennettii,* the latter of which also rests on shrubs and bushes, which is atypical amongst homalopsids (Murphy, 2007a). Many species that inhabit brackish waters have also been found swimming in open waters near the coast (*Cerberus australis* [Kinghorn, 1929], *Cerberus rynchops* [Acharji and Mukherjee, 1996], *Cerberus dunsoni* [Crombie and Pregill, 1999], *Fordonia leucobalia* [O'Shea, 1986]). It is likely that many species, especially those possessing salt glands (Dunson and Dunson, 1979) are able to tolerate both freshwater and saltwater environments for at least a limited amount of time, as many species are not solely found in one particular type of habitat. The differences in habitat between the fangless and rear-fanged homalopsids are also reflected in their diet. While *Calamophis* and

Karnsophis remain largely understudied due to low numbers of encountered and collected individuals, *Brachyorrhos* are vermivorous, primarily feeding on earthworms (Murphy et al., 2012a; Murphy unpublished; Sanders unpublished). *Karnsophis* has been confirmed to eat frogs, but it is uncertain if they have a frog-specialized diet or are generalists (Murphy and Voris, 2013). The prey consumed by the rear-fanged homalopsids is much more diverse, being comprised of a variety of fish (Anabantidae, Channidae, Clariidae, Cyprinidae, Nandidae, Osphronemidae, Synbranchidae), frogs (Ranidae, Rhacophoridae), and aquatic arthropods (Thalasinnidae [mud lobsters], Palaemonidae and Alpheidae [shrimp], Varunidae [crabs]) (Shine, 1991; Khan, 2002; Murphy, 2007a; Brooks et al., 2009; Murphy and Voris, 2013; Pongcharoen et al., 2016; Ghodke et al., 2018). A clear shift in diet during the evolution of homalopsids can be seen in *Fordonia leucobalia*, *Gerarda prevostiana*, and *Cantoria violacea,* which form a clade. These snakes primarily feed on crustaceans, particularly hard-shelled crabs (*Fordonia*) and freshly molted crabs and alpheids (*Gerarda* and *Cantoria*) (Murphy, 2007a; Jayne et al., 2002). Homalopsids have a variety of predators; some of these include: predatory fish and sharks (*Carcharhinus cautus*) birds of prey (*Haliaeetus leucogaster, Haliastur indus, Milvus migrans*), crocodiles (*Crocodylus porosus*), lizards (*Varanus indicus*), other snakes (*Bungarus* spp. *Cylindrophis* spp., *Naja naja*), and mammals (*Bandicota indica, Homo sapiens*) (Mao, 1970; Lyle and Timms, 1987; Shine, 1991; Voris and Jeffries, 1995; Murphy 2007a).

Figure 8.2. The tentacles of *Erpeton* make it one of the most distinctive snakes. Note the free end of the scales point anteriorly. Photography by Ken Catania.

Homalopsids display a variety of behaviors that are well known amongst snakes. These include swimming in open waters, hiding amongst root entanglements, utilizing burrows of other animals, and sidewinding when escaping predators (Murphy, 2007a; personal observation by JMB [*Cerberus microlepis*]). However, a few species have been widely recognized for behaviors that have yet to be identified in any of the 3,800+ species of snakes. The 'crustacean-eating' clade's (*Fordonia, Gerarda, Cantoria*) shift in diet to lobsters, crabs, and shrimp also shows a shift in how they feed. *Fordonia leucobalia* uses a specialized closed-mouth strike to attack and its chin to pin down its crustacean prey (Jayne et al., 2018). Both *F. leucobalia* and *G. prevostiana* rip their prey's legs off, engulfing them separately, allowing them to eat prey larger than would normally be possible. *Gerarda prevostiana* also tears the carapace off of the crab and uses body coiling (Jayne et al., 2018). *Erpeton tentaculatum,* a highly aquatic homalopsid snake, distantly related to the aforementioned clade, uses its unique rostral appendages for hunting. These appendages are mechanoreceptors which are innervated by the trigeminal nerve and increase the snake's sensitivity to water movement (Catania et al., 2010). This allows the snake to wait in a rigid J-shaped posture in the water, flick its tail to startle unsuspecting fish prey into a C-start escape response towards the

Figure 8.3. *Cerberus* has well developed, gooved rear-fangs. Here the functional fang is adajcent to a replacement fang. Photography by JCM

snake's mouth, and meet it to ultimately eat its prey (Smith et al., 2002; Catania, 2009; Catania et al., 2010). And finally, an observation suggests the poorly known Bornean species *Homalophis gyii,* changes color from dark reddish-brown to a complete white color within a few minutes. The role of metachrosis in snakes is under studied. It may be a defense mechanism or stress response once the specimen was placed into a bucket (Auliya, 2003).

Taxonomic History

The nomenclatural history of Homalopsidae has been far from stable for centuries. The first described species of the family was *Homalopsis buccata,* and was actually described on three separate accounts before the second species of homalopsid snake was described. *Homalopsis buccata* was described by Carl Linnaeus (1707–1778), twice in the same work (Linnaeus, 1758): first as *Coluber buccata* from India (specimen lost), and again as *Coluber monilis* from America. Then, in 1789, Johann Friedrich Gmelin (1748–1804), a German naturalist, used an illustration from Dutch zoologist Albertus Seba's **Locupletissimi Rerum Naturalium Thesauri** as the iconotype for *Coluber subalbidus* (Gmelin, 1789); these three *Coluber* taxa are all now known to be *H. buccata* (Murphy, 2007a). It was not until 10 years later that the second species, *Hydrus enhydris* (=*Enhydris enhydris*) was described by Schneider (1799).

Further contributions to homalopsids took place in the early 19th century by Heinrich Boie (1794–1827), a German naturalist who worked on the herpetofauna of Java, which ultimately remained unpublished (Adler, 1989). Boie's older brother, Friedrich Boie, published some of Heinrich Boie's earlier papers posthumously (Adler, 1989), which included many new genera and species; one of these still-valid taxa is what is now recognized as *Hypsiscopus plumbeus* (Boie, 1827). Before his death, Heinrich Boie also grouped all aquatic snakes into the family Hydrophidae, which included homalopsids except for *Erpeton tentaculatum* (Murphy, 2007a). Although aquatic snakes are now, without question, recognized as distinct evolutionary lineages in part due to broadly-sampled systematic studies (e.g., Pyron et al., 2013; Burbrink et al., 2020; Bernstein et al., 2021), the Hydrophidae was the earliest grouping of aquatic snakes as a distinct taxonomic group (Murphy, 2007a). Later, John E. Gray (1800–1875), British zoologist and founder of the zoological collections of the Natural History Museum (=British Museum, London), placed all genera of aquatic snakes in the family Hydridae, which included 14 homalopsids described by himself, eight of which are currently valid as the following: *Bitia hydroides, Cerberus australis, Homalopsis hardwickii, Myron richardsonii, Myrrophis bennettii, Myrrophis chinensis, Phytolopsis punctata,* and *Raclitia indica* (Gray, 1849). Continuing with the taxonomic flux of aquatic snakes, homalopsids were placed in the group 'Platyrhiniens' by French zoologists Constant Duméril (1774–1860), Gabriel Bibron (1805–1848), and Auguste Duméril (1812–1870) in their seminal work Erpétologie Générale (Duméril et al., 1854); this work includes the description of new homalopsid snakes, two of which are still valid and recognized: *Dieurostus dussumieri* and *Sumatranus albomaculatus.*

The recognition of Homalopsidae as a higher taxonomic group of snakes distinct from other aquatic lineages did not happen until Charles L. Bonaparte (1803–1857), French zoologist, classified them under the "Homalopsina," a subfamily of Dipsadidae (Bonaparte, 1845). Other than the higher-level name (likely derived from the genus *Homalopsis* by Kuhl and Hasselt [1822]), no list of characters or descriptions that grouped homalopsids in the Homalopsina was given. Because of this inconspicuous mentioning of homalopsids as a distinct group, credit towards naming homalopsids as a family of snakes is often given to Giorgio Jan (1791–1866), the infamous Austrian botanist and zoologist, most known for the iconic snake illustrations in his **Iconographie Générale des Ophidiens** (Jan, 1864). Jan (1863)

Figure 8.4 *Cerberus* **in a mangrove swamp in Singapore. Photography by Daryl R. Karns.**

Figure 8.5. *Cantoria violacea* **is an exceptionally slender and elongated homalopsid. Photography Daryl R. Karns.**

Figure 8.6 A *Gerarda* **near the entrance to two crab burrow in a Singapore mangrove. Photography by Daryl R. Karns**

used the name 'Homalopsinae' as a subfamily of Potamophilidae (Jan, 1863: p. 67), a family that contained snake representatives of what we now recognize as homalopsids, natricids, and dipsadids. Because of this, Jan's 1863 paper has been repeatedly cited as the authority on the family (e.g., Boulenger, 1896; Taylor, 1965; Gyi, 1970). Although many credit Jan (1863) as resurrecting the name, English physician and amateur herpetologist Malcom A. Smith (1875–1958) recognized the ichthyologist and herpetologist Albert Günther's 1864 work Reptiles of British India as the authority on Homalopsidae; this being because Günther (1864) elevated the Homalopsinae to family-level status based on the arrangement of head plates compared to other colubroid snakes. Still-valid homalopsid genera in Gunther's (1864) work include: *Bitia, Cantoria, Cerberus, Enhydris, Ferania, Fordonia, Erpeton, Homalopsis, Hypsiscopus,* and *Myrrophis*. While this is seemingly the first publication to specifically refer to 'Homalopsidae' in detail, Jan had a publication, that was apparently forgotten about, titled **uber die familie Homalopsidae** (Jan, 1961; Murphy, 2007a). Despite these family or subfamily mentions of the group, Bonaparte (1845) has been cited as the authority in a few widely recognized herpetological works, such as Underwood (1967) and David and Ineich (1845).

The taxonomic contributions to Homalopsidae continued by some of these and other naturalists, especially in regard to close examinations of morphology and describing new species. Edward D. Cope (1840–1897), one of America's most prolific herpetologists, tried to group homalopsids using vertebral and dentition characters, leading to a diverse 'Homalopsinae' of 31 genera containing currently-recognized homalopsids, but also dipsadids, natricids, and pseudaspidids (Cope, 1886). Belgian taxonomic herpetologist George A. Boulenger (1858–1937) followed Günther's (1864) grouping of homalopsids, and added *Gerarda* and *Myron* to the group, described *Hypsirhina* (=*Hypsiscopus*) *matannensis,* synonymized several names, and ultimately reduced Homalopsidae to subfamily status (Homalopsinae; Boulenger 1890, 1893). The recognition of homalopsids as a subfamily of Colubridae was continued by Smith (1943) while revising Boulenger's Fauna of British India. Smith (1943) also provided traits that are shared by homalopsids: enlarged grooved fangs on the posterior of the maxillary; valvular nares; small, dorsolateral eyes; the tendency to have fragmented head shields; rostral scale with shallow notch; similar hemipene structure amongst species; hypapophyses throughout the vertebral column; a highly aquatic lifestyle; viviparous reproduction; and a distribution restricted to South Asia, Southeast Asia, and northern Australasia. Although these groupings are shared by a majority of homalopsids, none of these represent synapomorphies of Homalopsidae (Zaher, 1999), and some of these traits are now known to be lacking in some representatives (such as the fangless, semi-fossorial homalopsids [e.g., *Brachyorrhos*]).

Figure 8.7. *Homalopsis* **was considered to be monotypic but it is composed of several species. Photography by Daryl R. Karns**

Perhaps one of the most notable taxonomic works on Homalopsidae was that done by Ko Ko Gyi, a Burmese herpetologist at Rangoon University (now the University of Yangon; Myanmar). Gyi worked on homalopsid snakes, in the Division of Herpetology of the Natural History Museum at the University of Kansas (Kansas, USA), during a three-year fellowship from the United Nations Educational, Scientific and Cultural Organization. Gyi's work included a revision of the entire (back then subfamily) Homalopsinae (Gyi, 1970). In this revision, Gyi (1970)

Figure 8.8. The illustration of *Cerberus rynchops* from Russells 1796 volume, An Account of Indian Serpents, Collected from the Coast of Coromandel.. Russell used the common Indian name for this snake - Bockdam.

recorded scalation, color pattern characters, and body measurements on 983 specimens (1038 total in the study), ultimately recognizing 34 species amongst 10 genera (22 species of which were placed in *Enhydris*). Gyi's (1970) work also provided distribution maps, specimen photographs, a key to genera and species, natural history notes, and biogeographic remarks and hypotheses. While taxonomic rearrangements have been proposed or implemented, especially regarding *Enhydris* (e.g., Saint Girons, 1971), a family-wide review and revision of Homalopsidae did not occur until 37 years later.

One of us (JCM) and Harold K. Voris, researchers at the Field Museum of Natural History (Chicago, Illinois, USA) have provided the most recent revisions to homalopsid taxonomy at a familial level. Murphy (2007a) published a book on mud snakes, which by this point is recognized as a family due to several studies supporting their evolutionary distinctiveness using molecular data (e.g., Voris et al., 2002). Using detailed morphological examinations of homalopsids, Murphy (2007a) recognized 39 species of homalopsid snakes in 12 genera (though, two genera and three species were considered problematic, to be revised later [Murphy and Voris, 2014]). Of these, 23 species were placed in *Enhydris.* This book provided updated geographic distributions, taxonomy, genera and species keys and illustrations, natural history information from the literature and personal observations, and a synopsis on homalopsid taxonomic history. With the increasing ease of acquiring molecular data, it was established that several homalopsids, primarily *Enhydris,* were not monophyletic (Alfaro et al., 2008); this led to the most recent revision of homalopsid snakes by Murphy and Voris (2014). Murphy and Voris (2014) recognizes 53 species (not including an undescribed lineage from Sulawesi; Murphy and Voris, 2014) amongst 28 genera, now with only six species of *Enhydris*, using morphological criteria. While Murphy and Voris (2014) was the most complete checklist of Homalopsidae, more species have been described since its publication (e.g., *Gyiophis salweenensis* [Quah et al., 2017], *Myanophis thanlyinensis* [Günther et al., 2021], *Brachyorrhos pygmaeus* [Murphy and Voris, 2020]), *Hypsiscopus murphyi* (Bernstein et al., 2022) raising the current species richness of the family to 56. “Genomic data from Bernstein et al. (2023) suggests that homalopsids actually diversified in the Oligocene ~26 million years ago, either in Indochina or Indochina+South Asia, and that many divergence events in the rear-fanged group were likely due to shifts in paleorivers ~17 million years ago rather than movement into different aquatic

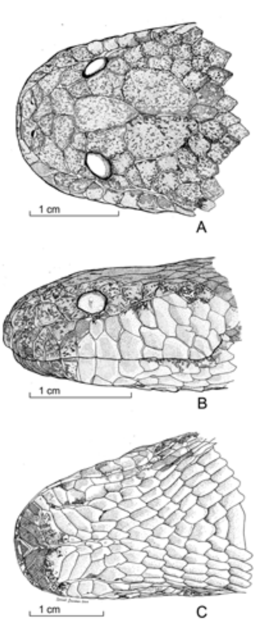


Figure 8.9. The holotype of *Homalophis gyii.* Names in honor of the Burmese herpetologist who revised the homalopsid snakes in the 1960s. Art work by Sara Drasner.

environments. This suggests Pleistocene sea-level fluctuations were not the main driver of homalopsids diversification, but sea-level changes undoubtedly influences population structure at least in the last tens of thousands of years.

Phylogenetic Placement

Homalopsids have long been recognized as caenophidian snakes and hypothesized to be affiliated with several families. Mud snakes have been considered as closely related, or part of, colubrids for much of their history (Boulenger 1890, 1893; Gyi, 1970). Before this, though, homalopsids were considered as a family, transitional between his colubrid group 'Natricina' (=Natricidae) and hydrophiines (=Hydrophiidae), particularly noting the 'transitional' appearance of the fang dentition (Nicholson, 1874); it is important to note that there is no evidence to support this as an evolutionary transition. Underwood (1874) also suggested that acrochordids were derived from the homalopsids. While still considered as part of colubrids, Dowling (1974) and Dowling and Duellman (1978) considered the mud snakes to be a tribe of the natricids (as Natricinae, family Colubridae). While homalopsids certainly do not produce the complex venom compounds as viperids, Knight and Mindell (1994) and Underwood (1999) hypothesized a close association between the two groups of snakes. The increased possibilities of DNA sequencing in the latter parts of the 20th century led to many studies confirming the monophyly and distinctiveness of homalopsids as a family distinct from the Colubridae, Natricide, Viperidae, and Hydrophiinae (Elapidae) (Voris et al., 2002; Pyron et al., 2013; Figueroa et al., 2016; Burbink et al., 2020). Homalopsids have been recovered in these molecular phylogenies as either sister to a Lamprophiidae+Elapidae clade (Pyron et al., 2013; Figueroa et al., 2016), or outside the sister relationship between Elapidae and a group containing Colubridae+Natricidae (Harrington and Reeder, 2017). This placement of homalopsids amongst the evolutionary tree of Serpentes seems to be supported using genomic data as well. Having the most homalopsid species sampled for a phylogenomics dataset, Burbrink et al. (2020) recovered Homalopsidae as the most closely related family to the Elapoidea and Colubroidea, with all families sampled.

Biogeography

While the taxonomy and phylogenetic placement of Homalopsidae has stabilized in recent years (e.g., Murphy, 2007a; Murphy and Voris, 2014; Burbrink et al., 2020), the biogeographic origins of the group and the evolutionary processes that have led to the subsequent diversification of lineages is far less understood. Mud snakes are distributed from Pakistan, eastward into South Asia, Southeast Asia, and reach their eastern limit in northern Australia and New Guinea. The geological history that spans these regions is extremely complex, resulting from millions of years of plate collisions, tectonic uplift, river catchment events, and fluctuating sea levels (Inam et al., 2007; Polhemus, 2007; Hall, 2009). Some of these events happened simultaneously in short time spans, while other events were separated by millions of years; some geological phenomena have been one-time events, and others repetitively over the course of several epochs.

The geographic origins of homalopsid snakes are suspected to be in mainland Southeast Asia (Murphy, 2007a), as 48% of homalopsid species are distributed throughout Indochina (and adjacent China), with the rest known from isolated regions or islands east or west of Indochina. Few family-wide systematic studies exist for this group, but molecular

Figure 8.10. Until 2014, the genus *Enhydris* contained most species of homalopsids despite evidence that it wss not monophyletic. Above is an adult female *Subsessor bocourti* (left) and an adult female *Enhydris enhydris* (right). both considered members of the genus *Enhydris* until 2014. Photography by JCM

data suggests that the fangless homalopsids (*Brachyorrhos* [*Karnsophis* and *Calamophis* not included in studies]) diverged from the rear-fanged clade in the mid-Eocene (43.7–47.9 Ma; Bernstein et al., 2021). Other estimates that do not include the fangless clade range from 22 Ma (Alfaro et al., 2008 [multilocus data]) to ~50 Ma (Burbrink et al., 2020 [genomic data]). It is likely that the fluctuating sea levels that facilitated land connections during sea level minima in Sundaland lead to many of the homalopsid (and other faunal and floral) distributions seen today (Woodruff, 2010; Bernstein et al., 2021). Multilocus data suggests the possibility of extinction of lineages throughout homalopsid evolution and increased diversification of rear-fanged lineages ~10 Ma (Bernstein et al., 2021). However, studies utilizing genome-scale data on both rear-fanged and fangless taxa with rigorous biogeographic analyses are necessary to confirm many of these findings and hypotheses. 'Genomic data (Bernstein et al., 2023a) supports that homalopsids likely diversified in the Oligocene ~26 million years ago in Indochina or Indochina+South Asia, and diversified in the last east and west from there in the last ~20 million years.'

The evolution of genera and species has been primarily focused on *Cerberus* and *Enhydris* (sensu Murphy and Voris, 2014). The six species of *Enhydris* comprise a large proportion of the vertebrate biomass in mainland Southeast Asia's low-elevation freshwater systems (Murphy, 2007a). While in-depth studies with more locus and specimen sampling are needed, their reliance on aquatic systems makes it likely that river length, topography (drainage basins, plateaus; Lukoschek et al., 2011), and sea level fluctuations (Woodruff, 2010) all influenced the diversification of this genus. Molecular data suggests that populations of *Enhydris subtaeniata* have been significantly structured by the lifting of the Khorat Plateau during the Quaternary, and the associated river catchment event of the Mekong River (Hutchison, 1989; Rainboth, 1996; Lukoschek et al., 2011). It is likely that this also had a similar impact on the population structure of *Hypsiscopus plumbeus* (Bernstein et al., 2021). Of particular interest would be why the distribution of *Enhydris enhydris* is widespread from India, mainland Southeast Asia, and the islands of Sundaland compared to its conspecifics, which have narrow distributions in Thailand, Cambodia, Vietnam, and Laos.

Figure 8.11. An *Enhydris enhydris* eating a Siamese Fighting Fish of the genus *Betta*. Photography by JCM

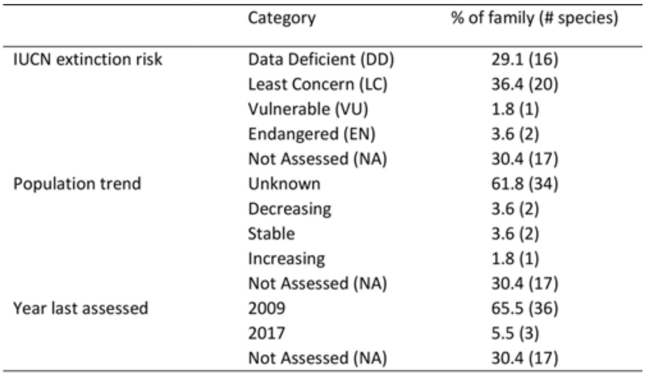
The brackish water *Cerberus* have one of the widest distributions of all snakes, which is nearly as widespread as Homalopsidae itself. Specifically, *Cerberus schneiderii* ranges from the Andaman sea coast of Thailand, eastward through the Indonesian archipelago. Phylogenetic methods using molecular data have shown that *C. microlepis* and *C. dunsoni* may actually be isolated, founder populations of *C. schneiderii*, as both former species are recovered within the latter (Alfaro et al., 2004; Bernstein et al., 2021). Similar to many other taxa, the distributions of *Cerberus schneiderii* and its congeners have likely been the result of Pleistocene sea level fluctuations in the past few hundreds of thousands of years. Similarly, land bridges during sea level minima have likely led to migration of *Pseudoferania polylepis* and *Myron richardsonii* populations between New Guinea and Australia. Genomic data (Bernstein et al., 2023a) supports that homalopsids likely diversified in the Oligocene ~37 mya in Indochina and/or Sundaland.

Conservation

Unfortunately, despite their ecological importance, the conservation status of most homalopsids snakes have either not been assessed for extinction risk by the International Union for Conservation of Nature (IUCN) or population trends are unknown due to data deficiency (IUCN, 2020). Out of the 56 described species, Homalopsidae has the following IUCN statistics:

A large proportion of homalopsid species have not been assessed in over 10 years for IUCN extinction status or are being assessed based on old taxonomy. For example, *Cerberus* populations in Wallacea and the Greater Sunda Islands are erroneously still recognized as *C. rynchop*s, rather than *C. schneiderii.* Ironically, *C. rynchops* is listed as a CITES appendix III species (India), despite being one of the most abundant homalopsids, and snakes, in Asia (Jayne et al., 1998; Murphy, 2007a). While only *Cerberus microlepis* (EN), *Gyiophis vorisi* (EN), and *Enhydris longicauda* (VU) have extinction risks as endangered or vulnerable, almost all other species have either yet to be assessed, are data deficient, or have not been reevaluated. Thus, any indication as to whether populations are increasing, decreasing, or are stable is only available for ~9% of species. Species that are poorly known/encountered, are endemic, or have extremely limited distributions, such as *Enhydris chanardi, Mintonophis pakistanicus, Calamophis* spp., *Brachyorrhos* spp., as well as island populations of widespread species (e.g., *Cerberus schneiderii*), should be focused on in future assessments.

The primary threats to homalopsid snakes are those that are considered detrimental for most other species: habitat destruction/fragmentation, pollution, and overexploitation/collecting for sale in the pet trade or in local markets for their meat and skin (Murphy, 2007a). Mud snakes are also commonly killed as bycatch in fishing nets. Their abundance in aquatic systems likely makes them important as aquatic indicators of ecosystem health, but fishing and hunting operations threaten many populations. In particular, the populations of homalopsids at Tonlé Sap Lake in Cambodia are threatened, with almost 4 million snakes collected per year (Brooks et al., 2007). This estimate includes *Erpeton tentaculatum, Subsessor bo-*



	Category	% of family (# species)
IUCN extinction risk	Data Deficient (DD)	29.1 (16)
	Least Concern (LC)	36.4 (20)
	Vulnerable (VU)	1.8 (1)
	Endangered (EN)	3.6 (2)
	Not Assessed (NA)	30.4 (17)
Population trend	Unknown	61.8 (34)
	Decreasing	3.6 (2)
	Stable	3.6 (2)
	Increasing	1.8 (1)
	Not Assessed (NA)	30.4 (17)
Year last assessed	2009	65.5 (36)
	2017	5.5 (3)
	Not Assessed (NA)	30.4 (17)

Figure 8.12. *Enhydsris subtaeniata* **was long confused with** *Enhydris enhydris* **until it was removed from the synonomy of** *E. enhydris.* **Photography by JCM**

courti, Hypsiscopus plumbeus, Homalopsis buccata, Enhydris longicauda, and *Enhydris enhydris*, with the latter species comprising ~70% of all specimens (Brooks et al., 2007). The catching of 'low-value' water snakes, such as homalopsids, benefit the economy when there are declines in fish catchment (Brooks et al., 2008). Finding balances between snake hunting and fishing, along with a better understanding of the diversity of lineages in this family and their associated taxonomy, is much needed to ascertain extinction risks of homalopsids and to create conservation management plans.

Fangless Species

Seram Short-tailed Snake

Brachyorrhos albus (Linnaeus, 1758)

Distribution and Habitat. Currently known from Indonesia, Maluku Province, specifically Seram and its satellite islands (Ambon, Haruku, Nusa Laut, Saparua). It has also been reported from the Banda Islands (Boettger, 1985). A population may exist on the Indonesian Island of Pulau Bisa (O'Shea, 2018), but molecular confirmation of this specimen is required to designate this as *B. albus* (Murphy and Voris, 2014). Populations may inhabit other islands (Banda, Batjan, Aru Islands) that have been underexplored or lack surveys. Type locality: "Indiis" (Indonesia, Ambon). (Figure 8.14)

Identification**.** Distinct preocular scale usually present (also present in *B. raffrayi* and *B. wallacei*); seven upper labials, fourth (rarely 3+4) in orbit, sixth is tallest; dorsal scales more lanceolate (elongated, taper posteriorly) than in congeners; usually single temporal scale contacting postoculars in Ambon population; two primary temporals in some Seram individuals. Size. Males: SVL: 337–472 mm; Tail: 32–61 mm. Females: SVL: 343–443 mm; Tail: 33–41 mm.

Figure 8.13. Distribution of *Brachyorrhos albus.*

Natural History**.** Extraordinarily little is known about the natural history, evolution, and habits of *Brachyorrhos* spp, and most of what is known about the genus comes from observations of *B. albus*. *Brachyorrhos* are an early diverging lineage of fangless homalopsids that are primarily terrestrial/semi-fossorial. There have been published reports of *Brachyorrhos* occasionally inhabiting arboreal habitats as well (Edgar and Lilley, 1993). *Brachyorrhos albus* are vermivorous, primarily feeding on earthworms (Murphy et al., 2012a; Murphy unpublished; Sanders unpublished). They are reported to be secretive, staying hidden beneath stones and logs, and are active at dusk to hunt prey (Kopstein, 1926). Populations on Seram were found in lowland secondary forests, but also in plantations, gardens, and have been found in human-populated areas at all altitudes (Murphy et al., 2012a). Although its reproduction is hardly understood, *B. albus* is viviparous based on one Seram female that contained four near-term embryos (Murphy et al., 2012a). Molecular data supports *Brachyorrhos* as the sister group to the rear-fanged homalopsids (Murphy et al., 2011). Skull and scale morphology suggest that *Brachyorrhos* and the other fangless homalopsids, *Calamophis a*nd

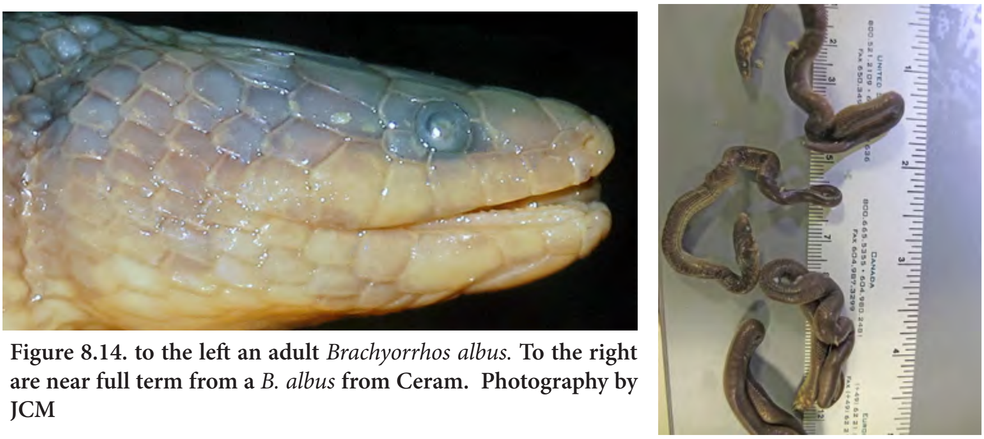


Figure 8.14. to the left an adult *Brachyorrhos albus.* **To the right are near full term from a** *B. albus* **from Ceram. Photography by JCM**

Karnophis, share a more recent ancestry than either of them does with the rear-fanged species (Murphy and Voris, 2013). Molecular data also supports a very close relationship between *B. albus* and *B. raffrayi* (Bernstein et al., 2021); further investigation is needed to see if these two species are populations are conspecific. The natural history of other Brachyorrhos species are largely unknown.

Buru Short-tailed Snake

Brachyorrhos gastrotaenius (Bleeker, 1860)

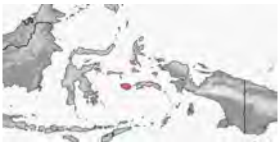


Figure 8.15. The distribution of *Brachyorrhos gastrotaenius*

Distribution and Habitat**.** Type locality: "Amboina" (= Ambon), in error. Buru – Fakal. Only known from Indonesia, Maluku Province, Buru Island (Figure 8.15.)

Identification**.** Six upper labials, fourth (rarely 3+4) in orbit, fifth is tallest; mid-ventral stripe often present. This combination of characters separates this species from all other members of the genus. Size. Males: SVL: 342–415 mm; Tail: 42–73 mm. Females: SVL: 338–595 mm; Tail: 30–48 mm (Figure 8.16). Natural History**.** See *Brachyorrhos albus.*

Figure 8.16. *Brachyorrhos gastrotaenius.* **Photography by JCM**

Pygmy Short-tailed Snake

Brachyorrhos pygmaeus Murphy & Voris, 2020

Distribution and Habitat**.** Type locality: Indonesia, Seram Island. Only known from the Type locality:

Identification**.** A small *Brachyorrhos* with a rounded snout, a loreal scale; one preocular scale; upper labials six or seven, the fourth upper labial bordering the orbit; the second and third upper labials contact loreal; six lower labials; 143 ventral scales; 22 subcaudal scales. Size. Males: Data Deficient. Females: SVL: 115 mm; Tail: 13 mm.

Natural History. See *Brachyorrhos albus*

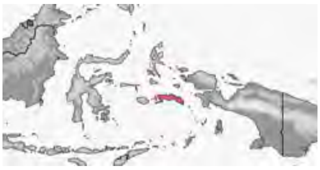


Figure 8.17. Distribution of *Brachyorrhos pygmaeus*

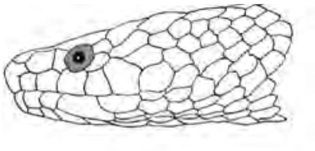


Figure 8.18. *Brachyorrhos pygmaeus*. **Artist credit Nathalie Aall.**

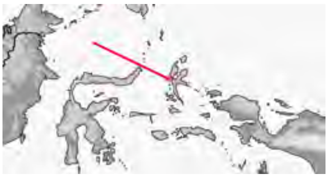
Ternate Short-tailed Snake

Brachyorrhos raffrayi (Sauvage, 1879)

Distribution and Habitat. Only known from Indonesia, Maluku Province, Ternate. Type locality: Indonesia, Ternate.

Identification. Six upper labials, the third, rarely 3+4, enter the orbit, tallest upper labial is third; very pointed snout. A preocular is present in about 35% of the specimens examined, making it possible to confuse this species with *B. albus*, which often have the preocular scale. Size. Males: SVL: 453–660 mm; Tail: 56–82 mm. Females: SVL: 394–462 mm; Tail: 29–51 mm.

Natural History. See *Brachyorrhos albus.*



Figuire 8.19. The distribution of *Brachyorrhos raffrayi.*

Halmahera Short-tailed Snake

Brachyorrhos wallacei Murphy, et al. 2012

Figure 8.20. *Brachyorrhos raffrayi.* **Photography by Kate Sanders**

Distribution and Habitat. Only known from Indonesia, Maluku Province, Halmahera Type locality: Indonesia, Halmahera, Jailolo including the island or Morotai (Murphy and Voris 2020).

Identification. Usually lacks preocular, usually seven (rarely six) upper labials, tallest is sixth (rarely fifth). *Brachyorrhos wallacei* is similar to *B. raffrayi*, which has upper labial three

Figure 8.21. The distribution of *Brachyorrhos walacei*

in the orbit and the third is the tallest. Specimens of *B. wallacei* usually have the fourth upper labial (rarely 3+4) in the orbit, and the fifth is the tallest. Size. Males: SVL: 317–395 mm; Tail: 17–54 mm. Females: SVL: 345–575 mm; Tail: 35–65 mm.

Natural History**.** See *Brachyorrhos albus.* Molecular data has shown that *B. wallacei* is deeply divergent from *B. raffrayi* (Murphy et al. 2012a). This was also seen in Bernstein et al. (2021) using mitochondrial and nuclear loci, with *B. wallacei* as sister to *B. raffrayi+B. albus*. However, these datasets do not include *B. gastrotaenius* in a phylogenetic framework and are based on limited molecular datasets. Thus, a thorough investigation with increased molecular and taxonomic sampling will be needed to elucidate the species boundaries and evolutionary relationships of this genus.

Figure 8.22. *Brachyorrhos wallacei.* **Photography by JCM**

Yapen Island Stout-tailed Snake

Calamophis jobiensis Meyer, 1874

Distribution and Habitat. Only known from New Guinea, apen Island (= Jobi/Japen). Type locality: Indonesia, Yapen Waropen Regency, Yapen Island, Ansus (about 1°43'2" S, 136°7'57" E). (Figure 8.23)

Identification**.** Diagnosis based on a translation of the original description164 ventrals and 10 subcaudals. Upper labials six; third and fourth enter orbit, eight lower labials, one preocular, one postocular; pentagonal internasal contacts rostral with one side and penetrates between prefrontals; subcaudals divided. Size: Measurements not available.

Figure 8.23. The distribution of *Calamophis jobiensis*

Natural History**.** Like most of the other fangless homalopsids, the known natural history of all *Calamophis* is minimal and based off few specimens. *Calamophis jobiensis* has the least amount of data attributed to any member of the genus. The holotype of *C. jobiensis* MTD (= MTKD; Staatliches Museum für Tierkunde) 1026 was destroyed in the Dresden bombings of World War II; no measurements were recorded from the holotype's original description (Meyer, 1872). It is possible that *C. jobiensis* has a terrestrial/fossorial lifestyle.

Andian Stout-tailed Snake

Calamophis katesandersae Murphy, 2012

Distribution and Habitat**.** Only known from Indonesia, West Papua, Andai. Type locality: Indonesia, West Papua Province, Manokwari Regency, Andai (~0°54'58" S, 134°00'25" E). (Figure 8.11)

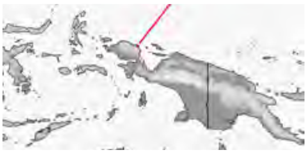


Figure 8.24 The distribuition of *Calamophis katesandersae.*

Figure 8.25. *Calamophis katesandersae.* **Photography by JCM**

Identification**.** Distinctive laterally compressed body (mid-body width 75–79% of body's height), exceptionally short tail (3.7–3.8% of snout–vent length [SVL]); frontal pentagonal but almost triangular; five or six upper labials; seven lower labials; low subcaudal count (eight or nine). Size. Males. Data Deficient, Females. SVL: 157–215 mm; Tail: 6–8 mm.

Natural History**.** *Calamophis katesandersae* may have a more aquatic lifestyle compared to its congeners. This is based off its morphology: laterally compressed body, narrow ventrals (compared to its congeners), and eyes that are slightly more dorsolateral (compared to more dorsal in *C. ruuddelangi* and *C. sharonbrook*sae) (Murphy, 2012). More specimens and through investigation of morphology and natural history observations will be needed to identify the true habitat preferences and lifestyles of *Calamophis* spp.

Kebar Stout-tailed Snake

Calamophis ruuddelangi Murphy, 2012

Distribution and Habitat**.** Known only from Indonesia, West Papua Province localities of Ambuaki and Kebar Valley. Type locality: Indonesia, West Papua Province, Manokwari Regency, Ambuaki in the Tamrau Mountains (~ 0°46' S, 132°57' E) West Papua. (Figure 8.26).

Identification**.** Gracile cylindrical body, relatively short tail (12% of SVL); six upper labials, fifth tallest, three and four shorter, ventrals 143–145, subcaudals 21–23. Size. Males. SVL: 219–232 mm; Tail: 27–29 mm. Females. Data Deficient. (Figure 8.27).

Natural History**.** This species may have a more terrestrial/fossorial lifestyle compared to *C. katesandersae*. Molecular data (Bernstein et al., 2023) shows that *C. ruuddelangi* (only one specimen in the sampling) is the sister to the genus *Brachyorrhos*. It is likely that *Calamophis* and *Brachyorrhos* are sisters but the phylogenetic placement of *Karnsophis* will be needed to confirm how the three known fangless genera are related. However, more specimens and natural history observations are needed to confirm this.

Figure 8.26, The distribution of *Calamophis ruuddelangi.*

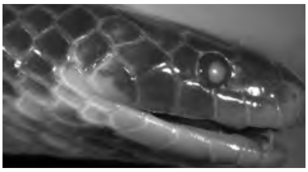


Figure 8.27. *Calamophis ruuddelangi.*

Arfak Stout-tailed Snake

Calamophis sharonbrooksae Murphy, 2012

Distribution and Habitat**.** Only known from Indonesia, West Papua Province. The two type specimens are collected from Manokwari Regency, Mount Arfak. A female specimen was collected from Atinyu (1°26'04" S, 132°22'58" E), Sorong

Selatan Regency, near Lake Danau (O'Shea and Kaiser, 2016). Atinyu is approximately 180 km west southwest of the Type locality: Type locality: Indonesia, West Papua, Mount Arfak (~ 1°05'00" S, 133°58'00" E). (Figure 8.28)

Figure 8.28. The distribution of *Calamophis sharonbrooksae*

Identification**.** A robust *Calamophis* with a cylindrical body, tail 9.0–9.6% of the SVL; upper labials three, four and five about equal in height; the rostral to frontal distance is greater than the parietal seam. Dorsal scales are uniform brown—no center spot of dark pigment. All other species have dorsal scales with a dark central spot and a light outer edge. In *C. katesandersae* the fifth upper labial is the tallest; the body is laterally compressed; and the tail is about 4% of the SVL. *Calamophis ruuddelangi* has a gracile, cylindrical body and a tail that is about 12% of the SVL. Size. Males: SVL: 288–290 mm; Tail: 26–28 mm, Females. SVL: 390 mm; Tail: 18 mm (Figure 8.29).

Figure 8.29. *Calamophis sharonbrooksae.* **Photography by JCM**

Natural History. This species may have a more terrestrial/fossorial lifestyle compared to *C. katesandersae.* O'shea and Kaiser (2018) mention that *Calamophis* may not be able to be in sympatry with the species-rich, vermivorous elapid genus *Toxicocalamus*, based on the mutual exclusion of both genera in their respective distributions (O'Shea and Kaiser, 2018). These hypotheses require more thorough investigation with higher sampling and observations.

Sumatran short-tailed snake

Karnsophis siantaris Murphy & Voris, 2013

Distribution and Habitat**.** Only known from Indonesia, Sumatra, Sumatera Utara (North Sumatra Province), Siantar. However, Bleeker (1860) reported *Brachyorrhos albus* from Agam (~0°15' S, 100°05' E) and Padang (0°57' S, 100°21' E), both localities from West Sumatra Province. As *Brachyorrhos* is currently considered only found in eastern Indonesia, these accounts from Bleeker (1860) likely *K. siantari*s. Type locality: Indonesia, Sumatra, Sumatera Utara, Siantar (~1°58' N, 99°47' E). (Figure 8.30).

Identification**.** Fangless, 19 scale rows not reduced posteriorly, premaxillary bone absent, nasal bones greatly reduced in size, neural spine present on the atlas (absent in *Brachyorrhos*). Distinguished from *Brachyorrhos* by its depressed skull, rostral not visible from above; eye diameter greater than eye–mouth distance, countersunk lower jaw, laterally compressed tail. Distinguished from *Calamophis* by 19 scale rows just anterior to the vent (*Calamophis* has 17); divided internasal (single in *Calamophis*); divided nasal scale (single in *Calamophis*); two postoculars (one in *Calamophis*). Size. Males: SVL: 415 mm; Tail: 12 mm. Females: no data. (Figure 8.31).

Figure 8.30. The distribution of *Karnsophis siantaris.*

Natural History**.** This species has been confirmed to feed on frogs (unknown species; Murphy and Voris, 2013). It is unknown if *K. siantaris* is a frog specialist, or if frogs are just a part of this species' diet.

Figure 8.31. *Karnsophis siantaris*. **Photography by JCM**

Rear-Fanged Species

Gray's Mangrove Snake

Bitia hydroides Gray, 1842

Distribution and Habitat**.** Coastal waters of southern Myanmar, Thailand, peninsular Malaysia (Johor, Penang, Selangor, Penang Island; Charlton, 2020), Singapore, and Borneo. There may be populations in other areas of the Greater Sundas (Murphy, 2007a). Type locality: Unknown. (Figure 8.32)

Identification**.** Extremely similar to true sea snake morphologically but lacking a paddle-like tail and has eyes that are more dorsal-facing. Scale rows at midbody 37–43 at midbody; ventral scales keeled; parietal scales fragmented; single internasal; dorsal scales small, triangular, exposed skin between them; head slightly distinguishable from neck; parietals fragmented; head, neck, and anterior body slender with body increasing in diameter posteriorly; single internasal separates nasal scales; loreal present; loreal in contact with first 3 or 4 upper labials; ocular ring scales large, plate-like; upper labials 3–4 or 4–5 below the orbit; tail short 8–11% of SVL; dorsal scales small, smooth, and triangular; dorsal scales have exposed skin between the scales; ventrals very narrow with two rows of keels; maxillary teeth number 11–13, followed by a gap and two enlarged grooved teeth. It has enlarged palatine teeth. Size. Males: Max SVL: 641 mm; Tail: 55 mm; | Average SVL: 338 mm; Females: Max SVL: 718 mm; Tail: 54 mm; | Average SVL: 500 mm Juveniles: SVL: 134–172 mm | Average SVL: 153.9 mm. (Figure 8.33)

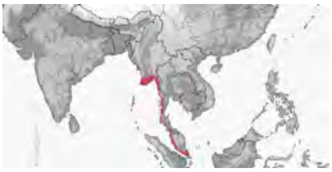


Figure 8.32. The distribution of *Bitia hydroides.*

Natural History**.** *Bitia hydroides* is an intertidal species, inhabiting mud flats and estuaries, and mangroves. It burrows into the mud. It is possible that the exposed, interstitial skin of Bitia may aid in cutaneous respiration in the already low-oxygen environments it inhabits. Like *Cerberus*, it may use a sidewinding-like motion on the surface of the mud. It is nocturnal and may be seasonally active. The species is remarkably similar in appearance to sea snakes of the genus *Hydrophis*, and it is often collected with *Hydrophis* in the sluice nets (or creeks) in the Bassein River of Myanmar (Theobald, 1868). The diet is composed of fish (Cantor, 1847; Boulenger, 1890) most of which are gobies, including *Oxuderces dentatus* (Jayne et al., 1995) and the deep-water goby *Trypauchen raha.* Females mature at an early age (as young as 1 year) and have small litters, ranging from 1–10, with small neonates (Jayne et al., 1995). Oviducal eggs have been confirmed in this species, though this species has been considered as having both viviparous or ovoviviparous modes of preproduction. Females captured between 20 November and 18 December were often gravid, and females have been found to grow to significantly longer SVLs than males (Jayne et al. 1995).

Figure 8.33. *Bitia hydroides.* **Muar, Malaysia.**
Photography by Bruce Jayne.

Cantor's Mangrove Snake

Cantoria violacea Girard, 1858

Distribution and Habitat**.** The Andaman Islands, Andaman coasts of Myanmar, Thailand, peninsular Malaysia, Sumatra, and Borneo. Type locality: Singapore (Figure 8.34)

Identification**.** Distinguished from all other homalopsids by the combination of 19 dorsal scales rows at midbody; nasals separated by internasal scale; prefrontals make broad contact; five upper labials; loreal contacts first 2–3 upper labials; subocular scale separates upper labials 3–4 from orbit; 7–8 lower labials; ventral count exceeds 243 (more ventrals than any other homalopsid). Size. Males: SVL: 358–902 mm; Tail: 71–193 mm (tail 18–21% of SVL | Average: 20%); Females: SVL: 620–957 mm; Tail: 127 mm (tail 12–17% of SVL | Average: 13.7%). Males have a long, thin, stringy, gracile appearance while females of the same size are more robust. (Figure 8.35-37)

Natural History**.** *Cantoria violacea* are found in mangrove forests with mud lobster mounds, mudflats, tidal creeks and river mouths, but will also occasionally enter nearby freshwater environments. It utilizes mud-lobster burrows and crab holes during the day, primarily being active at night. It will also use these holes or partially burrow into wet med to escape predators (Murphy, 2007a; Voris and Murphy, 2002; Ghodke et al., 2018). It uses the intertidal burrow system. Sworder (1923) considered this "a very rare snake" in Singapore. This is undoubtedly due to its microhabitat, the intertidal burrow system, which is seldom explored by herpetologists or other naturalists. Karns et al. (2002) found this species only three times (1.1 % of the 270 snakes collected) at Pasar Ris Mangrove Park in Singapore, while Ghodke and Andrews (2002) considered it common in the North Andaman Islands. *Cantoria violacea* specializes in eating small fish and crustaceans, including alpheids (e.g., *Alpheus microrhynchus*, giant snapping prawn; Voris and Murphy, 2002) (Figure 8.38), and hard-shelled crabs (*Metaplax elegans;* Ghod-

Figure 8.34. The distribution of *Cantoria violacea.*

Figure 8.35. Cantor's Mangrove Snake, ***Cantoria violacea*** **entering a burrow in Thailand. Photograph by Harry Ward-Smith.**

Figure 8.36. *Cantoria violacea.* **Photograph by Kenneth Chin.**

Figure 8.38. *Cantoria violacea.* **Photography by Kenneth Chin**

ke et al., 2018). These snakes often start their attack using their bodies to restrain and pin their prey (though, without coiling), as opposed to biting and striking (Jayne et al., 2018). Depending on its prey, it might either swallow their prey whole (shrimps; Murphy, 2007a) or rip their prey in pieces prior to consuming individual parts (crabs; Ghodke et al., 2018).

Figure 8.37. An *Alpheus* pistol shrimp preyed upon by *Cantoria violacea.*

The venom chemistry of this species is entirely unknown. However, Ghodke and Andrews (2002) reported stories from Karens living in the Andaman Islands who stated that they knew people who had been bitten by this snake, one had died, and another had been unconscious for several days. Bite symptoms included abdominal pain, vomiting blood, and swelling at the site of the bite. A folk remedy made from a "cactus-like plant that grows in mangroves" was applied to the bite lesions and taken internally. They acknowledged that *Cantoria* is usually considered harmless and has a similar appearance to the Andaman krait (*Bungarus andamanensis*). This species forms a clade with the other crustacean-eating homalopsids, *Fordonia leucobalia* and *Gerarda prevostiana* (Alfaro et al., 2008; Figueroa et al., 2016; Burbrink et al., 2020; Bernstein et al., 2021). *Cantoria* is the sister genus of *Gerarda* (Bernstein et al., 2023a).

Australian Bockadam

Cerberus australis (Gray, 1842)

Distribution and Habitat**.** Found on the northern coasts of Australia and the south coast of New Guinea. Its eastern-most distribution based on museum specimens is Edward River (Queensland, Australia), and it may reach the tip of the Cape York Peninsula (Wilson and Swan, 2003) though it the true limits of this species distribution is uncertain; records are confirmed around the Gulf of Carpentaria. A single specimen is known from Waingapu, Sumba Island, Indonesia. It is unclear if this is a waif or represents an established population (WAM 101620; Murphy et al., 2012b). Type locality: Merauke, Dutch New Guinea. (Figure 8.39)

Identification**.** Dorsal scales in 23 rows at midbody, upper labials 2–4 contact loreal, scales on the crown imbricate; those anterior to the angle of jaw lack keels; first labial does not contact loreal; last upper labial horizontally divided; venter is mottled. This species is known to exhibit several color morphs, such as grey, red, or even pale olive green (shown above). Size. Males: SVL: 380–665 mm; Tail: 117 mm (tail 21–26.7% of SVL); Females: SVL: 445–756 mm; Tail: 106 mm (tail 19–22.6% of SVL). (Figure 8.40)

Natural History**.** All members of this genus have similar or identical habitat preferences and behaviors. *Cerberus australis* are nocturnally active on mudflats, mangrove forests, and streams that pass through these habitats. They may be found in the sea or at river mouths (Kinghorn, 1929), or in estuaries and fresh-water streams, and can be found basking on mudflats (Heatwole, 1977). They are often present in groups, and, at low tide, burrow into soft mud, leaving just the top of their head visible (Gow, 1989). This species is considered piscivorous. While it has been reported to feed primarily on mudskippers, they might also feed on other small fishes and crustaceans (Gow, 1989) in estuarine mangrove roots and the shelving banks of tidal streams (Worrel, 1963); though, verification of crustacean prey is still needed (Murphy, 2007a). Confirmed predators include nervous sharks (*Carcharhinus cautus*; Lyle and Timms, 1987). Like other members of this genus, *C. australis* may sidewind across mudflats to increase locomotion speed (Kinghorn, 1929). The venom of this member of the genus is of little concern; stinging sensations have been reported (Gow, 1989). Data shows venom yields of 10 µl are typical, but up to 200 µl are possible; these data were from manual venom acquisition (venom milking) and venom is shown to increase free platelet clotting times from 12–40% and contains at least four major acidic proteins (Guinea et al., 1992). *Cerberus australis* has been found to be the sister lineage to all other *Cerberus* in phylogenetic studies (Al-

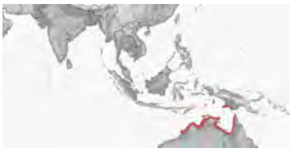


Figure 8.39. The distribution of *Cerberus australis*.

faro et al., 2004; Bernstein et al., 2021; Bernstein et al. 2023a).

Palau Bockadam

Cerberus dunsoni Murphy, Voris, and Karns, 2012

Distribution and Habitat**.** Palau Islands, Micronesia. Specifically known from Oreor Island (=Koror Island), Arakabesang (formerly Ngerekebesang) Island, and Babeldaob Island. Type locality: Micronesia: Palau Islands: Arakabesang (formerly Ngerekebesang) Island (~7°20’ N, 134°27’ E). (Figure 8.41)

Figure 8.40. Australian Bockadam, *Cerberus australis.* **Photography from MAGNT.**

Identification**.** Dorsal scales in 23 rows at midbody, upper labials 1–4 contact loreal; plate-like scales on crown rounded, juxtaposed, and thickened compared to scales of other *Cerberus* species, ninth upper labial horizontally divided, ventral surface uniform black. The 9th upper labial is horizontally divided. These characters, combined with large parietal scale fragments and a uniform black venter, make this a very distinctive species. The large, plate-like fragments of the parietals may fuse with the temporal scales. The parietal scales in other *Cerberus* are usually fragmented into small scales like scales on the crown. The scales on the crown anterior to rictus usually lack keels; all other *Cerberus* except *C. australis* have scales with keels anterior to the level of the angle of the jaw. Crown scales are distinctly rounded and juxtaposed; in other *Cerberus,* these scales tend to be sharp-edged and slightly imbricate. The light pigment forms an irregular ventrolateral stripe involving scale rows 1–2; this stripe involves rows 1–3 or 1–4 in other *Cerberus* except *C. microlepis,* which has 27–29 scale rows at midbody. The ventral pattern is uniform black or dark brown in preserved *C. dunsoni,* while all other species have a mottled ventral surface or one with an irregular central stripe of dark pigment. This species tends to have a broader, more robust head than the other species in the genus and it lacks the dorsolateral pattern of bars or incomplete cross bands. Size. Males: No Data; Females: SVL: 228–687 mm; Tail: No Data. Neonate. SVL: 232 mm; Tail: 62 mm.(Figure 8.42)

Natural History**.** *Cerberus dunsoni* is poorly known in comparison to other *Cerberus.* Populations have not recently been assessed, but Crombie and Pregill (1999) states that *Cerberus* is common in Palau, but is not often collected, as it is a nocturnal snake in difficult-to-survey mangrove habitats. They also report that *C. dunsoni* is occasionally found

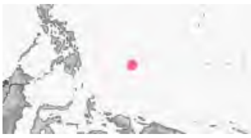


Figure 8.41. The distribution of *Cerberus dunsoni.*

in the open ocean or along beaches, particularly near river or streams, as has bene reported for *C. australis* (Kinghorn, 1929). They may cross stand vegetation between beach and mangrove swamp habitats. While their reproductive mode has not studied, an umbilical scare was present in a single neonate found by Pregill and Crombie (1999), so this species is likely viviparous like viviparous like *Cerberus schneiderii.* They have facultative premaxillary salt glands (Dunson and Dunson, 1979); it is uncertain if these are present in all *Cerberus* or just the isolated *C. dunsoni.* This species has been recovered as a clade within Philippine *C. schneiderii,* and may represent a founder population of this *C. schneiderii* (Bernstein et al., 2021).

Figure 8.42. Pulau Bockadam, *Cerberus dunsoni.* **Photography by JCM.**

Lake Buhi Bockadam

Cerberus microlepis Boulenger, 1896

Figure 8.43, The distribution of *Cerberus microlepis.*

Distribution and Habitat**.** Known only from Lake Buhi and the adjacent rivers (personal observation by JMB). Lake Buhi is a small freshwater lake in the Camarines Sur Province on Luzon Island, Philippines. The lake is about 18 square kilometers and is positioned between two volcanoes: Mt. Iriga (~1200 feet above sea level) on the western side of the lake and Mt. Malinao (~3900 feet above sea level. Lake Buhi is 15 km from the coast. Type locality: Philippines. (Figure 8.43)

Identification**.** Dorsal scales 27 to 31 rows at midbody; all other species have 21–25 scale rows at mid-body; the imbricate plate-like scales on the crown have a slightly thickened appearance; last upper labial is horizontally divided, and the venter is mottled. Size. Males: Maximum TL: 768 mm; Tail: 158 mm (tail 23–27% of SVL). Females. Maximum TL: 1046 mm; Tail: 161 mm (tail 18–27% of SVL) (Figure 8.44).

Natural History**.** Collectors' notes accompanying specimens report this species in the shallow water fishponds at 1940–0100 hours. Personal observations by JMB include abundant *C. microlepis* in the river of San Pascual Municipality, which drains into Lake Buhi's southern coast. Snakes were found late at night, laying submerged on the river's edges or swimming. *Cerberus schneiderii* were sometimes within 1–2 meters of each other, or in one case two specimens on top of one another. Locals from barangays around Lake Buhi refer to the bockadams as 'Aninikig' and report them in high numbers after floods and storms. This species is very closely related to *Cerberus schneiderii,* the Southeast Asian Bockadam, which

Figure 8.44. Lake Buhi Bockadam, *Cerberus microlepis*
Photograph by JMB

is often associated with brackish waters. *Cerberus microlepis* is often recovered as a clade within *C. schneiderii* in phylogenetic trees (e.g., Alfaro et al., 2004, Bernstein et al., 2021; Bernstein et al. 2023a) and may represent a freshwater-adapted population of *C. schneiderii.*

South Asian Bockadam

Cerberus rynchops (Schneider, 1799)

Distribution and Habitat**.** On the eastern edge of its range, it extends to the Mouth of the Irrawaddy, Myanmar, and perhaps into the Mergui Archipelago. It is replaced by *Cerberus schneiderii* along the Andaman Sea coast of Thailand and coastal Southeast Asia. The western edge of the distribution is likely to be the Gulf of Khambhat in the rivers and estuaries of Gujarat, India (Vyas et al., 2013). Type locality: "Ganjam" (Orissa State, SE India), (~19°22' N 85°03' E). There are at least two other localities on India's east coast that contain the name "Ganjam:" Chinna Ganjam and Pedda Ganjam. Both are south of Ganjam, all three locations are coastal and within the range of this species. Murphy et al. (2012) has restricted the type locality to 'Ganjam, India' (Figure 8.44).

Identification**.** Dorsal scale rows 25 (rarely 23) at midbody, imbricate plate-like scales on the crown have flat, thin appearance, keeled scales anterior to the angle of jaw; the last two upper labials are horizontally divided; venter mottled. *Cerberus rynchops* can be distinguished from all other members of the genus by its 25 (rarely 23) scale rows at midbody, the imbricate plate-like scales on the crown have a flat, thin appearance and are keeled anterior to angle of jaw; the last two upper labials are horizontally divided; the venter is mottled. *Cerberus australis* has 23 scale rows at mid-body, and the first upper labial does not contact the loreal (it usually does so in all other *Cerberus* species). *Cerberus dunsoni* has 23 scale rows at midbody, rounded juxtaposed scales on the crown, and a uniform black venter. *Cerberus schneiderii* usually has 23 scale rows at mid-body (rarely 21 or 25). The last upper labial is horizontally divided (instead of the last two in *Cerberus rynchops*) and the venter is mottled. Size. The largest male was 777 mm in TL, and the largest female was 886 mm (Figure 8.46 - 8.47).

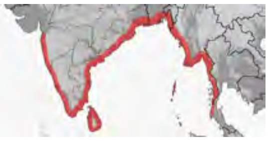


Figure 8.45. . The distribution of *Cerberus rynchops*

Natural History**.** This species, along with *Cerberus schneiderii,* are perhaps the most well-known homalopsid snakes regarding natural history, in part due to their high abundance and wide distributional ranges. *Cerberus rynchops* are coastal specialists that inhabit mangrove forests and associated mud flats, tidal zones and creeks, and estuaries and rivers. It has also been found at open sea (Acharji and Mukherjee, 1966), and is sometimes caught in fishing traps together with true sea snakes (Hydrophiidae) (Anderson, 1889). At Chilka Lake, Orissa, India, it uses seasonally flooded areas with numerous aquatic plants (Dutta, 1989). In Sri Lanka, it inhabits rivers and inland swamps, lagoons, and coastal waters (Deraniyagala, 1955). It is also common in human populated areas, such as near or in rice paddy fields or near fishing communities. It is most often found in salt and brackish waters but is also found in freshwater streams and lakes. It has even been found in fresh water more than 100 miles from the salt waters of coastal areas (Smith, 1943; Whitaker, 1969).

Figure 8.46. South Asian Bockadam, *Cerberus rynchops.* **Photography by Vivek-Sharma**

The diet is mostly composed of fish, primarily gobiids and carangids (Annandale, 1907; Murphy, 2007a). Wall (1918) reports fish herding behavior. It flicks its tail, first on one side and then the other in such a way as to make an unwary fish recede from the movement towards its head; when coming within the snake's field of vision, the fish is captured. Major predators of this species include birds, such as white-bellied sea eagle (*Haliaeetys* [=*Haliaeetus*] *leucogaster*), house crows (*Corvus splendens*), Brahminy kites (*Haliastur indus*), and pariah kites (*Milyus migrans*) in different parts of India (Saha 1984; Murthy and Rao, 1986). Though not as common, other predators include mangrove crabs (*Scylla serrata*; Voris and

Figure 8.47. Divided upper labials of of *Cerberus rynchops.* **Photography by JCM**

Jeffries, 1995).

Algal fouling has been reported in this species, though the effects it has on *Cerberus* requires more research (Rahman and Reza, 2013). This species is extremely abundant in India, with several published accounts noting that they might be the most or second most common aquatic snake in swamps, shorelines, estuaries, and other systems (Keswall, 1886; Dutta, 1989; Murthy, 1987; Whitaker, 1969).

The venom of *Cerberus rynchops* (and likely the entire genus) contains three known venom protein families: metalloprotease, CRISP, and C-type lectin. It also contains unique proteins (ryncolin1 and ryncolin2) that belong to a venom protein family unique amongst snakes, called veficolins (OmPraba et al., 2010); it is presumed that veficolins may induce platelet aggregation and/or initiate complement activation (OmPraba et al., 2010). Few venom studies have bene performed, but injections in laboratory mice showed sluggishness, partial paralysis, and death in 10–36 minutes, with post-mortem subcutaneous extravasation of blood over the back (Alcock and Rogers, 1902). The bite and venom, however, are considered medically insignificant for humans. *Cerberus rynchops* has been consistently recovered as the sister species to *Cerberus schneiderii* (Alfaro et al., 2004; Bernstein et al., 2021; Bernstein et al. 2023a). It is likely that the mosaic geological history (e.g., plate tectonics, sea level fluctuations; Hall, 2009) in the Quaternary has shaped the history of *Cerberus rynchops* and *Cerberus schneiderii.*

Southeast Asian Bockadam

Cerberus schneiderii (Schlegel, 1837)

Distribution and Habitat**.** Throughout Southeast Asia as a coastal specialist (though also can be found in inland streams and aquatic habitats). Specifically, it is found along the Andaman Sea coast of Thailand eastward to the Philippines and southward throughout peninsular Malaysia. Its distribution widely continues throughout Indonesia, as far east as the Moluccan islands of Halmahera and Seram. Type locality: Timor (Figure 8.48).

Identification**.** Dorsal scale rows in 23 (rarely 25) scale rows at midbody; the imbricate plate-like scales on crown have flat, thin appearance, lack keels anterior to rictus; last upper labial horizontally divided; venter mottled. The background color of the venter can be a cream, light yellow, or yellow. There seems to be significant variation in the cloacal plate, anterior chin shield, lower labials at the first chin shield, type of scale, prefrontal plate, upper labials at loreal, and ocular ring within Philippine *Cerberus schneiderii* (Barrera Jr. et al., 2017). Size. Males: SVL: 212–683 mm; Tail: 55–168 mm (tail 18–34% of SVL); Females: SVL: 190–901 mm; Tail: 45–184 mm (tail 18–28% of SVL). Neonates : SVL: 116–160 mm (Figure 8.49).

Natural History. Most of what is thought to be known about *Cerberus rynchops* is attributed to *Cerberus schneiderii,* as all of the mainland Southeast Asian populations were considered *C. rynchops* until Murphy et al. (2012b). They are nocturnal and often found in the same muddy, mangrove, and intertidal habitats that the rest of the genus are found in (Murphy, 2007a). They have been reported as the dominant snakes in *Rhizophorus mucronata* or *Sonneratia* sp. mangroves of Komodo, as well as in shallow sea water (Hoogerwerf, 1954; Auffenberg, 1980). In the Philippines they are abundant in most low-elevation aquatic systems, such as mangroves, intertidal zones, rivers, and lakes (see *C. microlepis*) (Griffin,

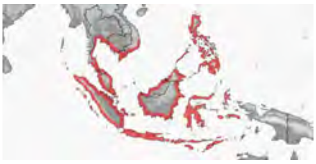


Figure 8.48. The distribution of *Cerberus schneiderii.*

1909; Gorman et al., 1981; Barrera Jr. et al., 2017; personal observations by JMB). On Java they are commonly found in muddy, brackish tidal waters of the coastal zone, and live-in holes in the mud until they are active at night (Hoesel, 1959). Based on diet data (two *Valencieannea longipinnus* , a coral reef goby) of a single Malaysian *C. schneiderii,* there is a possibility that *C. schneiderii* will enter coral reefs (L.T. Ming, personal communication [Murphy, 2007a]). These accounts of habitat and microhabitat preference, coastal specialization, and nocturnal behavior have been reported for several localities, such as Thailand (Taylor, 1965), Bali (Auffenberg, 1980), Singapore (Chim and Diong, 2013; de Lang, 2013), peninsular Malaysia (Charlton, 2020), the Moluccas (Edgard and Lilley, 1993; Setiadi and Hamidi, 2006;) and Sumatra (David and Vogel, 1996). They are known as 'Aninikig' in the Philippines and locals find them in high numbers, especially after heavy rain events (personal communication by JMB). Prey includes eels, crustaceans, and a variety of actinopterygian fish, most of which are gobies (Frith et al., 1977; Auffenberg, 1980; Gormon et al., 1981; Jayne et al., 1988; Murphy, 2007a). Snakes will hold their mouth open while swimming to capture schooling fish. Prey tends to be small—less than 10% of the predator's mass. Snakes will sometimes anchor itself to a convenient bamboo stake, anchor rope, or submerged branch by its tail, and from this purchase swings about in the current on the lookout for fish passing by. *Cerberus schneiderii* in the Philippines will readily sidewind to escape and stay still when approached; the Philippines *C. schneiderii* in the field were found swimming in the intertidal zone at ~2300 h in March in the Libmanan River mouth by San Miguel Bay, Camarines Sur Province, Luzon Islands (personal observation by JMB). In the immediate

Figure 8.49. Southeast Asian Bockadam, *Cerberus schneideri.* **Photography by Kenneth Chin.**

area where these specimens were caught, *Acrochordus granulatus* is also present, suggesting sympatry of these two aquatic snakes. This was also found to be the case in other parts of the Philippines, were there is a significant dietary overlap between *Cerberus* and *Acrochordus* (Gormon et al., 1981). This species is viviparous and has 2–12, with a direct correlation between female snake size and litter size (Chim and Diong, 2009); though, this is likely higher as *C. rynchops* can give litter sizes up to 38. *Cerberus schneiderii* is recovered as sister to *Cerberus rynchops*; it is likely that *C. microlepis* and *C. dunsoni* represent founder populations of *C. schneideri* (Bernstein et al., 2021).

Figure 8.50. Habitat for *Cerberus schneiderii.* **Photography by JCM**

Kerala Mud Snake

Dieurostus dussumieri (Duméril, Bibron & Duméril, 1854)

Distribution and Habitat**.** Coastal plain of South India (Kerala and Tamil Nadu), from Vembanad-kole wetlands of Kerala and Vellayani Lake to Neyyar River southern Kerala. Type locality: west coast (Malabar coast) of North Kerala, India (Figure 8.52.)

Identification**.** Dorsal scales smooth in rows of 25 or 27, nasal scales in contact, posterior labials horizontally divided by divided internasal, upper labials 1–3 contacting loreal; five lower labials contact the chin shields; a mostly uniform dorsum with lower ventrolateral stripe. The anterior edge of the first pair of chin shields is narrower than the posterior edge—ventral scales 146–148 in the two females. Size. Males. no data. Unsexed specimens. Maximum SVL: 555–795 mm; Maximum total length: 670–920 mm; Females. SVL: 491–670 mm; Tail: 74–77 mm (tail 12% of SVL) (Figure 8.53).

Natural History. *Dieurostus dussumieri* has a high salinity tolerance but has been found in both fresh and brackish environments. They use marshy habitats, stagnant ponds, and nearby areas with emergent and submerged aquatic vegetation such as wetland rushes and water hyacinths as habitat. They can also be found in paddy-fields (Kumar and Captain, 2011). *Dieurostus dussumieri* is piscivorous, and identifiable prey includes *Anabas testudineus* (Kumar and Captain, 2011). It breeds early in June with the southwest monsoon; gestation lasts more than five months. This species is viviparous and can have litter sizes of 25 neonates (can have up to 32 eggs, some of which may atrophy [Parameswaran 1954, 1962]). During the early stages of pregnancy, a chorioallantoic placenta forms that sup-

Figure 8.51. A *Cerberus schneiderii* **escapes into the water. Photography by JCM**

Figure 8.53. Kerala Mud Snake, *Dieurostus dussumieri.*
Photography by Vivek-Sharma,

Figure 8.52. The distribution of *Dieurostus dussumieri*

plies embryos with nutrients after the yolk has been used (Parameswaran, 1962). Kumar and Captain (2011) mention that theses snakes can be found buried in the mud, and also observed escape behavior in which *D. dussumieri* escapes into the grasses and *Ipomoea aquatica* along the margins of lakes and their flood plains. Personal communication with fisherman in Kumar and Captain (2011) state that the bite of *D. dussumieri*, while only mildly venomous, is painful (though, it is uncertain if this is due to lacerations from the teeth or the venom itself). Several hypotheses using molecular data exist for its phylogenetic placement: it has been recovered as sister to *Myrrophis chinensis* (Kumar et al., 2012); sister to a clade consisting of *Hypsiscopus, Myrrophis, Gyiophis*, and *Enhydris* (Quah et al., 2018); sister to *Raclitia indica* or all rear-fanged homalopsis with the exclusion of *Hypsiscopus* (Bernstein et al., 2021); and other placements within the rear-fanged group (Quah et al., 2017). Gyi (1970) hypothesized that *D. dussumieri* is in the *Ferania sieboldii* group, and Murphy (2007a), based on morphological data, hypothesized that *D. dussumieri, F. sieboldii,* and *Mintonophis pakistanicus* all share a common ancestor. However, all of the molecular studies have varying levels of support. Bernstein et al. (in review), used nuclear and mitochondrial DNA to recover a clade that consists of *D. dussumieri, F. sieboldii,* and *M. pakistanicus,* which are closely related to the clade containing *Hypsiscopus, Enhydris, Myrrophis,* and *Gyiophis.*

Trans-fly Mangrove Snake
Djokoiskandarus annulata (De Jong, 1926)

Distribution and Habitat. Found on the southern coast of New Guinea, Trans-Fly region. Type locality: Prins Frederik Hendrik Island, West New Guinea (about 7°56' S and 138°21' E). (Figure 8.54).

Figure 8.54. The distribution of *Djokoiskandarus annulatus.*

Identification**.** Mostly smooth scales but some of the posterior dorsal scales keeled; dorsal scales in 21 rows at midbody reduced to 19 rows posteriorly; internasal separates prefrontal and nasals scales, frontal contacts internasal. Size. Males: SVL: 470 mm; Tail: 108 mm (tail 18.7% of SVL) (n=1 specimen) (Figure 8.38)

Females: Total length: 227–548 mm; Tail: Data Deficient (tail 16–17.8% of SVL); Juvenile: SVL: 254 mm; Tail: 44 (tail: 17.3% of SVL) (Figure 8.55)

Natural History**.** Little is known about the natural history of *D. annulata*. It occurs at Abam in mangrove and *Nipa* palm habitats (Parker, 1982). Parker (1982) also reported a gravid female that was 568 mm (total length; five eggs). The Trans-Fly region is a mosaic of freshwater, marine, and swamps and monsoon and mangrove forests, and it is likely that *D. annulata* inhabits these areas.

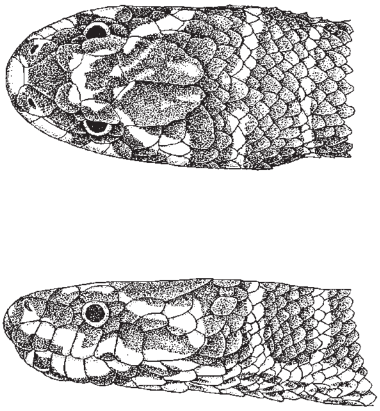


Figure 8.55. Trans-Fly Mangrove Snake, *Djokoiskandarus annulatus* **MCZ R136063. Artist credit Lisa Kanellos**

Chanard's Mud Snake
Enhydris chanardi Murphy & Voris, 2005

Distribution and Habitat**.** Restricted to vicinity of Bangkok, possibly as far west as Chantaburi, Thailand. No known extant population. Type locality: Bangkok, Thailand (13° 45' N, 100° 31' E) (Figure 8.56). A photograph of a live specimen Cox et al. (1998, p. 41) labeled as *Enhydris jagori*i exists. However, a photograph („http://www.flickr.com/photos/exotarium-oberhof/8243681837/.) of a specimen reportedly from Mueang Nakhon Nayok, Nakhon Nayok in Khao Yai National Park was recently seen, and this species may be more widely distributed than previously thought. A photograph was also posted on social media on November 11th, 2020 (locality: Thamai District, Chanthaburi Province, Thailand), though this may be *E. subtaeniata*. All specimen of this snake come from metropolitan Bangkok area. *Enhydris chanardi* appears to be endemic (or a near-endemic) to the Chao Phraya freshwater swamp forest.

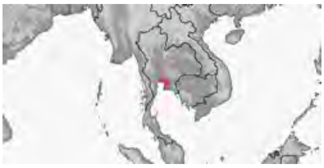


Figure 8.56. The distribution of *Enhydris chanardi*

Identification**.** *Enhydris chanardi* can be distinguished from all other *Enhydris* with 21 scale rows at midbody by the combination of the following characteristics: 116–125 ventral scales, 38–60 subcadual scales (53–60 in males and 38–49 in females); two pairs of chin shields with the second pair being the longest or equal to the first pair; lateral spots rows 4–5 or 4–6; stripe on scale row three. Dorsal scales lack striations (present in *E. enhydris* and *E. subtaeniata)*. Size. Males:

Figure 8.57. *Enhydris chanardi.*
Photography by Rica Achim Kempter

SVL: 127–437 mm; Tail: 39–87 mm (tail 19.9–26% of SVL; Females: SVL: 192–460 mm; Tail: 42–101 mm (tail 18.3–26% of SVL) (Figure 8.57).

Natural History**.** Despite the genus *Enhydris* being one of the most well-studied groups of homalopsids, along with *Cerberus,* very little is known about *E. chanardi.* It is likely piscivorous. One specimen at the Smithsonian National Museum of Natural History (USNM 83431) contains 13 well-developed embryos. Bernstein et al. (2021) obtained strong support in a concatenated nuclear+mitochondrial tree for *E. chanardi* as the sister taxon to all other *Enhydris*. In this study, *Enhydris* was consistently recovered as sister to a group containing the reciprocally monophyletic *Gyiophis* and *Myrrophis* (strong and weak support in the concatenated and species tree analysis, respectively). New data (Bernstein et al. 2023a) using genomic-level DNA supports this, and recovers *Enhydris* as sister to a clade containing *Myrrophis, Myanophis,* and *Gyiophis,* and also recovers *E. chanardi* as sister to all other *Enhydris* species.

Rainbow Mud Snake

Enhydris enhydris (Schneider, 1799)

Distribution and Habitat**.** Widespread from Nepal and eastern India to Indochina (and possibly southern China), southward to the Greater Sunda Islands as far east as Borneo. Its presence on Sulawesi is doubtful. Type locality: "Indiae orientalis. … lake of Ankapilly, coast of Coromandel, India." (Figure 8.58)

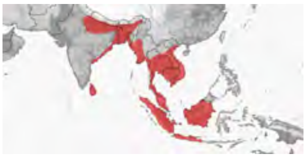


Figure 8.58. . The distribution of *Enhydris enhydris***.**

Identification**.** *Enhydris enhydris* is a distinctly striped species with a small narrow head. The combination of 153–174 ventral scales, a pattern of longitudinal stripes with no lateral or dorsal spots or bars, second pair of chin shields longer than the first will distinguish this snake from other *Enhydris.* It may be most easily confused with is its sympatric (in the Mekong drainage) sister species, *E. subtaeniata,* which

Figure 8.60 Rainbow Mud Snake, *Enhydris enhydris.*
Photography by A. Konrad Mebert; B. JCM.

has fewer than 153 ventral scales; a pattern of spots on scale rows 4–6, and two or three pairs of chin shield. When there are two pairs, the first pair is longer than the second (Figure 8.59).

Size. Males. Maximum SVL: 575 mm; Tail: 125 mm (tail 25–38% of SVL); Females. Maximum SVL: 734 mm; Tail: 148 mm (tail 20–35% of SVL). Neonates: SVL: 143–206 mm (average=178 mm; Karns et al. [2005]). There may be considerable size differences between populations.

Natural History**.** This is a highly aquatic snake that uses a variety of stagnant, slow-mov-

Figure 8.59. Habitat for *Enhydris enhydris* at Ban Tha Hin, Lake Songhkla Thailand. Stakes on the left shoreline mark funnel traps for snakes. Photography JCM

ing, and shallow aquatic habitats ranging from rice paddies, canals, ditches, and drainpipes to lakes and rivers. It can be found in and around urban areas; it thrives in disturbed habitats (Figure 8.60). It is considered a freshwater species. Although it has been observed in brackish and salt water, it is not known if these observations were due to flooding events of nearby freshwater localities (Subaraj and Rajathurai, 2018). They can be found in high numbers and studies using PIT tags and radio telemetry in Thailand show that these snakes can dominate the aquatic snake assemblages of the systems they live in (Murphy et al., 1999; Karns et al., 2000). *Enhydris enhydris* is likely to be one of the most common and abundant species in its range. It will use drain tiles to move around in metropolitan areas. Rarely is it far from water. Fish are the primary food, and specimens examined contained only fish. The most common species were cyprinids (*Rasbora sumatrana, Trichopsis vitta* [=*Trichopsis vittate*]) and osphronemids (*Trichogaster trichopterus* (=T*richopodus trichopterus*) (Murphy, 2007a), but also include nandids and anabantids (Brooks et al., 2009). Karns et al. (2005) dissected 141 specimens caught as bycatch from gill nets in Thailand, and stomach contents only contained fish, supporting that his is a piscivorous species. *Cylindrophis jodiae* (formeraly *C. ruffus*) has been a confirmed predator of *E. enhydris* (Brooks et al., 2009), as has *Xenopeltis unicolor* (Murphy, 2007a). Bandicoot rats (*Bandicota indica*) are also reported to feed on *E. enhydris* (Nandi, 1984). Females continue to hunt when gravid. The smallest females at maturity are 410 mm (Brooks et al., 2009). Litter sizes range from 2–39 neonates. Parturition occurs likely occurs year-round across the range, with most births timed with the onset of the monsoon season. Reports of envenomation from this snake are in the literature; symptoms are localized (localized pain, swelling, throbbing [Acharji and Mukherjee, 1966; D'Abreu, 1912]). Molecular systematics have consistently recovered a monophyletic *Enhydris*, with either *E. enhydris* or *E. subtaeniata* as the sister taxon to a clade containing *E. innominata, E. longicauda*, and *E. jagori*i (Alfaro et al., 2008; Karns et al., 2010a; Bernstein et al., 2021). Genomic data (Bernstein et al. 2023a) recovers *E. enhydris*

Jagor's Mud Snake

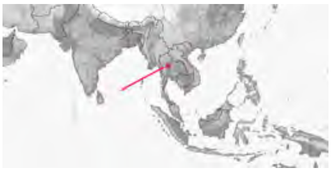


Figure 8.61 The distribution of *Enhydris jagorii.*

Enhydris jagorii (Peters, 1863)

Distribution and Habitat**.** Probably restricted to Thailand's Central Plain. Historical evidence suggests it occurs in the vicinity of Bangkok. Only one extant population is from the northern edge of Thailand's Central Plain at the Bung Ka Lo wetland, Uttaradit province, Thailand. Type locality: "Siam" [Thailand]. (Figure 8.61).

Identification**.** Dorsal scales in 23–25 rows on the forebody, large, scalloped blotches or spots on sides and dorsum, ventral scales 117–127; females have more than 50 subcaudals, males have about 68, pupil mottled and colored like

Figure 8.62. Jagor's Mud Snake, *Enhydris jagorii.* **From northern Thailand. Photography by JCM**

scales surrounding it. Eye diameter less than the diameter of the nasal scale.

Note that *E. jagorii, E. longicauda*, and *E. innominata* as sister to *E. longicauda* and *E. innominata,* but this sampling does not include *E. jagorii* (though, *E. jagorii* is likely in a clade with the latter two taxa) are closely related. At some point, they are likely to be synonymized, and *E. jagorii* is the oldest of the three names. Size. Male: Maximum SVL: 353 mm; Tail: 118 mm (tail 29–33.4% of SVL); Female: Maximum SVL: 195–445; Tail: 43– 93 mm (tail 22–26% of SVL) (Figure 8.64). as sister to *E. longicauda* and *E. innominata*, but this sampling does not include *E. jagorii* (though, *E. jagorii* is likely in a clade with the latter two taxa).

Natural History**.** Little is known about *E. jagorii.* Of 108 specimens, 22 contained fishes of six families: Cyprinidae, Anabantidae, Channidae, Bagridae, Nandidae and Osphronemidae (Pongcharoen et al., 2016). Gravid females were found in every month of the year except March, December, and January. The absence of gravid females was likely the result of sampling bias or sample size (Pongcharoen et al. 2016). Molecular systematics using mitochondrial and nuclear loci have shown that *E. jagorii, E. innominata,* and *E. longicauda* are extremely similar or identical regarding sequence divergence (Karns et al., 2010a; Bernstein et al., 2021), and Murphy (2007a) suggested that *E. innominata* and *E. longicauda* may be best regarded as subspecies ('races') of *E. jagorii*, the oldest name of the three species.

Tay Ninh Mud Snake

Enhydris innominata (Morice, 1875a)

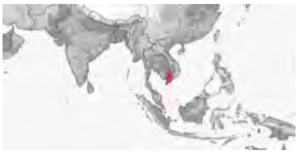


Figure 8.63. The distribution of *Enhydris innominata*

Distribution and Habitat**.** Lower Mekong drainage of Vietnam and possibly into Cambodia (Murphy, 2007a). Type locality: Tay-ninh, Cochinchina (= Tay Ninh Province, South Vietnam) (Figure 8.63).

Identification**.** Extremely low ventral count (106 –117), 42–56 subcaudals, a highly distinctive pattern of black lateral blotches (scalloped-shaped) arise from the ventral surface. These distinguish this snake from most other *Enhydris. Enhydris jagorii* has a higher ventral count (117–127), and smaller temporal scales. Enhydris longicauda has more ventral scales (122–136) and more subcaudal scales (52–76) than *E. innominata*. *Enhydris chanardi* has a higher ventral scale count (110–125), small dorsolateral spots that involve two or three scales: and larger, plate-like temporal scales. *Enhydris enhydris* and *E. subtaeniata* have stripes in their patterns and smooth, striated dorsal scales, and elongated anterior chin shields. This species has smooth scales without striations. The largest female measured had TL of 655 mm, with a 50 mm tail. Size. Males. SVL: 233–390 mm; Tail: 47 mm (tail 25–33% of SVL); Females: SVL: 176–605 mm; Tail: 39–50 mm (tail 18–24% of SVL). (Figure 8.62).

Natural History**.** *Enhydris innominata* uses artificial canals, flooded grasslands, and Melaleuca swamp forest (Bryan Stuart, personal communication in Murphy [2007a]). This habitat is within the Tonlé Sap-Mekong Peat Swamp Forest ecoregion of Wikramanayake et et al. (2002). Three gravid females were 465–555 mm SVL and contained 13–32 eggs (X = 25.6).

Figure 8.64. Tay Ninh Mud Snake, E*nhydris innominata.*
Photography by

Embryos were not detected in any of the eggs, and they were collected in South Vietnam in late-October and November. See *E. jagorii* for systematics and evolution.

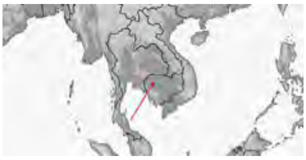


Figure 8.65. The distribution of *Enhydris longicauda.*

Long-tailed Mud Snake

Enhydris longicauda (Bourret, 1934)

Distribution and Habitat**.** Restricted to waters and adjacent shorelines of the Tonlé Sap area of Cambodia. Type locality: Tonlé Sap, Cambodia. (Figure 8.65).

Identification**.** Ventral scales 124–133, dorsolateral pattern mostly black-purple with large, lateral, dark scalloped blotches. In color pattern, it is most like *E. jagori*i and *E. innominata*. However, both *E. jagorii* and *E. innominata* demonstrate sexual dimorphism of the subcaudal scales and show less lateral compression of the tail. These two species also have different ventral scale count ranges, *E. jagorii* 117–127, and *E. innominata* 106 –117. *Enhydris chanardi* has fewer scale rows (20–22) around the neck compared to *E. longicauda* (23–25), fewer ventral scales (110–122), and a distinctive pattern of lateral spots involving 2–4 scales on scale rows 4–6. *Enhydris enhydris* and *E. subtaeniata* have a dorsal pattern of longitudinal stripes, but *E. subtaeniata*'s pattern includes lateral spots on scale rows 4–6, ventral scale count range of 136–153. *Enhydris enhydris* has more than 153 ventrals. *Enhydris enhydris* and *E. subtaeniata* have smooth, striated scales, while *E. longicauda, E. chanardi, E. jagorii*, and *E. innominata* do not. Size. Male: SVL: 503 mm; Tail: 173 mm (tail 23–35% of SVL); Female: SVL: 640 mm; Tail: 163 mm (tail 25–35% of SVL) This taxon shows no sexual dimorphism in tail length, an unusual condition for a homalop-

Figure 8.66. Long-tailed Mud Snake, *Enhydris longicauda.* **From Tonle Sap, Cambodia. Photography by Konrad Mebert**

sid (Fig. 8.67).

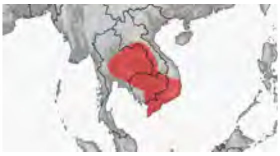


Figure 8.67 The distribution of ***Enhydris subtaeniata*****.**

Natural History**.** A highly aquatic snake that may leave the water on rare occasions, but as Tonlé Sap undergoes seasonal changes in water level, it appears to estivate in the mud. It may be inactive during low water (Saint Girons and Pfeffer, 1972). Fish likely compose a major portion of its diet; one specimen contained a *Trichogaster tricopterus* (Family Anabantidae), and other prey items include bagrids, channids, cyprinids, nandids, and osphronemids (Brooks et al., 2009). Little is known about its biology, but a female collected in June had 18 oviductal eggs. See *E. jagorii* for systematics and evolution.

Kompong Mud Snake

Enhydris subtaeniata Bourret, 1934

Distribution and Habitat**.** Found in the wetlands of the Indochinese Peninsula, mostly present in Mekong Drainage from Laos, Vietnam, Thailand, Cambodia; outside the Mekong drainage at Bung Boraphet, Thailand. Type locality: Kompong Speu, Cambodia (Figure 8.68).

Identification**.** This species has 136–153 ventral scales, and the color pattern contains stripes and lateral spots. The presence of lateral spots and ventral counts separate this species from *E. enhydris,* which has 153–174 ventral scales. *Enhydris subtaeniata* has two or three pairs of elongated chin shields, rather than the flared condition found in *E. jagorii* and its relatives (*E. chanardi, E. innominata, E. longicauda*). Both *E. enhydris* and *E. subtaeniata* have dorsal scales with striations, which do not occur in other members of the genus. This species has been long confused with *Enhydris jagorii,* and most of the older literature ref-

Figure 8.68. Kompong Mud Snake, *Enhydris subtaeniata* from Thailand.
Photography by JCM.

erences, particularly those outside of Thailand, to *Enhydris jagorii* refer to this species. Size. SVL: 133–539 mm; Tail: 120 mm; Average SVL: 397 mm; Female: SVL: 128–743 mm; Tail: 127 mm; Average SVL: 402 mm (Figure 8.69).

Natural History. This species is found in shallow stagnant water and streams. It is syntopic with *E. enhydris* at many locations (Saint Girons and Pfeffer, 1972; Stuart et al., 2000; Murphy, 2007a), but E. enhydris is numerically dominate (Murphy, 2007a). There are several localities in central Thailand where *E. enhydris* and *E. subtaeniat*a co-exists in similar numbers and both species have been collected in the same gill net. Prey includes fish and frogs. This aquatic snake uses streams impoundments, padi, ditches. klongs, ponds, and probably many other aquatic microhabitats. In Cambodia, Saint Girons (1972) and Saint Girons and Pfeffer (1972) considered this snake to be strictly aquatic and diurnal, and they suggest it migrates with the water as the water levels in the lake undergo season fluctuations. However, Murphy (2007a) has seen them buried in the mud. Murphy (2007a) found three females contained 7, 12, and 20 oviductal eggs, respectively. The smallest gravid female had a SVL of 572 mm. Deuve (1970) reported young born in April and May with the first rains; this assumes his *E. enhydris* account pertains to this species and not *E. enhydris.* The phylogenetic affinity of this species is uncertain but may be sister to all other *Enhydris* excluding *E. chanardi* or sister to the *E. jagorii+E. innominata+E. longicauda* group (Karns et al., 2010a; Bernstein et al., 2021). Genomic data supports this topology (Bernstein et al., 2023a).

Tentacled Snake

Erpeton tentaculatum Lacépède, 1800

Distribution and Habitat**.** Southern Thailand, Cambodia, southern Vietnam. Type locality: Unknown (fide Manthey and Grossmann, 1997). (Figure 8.69).

Identification**.** Prominent paired rostral appendages (appendage scales arranged in a pointed fashion, in successive annuli); dorsal scales in 34–39 at mid body, heavily keeled; ventrals very narrow with keel on each side (left and right); the ventrals and rostral appendages readily separate this snake from all other homalopsids. Size. Males: Maximum SVL: 478 mm; Tail: 246 mm (tail 43–59% of SVL). Females: Maximum SVL: 536 mm; Tail: 231 mm (tail 33–44% of SVL). Neonates. TL: 197–244 mm (Figure 8.70).

Natural History**.** *Erpeton tentaculatum* is a highly aquatic snake, living in shallow, slow-moving, turbid water, with some emergent vegetation (Taylor, 1965; Cox, 1991; Murphy, 2007a). It likely never leaves the water, and while it may be cryptic in nature, Smith (1943) reported that it is not uncommon in the country around Bangkok in ponds and sluggish waters, and that Bourret stated it is not rare in Cambodia and Cochin China (=Vietnam). This species is piscivorous and feeds on anabantid, bagrid, osphronemid fishes (Brooks et al., 2009). Using a J-shaped hunting posture, it hunts from ambush, taking advantage of the C-start response of fish to predators (Smith et al., 2002). *Erpeton tentacula*tum feints their body so fish will initiate a C-start response towards the snake's jaws as it strikes (Smith et al., 2002; Catania, 2009). While the rostral appendages of *Erpeton* have been the subject of much research, Catania et al. (2010) found that the appendages are sensitive mechanoreceptors that are innervated by branches of the trigeminal nerve and respond to water movement. Accounts of feeding on amphibians (frogs, tadpoles) are cited by Morice (1875b,c), along with plant matter. The amount of plant matter and al-

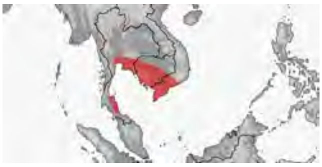


Figure 8.69.The distribution of *Erpeton tentaculatum.*

Figure 8.70. Tentacled Snake, *Erpeton tentaculatum* from southern Thailand. Photography by JCM

Figure 8.71. Hunting posture of *Erpeton* in an aquarium with a Fighting Fish, *Betta* sp. Photography by JCM

gae in the digestive tract of *E. tentaculatum* has been found in multiple specimens (see Neill and Allen [1956] and Saint Girons [1972]). However, given the ballistic nature of *E. tentaculatum's* strikes and the dense vegetation of its environment, this is likely secondary ingestion, as also suggested by Morice and Neil and Allen (1956). *Cylindrophis jodiae* (formerly *C. ruffus*) has been a confirmed predator of *E. tentaculatum* (Brooks et al., 2009). When this snake is handled, it does not attempt to bite or escape; instead, it stiffens its body (Smith, 1943). A captive snake placed in an aquarium with one floating water hyacinth proved to be remarkably cryptic. Its body posture and coloration combine to make it appear part of the vegetation. Its cryptic nature is also enhanced by the growth of algae on the skin. When placed in clean water the symbiotic algae are readily visible, and the fish (*Betta*) in the aquarium would graze along the snake's body. Thus, besides serving as camouflage, the algae may also help to attract prey. Reproduction studies of *Erpeton* has found that litters of 5–13 young are born in July–October (Morice, 1875c; Smith, 1943; Campden-Main, 1970; Martinez and Behler, 1988). The mean litter size is about eight (Martinez and Behler, 1988). Courtship was observed only once, on 24 February. *Erpeton tentaculatum* has been recovered as the sister taxon of *Subsessor bocourti* (Alfaro et al., 2008; Quah et al., 2017; Bernstein et al., 2021). However, Quah et al. (2018) recovered *Raclitia indica* as the sister to *E. tentaculatum*. All these studies have low support for these relationships and varying molecular datasets and taxa. Bernstein et al. (in review) used genomic data and found a strongly supported relationships of *Erpeton* as sister to the Australasian genera *Pseudoferania* and *Myron*. Thus, further investigation with more comprehensive sampling is needed to obtain more accurate phylogenetic relationships.

Siebold's Mud Snake

Ferania sieboldii (Schlegel, 1837)

Distribution and Habitat**.** Large rivers and associated flood plains from northwest peninsular India, Bangladesh, Nepal, and extreme western Myanmar. Possibly Bhutan (Lenz, 2012). Type locality: Jumma River, near Agra (Figure 8.32).

Identification**.** Dorsal scale rows 27–29; ventrals 143–156; subcaudals 28–56; prefrontals contact loreal; upper labials in orbit 4 or 4–5; divided internasal; two postoculars; no suboculars; 7–9 upper labials; last one or two upper labials divided; 11–13 lower labials; hemipenis extends to 14th subcaudal. Size. Males: no data. Females: Maximum SVL: 575; Tail: 105 (partly damaged tail); Neonates: SVL: 172 – 191; Tail: 35–41 mm | Average SVL: 180 mm; Average Tail: 39 mm (Figure 8.73)

Natural History**.** *Ferania sieboldii i*s a poorly known homalopsid snake. Habitat includes large rivers and associated flood plains; it has been found embedded in the mud (Gharpurey, 1944), in dead rushes in the water/mud substrate (Wall, 1897), and even underneath wood stacks near water sources (Wall, 1908). It has been caught in fishing nets by fisherman (water depth = 0.5 m) in the Kaliya Sot dam (Bhopoal, Madhya Pradesh State) of India (Thakur and Watve, 2009). Prey may be exclusively fish. Reproduction: Litters of 5–7 neonates are likely. The diet of this snake likely includes fish and frogs; Wall (1897) reported a captive *F. sieboldii* ate a frog, and another specimen died trying to eat a fish. Mell (1928) described a passive defensive posture and behavior of this species when disturbed: it alternated between mirrored postures and will assume a loose coiled position. Thakur and Watve (2009) observed aggressive behavior that was also supported by accounts from local fisherman of Bhopal: the snake actively lunged and tried to bite, which often causes it to be killed once caught in fishing nets. Gyi (1970) hypothesized it is closely related to *Dieurostus dussumieri,* and Murphy (2007a) suggests that *F. sieboldii, D. dussumieri,* and *Mintonophis pakistanica* derive from a common ancestor. Molecular data (Bernstein et al. 2023a) supports this hypothesis by Murphy (2007a).

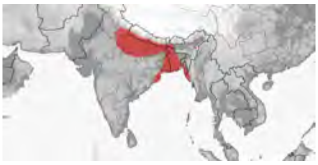


Figure 8.72. The distribution of *Ferania sieboldii*

Figure 8.73 . Siebold's Mud Snake, *Ferania sieboldii.* a juvenile of Ferania from Lucknow, Uttar Pradesh of India.
Photography by Vivek R Sharma

Crab-eating Snake

Fordonia leucobalia (Schlegel, 1837)

Distribution and Habitat**.** Found on mainland coastal habitats from Bangladesh, Myanmar, Thailand, and southern Vietnam. Also, Nicobar Islands and Greater Sunda Islands eastward to New Guinea and northern Queensland, Australia. Type locality: Timor (Indonesia) (Fig. 8.74)

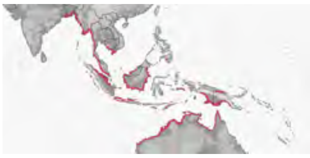


Figure 8.74. The distribution of *Fordonia leucobalia.*

Identification**.** Dorsal scales in 25–29 rows at midbody; five or six upper labials, third enters orbit; loreal usually absent; scales in ocular ring plate-like; frontal shorter than parietal; chin shields small, usually two pair (can number 1–3), second pair contacting each other (a trait that will separate this snake from all other homalopsids). Rear fangs grooved, exceptionally robust. Size. Males: SVL: 394–528 mm; Tail: 57–

82 mm (tail 13.5–15.9% of SVL); Females: SVL: 427–589 mm; Tail: 46–58 mm (tail 9.8–12.6% of SVL). Neonates: SVL: 190–222 mm; Tail: 24–27 mm (Figure 8.76).

Natural History.

Found in shallow, stagnant water and streams. On occasion, it may be found in monsoon forests or the open ocean (O'Shea, 1986; Campden-Main, 1970), though it is unlikely that they thrive in this habitat (Murphy, 2007a). This species uses the intertidal burrow system. Karns et al. (2002) used radiotelemetry on three specimens in Singapore, and found F. leucobalia to be quite sedentary (average 4.4 m over 7–10 days), primarily nocturnal, and were often found in mud lobster mounds or foraging on tidal mud flats. The use of mangrove systems, mud flats, and crustacean burrows by populations throughout its range is supported in the literature (Malayan Peninsula and Thailand [Macnae, 1968]; Java

Figure 8.75. Crab-eating Snake, *Fordonia leucobalia.* **Top two are from Penang. Photograph from Evan Quah. The next two are from the Northern Territory of Australia Photography by JCM and Mark Sanders.**

[Kopstein 1931, Hoesel, 1959]; Australia [Cogger, 1981]; New Guinea [Parker, 1982; O'Shea 1986]). It has been observed using sidewinding behavior on the mudflats (Cogger and Lindner, 1974). Their diet is almost entirely crustaceans, including: *Sarmiatium germaini, Macrophthalmus* sp., graspid crabs, *Dotillopsis brevitarsis, Uca* sp. (ocyopodids, fiddler crabs), and *Thalassina anomala* (mud lobster - Fig. 8.70)) (Gow, 1989; Voris and Murphy, 2002). Like other snakes, they are likely predated on by birds and mammals; they have been reported to be eaten nervous sharks (*Carcharhinus cautus;* Lyle and Timms, 1987) and other squamates, such as *Bungarus candidus* and *Varanus indicus* (Murphy, 2007a). They have been observed feeding in the daytime by Nobbs and Blamires (2004), who also made two separate observations of *F. leucobalia* separating the tail from the cephalothorax prior to eating (behavior unique to this taxon and Gerarda prevostiana amongst all alethinophidians, except the natricid *Opisthotropis* cf. *spenceri;* Noonloy et al., 2018). This has been further observed in the field and in experimental setups: *F. leucobalia* subdues its prey with its venom, then pins the prey to the mud substrate, subsequently ripping the prey apart, usually by the legs and sometimes by chewing (Shine and Schwaner, 1985; O'Shea, 1996; Voris and Murphy, 2002; Jayne et al., 2018). *Fordonia leucobalia* is considered a specialist on hardshelled crabs (Jayne et al., 2002). Litter size range from 2–17 neonates (Murphy, 2007a). Bergman (1960) suggests that adults are sexually mature at 330 mm SVL. The mainland Asia populations tend to be a uniform black, while Australasian populations show dramatic color polymorphisms with red, white, and tan color morphs. Genomic data (Bernstein et al. 2023a) recovered a relationship in which *Fordonia* is the sister to the sister-pair *Gerarda+ Cantoria*. *Fordonia leucobalia, Gerarda prevostiana*, and *Cantoria violacea, t*he three crustacean specialists of the Homalopsidae, are often strongly supported as a clade in molecular systematics studies (Alfaro et al., 2008; Burbrink et al., 2020; Bernstein et al., 2021).

Figure 8.77 Mud lobsters of the genus *Thalassina*. build mounds of dirt around its burrow. The mounds are used by several homalopsid snakes for refugia and the crustaceans are eaten by both *Fordonia* and *Gerarda.* Photography by Bruce Jayne.

Gerard's Crab-eating Snake
Gerarda prevostiana (Eydoux & Gervais, 1837)

Distribution and Habitat. A widespread coastal species from the vicinity of the Gulf of Kutch, India eastward to Sri Lanka, Myanmar, Thailand, Cambodia, peninsular Malaysia,

Borneo, and the Philippines. The snake is likely rare in Sri Lanka (Somaweera et al., 2006), and the Indian and Sri Lankan populations are restricted to both countries' western coasts (Karunarathna et al., 2018). It is probably widespread in the Indonesian Archipelago, but specimens are absent due to the secretive habits of this snake, other than a report from Sarawak, East Malaysia (Borneo; Das et al., 2013). Type locality: "Manille" (= Manila, 14°37' N, 120°58' E, Luzon, Philippines) (Figure 8.78).

Description. A relatively small and slender species; dorsal scales in 17 rows at mid-body;

loreal present, in contact with upper labials 1–3; of 7–8 upper labials, the fourth enters orbit; postoculars are usually two with bottom scale extending partially under the eye; first

Figure 8.76. . The distribution of *Gerarda prevostiana*

pair of chin shields large, second pair much smaller and separated by a pair of smaller scales. Size. Males: SVL: 282–449 mm; Tail: 42–65 mm (tail 13.5–18.4% of SVL); Females: SVL: 254–434; Tail: 40–60 mm (tail 13–16.9% of SVL) (Figure 8.77.)

Natural History**.** A nocturnally active snake in mangrove forests with or without mud lobster mounds. Multiple studies have observed it as a coastal, intertidal snakes (Wall, 1921;

Lim, 1963; Taylor, 1965; Tweedie, 1983; Gharpurey, 1944; Murphy, 2007a). It has been excavated from the mounds of mud lobsters, specifically *Thalassinia anomala* and *T. gracilis* (Karns et al., 2002; Voris and Murphy, 2002), which occur toward the landward edge of the

mangal. It appears to be more active on two spring tide survey nights (full and or new moon; 16 snakes) compared to eight survey nights on the neap tide (half-moon: 12 snakes). Sri Lankan populations have also been found to only be active at night (Karunarathna et al., 2018). A variety of microhabitats are used from the landward edge of the mangal to the mud pools in the lower tidal zone at Pasir Ris Park in Singapore. However, Karns et al. (2002) found that it was not restricted to areas around mud lobster mounds. The diet of *G. prevostiana* has been presumed to include fish, shrimp, and other aquatic animals (Cox, 1991), but recent literature has not supported this; Voris and Murphy (2002) never found fish in the stomach contents of examined specimens. This snake tears its prey into pieces before engulfing (Jayne et al., 2002). This is similar to *F. leucobalia* (hard-shelled crab specialist), but *G. prevostiana* specializes on freshly molted crabs and does not press their prey into the mud;

Figure 8.77, Gerard's Crab-eating Snake, *Gerarda prevostiana*
Photography by Vivek-Sharma

Figure 8.78. A mud lobster mound on the west coast of peninsular Thailand. The burrow is visible. Harold Voris (left) Tanya Chanard and a graduate student (right). Photography by JCM

rather, they rip apart the crab carapace assisted by body coiling (Jayne et al., 2018). The only other non-homalopsid snake that rips their prey apart (other than scolecophidians, which may decapitate termites) scale rows square; 129 (female) ventral scales; 30/29 (female) paired subcaudals; a divided cloacal plate; eight or nine upper labials; ten lower labials; a maximum total length of 416 mm; relative tail length ratio of 0.13; a ventral patterning lacking a central spot on each ventral scale; the presence of a faint stripe on the lower, dorsal scale rows; and four rows of dark spots on the dorsum. *Gyiophis salweenensis* can be distinguished from *G. maculosa* by the shape of the dorsal scales of first three rows (square in *G. salweenensis* vs. ovate in *G. maculosa*), the ventral scale pattern (absence of a central spot on each ventral scale vs. its presence), and a stripe running through the scales of the lower dorsal scale row (faint stripe vs. absent). It is distinguished from *G. vorisi* by its lower number of ventrals (129 in *G. salweenensis* vs. 142–152 in *G. vorisi)*, lower number of subcaudals (30/29 [left/right] vs. 41–58), shape of the rostral scale (narrow vs. broad), and the number of rows of spots on the dorsum (four vs. three). Size. Male: no data. Female: SVL: 364 mm; Tail: 52 mm (Fig.8.77)

Natural History**.** Any aspect of biology or natural history of this species is solely known from the holotype (Quah et al., 2017). The single specimen of *G. salweenensis* was found at ~1930 hours crossing a narrow dirt road between flooded fields. Given the abundance of other homalopsid species that utilize flooded fields or intertidal habitats, it is likely that these flooded fields are natural habitat for *G. salweenensis*. This species has the dorsally-oriented, semilunar valvular nostrils that indicate an aquatic/semiaquatic lifestyle. Although more data is needed,

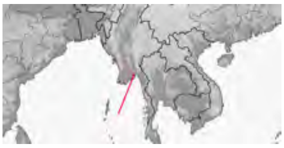


Figure 8.79. The distribution of *Gyiophis maculosa.*

the collection time of this specimen may indicate it has nocturnal habits. Quah et al. (2017) mention that the holotype had a puncture wound on its back, which may have come from a predation attempt from a heron. This species is recovered as sister to *Myanophis*, both of which are sister to *Myrrophis* (Bernstein et al. 2023a).’

Spotted Mud Snake
Gyiophis maculosa (Blanford, 1881)

Distribution and Habitat. Known only from Bajo in Ayeyarwady River Delta, Myanmar; and known from only two specimens, one of which (the holotype) appears to be lost. The population may extend to Dagon Township, Yangon (= Rangoon), Ayeyarwady State, Myanmar (JMB, Kate Woolf; personal communication). Type locality: ‘Pegu (probably in the neighborhood of Bassein)’ (= Bago, in southern Myanmar) (Fig. 8.81). Identification. This species has three pairs of chin shields, 123 ventrals, 25 scale rows on the neck, and a dorsal pattern of blotches without a stripe. These traits will separate it from *G. vorisi* which has more than 142 ventrals, a stripe on scale rows 2–4, 26-28 (usually 27) scale rows on the neck, a depressed head, and a bold zigzag stripe on the edge of the ventral scales that extends onto scale rows one and two, and a cream-colored stripe on the upper part of row two and row three; this stripe is bordered dorsally by a row of dark spots. It is distinguished from *G. salweenensis* by having ovate scales for the first three dorsal scale rows (square in *G. salweenensis), presence of a central spot on each ventral scale (absent in G. salweenensis), absence of a str*ipe running through the scales of the lower dorsal scale row (faint in *G. salweenensis*). In *G. maculosa*, three upper labials contact the loreal, smallest upper labial is the eighth, ten lower labials; 25 scale rows on the neck, and 25 scale rows at midbody; ventrals 122–125 ventral scales; and 32–33 subcaudal scales. Size. no data (Fig. 8.80).

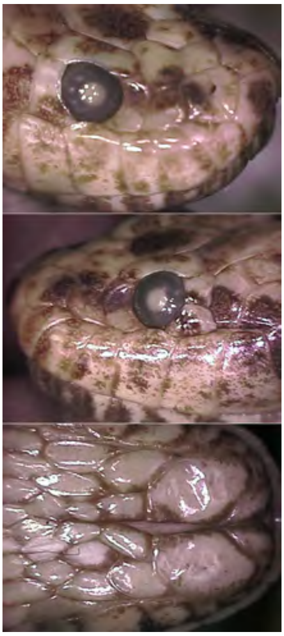


Figure 8.80. Spotted Mud Snake, *Gyiophis maculosa,* **BMNH 1913.6.12.1 labeled “blanfordi.” Photography by JCM.**

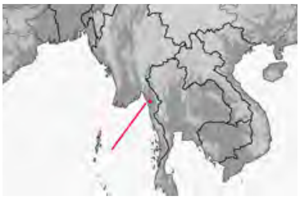


Figure 8.81. The distribution of *Gyiophis salweenensis.*

Natural History. Almost nothing is known about this species, and very little is known about the genus as a whole. It appears to be endemic to the Ayeyarwady freshwater swamp forest ecoregion of the Indochina Bioregion (Wikramanayake et al., 2002). A specimen of *G. maculosa* (based on the presence of a central spot on the ventral scales) may have been found in Dagon, Yangon City, but the molecular analyses and a thorough examination morphology is still needed to determine its species-level identity.).

Salween Mud Snake
Gyiophis salweenensis Quah, et al. 2017

Distribution and Habitat**.** Only known Mawlamyine, Mon State, Myanmar (type locality). Type locality: close to Sanpel Cave, Mawlamyine, Mon State, Myanmar (16°22.427 N, 97°46.388 E; 44 m in elevation) (Fig. 8.81).

Figure 8.82. Salween Mud Snake, *Gyiophis salweenensis*
Photography by Evan Quah.

Identification**.** This species is separated from the other two *Gyiophis* by having a unique combination of the following characters: a narrow rostral scale; the first three dorsal scale rows square; 129 (female) ventral scales; 30/29 (female) paired subcaudals; a divided cloacal plate; eight or nine upper labials; ten lower labials; a maximum total length of 416 mm; relative tail length ratio of 0.13; a ventral patterning lacking a central spot on each ventral scale; the presence of a faint stripe on the lower, dorsal scale rows; and four rows of dark spots on the dorsum. *Gyiophis salweenensis* can be distinguished from *G. maculosa* by the shape of the dorsal scales of first three rows (square in *G. salweenensis* vs. ovate in *G. maculosa*), the ventral scale pattern (absence of a central spot on each ventral scale vs. its presence), and a stripe running through the scales of the lower dorsal scale row (faint stripe vs. absent). It is distinguished from *G. vorisi* by its lower number of ventrals (129 in *G. salweenensis* vs. 142–152 in *G. vorisi)*, lower number of subcaudals (30/29 [left/right] vs. 41–58), shape of the rostral scale (narrow vs. broad), and the number of rows of spots on the dorsum (four vs. three). Size. Male: no data. Female: SVL: 364 mm; Tail: 52 mm (Fig.8.82) Natural History**.** Any aspect of biology or natural history of this species is solely known from the holotype (Quah et al., 2017). The single specimen of *G. salweenensis* was found at ~1930 hours crossing a narrow dirt road between flooded fields. Given the abundance of other homalopsid species that utilize flooded fields or intertidal habitats, it is likely that these flooded fields are natural habitat for *G. salweenensis*. This species has the dorsally-oriented, semilunar valvular nostrils that indicate an aquatic/semiaquatic

Maubin Mud Snake.
*Gyiophis vorisi (*Murphy, 2007b)

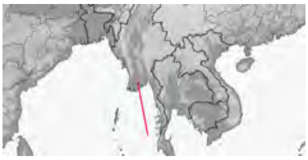


Figure 8.83. Distribution of *Gyiophis vorisi.*

Distribution and Habitat**.** Known only from the vicinity of Maubin in the Ayeyarwady River Delta, Myanmar. Type locality: Maubin, Ayeyarwady Division, Myanmar (about 16° 73’ N, 95° 65’ E) (Fig.8.83).

Identification**.** Two pairs of chin shields, 142–152 ventrals, dorsal pattern of stripes that are lateral and dorsal, and may break up into smaller spots. All these traits separate it from *G. maculosa,* a species with which it has been long confused.

Figure 8.84. Maubin Mud Snake, *Gyiophis vorisi.* **Photography by JCM**

Gyiophis vorisi is distinguished from *G. salweenensis* by having a higher number of ventrals (142–152 in *G. vorisi* vs. 129 in *G. salweenensis*), higher number of subcaudals (41–59 vs. 30/29 [left/right]), shape of the rostral scale (broad vs. narrow), and the number of rows of spots on the dorsum (three vs. four) (Fig.8.84)

Size. Males: SVL: 378–450 mm; Tail: 90–102 mm (tail 24–25% of SVL) | Average SVL: 390.2 mm; Average Tail: 95.8 mm; Females: SVL: 371–505 mm; Tail: 73–86 mm (tail 16–24% of SVL) | Average SVL: 429.6 mm; Average Tail: 81.1 mm.

Natural History**.** Known from the Maubin area, which is in the Ayeyarwady Freshwater Swamp Forest ecoregion. None of the specimens examined by Murphy (2007b) contained prey. A 450 mm SVL female (KU 92397) had five oviductal eggs (Murphy, 2007b). The species inhabits a severely degraded habitat. Wikramanayake et al. (2002) report the sedimentation rate of the Ayeyarwady River is the fifth highest in the world because of the deforestation that has occurred upstream in recent decades.

Mamberamo River Water Snake

Heurnia ventromaculata Jong, 1926

Figure 8.85. The distribution of *Heurnia ventromaculata*

Distribution and Habitat**.** Only known from the type locality in northwestern West Papua, Indonesia. Pionierbivak, Mamberano River, northern New Guinea. Type locality: Pionierbivak, Mamberamo River, NW New Guinea (Fig. 8.85.)

Identification**.** Dorsal scales in 27 rows; the internasal is large; prefrontals are fused with the loreals and separate the internasal scale from the frontal; lower postocular extends under the orbit; upper labials eight or nine, with the fifth entering the orbit. Size. Males: SVL: 554 mm; Tail: 148 mm. Known only from the holotype

Natural History**.** Known only from the type specimen, no information exists on the natural history of *H. ventromaculata*. The area *H. ventromaculata* is known from is filled with estuaries of the Mamberamo River, freshwater swamps, and extensive mangroves areas (Muchtar and Ilahude, 2001; Richards and Suryadi, 2002). It is possible that these areas are home to *H. ventromaculata*, as many homalopsids have adapted to these types of ecosystems. See page 715.

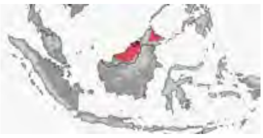


Figure 8.86. The distribution of *Homalophis doriae.*

Borneo Mud Snake

Homalophis doriae Peters, 1871

Distribution and Habitat**.** Known only from the island of Borneo, and is widespread on the island (Figure 8.86). Type locality: Sarawak, Borneo.

Identification**.** Dorsal scales in 29–33 rows at mid-body; suboculars present; 11–16 upper labials with last 5–9 horizontally divided. It may be most easily confused with *H. gyii,*

Figure 8.87. Borneo Mud Snake, *Homalophis doriae*
Photography by Anton Sorokin.

which has 25–27 scale rows at mid-body and more than 153 ventrals. Size. Males: SVL: 175–580 mm; Tail: 125 mm (tail 20–26% of SVL); Females: SVL: 193–696 mm; Tail: 101 mm (tail 14–18% of SVL) (Figure 8.87).

Figure 8.88. The distribution of *Homalophis gyii.*

Natural History**.** *Homalophis doriae i*s found exclusively in swampy habitats and muddy rivers below 500 m in coastal Sarawak and Sabah; it has been found in the same locality as *Hypsiscopus plumbeus* (Stuebing and Inger, 1999). It can be abundant in stagnant or slow-moving water of rice fields and ponds and sometimes burrows in muddy river bottoms during the day, becoming more active at night (Iskandar, 2004). Its diet is composed of fish, has been caught in fishing nets, and is considered a pest by aquaculturists in eastern Kalimantan (Iskandar, 2004). Confirmed prey items include *Systomus* cf. *orphoides* (barbs; Voris and Murphy, 2002). Three gravid females from Murphy (2007a) contained 6–16 eggs or embryos. Bernstein et al. (in review), using mitochondrial DNA, found that *Homalophis doriae* is sister to *Phytolopsis punctata.*

Gyii's Mud Snake

Homalophis gyii (Murphy, Voris & Auliya, 2005)

Distribution and Habitat**.** Known only from the Kapuas River drainage in Kalimantan, Indonesia. Type locality: Kalbar, Sungei Kapuas, near Putussibau, Indonesia (Figure 8.88).

Identification**.** Dorsal scales in 25–27 rows at mid-body; subocular scales present; 15–16 upper labials, ones below and behind eye horizontally divided. It may be most easily confused with *H. doriae,* which has 29–33 scale rows at mid body, and less than 153 ventrals. Size. Males: no data. Females: Maximum SVL: 666 mm; Tail: 96 mm (tail 14–18% of SVL) (Figure 8.89).

Figure 8.89. Gyii's Mud Snake, *Homalophis gyii* from Kalamantan, Indonesia. Photography by Mark Auliya.

Natural History**.** This snake is likely the sister to *H. doriae.* Little is known about the habitat, feeding habits, and reproduction of this species. Two specimens were obtained during periods of heavy rainfall in flooded riparian habitats. The wet season in Putussibau may be characterized by months that exceed 400 mm of precipitation (January, February, August, October, and November), and a total annual rainfall of 4480 mm. The Reserve is west of the type locality and is a large complex of swamp forest, peat swamps, and lakes. This area is subject to two annual monsoons, a northeast monsoon in October and the second monsoon in March. Water levels in the area recede by August, at which time the floodplain lakes are completely dry for a 3–4-month period; the area then becomes a dry savanna with high daily temperatures. This climatic regime has produced an environment unique from the surrounding lowland forest and several endemic fish and bird species are known from the region (Sebastian, 1994). It is uncertain if *H. gyii* and *H. doriae* are sympatric. This snake has also been referred to as the 'chameleon snake,' due to its potential ability to change from a reddish-brown color to completely white within minutes (Auliya, 2003). This phenomenon in *H. gyii* may be a defense/warning mechanism, but it is poorly understood in this species and has yet to be published on since.

Puffed-faced Watersnake

Homalopsis buccata (Linnaeus, 1758)

Distribution and Habitat**.** Found from extreme southern Thailand, peninsular Malaysia, Indonesian Archipelago from Sumatra to Borneo. A population may exist on Sulawesi (Rooij, 1917), but this has yet to be confirmed (de Lang and Vogel, 2005; Murphy et al., 2012c). Type locality: "Indiis" (in error; given erroneously as "India" by Manthey and Grossman1997). "Indiis" was likely meant to mean 'East Indies,' now the Indonesian Archipelago. The type locality is now Singapore (Murphy et al., 2012c) (Figure 8.93).

Identification**.** Upper labials 1–4 single contact loreal; two prefrontals; 33–40 dorsal scale rows at midbody, usually reduced to less than 30 posteriorly; one postocular plus a post-

Figure 8.90. The distribution of *Homalopsis buccata.*

subocular; 12 (11–14) upper labials; ventral count less than 166. *Homalopsis buccata* can be distinguished from *H. hardwickii* by the latter species having a divided loreal; *Homalopsis nigroventralis* has upper labials 1–3 contacting the loreal; *Homalopsis semizonata* has a divided or fragmented loreal contacting upper labials 1–4 or 1–5 and three prefrontals; *H. mereljcoxi,* has a single loreal contacting upper labials 1–4, scale rows at midbody 40–47, reduced to 30 or more posteriorly. Size. Males: SVL: 167 – 695 mm; Tail: 56–236 mm (tail 28–34% of SVL); Females: SVL: 192–794 mm; Tail: 62–202 mm (tail 23–26% of SVL); Neonates: 227–450 mm (Figure 8.91-92).

Natural History**.** *Homalopsis buccata* is an aquatic species that feeds on fish. Much of the literature that reference *H. buccata* are referring to other species within the genus. The habitat used by *H. buccata* may include a variety of aquatic habitat, from freshwater streams, ponds, agricultural drains and irrigated fields (Cantor, 1847; Charlton, 2020), to brackish waters (Hagen, 1890) and peat swamp forests (specimen notes of California Academy of Sciences specimen CAS 174127 [Narathiwat, Thailand]). In Malaysia, they have been found both inland and coastally, as well as in vacated crab holes in swamps, river banks, streams, and ponds (Lim, 1964). While considered a nocturnal, Lim (1964) found it foraging during the day along the edges of water bodies. This species may even inhabit polluted habitats, as it is still found in Kuala Lumpur's Klang River (Malaysia), which is

Figure 8.91. A juvenile *Homalopsis buccata.* **Kalamantan. Photography by Rob Steubing,**

Figure 8.92. Puffed-faced Watersnake, *Homalopsis buccata.* Krabi, Thailand. Photography by **Harry Ward-Smith**

often flooded, muddy, and polluted (Berry and Lim, 1967). In Sumatra, it has been described as the most common water snake in Medan (specifically, Deli River, in root systems). This is another species that has been found to sidewind (Bergman, 1951). Specific prey items for *H. buccata* include fish (*Tilapia, Lebistes, Mystus, Claris* sp. *Chana* sp. *Puntius binotatus*) and eels (*Fluta alba*) (Bergman, 1951; Berry and Lim, 1967; Lim, 1964). Deuve (1970) mentions freshwater crustaceans as a part of their diet, but this refers to the Laos populations, which likely represent what is now considered *H. nigroventralis* (Murphy et al., 2012c). It is likely *Cylindrophis* sp. (*C. ruffus* or *C. jodiae*) are predators of *Homalopsis* (Greene, 1893). Cobras and kraits may also feed on them, as *Homalopsis buccata* are susceptible to the elapids' venom (captive observation; Bergman, 1951). No definitive breeding season has been confirmed, and juveniles have been found year-round in a population in Kuala Lumpur, Malaysia (Berry and Lim, 1967). Litter sizes range form 4–37 (embryos and eggs; Murphy, 2007a). Size of reproductive maturity varies across studies that have looked at different species (based on locality); Bergman (1951) reported a 569 mm SVL females with 4 mm eggs. *Homalopsis* has been recovered as the sister to *Cerberus* when analyzed with genetic data (Alfaro et al., 2008; Bernstein et al., 2021; Bernstein et al. 2023a). Before the use of molecular data, it was hypothesized that *Cerberus, Homalopsis*, and *Enhydris* were closely related (Gyi, 1970). Studies using more sampling are needed to identify strongly supported, intergeneric relationships, which are currently lacking for the family. Genomic data (Bernstein et al. 2023a) supports that *Homalopsis* and *Cerberus* are sister to each other, but are distantly related to *Enhydris*.'

Figure 8.93. The distribution of *Homalopsis hardwickii.*

Indian Puff-faced Watersnake

Homalopsis hardwickii Gray, 1842

Distribution and Habitat**.** Known only from type specimen, this species may be restricted to northeast India or Nepal. Its distribution is poorly known. Type locality: India (datum questionable; Murphy et al., 2012c) (Figure 8.93).

Identification**.** *Homalopsis hardwickii* has a divided loreal contacting upper labials 1–4; two prefrontals; scale rows at midbody 39, reduced to 28 posteriorly; one postocular and no presubocular; 159 ventrals. *Homalopsis buccata* has a single loreal contacting upper labials 1–4. *H. nigroventralis* has upper labials 1–3 contacting loreal. *Homalopsis semizonata* has three prefrontals. *Homalopsis mereljcoxi* has a single loreal and two postoculars plus a postsubocular and 40 –47 scale rows at midbody, reduced to 30 or more posteriorly. Known only from the holotype. Size. Males: SVL: 511 mm; Tail: 172 mm (tail 33.7% of SVL). Data Deficient. (Figure 8.94).

Natural History**.** Nothing is known about the natural history of *Homalopsis hardwickii.* It is likely similar to the other members of the genus, but much remains to be discovered.

Figure 8.94. One of the syntypes of *Homalopsis hardwickii* **BMNH 111.18.1b Photography by Christinia Cumberbatch**

Jack's Watersnake

Homalopsis mereljcoxi Murphy et al. 2012

Distribution and Habitat. Known from lowland locali-

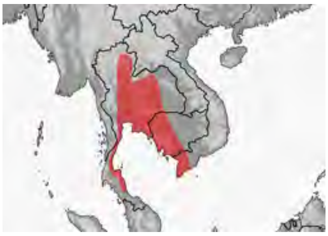


Figure 8.95. The distribution of *Homalopsis merlejcoxi.*

ties in Thailand, Cambodia, and Vietnam. It is known as far north as Bung cho, Uttaradit Province, Phichai District, Thailand (~12° N, 104° E) and as far south as Lake Songkhla (~7° N, 100° E), Thailand. In Vietnam, it is known as far east as Can Tho Province (~10° N, 105° E), and as far south as Vinh Thuan District Town in Kien Giang Province (~9° N, 105° E). In Cambodia, it is present in Tonle Sap, and likely occurs in the lower elevations of the Chao Phraya and Mekong river drainage systems. It is unclear if this species inhabits Myanmar, which H. semizonata is native to. Type locality: Thailand, Nakhon Ratchasima Province, Wang Nam Khieo, Udon Sap (subdistrict), Ban Badan Reservoir (14°31'04" N, 101°58'25" E) (Fig. 8.95).

Identification. *Homalopsis mereljcoxi* has a single loreal contacting upper labials 1–4; scale rows at mid-body 40–49, reduced to 30 or more posteriorly; two postoculars plus a postsubocular; and ventral counts are usually greater than 165. Homalopsis buccata has 33–40 dorsal scale rows at midbody, reduced to less than 30 posteriorly; one postocular plus a postsubocular; ventral count less than 166. *Homalopsis hardwick*ii has a divided loreal; Homalopsis nigroventralis has upper labials 1–3 contacting loreal; 35–39 dorsal scale rows at mid-body, reduced to less than 30 posteriorly; reverse color pattern on the venter (dark olive-gray with white spots). *Homalopsis semizonata* has a divided or fragmented loreal contacting upper labials 1–4 or 1–5; three prefrontals; one postocular and one postsubocular. Size. Males: SVL: 404–914 mm; Average Tail: 223.72 mm (tail 30–44% of SVL); Females: SVL: 400–973 mm; Average Tail: 181.24 mm (tail 25–34% of SVL) (Figure 8.96).

Natural History. Habitat in Thailand includes small reservoirs, ditches, ponds, streams,

Figure 8.96. Jack's Watersnake, *Homalopsis merlejcoxi.* **Eastern Thailand Photography byJCM.**

and shallow wetlands (Karns et al., 2005, 2010b). Snakes are taken as bycatch in gill nets; one specimen from Murphy et al. (2012c) was hand-collected from a pond at night while it floated near the surface in an ambush posture with its head and forebody submerged. They have also been found in similar habitats in Cambodia: streams, rivers, irrigation canals, marshes, reservoirs, lakes, riverbanks Saint Girons (1972). It rests in burrows or crevices in the bank during the day and has been reported to move very little while on land (Saint Girons, 1972). Individuals released into shallow water escaped without hesitation but placed in a river with steep banks, the snakes immediately sought refuge along the shore. In a population depletion experiment at Tonlé Sap (Brooks et al., 2007), a density of one specimen per 1718 m2 was calculated. Only fish have been found in the gut of *H. mereljcoxi.* About 61.5% of males and 37.5% of females contained fish as prey in Karns et al (2010). Five families of fish are confirmed as prey items in a study of 700+ specimens: Anabantidae 57%, Channidae 7.5%, Cyprinidae 2.5%, Mastacembilidae 3%, Osphronemidae 31% (Brooks et al., 2009); fish consumed were usually less than 10% of the predator's mass. Predators likely include *Cylindrophis jodiae* (formerly *C. ruffus*) (Smith, 1914a; Brooks et al., 2007). Females start vitellogenesis

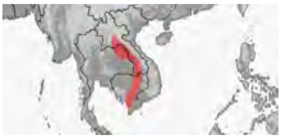


Figure 8.97. The distribution of *Homalopsis nigroventralis.*

Figure 8.98. Mekong Watersnake, *Homalopsis nigroventralis.* **Thailand. Photography by JCM.**

in November and mating occurs in December or early January; ovulation occurs in February (Murphy et al., 2012c). Six females contain 13–33 large ovarian follicles or recently ovulated eggs in February. Gestation lasts until May (Karns et al., 2005).

Mekong Watersnake

Homalopsis nigroventralis Deuve, 1970

Distribution and Habitat**.** This species is known from the Mekong River Valley from Laos and Thailand to at least Cambodia. It has been reported from the Mekong River in Kratié Province, Cambodia and Koh Kapeung and the Koh Khlap Islands. Type locality: Ngum River Valley, Laos (Figure 8.100)

Identification**.** Upper labials 1–3 contacting the loreal; two prefrontals; 35–39 dorsal scale rows at midbody, reduced to 30 or less; one or two postocular plus one postsubocular; 10–12 upper labials; 159–167 ventrals; reverse color pattern on the venter (dark olive-gray with white spots). All other *Homalopsis* have upper labials 1–4 contacting loreal and a ventral pattern that is light with dark spots. Size. Males: Maximum SVL: 828 mm; Maximum Tail: 204 mm (tail 24.6% of SVL); Females: Maximum SVL: 820 mm; Maximum Tail: 171 mm (damaged tail; tail 20.8% of SVL) (Figure 8.101).

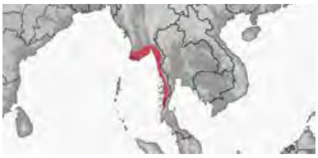


Figure 8.99. The distribution of *Homalopsis semizonata*

Natural History**.** *Homalopsis nigroventralis* utilizes aquatic habitats, and, unlike the other members of this genus, may use streams with a moderate current and sand and rock substrate, compared to the slow moving or stagnant water with mud substrates that other *Homalopsis* utilize (Stuart et al., 2006; Murphy et al., 2012c). The streams and localities where this species have been found have closed or open canopies, and some had grass-lined banks (Stuart et al., 2006). All these localities are peripheral to the Mekong. Despite this, they have been collected on mud substrates too (Bezuijen et al., 2009). It also occurs in

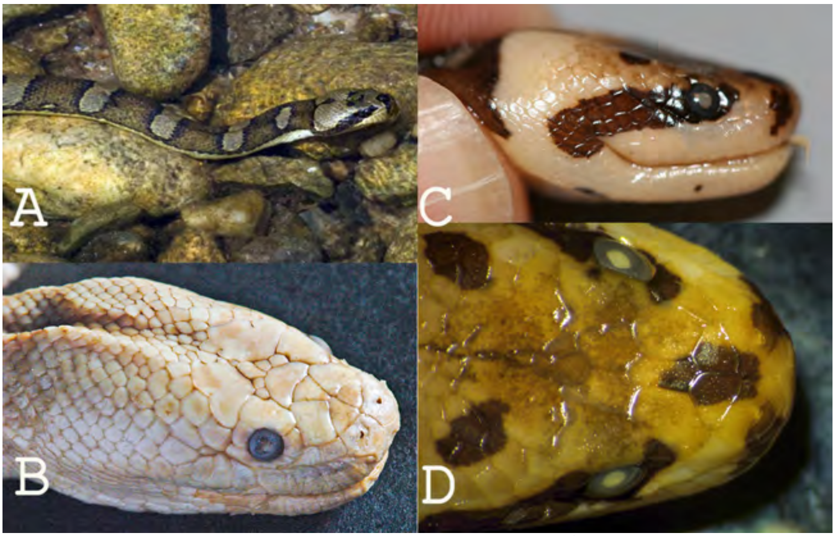


Figure 8.100. Myanmar Watersnake, *Homalopsis semizonata.*
Photograph from (A) Jens Vindum, (B) B. Murthy (C-D) JCM

bamboo mixed with evergreen forest between 100 and 170 m ASL in eastern Cambodia (Stuart et al., 2006). Specimens have been collected during the day and are sometimes caught in gillnets as bycatch (Stuart et al., 2006). Deuve (1970) noted that *H. buccata* and *H, nigroventralis* never occurred together. Bernstein et al. (2021; in review), using phylogenetics methods with molecular data, showed that *H. nigroventralis* is strongly supported as the sister to all other *Homalopsis.*

Myanmar Watersnake

Homalopsis semizonata Blyth, 1855

Distribution and Habitat**.** This species is known from Kawkareik, Twante near Rangoon, Mottama, and the Irrawaddy Delta, Myanmar. It also occurs at Kawkareik on east side of Gulf of Martaban. It extends southward along the coast to Phuket Province in southwestern Thailand (Frith, 1977). It may extend along the Andaman Sea's coastal plain in southern Myanmar and along the Andaman coast of peninsular Thailand. Type locality: Mottama (formerly Martaban), Myanmar (Figure 8.99).

Identification**.** This species is distinguished from all other members of the genus by a prefrontal composed of three scales, loreal scale divided into 2 –6 smaller scales, upper labials 1–5 contacting loreal scales. All other *Homalopsis* have two prefrontals, and upper labials 1–4 at the loreal. The three prefrontal scales, however, may be variable in different populations; a series from Ranong, Thailand was shown to have two or three prefrontals, and sometimes even four (Murphy et al., 2012c [University of Kansas Biodiversity Institute & Natural History Museum specimen voucher KU 92453; Pauwels and Sumontha, 2016). Size. Males: SVL: 562 mm; Tail: 166 mm (tail 29.4% of SVL); Females: SVL: 480 – 629 mm; Tail: 136–177 (tail ~28% of SVL); Neonates: SVL: 54 mm; Tail: 170 mm (tail 31.8% of SVL) (Figure 8.100).

Natural History**.** Little is known about *Homalopsis semizonata.* They have been collected at night during rain near a dam at the Suwansiri waterfall in the Kraburi District of Thailand (Pauwels and Sumontha, 2016). In Pauwels and Sumontha (2016), a specimen had nine babies in mid-June. They also two young individuals (one male, sex of second specimen not mentioned) on Phuket Island (Phuket Province, southeastern Thailand) actively foraging in a small stream near a waterfall in mid-September and mid-October. The young male

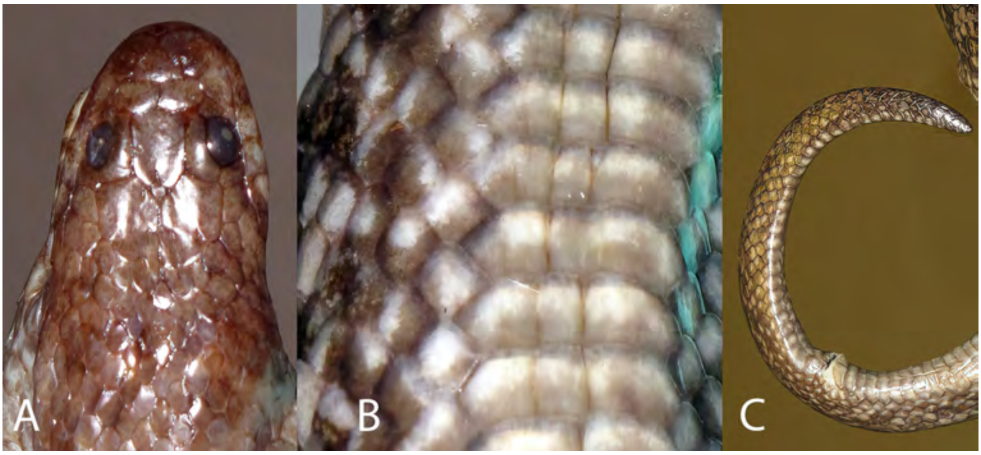


Figure 8.101. *Hypsiscopus indonesiensis.* A. Dorsal view of head. B. Narrow ventrals C. Laterally compresswed tail Photography by JCM.

was found syntopic with the diploglossid *Limnonectes blythii.* The unsexed individual was catching a channid fish (*Channa gachua*) and found syntopic with the geomydid turtle *Siebenrockiella crassicollis*. It is possible that *H. semizonata* may be a population of *H. buccata,* as phylogenies using genomic data recovers the former embedded within the latter (Bernstein et al. 2023a), but more sampling is needed to confirm this. Because observations are limited, it is uncertain if *H. semizonata* is piscivorous and nocturnal, or if day encounters and observations of other prey items have just yet to be confirmed.

Lake Towuti Paddle-tailed Water Snake

Hypsiscopus indonesiensis Hamidy et al. 2023

Distribution and Habitat. The species is known only from Towuti Lake, South Sulawesi. Although Matano Lake, Towuti Lake, and Mahalona lakes are nearby and connected, *Hypsiscopus indonesiensis* is only recorded from Lake Towuti Lake. The Type Locality is Lengkona Bay, Towuti Lake, South Sulawesi. (no map).

Figure 8.102. The distribution of *Hypsiscopus matannensis.*

Identification. small body size (SVL <700 mm), internasal(s) do not contact loreal, upper labials 2–3 or 2–4 usually contact with loreal, lower labials 1–5 usually contact the anterior chin shields, relatively short tails (10–17 % of SVL) (Murphy & Voris, 2014) and molecularly nested in the genus *Hypsiscopus* (Bernstein et al., 2021; Fukuyama et al., 2022). *Hypsiscopus indonesiensis* is diagnosable from all congeners by having a laterally compressed tail, a high number of scale rows (24–25 in the neck, 25–27 at mid-body, 20–22 near the vent), a high number of ventral scales (152–159), the blotched pattern on the dorsum and mottled pattern on the ventral surface.

Figure 8.103. *Hypsicopus matannensis.* **Photograsphy by JCM**

Lake Matanna Mud Snake

Hypsiscopus matannensis (Boulenger, 1897)

Distribution and Habitat**.** Type locality: Lake Matanna, South-eastern Celebes (=Sulawesi). Endemic to Sulawesi. Known from Lake Matana (~02°27' S, 121°12' E) and near Raha (~04°51' S, 122° 43' E), on Muna Island in southeast Sulawesi (Figure 8.102).

Identification**.** Scale at mid-body in 21 rows; single postocular; and divided internasal separate it from its congener, *H. plumbeus.* Size. Males: SVL: 369–392 mm; Tail: 64–71 mm (tail 17.1–18.1% of SVL). Females: SVL: 387–566; 65–78 mm (tail 16–16.7% of SVL).

Natural History**.** *Hypsiscopus matannensis* is another species of homalopsid that is poorly known and published on. The second specimen ever discovered was collected from a fishpond about 200 m from the nearest river (Iskandar, 1979). All other aspects of its natural history have yet to be discovered.

Figure 8.104. *Hypsiscopus murphyi* **from Hong Kong. Photography by Artur Tomaszeck**

Murphy’s Mud Snake

Hypsiscopus murphyi Bernstein et al. 2022

Distribution and Habitat. It inhabits sluggish streams, ponds, rice fields, and marshlands at elevations from sea level up to at least 1200 m (Mell, 1922; Deuve, 1970; Murphy, 2007). It is present in Taiwan and southern China (Zhejiang Province) at its northernmost limit extending southward into China (including Hainan Island), into Vietnam, Laos, Cambodia, and Thailand. Sampling by Bernstein et al. (2022) suggests the southern limit of this species is in Phetchaburi, Thailand. Specimens from adjacent and nearby islands will need to be identified pending future molecular and morphological comparisons (e.g., Andaman Islands and other parts of India and Myanmar

Type locality: Laos, Khammouan Province, Gnommalath District, Ban Phak Phoung, 17.581918N, 105.219978E, 167m elev., collected in water in a rice paddy near karst forest at 2110 h, Bryan L. Stuart, Niane Sivongxay, Sengvilay Seateun, and Monekham Davanhkham, 11 July 2014.

Identification. *Hypsiscopus murphyi* can be distinguished from its congeners by having a higher range of ventral scales which is nearly non-overlapping with that of *H. plumbeus* (113–123), a lower minimum number of subcaudal scales than *H. plumbeus*(30–44), a lower range of subcaudals than *H. matannensis*(43–48), and a lower number of scales at mid-body than *H.matannensis* (21 DSR at midbody)

Natural History. It inhabits sluggish streams, ponds, rice fields, and marshlands at elevations from sea level up to at least 1200 m (Mell, 1922; Deuve, 1970; Murphy, 2007). However, it may wander some distance from the water. It has been found beneath logs, especially during the dry season (Saint Girons, 1972).One of the paratypes was found during the day (1420 h) two meters above the ground inside a rotted, hollow, termite-infested vertical tree in a gallery evergreen forest near a stream. The species is nocturnal or cathemeral (Murphy, 2007). *Hypsiscopus murphyi* is likely syntopic with its congener, *H. plumbeus*, in regions south of the Khorat Plateau in central and eastern Thailand and western Cambodia, up to latitudes of approximately 12.48N. Like other members of the genus, this species feeds on fishes, frogs, and sometimes crustaceans (Schmidt, 1927; Gressitt, 1941). Like all homalopsids it is ovovivip-

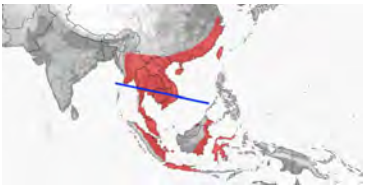


Figure 8.105. . The combined distribution of *Hypsiscopus murphyi* and *H. plumbeus*. The blue line roughly marks the boundary between the two species. *H. murphyi* is to the north line and *H. plumbeus* is to the south. The two species are likely sympatric in the vicinity of the line

arous, containing 2–18 young (Murphy, 2007); averages of nine young per litter have been reported (Cox,1991). Two examined specimens of *H. murphyi* (ROM 30818 and ROM 30933) in this study contained seven and nine ova, respectively. The venom toxicity of this species is not considered dangerous to humans, usually only causing localized effects (if any) such as burning sensations and local swelling (Karsen, 1986)

Hypsiscopus has three species. *Hypsiscopus plumbeus* was considered to inhabit nearly all of Southeast Asia, including Sulawesi. Previous research recovered *H. plumbeus* as paraphyletic with respect to the Sulawesi-endemic *H.matannensis* (Bernstein et al., 2021), a finding confirmed here with additional sampling. Bernstein et al. (2022) molecular and morphological analyses show evidence that the populations around and north of central Thailand's Khorat Plateau represent a distinct lineage that warrants species-level recognition. Wile they did not use genetic distances to diagnose this species, their genetic divergences (mitochondrial genes: 4.75–13.53%; nuclear genes: 0–2.48%) exceed that of species-level distances seen in studies on homalopsids (Kohler et al., 2021) and other snakes (Ruane et al., 2018).

Figure 8.106. *Hypsiscopus plumbeus*. A. is from Sabah, Malaysia (island of Borneo). Photography by DRK. B is a female from Lake Songhkla, southern Thailand. Photography by JCM.

Plumbeous Mud Snake

Hypsiscopus plumbeus (Boie, 1827)

Distribution and Habitat**.** Previously considered a widespread species. Bernstein et al. split it into two species. *H. plumbeus* now occupies the southern portion of the previously widespread species. range in southern Indochina, peninsular Thailand and Malaysia It is present on many, if not all, the Indonesian islands and extends its distribution eastward to Sulawesi. One specimen (American Museum of Natural History specimen voucher AMNH 3840) is from the Moluccan Islands, which would extend the eastern edge of the range if the locality data is correct. Type locality: Java (Figure 8.105).

Identification**.** Scale rows at mid-body 19, ventrals 119–142; upper labials 2–3 or 2–4 contact loreal; four or five lower labials contact anterior chin shields. Dorsum a uniform grey or black. Its congener, *H. matannensis* has 21 scale rows at mid-body. Size. Males: SVL: 152–420 mm; Tail: 24–59 mm (tail 11.9–19.1% of SVL); Females: SVL: 190–650 mm; Tail: 29–70 mm (tail 10–17.6% of SVL). Neonates: 122–160 mm (Figure 8.106).

Natural History**.** This is a semi-aquatic snake and the most terrestrial of the fanged homalopsids. It is associated with wallows, marshes, ditches, stream, pond banks in the mud-root tangle 10–20 cm below surface debris, both day and night, and occurs from sea level to at least 1200 m (Deuve, 1970; Mell, 1922; Smith, 1943). The species is particularly common in the rice paddies and drainage ditches (Bien Hoa, Vietnam; Main, 1970), and it will move over land. Accounts from Annandale and Robinson (Boulenger, [1903]) report it is aquatic, but is found under dead trees at some distance from water; this has also been stated by Saint Girons (1972), mentioning that prefers rice fields and marshland, but is found away from water in the dry season. Because of common encounters in ride paddies and agricultural areas, this snake is also called the ‘rice paddy snake.’ This species is considered nocturnal (Karsen et al., 1986; Murphy, 2007a). They have also been collected in stagnant ponds in Thailand (Murphy, 2007a). Snakes that were using a nearby stream were more mobile than those using the wallow microhabitats. It also feeds on dead fish. Their diet includes fish and amphibians (adults and larvae). Confirmed prey items include: the four-lined tree frog *Polypedates leucomystax* (Rhacophoridae), alpine cricket frog *Rana* [*=Fejervarya*] *limnocharis* (Ranidae), and walking catfish *Claris teysmanni* (*=Clarias teijsmanni;* Clariidae) (Pope, 1935; Voris and Karns, 1996; Murphy, 2007a). Confirmed predators include *Cylindrophis ruffus* (though, this record may represent *C. jodiae*), *Bungarus multicinctus* (Mao, 1970; Slowinski, 1994), and *Naja naja* (Mao, 1970). While not confirmed, the root tangle that *H. plumbeus* resides in is likely very safe from predatory birds and some fish, but others, such as snakeheads (Ophicephalidae) likely feed on *H. plumbeus*. Gravid females ranged in size from 282–480 mm total length and litter sizes range from 2–18 neonates (Murphy, 2007a). In Cambodia, neonates are recorded to be born in the spring (Saint Girons, 1972; Saint Girons and Pfeffer, 1972). In Laos, neonates have bene found throughout the rainy season, with young being born from April through August (Deuve, 1970). Parturition is finished by August. These snakes are known to use sidewinding and erratic ‘jumping’ to escape (Pope, 1935; Kuntz, 1963), and have been described as having either hiding behaviors by burying its head (Batchelor, 1963) or a tendency to flee when encountered in water, or relentless striking and biting if provoked out of water (Kuntz, 1963; Campden-Main, 1970). High levels of molecular divergence have been found in this group, and research currently underway (Bernstein et al. 2023b) will likely increase the known diversity of this genus. The venom of *H. plumbeus* is mild, not posing a threat to humans (Karsen et al., 1986). Bites from this species have been followed by immediate burning sensations and localized swelling (i.e., no systemic effects) and been compared to that of a bee sting (Daryl Karns, personal communication [Murphy, 2007]).

Figure 8.107. The distribution of *Kualatahan pahangensis.*

Pahang Mud Snake

Kualatahan pahangensis (Tweedie, 1946)

Distribution and Habitat**.** Kualatahan pahangensis is known from the vicinity of the type locality Kuala Tahan, River Tembeling, Pahang, peninsular Malaysia. Its range was expanded

Figure 8.108. ***Kualatahan pahangensis***
Photography by Chan Kin Onn

to include Hulu Terengganu and the Nenasi Forest Reserve in Pahang (Chan and Ahmad, 2009). Type locality: Kuala Tahan, River Tembeling, Pahang, between 500- and 1000-feet ASL (152–308 m) (Fig.8.107).

Identification**.** Has 25 scale rows at midbody, eight upper labials, upper labials 2–3 contact loreal, dorsal scales lanceolate; two pairs of chin shields five lower labials contacting first pair. Dark lateral stripe on the outer edge of ventrals row one, light stripe on rows 2–4. It may be confused with *Gyiophis,* which has 25 scale rows at midbody, but upper labials 1–3 contact the loreal; dorsal scales, particularly those in the first row, are ovate. Both H*omalophis* and *Phytolopsis* have 25 scale rows at midbody but have more than ten upper labials, and some are horizontally divided. Size. Males: SVL: 220–300 mm; Tail: 40–69 mm (tail 18.2–23% of SVL); Females: SVL: 392 mm; Tail: 68.5 mm (tail 17.5% of SVL) (Fig.8.108).

Natural History**.** *Kualatahan pahangensis* is known only from very few localities in Malaysia, and all natural history is based on a few specimens. Chan and Ahmad (2009) report that this species inhabits primary or undisturbed secondary forests, utilizing decaying leaves in stagnant portions of small, slowing moving streams. Charlton (2020) reports it from both primary and secondary forests up to 300 m asl, residing in slow-moving streams.

Indus Mud Snake

Mintonophis pakistanicus (Mertens, 1959)

Figure 8.108. The distribution of *Mintonophis pakistanicus.*

Distribution and Habitat**.** Extreme western edge of the family's distribution in the Indus River delta of Pakistan. Type locality: Jati, Sind, West Pakistan (Fig. 8.109).

Identification**.** Smooth dorsal scales, in 29 rows at mid-body; 153–162 ventrals exceptionally narrow on the anterior body, widening posteriorly; 8–9 upper labials, 4 or 4–5 in orbit; internasal divided contact loreal; loreal contacts upper labials 1–3; lower labials 11–12; chin shields absent (or exceptionally small), replaced

Figure 8.109. Indus Mud Snake, *Mintonophis pakistanicus.* **Photography by Petrova and Cyclowiki.org**

by numerous small scales; tail exceptionally long. The narrow ventrals, absent or tiny chin shields, and long-tail suggest this snake is highly derived and convergent with *Erpeton tentaculatum*. Males: SVL: 513 mm; Tail: 207 mm (tail 32–41% of SVL). Females: SVL: 779 mm; Tail: 208 mm (tail 21–33% of SVL) (Fig. 8.108).

Natural History**.** This species, while poorly known outside a few specimens, is known to occupy large shallow pons near channels of the Indus River, but not in the stream itself (Minton, 1966). Some of the sites in this area are brackish water habitats, and one used to be a seaport (Murphy, 2007a). They are reported to be diurnal, almost entirely aquatic, and shy in nature. Personal communication with collectors also mentions that they have been collected from late April through November, and will bury themselves in the mud the edges of their habitats (e.g., ponds) before the onset of cool weather (Murphy, 2007a). These habitat notes have also been cited by Khan (2002), stating that *M. pakistanicus* is almost completely aquatic (moving poorly on dry land), will bury in the mud to hibernate, and inhabits backwaters and ponds with emersed coastal vegetation. This study contains the only diet records of this species, finding that they eat fish, frogs, tadpoles, and aquatic arthropods, and also confirms previous reports on their shy and non-aggressive nature. ‘Bernstein et al. (2023a) uses mitochondrial DNA to recover *Mintonophis* as sister to *Dieurostu*s, both of which are sister to *Ferania.* The morphology suggests a highly aquatic snake with a prehensile tail (Murphy, 2007a). Gyi (1970) and Murphy (2007a) noted that two female museum specimens, AMNH 93154 (708 mm SVL) and CAS 99964 (500 mm SVL) contained 16 and 8 embryos, respectively.

Reuss’ Mud Snake

Miralia alternans (Reuss, 1834)

Distribution and Habitat**.** Greater Sunda Islands (Sumatra, Java, Borneo) and smaller islands of Bangka and Beliting. Type locality: Java (Fig. 8.110).

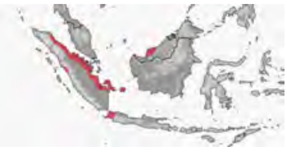


Figure 8.110. The distribution of *Miralia alternans.*

Identification**.** Smooth scales, nasals in contact; dorsal scales in 19 rows at mid-body; a tiny preocular scale; lower postocular does not extend below eye; fourth and fifth upper labials enter orbit; the ventrals number 120–143; eight upper labials; nasal cleft contacts second upper labial. Superficially like Raclitia indicia (but see Natural History, below). Size. Males: SVL: 380–474 mm; Tail: 50 mm (tail 13.1% of SVL); Females: SVL: 320–490 mm; Tail: 45–50 mm (tail 13.2–14.1% of SVL); Neonates: SVL: 123–126 mm; Tail: 14–19 mm | Average SVL: 124.4 mm; Average Tail: 16.2 mm (Fig.

Figure 8.111 .Reuss' Mud Snake, *Miralia alternans***.**
Photography by Rendra-Wahyudi

8.111)

Natural History**.** *Miralia alternans* is a rare species that is not encountered often, thus little is known about its Natural History**.** It has been found in rivers, specifically the Kali Cakung in Jakarta, Indonesia (Iskandar, 1987). Confirmed species that predate on *M. alternans* include *Cylindrophis ruffus*. The small head and short tail of this species suggest it have burrowing behavior. Clutch sizes in this species range from 6–16 (average = 9), and litter sizes may increase with female body size; the smallest gravid female recorded was 403 mm SVL (Bergman, 1960). *Miralia alternans* is superficially like *Raclitia indica*. However, the extremely gracile body of *R. indica*, more robust body of *M. alternans*, the difference of more than 30 ventral between the two species, and the exceptionally microcephalic condition of *R. indica* suggest the two snakes have been separated from each other for some time and have distinct evolutionary trajectories. Mitochondrial DNA (Bernstein et al. 2023a) suggests that *Miralia* may be sister to *Myrrophis*, but high levels of sampling are needed to confirm this.

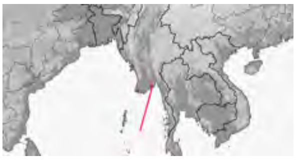


Figure 8.112. Distribution of *Myanophis thanlyinensis.*

Thanlyin Mud Snake

Myanophis thanlyinensis Köhler, et al. 2021

Distribution and Habitat**.** Only known from the Type locality: Specimen found near East Yangon University. Type locality: Thanlyin, Yangon, Myanmar (Figure 8.112).

Identification**.** Differs from all homalopsids by the following combination of characters: (1) dorsal scales smooth, row formula 21–21–19 or 21–21–17; (2) tail short, ratio tail length/SVL 0.185–0.204 in males, 0.160–0.167 in females; (3) nasal scales separated; (4) 125–126 ventral scales in males, 120–122 in females; (5) 38–39 subcaudal scales in males, 32–34 in females; and (6) hemipenis bilobed. It differs from *Myrrophis* by having 125–126 ventral scales in males, 120–122 in females (vs. 137–162, 137–164, respectively), and 38–39 subcaudal scales in males, 32–34 in females (vs. 39–55, 37–52, respectively). *Myanophis*

Figure 8.113. Thanlyin Mud Snake, *Myanophis thanlyinensis.* **Photography by Günther Kohler.**

thanlyinensis differs from *Gyiophis* by lacking dark blotches along flank (vs. blotches present), and by having 21 dorsal scales rows at midbody (vs. 25 scale rows). Additionally, the bilobed hemipenes present in *M. thanlyinensis* distinguish it from both *Myrrophis* and *Gyiophis.* Size. Males: SV:260–335 mm; Tail: 53–62 mm (tail 18.5–20.38% of SVL); Females: SVL: 300–362 mm; Tail: 50–58 mm (tail 16–16.7% of SVL) (Figure 8.113).

Natural History**.** The natural history of this monotypic genus is only known from the holotype and three paratypes published in Köhler et al. (2021). This species only known from open grassland that is flooded during the rainy season. Its discovery adjacent to East Yangon University may indicate this taxon can thrive in disturbed habitats close to human settlement. *Myanophis thanlyinensis* is likely nocturnal and has been found in shallow waters (<50 cm depth). A phylogenomic study (Bernstein et al. 2023a) places Myanophis as sister to *Gyiophis.* Other snakes syntopic with *M. thanlyinensis* are *Enhydris enhydris, Gyiophis vorisi, Amphiesma stolatum, Xenochrophis bellulus*, and *X. piscator.*

Figure 8.114. The distribution of *Myron karnsi.*

Figure 8.115. *Myron karnsi.* **Phototography by JCM**

Karns's Mangrove Snake

Myron karnsi Murphy, 2011

Distribution and Habitat**.** Only known from the type locality of Indonesia Aru. Type locality: Selrutti, Kobroor, Indonesia Aru (~5°46' S, 134°31' E) (Fig. 8.114).

Identification**.** *Myron karnsi* is a melanistic species with narrow yellow cross bands, with 21 scale rows at mid-body; seven upper labials; single preocular, semi-divided nasal, and a black dorsum with narrow yellow cross bands separate this species from other two species of *Myron.* Size. Males: no data. Females: SVL: 333 mm; Tail: 64 mm (tail 19% of SVL).(Figure 8.114)

Natural History**.** The natural history of *M. karnsi* is unknown but is likely similar to its congeners.

Figure 8.116. The distribution of *Myron resetari.*

Resetar's Mangrove Snake

Myron resetari Murphy, 2011

Distribution. *Myron resetar*i is known only from the type locality of Broome, Western Australia. However, it may be more widespread. It is likely that this snake also inhabits the Roebuck Bay area of the Dampier Peninsula (Murphy, 2011). Type locality: Broome, Western Australia (~17°58' S, 122°14' E) (Fig. 8.116).

Identification**.** This species has 19 scale rows on the neck and at mid-body; one preocular; large, plate-like occipital scales that are posterior and lateral to parietals. *Myron resetari* can be distinguished from *M. richardsonii* by a lower scale row count on the neck and at mid body (19 vs. 21); one preocular (two in *M. richardsonii*); largest upper labial is the fifth compared with the largest upper labial of six or seven in *M. richardsonii. Myron resetari* can be distinguished from *M. karnsi* by a lower number of scale rows at mid-body (19 vs. 21) a blotched pattern on a gray ground color (as opposed to yellow bands on black ground color in *M. karnsi*). Size. Males: SVL: 330 mm; Tail: 65 mm (tail 19.7% of SVL). Females: SVL: 246 mm; Tail: 44 mm (tail 17.9% of SVL) (Fig. 8.117).

Figure 8.117. Resetar's Mangrove Snake, *Myron resetari.*
Photography by Gary Rethus.

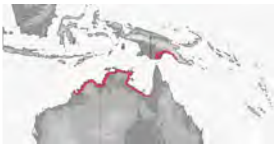


Figure 8.118 The distribution of *Myron richardsonii.*

Natural History**.** Similar to *M. karnsi,* little is known about this species. It inhabits mangroves and mudflats (Murphy, 2011).

Figure 8.119. Richardson's Mangrove Snake, *Myron richardsonii.*
Photography by Jacob Loyacano.

Richardson's Mangrove Snake

Myron richardsonii Gray, 1849

Distribution and Habitat**.** Found on coastal northern Australia, from the Gulf of Carpentaria to Western Australia and northward to the south coast of New Guinea. It is also present on the Aru Islands of Indonesia (Roux, 1910). Type locality: North Western Australia. Restricted to Buffalo Creek, Northern Territory, Australia (~12°40' S, 131°29' E) by Murphy (2011) (Fig. 8.118).

Identification**.** Has 21 scale rows on the neck and at mid-body, reduced to 17 or 19 rows near vent; posterior dorsal scale rows above row six prominently keeled in males; two preocular; upper labials usually number 8 or 9; lower labials 8–10; a dorsal pattern of 35–48 blotches. The presence of 21 scale rows, two preoculars distinguish it from *M. resetari.* The 8 to 10 upper labials and blotched pattern separate it from *M. karnsi*, which is melanistic with narrow yellow cross bands and has fewer upper labials. Size. Males: SVL: 191–372; Tail: 32–64 mm (tail 16.8–19% of SVL); Females: SVL: 255–370; Maximum Tail: 59 mm (tail 16–17% of SVL) (Fig. 8.119).

Natural History**.** The natural history of *M. richardsonii* is perhaps the most well-known out of any member from this genus. This species (as well as the other *Myron*) are considered dwarf homalopsids (Murphy, 2011), not exceeding 436 mm in total length; most other homalopsids exceed one meter in length (Murphy, 2007a). This species uses coastal mangroves, nearby mud flats, tidal rivers, and other aquatic habitats. Similar to *Cerberus, Cantoria, Fordonia,* it inhabits the intertidal burrow system and will bury itself into muddy substrate (Glauert, 1950; Gow, 1989, Worrell, 1963). Confirmed prey items include gobies (Murphy, 2007a), but crustaceans have also been mentioned as prey items (Worrell, 1963; Gow, 1989). One observation reports finding a *M. richardsonii* with a nudibranch in its mouth (Nobbs and Blamires, 2004). Shine and Schwaner (1985) observed it using constriction to subdue small fish, and Gyi (1970) suggested that the long, anterior teeth of this species may assist in holding onto gobies and gastropods covered in slippery mucous. Confirmed predators are *Crocodylus porosus* (Taylor, 1979). Litter sizes of this species are reported to be 6–8 (Gow, 1989; Shine, 1991). The interspecific, evolutionary relationships within *Myron* are currently unknown, but Gyi (1970) hypothesized that *Myron* and *Heurnia ventromaculata* formed a group. Bernstein et al. (2021) and Alfaro et al. (2008), using molecular data, both found strong support for the genus *Myron* to be sister to *Pseudoferania polylepis* and genomic data also supports this sister relationship (Bernstein et al. 2023a).

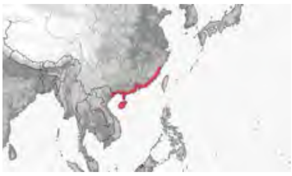


Figure 8.120. The distribution of *Myrrophis bennettii.*

Figure 8.121. Bennet's Mangrove Snake, *Myrrophis bennettii*
Photography by Adam Francis

Bennet's Mangrove Snake

Myrrophis bennettii (Gray, 1842)

Distribution and Habitat**.** *Myrrophis bennettii* is endemic to China's south coast from Hong Kong, south and west to Hainan. Gyi (1970) examined a specimen from Java, from the Zoölogisch Museum (University of Amsterdam; ZMA, no voucher number), but this is likely in error according to Murphy (2007a). Type locality: China (Figure 8.120).

Identification**.** *Myrrophis bennettii* has dorsal scales in 21 rows at mid-body, reduced to 17 or 15 in front of the vent; an internasal scale that does not contact the loreal; and an upper postocular larger than lower postocular. It is most often confused with *M. chinensis,* which has 23 rows of scales at midbody, 19 rows near the vent. Size. Males: Maximum SVL: 560 mm; Tail: 120 mm (tail 21–22% of SVL); Females: Maximum SVL: 755 mm; Tail: 96 mm (damaged tail) (tail 21–24% of SVL) (Figure 8.121).

Natural History**.** *Myrrophis bennettii* inhabits saltwater marshes and estuaries, and occasionally climbs onto shrubs, behavior not typical for homalopsid snakes (Murphy, 2007a). It is unclear if this behavior is an attempt at basking, or if the snakes use branches at high tide and were left on a branch as the tide receded. They have been reported as common in tidal marshes in and around mangroves (Deep Bay) and partially active in the day, but still may be nocturnal (Karsten et al., 1986). Other observations also mention their ability to climb is particularly good (Karsten et al., 1986). They are not considered a rare snake and have bene found in the sea around Hainan's coast, which may indicate they get washed out to sea from streams (Pope, 1935; Murphy, 2007a); this is possible as they have been found in streams at points that drain into the sea (Romer, 1961). The Hong Kong population uses tidal marshes (near Pak Hok Chau) along the shore at Deep Bay. Specimens have also been taken at the mouth of the Yuen Long Creek (unofficial name) and by the shore on the Mong Tseng peninsula at Deep Bay (Murphy, 2007a). Using molecular data, Bernstein et al. (2021) found strong support that *Myrrophis* is most closely related to *Gyiophis salweenensis* (the only species of *Gyiophis* in the study), which together form a clade that is sister to a monophyletic *Enhydris.* However, genomic data (Bernstein et al. 2023a) now supports that *Myrrophis* is sister to *Myanophis* and *Gyiophis;* these three genera are all reciprocally monophyletic to *Enhydris*.

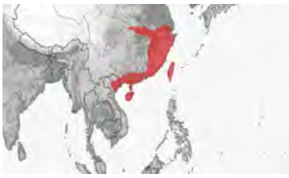


Figure 8.122. The distribution of *Myrrophis chinensis.*

Chinese Mud Snake

Myrrophis chinensis (Gray, 1842)

Distribution and Habitat**.** Known from southern China, North Vietnam, Taiwan, Hong Kong, Hainan. It may be present in northern Laos. Type locality: China (Fig. 8.122).

Identification**.** *Myrrophis chinensis* has 23 scale rows at midbody, reduced to 19 rows in front of vent; internasal not usually in contact with loreal, upper postocular smaller than lower postocular. Size. Males: SVL: 580 mm; Tail: 125 mm (tail 15–19% of SVL); Females: SVL: 710 mm; Tail: 100 mm (tail 12–15% of SVL); Neonates: 100–170 mm (Fig. 8.123).

Natural History**.** *Myrrophis chinensis* is a highly aquatic snake that inhabits lowlands and is common between sea level and 200 m. Though, it ascends to considerable altitudes in northeastern Kiangsi and on the Chungan plateau, the latter of which reaches an elevation of 1500 m (however, this is not to say *M. chinensis* is found at that elevation). It has been recorded at 525 m elevation (Gangeku, southwestern Fukien Province) and at 825 m (Hong San, southeastern Kiangsi Province) (Gressitt, 1941). Data accompanying specimen from North Vietnam suggest it reaches 1100 m ASL (Murphy, 2007a). This implies that this population may experience cold winter temperatures. It uses fishponds, sluggish streams, canals, and rice paddies; many literature accounts have found this species associated with rice paddy ecosystems, thus, agricultural practices may in part be responsible for the relatively high abundance widespread altitudinal distribution of this species (Murphy, 2007a). The optimal time of activity for *M. chinensis* is uncertain; Karsen et al. (1986) states that it may leave the water at night during rain spells, but also reports it being active in water during the day. Kuntz (1963) also made similar observations and records its presence in suburban Taipei, Taiwan during flooding. They feed primarily on fish (anabantids [*Anabas scandens* (=*Perca scandens*): Chang and Fang, 1931], cyprinids [*Carassius* sp., sp.: Pope, 1935], xenocypridids [*Erythroculter aokii*(?), *Culter alburnus*: Pope and Granger, 1929; Pope, 1935], osphronemids [*Macropodus opercularis* (=*baviensis*), *Macropodus viridiauratus:* Pope and Granger, 1929; Pope, 1935) and according to the literature may take amphibians on occasion (Gressitt 1940, 1941; Kunts, 1963). Mori

Figure 8.123. Chinese Mud Snake, *Myrrophis chinensis.*
Photography by Artur Tomaszek

(1998) found this species will swallow food underwater, which is a common behavior for most homalopsids.

Seven females from Taiwan contained 3–32 embryo/eggs (average=16.3; Murphy, 2007a). The smallest SVL of a gravid female in Murphy (2007a) was 396 mm, the largest was 701 mm. However, another gravid female from Canton, China is 385 mm SVL. Pope (1929) commented that females from higher latitudes give birth to larger litters. Parturition likely occurs during the summer months, though gravid females in December have been found (Smith, 1914b). Smith (1914b) mentions that parturition may take place in April, though as to which population this pertains to is uncertain. Kuntz (1963) remarked on the behavior of *M. chinensis,* saying that at first, it is prone to striking upon the slightest irritation, but soon becomes more docile. It may make false strikes with lateral and/or vertical jerks of the head, along with quick vertical jumps. It is difficult to capture in the wild when disturbed since it tends to disappear or submerge into the soft mud of the rice paddies. When handled, this snake is likely to initiate a profuse flow of semi-fluid feces with a pungent odor (Murphy, 2007a). The venom of this species may be more potent than other homalopsids, inducing headaches, nausea, and pain (Karsen et al., 1986).

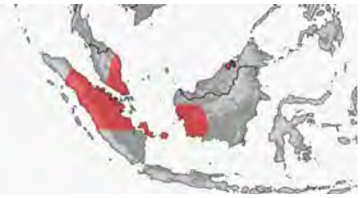


Figure 8.124. The distribution of *Phytolopsis punctata.*

Blackwater Mud Snake

Phytolopsis punctata Gray, 1849

Distribution and Habitat**.** Found in peat swamps in peninsular Malaysia, Singapore, Sumatra, and Borneo (Kalimantan, Brunei). Type locality: India (in error) (Figure 8.123).

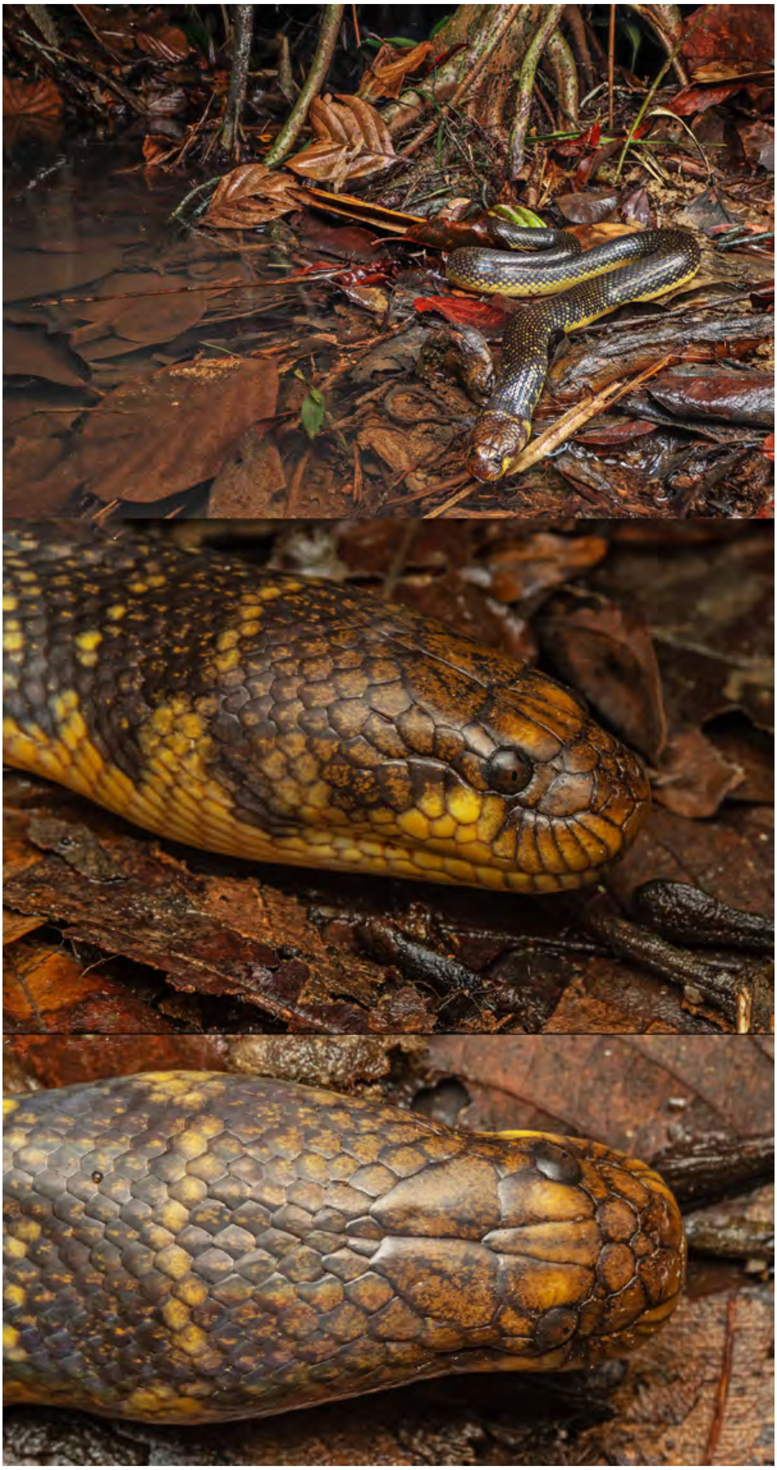


Figure 8.124. Blackwater Mud Snake, *Phytolopsis punctata*. Photography by Ing Sind.

Identification**.** A large bodied snake, dorsal scales in 25–27 rows; upper labials number 11–13, those behind eye horizontally divided; lower labials 12–15; ventrals 148–160; subcaudals 36–48; upper labial 5 or 5–6 under orbit; no subocular scales; two pairs of chin shields, first pair very wide. Readily distinguished from *Homalophis* by lower number of scales at mid-body (29–33 in *Homalophis*), single supraocular (2 or 3 in *Homalophis*), and the absence of subocular scales. Size. Murphy (2007a) reports on sizes from the literature, but as to which sex these size ranges pertain to is uncertain; it is likely inclusive of both males and females. Murphy (2007a) reported that the largest specimen in that study was 665 mm SVL and 95 mm tail. This exceeds previous measurements by Erns and Zug (1996) and David and Vogel (1996), in which the maximum total length was 450 mm; the latter study found adults averaged 340–400 mm. Murphy (2007a) comments that most of the museum specimens examined previously were juveniles. Males have tails that are 19–21% of SVL, and females have tails that are 8.5–17.8% of SVL (Murphy, 2007a) (Figure 8.124).

Natural History**.** *Phytolopsis punctata* has been found in a variety of habitats. Museum notes for peninsular Malaysian specimens from the Field Museum of Natural History (FMNH 250111–250112) mention that they were collected from 'blackwater streams.' Malaysian specimens have been collected from peat swamp forests (collected by Shahrul Anuaroast) of Pondak Tanjung Forest Reserve in Selama Perak. And, recently, they have been reported from within and around the Nee Soon freshwater swamp forest of Singapore (Thomas et al., 2014; Serin et al., 2019). The fragmented nature of these habitats and the high level of fish endemism in the peat swamps of Southeast Asia add an interesting dimension to this species complex, and to homalopsid diversity. The details of its lifestyle remain virtually unknown. A female specimen examined by Murphy (2007a) contained 15 yolked follicles (Murphy, 2007a). Its diet includes fish, with walking catfish (Clariidae: *Clarias leiacanthus*) as confirmed prey (Tan et al., 2014).

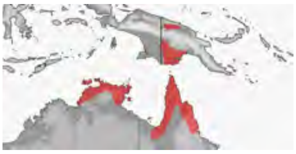


Figure 8.129. The distribution of *Pseudoferania polylepis.*

Phytolopsis punctata has been recovered in molecular phylogenies with varying levels of support: Alfaro et al. (2008) recovered *P. punctata* as sister to a clade with *Cerberus, Homalopsis, Erpeton, Subsessor, Myron, Pseudoferania, Fordonia, Gerarda, Cantoria,* and *Bitia*, but Bernstein et al. (2021) recovered *P. punctata* as sister to *Bitia hydroides.* Using thousands of nuclear markers, Bernstein et al. (in review) finds strong support that *P. punctata* is sister to *Raclitia indica*.

Macleay's Mud Snake

Pseudoferania polylepis (Fischer, 1886)

Distribution and Habitat**.** Found in Australia (coastal plain of Queensland, Northern Territory (Groote Island)) and Papua New Guinea. Groote Island. Type locality: Fly River, Western Province, Papua New Guinea (Figure 8.129).

Identification**.** *Pseudoferania polylepis* has parietals scales that are longer than the frontal; loreal single. Dorsal scales in 21–27 rows (usually 23) at mid body; 137–162 ventral scales; upper labials 7 – 9 (usually 8), with 4–5 or 5–6 under the orbit, upper labials 2 –3 or 2–4 contact loreal. Internasal single or double, it may or may not contact the loreal. Size. Males: SVL: 380–689 mm; Tail: 114 mm (tail 16.5–19.6% of SVL); Females: SVL: 44–870 mm; Tail: 107 mm (tail 16.5–21.5% of SVL) (Figure 8.130).

Figure 8.130. Macleay's Mud Snake, *Pseudoferania polylepis.*
Photography by David Nixon.

Natural History**.** This taxon is the only freshwater homalopsid in the Austral-Papuan region except for *Heurnia ventromaculata* from Western Papua which does not have the nasal scales in contact. They use slow moving or stagnant bodies of freshwater, such as lagoons, billabongs, swamps, and creeks and take refuge in vegetation near water, such may prefer dense pandanus root systems near overhanging banks (Gow, 1989; Murphy, 2007a). Dunson and Dunson (1973) found this species sensitive to salt water. Shine et al. (2004) reports them from shallowly inundated areas of Fogg Dam in Northern Territory, Australia; these areas are usually dry for a majority of the year and were flooded for two weeks before their study took place. During seasonal flooding, their movement expands. They report that while *P. polylepis* is infrequent, the two weeks of these floods results in high numbers of this species at night, foraging for sleeping fish. The fish allows the snake to approach closely and then flips upwards and out of the water when touched; experiments showed that these snakes locate their prey primarily by visual cues, especially movement, rather than by scent or waterborne vibrations (Shine et al., 2004). Strikes are elicited by tactile cues, especially the splash of water as a fish leaps upwards. Confirmed prey includes decapods (shrimp fragments; *Macrobrachium* sp.), frogs (captive specimens), and fishes (Eleodtridae, Megalopidae (*Megalops cyprinoides*) (Shine, 1991). They are known to be eaten by various birds, such as white-belled sea eagles (Accipitridae: *Haliaeetus leucogaster*) and black-belled storks (Ciconiidae: *Ephippiorhynchus asiaticus*) (Sergo and Shine, 2015), as well as long-necked turtles (Chelidae: *Chelonia rugosa*; Shine, 1991). Junqueira-de-Azevedo et al. (2016) found the venom of this species contained low amounts of snake venom metalloproteinase (SVMP), three finger toxin (3FTx), cysteine rich secretory protein (CRISP), and C-type lectin (CLT); they also contain veficolins, the venom protein family discovered in *Cerberus rynchops* (Fry et al., 2012). Reports on the bite of *P. polylepis* on humans are asymptomatic (Thompson, 1935), but frogs have been found to succumb quickly, with accompanying discoloration and oedema at the site of the bite, and death in fish have been observed <2 minutes from the time of attack (Shine, 1991). *Pseudoferania polylepis* has consistently been recovered, with strong support, as the sister group to *Myron* when using mitochondrial and nuclear genes (Alfaro et al., 2008; Bernstein et al., 2021; Bernstein et al. 2023a).

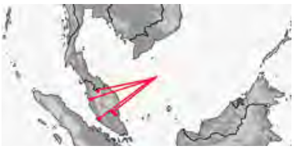


Figure 8.131. The distribution of *Raclitia indica.*

Selangor Mud Snake

Raclitia indica Gray, 1842

Distribution and Habitat**.** Known from peninsular Malaysia (Perak, Pahang, Selangor) and Singapore. Type locality: India (probably referring to the East Indies or, broadly speaking, Southeast Asia. (Figure 8.131)

Description. Supraocular exceptionally large, plate-like, preocular exceptionally small; supraocular and upper postocular fused; lower postocular extends under eye; nasal cleft contacts first labial; 173–175 very wide ventrals; eye diameter less than width of supraocular; seven upper labials. Size. Males: SVL: 303–372 mm; Tail: 42–53 mm (tail 13.9–14.4% of SVL); Females: Total Length: 490 mm (Figure 8.132)

Natural History**.** *Raclitia indica* has a small, narrow head, gracile body form, short tail, and a relatively low dorsal scale count; based on these, it has been suggested that this species typcally burrows in the ground, possibly in aquatic habitats, and may be vermivorous (Murphy, 2007a; Murphy et al., 2011). They have been collected in small forest streams at night (Klang, Selangor, Malaysia: Lim and Karmudin, 1975; Lim et al., 1995). The population in Singapore has been considered questionable by Murphy (2007a), but recent records of a specimen found in a concrete drain at the edge of a freshwater swamp forest from Upper Seletar, Singapore confirm a population here (Law et al., 2020). Whether a population get here accidentally due to human transport is uncertain. *Raclitia indica* is recovered in phylogenies using molecular data as either the sister to *Erpeton tentaculatum* (Quah et al., 2018), to a

Figure 8.132. Selengor Mud Snake, *Raclitia indica.*
Photography by Evan Quah.

Figure 8.133. The distribution of *Subsessor bocourti.*

clade containing *Bitia, Phytolopsis, Homalopsis*, and *Cerberus* (concatenated approach; Bernstein et al., 2021), or sister to *Dieurostus dussumieri* (coalescent approach; Bernstein et al., 2021). All of these phylogenetic relationships have low support, and further, more comprehensive studies must be conducted.

Bocourt's Mud Snake

Subsessor bocourti (Jan, 1865)

Figure 8.134. Bocourt's Mud Snake, *Subsessor bocourti.*
Photography by (top) Tom Charleton and (bottom) JCM.

Distribution and Habitat**.** This species is found in southern Thailand, peninsular Malaysia, Cambodia, Vietnam, and Laos. It may have been introduced into southern China where it is captive raised. Type locality: Bangkok, Thailand (Figure 133).

Identification**.** Subsessor bocourti is considered a massive, stout-bodied snake, exceeding a meter in length; dorsal scale rows in 27–29 rows; ventrals less than 136; chin shields petal shaped, some upper labials behind the eye are horizontally divided. Probably the largest, extant homalopsid when considering weight and length; 27 scale rows at midbody; divided upper labials behind the eye: 135 ventral scales, or fewer; an internasal that is single, and may make nrrow contact with the loreal scales. Size: Males. SVL: 646 mm; Tail: 124 mm (tail 19.2% of SVL); Females: SVL: 950–1080 mm; Tail: 150 mm (tail 4.6% of SVL); Neonates: 220 mm. Size of males and females from Murphy (2007a). Previous studies that report on specimens (unsexed) include individuals with total lengths of 1220 mm (Smith, 1914b) and one with a 1075 mm SVL and 125 mm tail Werner (1923). Saint Girons (1972) recorded a female of 950 mm and a male of 812 mm total lengths. Neonate size data from Flower (1899).

Natural History**.** *Subsessor bocourti* is a highly aquatic snake that uses swamps, shallow lakes, pools, and other stagnant water habitats, including those that are anthropogenic, such as reservoirs, rice paddies, and fishponds (Campden-Main, 1970; Murphy, 2007a). It is reportedly found with *Acrochordus javanicus i*n swamps and pools, and it may move into deep water during the hottest part of the year (Laidlaw, 1901; Boulenger, 1903). They are considered nocturnal (Deuve, 1970), but have been found in lakes in Laos during the daytime predating on fish (Nguyen et al., 2020). This species is known to eat fish across multiple studies and observational accounts (Deuve, 1970; Saint Girons, 1972; Murphy, 2007a). A specimen from Tonlé Sap, Cambodia (555 mm) contained a 50 mm catfish, (Bagridae: *Mystus mysticetus)*. A neonate obtained near Kabin Buri, Thailand contained a 145 mm freshwater eel (*Monopterus albus*). Several other specimens from the same locality contained unidentified fish remains. Captive newborns will feed on small frog (e.g., *Rana* and *Microhyla*; Flower, 1899). In captivity, females have produced 17 live young (Flower, 1899). A range of 6–17 eggs have been found inside females in the Cambodian population (Saint Girons, 1972), and 26 embryos were found in a female of a Thailand population (Murphy, 2007a). Using DNA, *Subsessor bocourti* and *Erpeton tentaculatum* have both been recovered as sister taxa, though with low support but genomic data (Bernstein et al. 2023a) strongly supports *Subsessor* as sister to both *Homalopsis* and *Cerberus.*'

Figure 8.135. The distribution of *Sumatranus albomaculata.*

Sumatran Mud Snake

Sumatranus albomaculata (Duméril, et al., 1854)

Distribution and Habitat**.** Found on the Sumatra satellite islands of Nias, Pulo, Simeuluë, Sibigo, and Sinabang; and probably Sumatra proper. Type locality: "les environs de Padani, île de Sumatra." [=Padang, west Sumatera].(Figure 8.135)

Identification**.** This species has smooth scales in 27 (26–28; possibly 25 based on literature accounts) rows; the nasals are in contact; the last two or three upper labials are horizontally divided; large internasal makes narrow contact with elongated loreal; five of six lower labials contact anterior chin shields; dorsum with scattered spots, venter mottled. Size. Males: SVL: 520 mm; Tail: 90 mm (tail 17.1–26.9% of SVL); Females: SVL: 625 mm; Tail: 75 mm (tail 12.5–14.4% of SVL). Size data from largest individuals from Murphy (2007a). Murphy (2007a) study also reported that the smallest individual (sex not given) was 260 mm SVL with a 70 mm tail. Gyi (1970) mentioned that male tails are significantly longer than female tails.

Natural History. The natural history of this homalopsid is nearly unknown. A single specimen (USNM 30767) contained three eggs and has an SVL of 520 mm (Murphy, 2007a)

Dak Krong Mud Snake

Myrrophis dakkrongensis Nguyen et al. 2024

Distribution and Habitat. Known only from its type locality in Dak Glong District, Dak Nong Province, Vietnam southern China and northern Vietnam. The holotype is an adult male, collected from Quang Son, Dak Glong District, Dak Nong Province, Vietnam at an elevation of 890 m ASL. The first specimens were collected in forest wetlands, including a wetland in a rubber plantation.

On the next page. Amazonian Aquatic Coral Snake, *Micrurus surinamensis* waiting in ambush **Photography by Konrad Mebert**

9. Aquatic Coral Snakes

9. Aquatic Coral Snakes

Most Neotropical coral snakes of the *Micrurus* genus are fossorial or cryptozoic. However, two species are semi-aquatic, *M. nattereri* and *M. surinamensis* (Passos and Fernandes 2005). Additionally, other species will readily enter the water and search for food – particularly *Micrurus diutius* and other members of the *Micrurus lemniscatus* group.

Orinoco Aquatic Coral Snake

Micrurus nattereri Schmidt, 1952

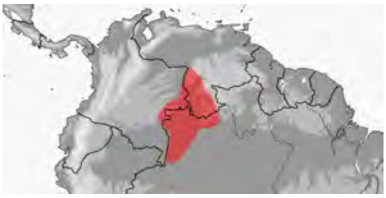


Figure 9.1 The distribution of *Micrurus nattereri.*

Distribution and Habitat. Streams and wetlands in the equatorial forest are associated with the upper Orinoco and Negro Rivers, from southern Venezuela and Colombia to northern Brazil. Type locality: Between Guaramaco and San Fernando de Atabapo in the upper Orinoco River, Venezuela (Fig. 9.1)

Identification. Distinguished from other *Micrurus* (except *M. surinamensis*) by a frontal scale narrower than supraoculars; only the fourth upper labial borders the orbit;

Figure 9.2 Orinoco Aquatic Coral Snake, *Micrurus nattereri.*
Photography by Santiago Ayerbe.

head flattened with nostrils and eyes directed upwards; distinguished from *M. surinamensis* by having 180–195 (instead of 156–174) ventrals in males and 193–215 (instead of 169–187) ventrals in females. This species is smaller than *surinamensis*. The largest male *M. natteri* was 650 mm TL, with an 80 mm tail; the largest female was 674 mm TL, with a 69 mm tail; ventrals 180–195 in males; 193–206 in females; subcaudals 33–41 in males; 30–38 in females; upper labials 7–8; lower labials 7–8; temporals 1+2 or 1+3; the number of triads 6–8; width of the central triad at the level of the midbody 5–10 scales; width of interspaces 6–12 scales; hemipenis extend 13–15 subcaudal scales (based on Passos and Fernandes 2005).

Amazonian Aquatic Coral Snake

Micrurus surinamensis (Cuvier, 1816)

Figure 9.3. The distribution of *Micrurus surinamensis.*

Distribution and Habitat. Rivers in equatorial forest in South America in the Guiana region, Colombia, eastern Ecuador, Peru, Bolivia, and central Brazil. In Brazil, it occurs in Acre, Amazonas, Roraima, Rondônia, Pará, Maranhão, Tocantins, and Mato Grosso. Type locality: Suriname (Fig. 9.3).

Identification. Ditinguished from other species of the genus by a frontal scale narrower than supraoculars, only the fourth upper labials border the orbit of the eye; head flattened with nostrils and eyes directed upwards and distinguished from *M. nattereri* by having 156–174 (nattereri 180–195) ventrals in males and 169–187 in females (instead of 193–215 in *surinamensis* ventrals). Rostral scale broader than high, with a triangular shape in frontal view and visible from above; internasals less than half of the length of prefrontals; frontal longer than broad; supraoculars approximately as broad as the prefrontal; parietals about twice longer than wide; nasal divided; one preocular, longer than high; two postoculars; fourth upper labial enters the orbit; first pair of lower labials contacts behind symphysial; first four pairs of lower labials touch first pair of chin shields; two pairs of chin shields; usually four gulars; 15 dorsal scales rows, smooth, without reduction; cloacal plate divided (Figure 9.4).

Figure 9.4. *Micrurus surinamensis.* **Photography by Konrad Mebert.**

Natural History. Silva et al. (2018) found the head shape of *surinamensis* is convergent with other aquatic snakes. However, *Micrurus surinamensis* differs from the two semi-aquatic species of *Micrurus lemniscatus* and *M. spixii* in having a wider head, a smaller distance between nostrils, and a longer tail. Despite having an extremely conserved skull and mandible shape, *M. surinamensis* has longer supratemporal and quadrate bones than in terrestrial coral snakes, suggesting a larger gape for feeding on fish are larger and broader prey in contrast with the elongated prey of other *Micrurus.* The South American coral snakes (*M. lemniscatus* species complex) are, to a lesser degree, semi-aquatic and are known to feed on synbranchid eels and shallow water fish but do not demonstrate the morphological adaptations seen in *surinamensis.* Tavares-Pinheiro et al. (2021) observed this snake feeding on a knifefish, swallowing it headfirst on the edge of a stream. The coral snake captured the fish at night in water ca. 1.5 m deep, but the fish was subdued and consumed on the stream bank.

Micrurus surinamensis inhabits the Amazon drainage, while *M. nattereri* occupies the Orinoco drainage basin. The separation of these two basins likely resulted in the evolution of the two taxa in the late Miocene when the Vaupes Arch semi-isolated the river systems. However, separating the two basins is still incomplete, with the Casiquiare River in southern Venezuela connecting to the Orinoco and Negro Rivers. The connection explains the presence of *M. nattereri* in the upper Negro River

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On the next page. The Banded Water Cobra, *Naja annulata* **from Kinshasa, DRC. Photography by Vaclav Gvozdik**

10. Aquatic Cobras (Najinae)

10. Aquatic Cobras (Najinae)

Lake Tanganyika, the African Great Lake, is well-known for the two British explorers, Richard Burton and John Speke, who discovered the lake in 1858. A species swarm of more than 250 cichlid fish has made this lake famous among biologists and hobbyists because the fish are a well-studied example of rapid evolution and are popular in the pet trade. But a fish predator is living here that is also of interest, Boulenger's Water Cobra (*Naja annulata*). Arthur Loveridge, a Harvard University herpetologist, was one of the first to provide observations on this snake. At Kasanga, rocky promontories extend into the Lake, and the Germans built one for their Bismarckburg military base. A natural breakwater of jumbled rocks protects these peninsulas, and it is here Loveridge observed the aquatic cobras. He wrote,

> According to native reports, which my own experience confirmed in some points and contradicted in none, when the sun rises and strikes the rocks the cobras emerge from their retreats beneath them and bask for a short time on the tops of the rocks. Shortly afterward...and I found none on the rocks an hour and a half after sunup...they take to the water in search of fish. I was told on a calm day one might see as many as ten in a morning's fishing. We saw four in a little over three hours. The snakes come out of the water in the evening, and they are said to bask under the rocks. Loveridge suggested that this is probably correct because the evenings were cool, and the snakes may absorb heat from the rocks and avoid the cool wind blowing in mid-May.

Boulengerina Dollo (1886) was established for a cobra with aquatic habits, *Boulengerina annulata* (Buchholz & W. Peters, 1876) and *Boulengerina christyi* Boulenger, 1904 was later assigned to the genus. Wallach et al. (2009) returned the two species of *Boulengerina* to *Naja.* They recognized *Boulengerina* as a subgenus containing four non-spitting cobras species, including semi-aquatic and semi-fossorial species. Wüster et al. (2018) used mitochondrial and nuclear gene sequences and morphological data to diagnose species limits within the African Forest Cobra, *Naja* (*Boulengerina*) *melanoleuca*. They found deep genetic divergences within *N. melanoleuca* and recognized four additional species (*N. subfulva, N. peroescobari, N. guineensis, N. savannula*), two of which were new. The lifestyles of these snakes, previously considered to be *Naja melanoleuca* are poorly known. However, Wüster et al. (2018) state that *Boulengerina* is composed of a mixture of small and primarily terrestrial, burrowing, and aquatic forms occupying a diversity of biomes and with distinct foraging ecologies. More recently, another member of the genus was described, the Dwarf Water Cobra, *Naja nana.*

Banded Water Cobra

Naja annulata Peters, 1876

Distribution and Habitat. Distributed in central Africa, from the Cameroons to Tanganyika, where it is often associated with flooded forests and rarely occurs far from water. It occurs in Burundi, Cameroon, Central African Republic, Democratic Republic of Congo, Republic of Congo, Equatorial Guinea, Gabon, Rwanda, and the province of Cabinda in Angola, as well as along the Burundian, Tanzanian and Zambian shores of Lake Tanganyika. Type locality: "Dorfe Mbusa (Eliva Sonange am Ogowe)," Gabon.

The subspecies *Naja annulata stormi* was considered endemic to Lake Tanganyika, but there is a single record from Pweto on Lake Mweru, Katanga Province in the Democratic

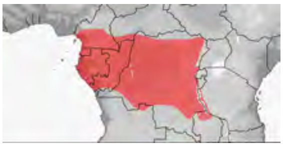


Figure 10.1. The distribution of *Naja annulata*.

Republic of Congo (Broadley and Cotterill 2004). Type locality: Lake Tanganyika, Zaire. Pauwels et al. (2017) report it from the buffer zone of the southeastern part of Minkébé National Park, where one was killed in a river and eaten by local people. Habitat includes flooded forests and savannas and is rarely far from water.

Natural History. The Banded Water Cobra is in the water most of the time. It is an excellent swimmer and can remain underwater for up to 10 minutes and dive to depths of 25 m (82 ft). On land, It moves slowly and hides among rocks, in burrows made by other animals, or in overhanging tree roots at the shoreline; It also uses artificial structures, such as bridges and jetties, to hide. It is generally not aggressive, and if approached in water, it will swim away swiftly and, on land, it will attempt to escape into the water. If threatened on land, it will rear up and spread its narrow yet prominent hood, and it may hiss loudly, but it tends not to make any forward movements. It will only bite when provoked. It feeds on fish and amphibians. When not looking for food, it uses rocks, bank holes, tree holes, and root clusters for refuge. Human encounters with water cobras are probably few, and the snake poses little danger to anyone except when it becomes entangled in fishers' nets or in the nets of herpetologists trying to trap it.

Venom. The LD50 of long-chain neurotoxin two from B. a. annulata venoms was 0.086 mg/kg. The venom of this little-known elapid has the lowest LD50 of any African proteroglyph studied thus far and has a high concentration of potent postsynaptic neurotoxins.

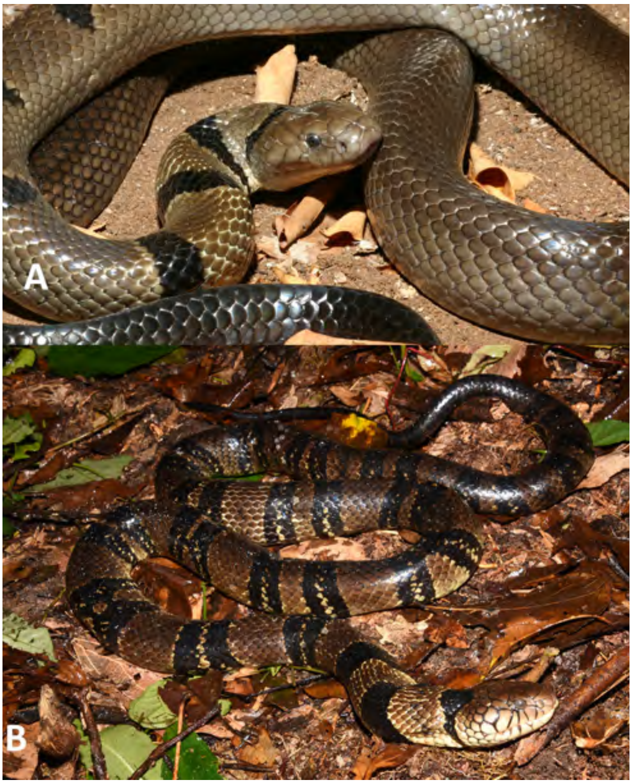


Figure 10.2. Banded Water Cobra, *Naja annulata*. (A) *N. a. stormsi* Lake Tanganyika, Tanzania (B) *N. a. annulata* from the DRC) Photography by (A) Wolfgang Wuster, (B) Vaclav Gvozdik.

Congo Water Cobra

Naja christyi Boulenger, 1904

Distribution and Habitat. The lower reaches of the Zaire River. The Congo Water Cobra has a small range in the western Democratic Republic of Congo, the southern half of the Republic of Congo, a small portion of southeastern Gabon, and the province of Cabinda in northern Angola. It is highly aquatic and always near water, in lowland bush or wooded areas along banks of lakes, rivers, and streams. It is restricted to the lower Congo River and nearby wet forested areas. Type locality: Leopoldville, Congo.

Figure 10.3. The distribution of *Naja christyi*.

Natural History. A poorly studied species. The diet is mostly fish. But, the literature suggests that amphibians, lizards and rodents may be consumed.

It is active day and night and spends much of its time in the water. Not an aggressive snake; when approached in water, it will swim away; If threatened on land, it will rear up, spread its narrow hood, and hiss. It may strike if provoked. Like other cobras, it is oviparous.

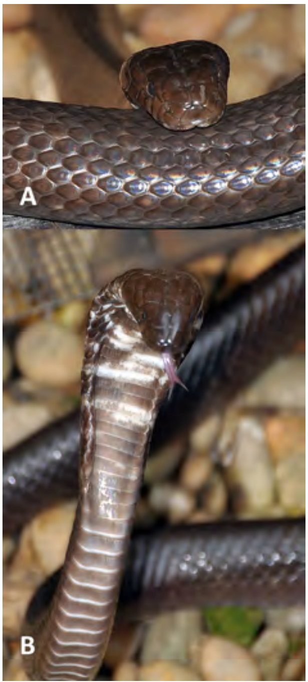


Figure 10.4. Congo Water Cobra, *Naja christyi*. From Kinhaa,DRC. Photography by Vaclav Gvozdik.

Venom. Not well studied, but believed that the venom is dangerously neurotoxic, like most elapids. The LD50 of long-chain neurotoxins-2 from *N. christyi* venoms was 0.090 mg/kg. The venom of this elapid has the lowest LD50 of any African proteroglyph studied thus far and has high concentrations of potent postsynaptic neurotoxins (Weinstein et al. 1991).

A DNA has not been included in the nolecular studies. It is unclear where this species falls phylogenetically. Schmidt (1923) erected a new genus, *Limnonaja*, for it because he considered it morphologically distant from *N. annulata.*

Dwarf Water Cobra

Naja nana Collet and Trape, 2020

Distribution and Habitat. Democratic Republic of Congo (Katanga [Zaire]). Known only from Lake Mai-Ndombe, The type locality is the environs of the village of Bokeben.

Natural History. Locally, the common name is Musso. The Dwarf Water Cobra feeds exclusively on fish. It is frequently caught in the nets of the fishermen at Lake Mai-Ndombe. According to the villagers, it stays in the boulders bordering the Lake when it is out of the water. At high water, it climbs into the branches of emergent vegetation bordering the Lake. When threatened out of the water, *Naja nana* adopts the classic cobra defense behavior by raising its head and anterior body and spreading its hood. Captives only accept fish and refuse to eat amphibians (Collet and Trape 2020).

Captive specimens have produced clutches of four eggs. The eggs are relatively large and elongated (~70 x 24mm). Incubation at 29° C was exactly 70 days (laid June 17, first hatching August 26 (Raw and Deacon 2021).

Figure 10.5. The distirbuition of the Dwarf Water Cobra, ***Naja nana.***

Fishers who handle it frequently teach their children not to fear it. A snake hunter who took more than 300 specimens from nets was bitten about fifteen times, and symptoms of envenomation followed five times. The bites were moderate and lacked respiratory symptoms. There was mild local pain and slight edema, which resolved in 24-48 hours.

Figure 10.6. The Dwarf Water Cobra, ***Naja nana.***
Photography by Jean-Francois Trape.

Forest Cobra clade

Naja melanoleuca Hallowell, 1857

Distribution and Habitat. Swamp forests and mangrove forests from Nigeria, Cameroon, Central African Republic, Equatorial Guinea, Gabon, Republic of Congo (Brazzaville), Democratic Republic of the Congo (Kinshasa) (Zaire), N Angola, and Rwanda. Type locality: Gabon. Cryptic diversity in this species was described by Wüster et al (2018), and the species was divided into five taxa. However, the exact distributions are unclear.

Figure 10.7. The distribution of *Naja melanoleuca.*

Natural History. It is considered a semi-aquatic snake because it escapes to the water and feeds on amphibians, other snakes, and fish (Haagner and Carpenter 1988). Clutches of 15-17 eggs are known and require about 78 days of incubation. The venom is neurotoxic.

The African Forest Cobra, *Naja* (*Boulengerina*) *melanoleuca* was recently shown to be a composite species. Using mitochondrial DNA sequences and morphology, Wuster et al. (2018) revealed deep divergences and recognized five species within *N. melanoleuca.*

*Naja subfulva (*Laurent, 1955)

Distribution and Habitat. from South Kivu Province of the Democratic Republic of the Congo (DRC), Forest/savanna mosaic, encircling the Congo Basin, from the grasslands of western Cameroon northward, to Bol, Chad, on the northern shore of Lake Chad, east through the CAR and South Sudan to west Ethiopia, south through Uganda, western Kenya, eastern DRC, Rwanda, Burundi and western Tanzania to northern Malawi, west through Zambia and Katanga to Angola and the Lower Congo region (Fig. 6). The distribution ex-

Figure 10.8. Forest Cobra, *Naja melanoleuca*.
Photography by Myke Clarkson.

tends disjunctly east and south to the East African coast from Kenya to northern KwaZulu-Natal (South Africa), including inland locations in western Zimbabwe.

Naja peroescobari Ceríaco, Marques, Schmitz & Bauer 2017

Distribution and Habitat. Known only from the island of São Tomé, adult male collected in the vicinity of Praia Inhame, São Tomé Island, Republic of São Tomé e Príncipe. It does not appear to be a semi-aquatic species.

Naja (*Boulengerina*) *guineensis* Broadley, et al., 2018

Distribution and Habitat from the Upper Guinea forest of West Africa, The distribution of Naja guineensis appears to be restricted to the Upper Guinea Forests of western Africa, from west Togo to Liberia and Guinea. It does not appear to be a semi-aquatic species.

Naja (*Boulengerina*) *savannula* Broadley, et al., 2018

Distribution and Habitat. A banded cobra from the savanna-forest mosaic of the Guinea and Sudanian savannas of West Africa. From Senegal and Gambia east to northern Cameroon in gallery forest areas in the Guinean Forest/Savanna Mosaic. This is not a semi-aquatic species.

Monocled Cobra

Naja kaouthia Lesson, 1831

Distribution and Habitat. They inhabit natural and anthropogenic habitats and prefer water-associated habitats, such as swamps, and mangroves, but can also be found in grasslands, shrublands, and forests. Agricultural land (paddy fields), human settlements, and cities are also used. They occur at elevations of up to 1000 m above sea level. The range includes Bangladesh, Myanmar, Cambodia, northeast India, Bhutan, Laos, northern Malaysia, Nepal, S China, Thailand, and southern Vietnam. Type locality: Bengal, India.

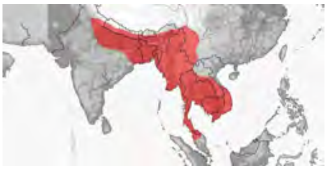


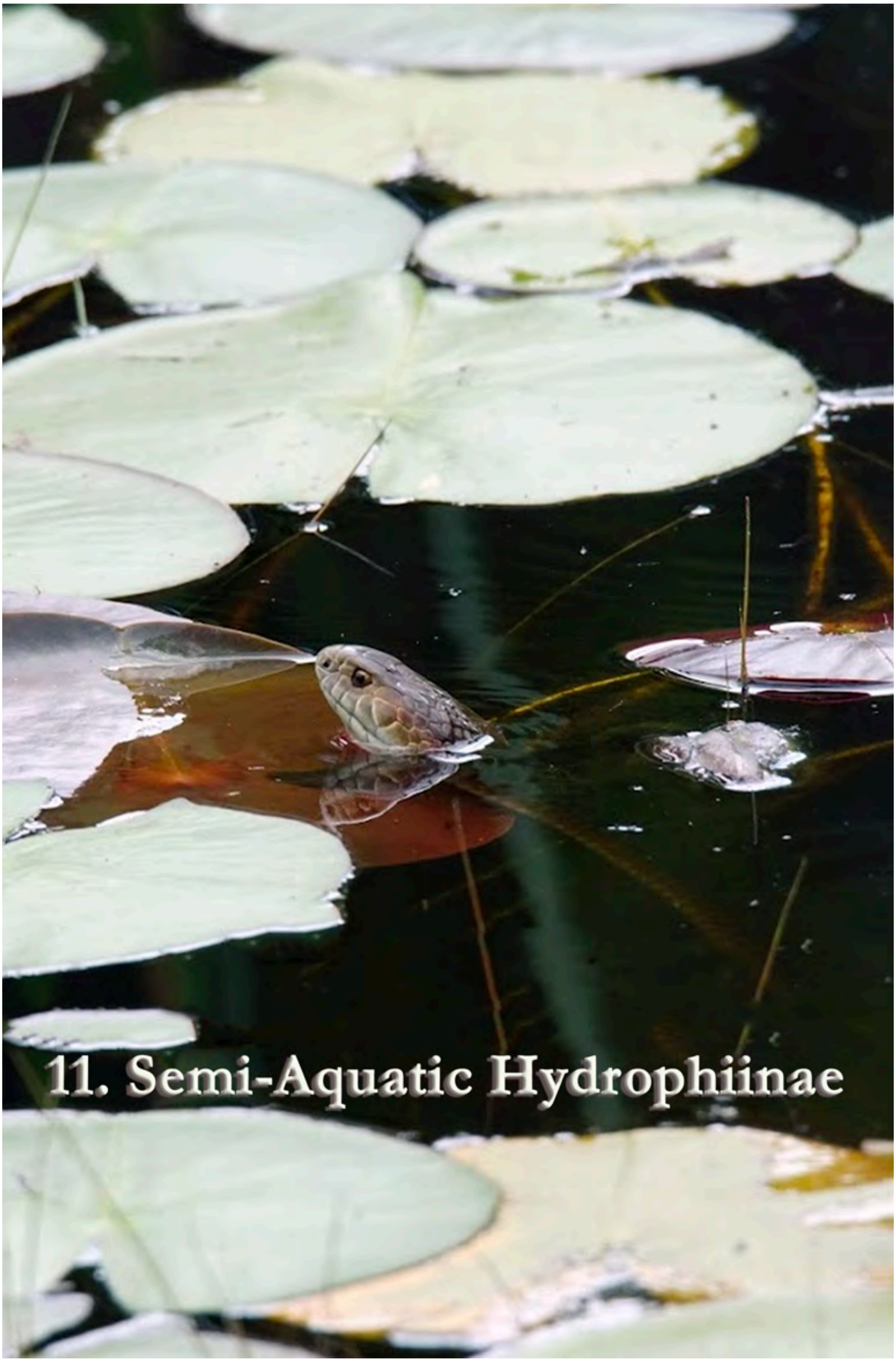
Figure 10.9 The distribution of *Naja kaouthia.*

Natural History. Diet includes snakes, lizards, and fish. In Myanmar, it has been observed to enter fish traps to prey on the fish in the trap (Kyi and Zug 2003). They are primarily crepuscular. In rice-growing areas, they hide in rodent burrows in the dykes between fields and have become semi-aquatic in this type of Habitat. Juveniles feed primarily on amphibians, while adults prey on small mammals, snakes, and fish. When disturbed, they prefer to take flight. However, when threatened, they will raise the anterior body, spread a hood, often hiss loudly, and strike to bite and defend themselves. Sometimes they inhabit tree holes and areas where rodents are plentiful.

Venom. Some populations of the monocled cobra can spit venom. Adult and juvenile *N. kaouthia* venom composition was investigated by Modahl et al. (2016). Alpha-cobratoxin (a-elapitoxin) was the only significantly toxic 3FTx (three-fingered toxin) found in its venom, and it was equally harmful in both lizard and mouse models. The abundance and diversity of 3FTxs and most enzyme activities did not vary between adult and juvenile cobra venoms; however, total venom PLA2 activity and specific PLA2 isoforms did vary, with juveniles lacking several of the least acidic PLA2s, and these differences could have both biological (related to predation) and clinical (antivenom efficacy) implications. Nevertheless, the ubiquitous presence of a-cobratoxin in both adult and juvenile cobra venoms, with high toxicity toward both reptiles and mammals, represents a venom compositional strategy wherein a single potent toxin effectively immobilizes a variety of prey types encountered across life history stages.

Figure 10.10 Monocled Cobra, *Naja kaouthia.*
Photography by Avrajjal Ghosh.

Next Page. A Lowland Copperhead hunting in a pond. Photography by Ben Fisher.



11. Semi-Aquatic Hydrophiinae

11. Semi-Aquatic Hydrophiinae

The elapid subfamily Hydrophiinae contains 38 genera and about 200 species. It includes snakes entirely terrestrial or fossorial, and some are aquatic. This chapter examines the semi-aquatic species minus the genus *Laticauda* (Chapter 12). The genus *Hydrophis* (Chapter 13) are the most highly aquatic member of this clade, with a paddle-like tail, but other species also show trends toward aquatic behavior.

New Guinea Small-eyed Snake

Micropechis ikaheka Lessons, 1830

Figure 11.1. The distribution of *Micropechis ikaheka.*

Distribution and Habitat. It inhabits rainforests and coconut plantations in Papua New Guinea, West Papua, and the Indonesian islands of Batanta, Misool, Jobi, Mios, Num, Mefoor, Mansinam, Valise, and the Aru Islands. Type locality: Ddore, Irian Jaya (=West Papua) (Figure 11.1).

Natural History. Diet includes squamates, conspecifics, terrestrial boid *Candoia aspera*, *Sphenomorphus jobiensis,* colubrid Stegonotus, and large skink *Tiliqua gigas*, and large earthworms. Small mammals and frogs are also eaten (Krey et al. 2015). Females produce clutches of 2-7 eggs in October, which are relatively large, 40 to 65 mm long (Shine and Keogh 1996). The snakes are easiest to find in the drier weather when

Figure 11.2. New Guinea Small-eyed Snake, *Micropechis ikaheka* **Photography by David Williams (top) Paul Freed bottom..**

they are hidden inside the coconut husk piles. It has been reported to catch fish (eels) in the water (Krey et al. 2015).

Small-eyed snakes bite plantation workers, grass-cutters, and villagers when they encounter these snakes abroad at night or in the early morning, especially during the wet season (Figure 11.2).

Pygmy Copperhead

Austrelaps labialis (Jan, 1859)

Figure11.3. The distribution of *Austrelaps labialis.*

Distribution and Habitat. South Australia. Kangaroo Island, Mt. Lofty Ra, and the Fleurieu Peninsula. Island populations use coastal dunes, woodlands, samphire flats, and agricultural areas. Mainland populations are found in high-altitude stringybark forests with a dense understory (Wilson and Swan 2003). Type locality: Australia. NeoType locality: Islet 477, Pelican Lagoon, Kangaroo Island, South Australia (Rawlinson 1991).

Natural History. It is a semi-aquatic snake that feeds on frogs, tadpoles, and lizards. Females are gravid from late spring (October) to early autumn (March). Parturition can occur as early as February. Litters usually contain seven young but have a maximum size of 20. Full-term embryos are 131-142 mm.

Figure 11.4. Pygmy Copperhead, *Austrelaps labialis*, Adelaide Hills, SA. Photography by Shawn Scott.

Highlands Copperhead

Austrelaps ramsayi (Krefft, 1864)

Distribution and Habitat. Mesic upland habitats in New South Wales and Victoria, Australia. Type locality: near Braidwood, NSW. NeoType locality: Moss Vale. Montane heaths, woodlands, creek edges, and marshes with dense grasses.

Figure 11.5 The distribution of *Austrelaps ramsayi*.

Natural History. A semi-aquatic snake. The diet comprises small frogs, tadpoles, lizards and snakes, and squamate eggs. Females give birth to neonates that are about 146 mm long.

Figure 11.6 Highland's Copperhead, *Austrelaps ramsayi*. The Blue Mountains. Photography by Scott Eipper.

Lowland Copperhead

Austrelaps superbus (Günther, 1858)

Distribution and Habitat. South Australia, Tasmania, and Victoria, Australia. Type locality: Australia and Tasmania, restricted to Tasmania by Günther (1863). It prefers areas of low vegetation near water. It has also been found on sandstone ridgetop woodland in the Blue Mountains, west of Sydney, which is becoming rare due to increasing fires and the spread ofurban settlements.

Figure 11.7 The distribution of *Austrelaps superbus*.

Natural History. The diet includes primarily small frogs, lizards, and snakes. Reproduction probably does not occur every year. Litter sizes average about 15 neonates.

Grey Snake

Hemiaspsis damelii (Günther, 1876)

Distribution and Habitat. Dry sclerophyll forests and woodlands on clay soils where water bodies or gullies are present in

Figure 11.8. Lowland Copperhead, *Austrelaps superbus*, Warrandyter. Photography by Scott Eipper.

southeast Queensland and New South Wales, and there are isolated populations in north-eastern South Australia and southwestern New South Wales Australia. Type locality: Peak Downs, Qld.

Figure 11.9. The distribution of *Hemiaspis damelii.*

Natural History. At Macquarie Marshes in central New South Wales, Shine (1987) found *H. damelii* is exclusively crepuscular and only active for an hour or two afterward. The diet is primarily frogs: *Litoria* (Hylidae), *Adelotus, Limmnodynastes, Rana*.

Figure 11.10. Grey Snake, *Hemiaspis damelii.* **Photography by Melissa Bruton.**

Black-bellied Swamp Snake

Hemiaspis signata (Jan,1859)

Distribution and Habitat. Rainforests and wet sclerophyll forest, margins of creeks, dams, wetlands, and low-lying seasonally flooded areas along the east coast of New South Wales and Queensland, Australia. This species may be partially estuarian. It occurs in marshes along the east coast of Australia. Type locality: Sydney, Australia.

Figure 11.11. The distribution of *Hemiaspis signata.*

Natural History. *Hemiaspis signata* may be active all day and well into the night (Shine 1987). The diet of *H. signata* is much broader than that of *H. damelii*, with the recorded prey items including one invertebrate, 22 anurans, 68 lizards, and 13 lizard eggs. Only two of the 22 frogs are arboreal species. Apart from a single gecko, all the lizards consumed by *H. signata* were skinks, with small diurnal species of the genus *Lampropholis* being the most critical (37 records). The scincid species eaten

Figure 11.12. Black-bellied Swamp Snake, *Hemiaspis signata*. **Photography by Tony Gerard <tonyg@shawneecc.edu>**

also included fossorial (e.g., *Anomalopus*) as well as larger diurnal surface-active taxa (e.g., *Ctenotus*) (Shine 1987). Females produce 6 to 16 embryos per clutch (Shine 1977).

Red-bellied Black Snake

Pseudechis porphyriacus (Shaw, 1794)

Distribution and Habitat. The east coast of Australia, in the urban forest, woodlands, plains, and bushland areas of the Blue Mountains, Canberra, Sydney, Brisbane, Melbourne, Cairns, and Adelaide. The Macquarie Marshes mark a western border to its distribution in New South Wales, and Gladstone in central Queensland marks the northern limit to the main population. To the south, it occurs across central and east Victoria and extends along the Murray River into South Australia. Disjunct populations occur in the southern Mount Lofty Ranges in South Australia and North Queensland. The type locality is New Holland, Australia. It is often close to dams, streams, billabongs, and other bodies of water, although they can venture up to 100 m (350 ft) away, including into nearby backyards. In particular, the Red-bellied Black Snake prefers shallow areas with tangles of water plants, logs, or debris (Shine 1981b).

Figure 11.13 The distribution of ***Pseudechis porphyriacus***

Natural History. The diet includes fish, frogs, reptiles (including other snakes), and small mammals. Fish are hunted in water - at the surface or underwater. Individual snakes stir up the substrate in search of prey. As they grow and mature, they eat the same prey and add larger animals. They have been reported to scavenge road-killed frogs.

Figure 11.14. Red-bellied Black Snake, *Pseudechis porphyriacus.*
Photography by Shawn Scott.

Males engage in ritualized combat for 2 to 30 minutes and may attack males already mating with females. They wrestle vigorously but rarely bite and engage in head-pushing contests, where each snake tries to push his opponent's head downward with his chin. Females can gravitate from early spring to late summer (Shine et al. 1981). After that, they become less active and congregate in nursery areas. They are viviparous; and give birth to young after 14 weeks gestation, usually in February or March. Litter sizes 8- 40. Neonates average 122 mm. Young triple their length and increase their weight 18-fold in their first year of life. Males are sexually mature when they reach 780 mm, and females mature at about 880 mm. Females can reproduce at about 31 months of age (Shine 1977, 1987b).

Tiger Snake

Notechis scutatus (Peters, 1861)

Distribution and Habitat. Coastal environments, wetlands, and creeks in Australia (New South Wales, Queensland, South Australia, Victoria, Western Australia, Tasmania). Type locality: Java (in error); neotype locality: "The Brothers," 10km NE of Benambra, Victoria. This is a polytypic species, and two subspecies are recognized. *N. s. scutatus* and *N. s. occidentalis*: The latter occurs in southwestern Western Australia and had no type locality given.

Figure 11.15 The distribution of *Notechis scutatus.*

Natural History. A semi-aquatic snake. Mainland adult snakes feed on frogs and mice, while adult island snakes mostly feed on silver-gull chicks. Tiger snakes give birth to 20 -30 young; the largest litter reported was 64. Tiger Snakes usually mate in spring and gives birth in the summer. A released captive snake crawled into a pond and submerged for 18 m 36 s (Cornelis and Lettoof 2020).

Temperature preferences are plastic in some snake species. Michniewicz and Aubret (2010) experimentally raised young Tiger Snakes in terrestrial or semi-aquatic environments over 11 months. Young snakes raised in a semi-aquatic environment selected slightly but significantly higher mean body temperatures (30.3°C) than their terrestrially grown siblings (29.5°C). The semi-aquatic raised young allowed their body tem-

Figure 11.16. Tiger Snake, *Notechis scutatus.*
Photography by Wolfgang Wuster.

perature to remain above 32°C for twice as long as the terrestrial raised snakes (4.4 hours vs 2.1 hours. Swimming speed was strongly linked to body temperature. Entering the water with a higher body temperature (30°C versus 19°C) delayed a sharp drop in swimming speed, thus lengthening maximum performance time.

Translocated snakes studied by Butler et al. (2005) traveled greater distances than resident telemetered snakes, although there was no difference in the frequency of movements. The degree of cloud cover and the maximum daily temperature significantly influenced daily activity, with snakes more likely to be active on relatively cool, sunny days. Snakes exhibited bimodal peaks in daily activity avoiding the hottest part of the day. Both resident and translocated snakes preferred grassy woodlands associated with hills but avoided escarpment woodlands and open plains. Floodplain riparian woodland was avoided by resident snakes but used in proportion to its availability by translocated snakes.

On the next page. New Caledonia Sea Krait, ***Laticauda saintgironsi*****. Photography by Jean Roger**

12. Sea Kraits

12. Sea Kraits

Myke Clarkson

Sea kraits form a monophyletic clade, the Laticaudini composed of a single genus, *Laticauda* with eight species of banded paddle-tailed snakes. Seven of the eight species of this group inhabit a mix of marine and land environments, with *Laticauda crockeri* being the sole exception, restricted to a single brackish lake in the Solomon Islands. Sea kraits are amphibious, rather than fully aquatic like their close relatives the true sea snakes (Hydrophiini.) While both groups of elapids evolved into marine environments about the same time 13‑8 million years ago (Kim et al. 2018), the two groups have taken two notably different evolutionary paths. Laticaudini nasal scales are separated by one or two internasal scales, have retained widened ventral scales and oviparity from their terrestrial ancestors. Their bodies are cylindric in shape, scales are smooth, and imbricate. Sea kraits are adapted for life on land as well as the water, they spend much of their lives in aquatic environments searching for prey. Their time on land is for digestion, thermoregulation, mating, ecdysis (shedding), and egg laying. Drinking freshwater on land has also been observed in this genus, which is reliant on freshwater for hydration. The reliance on fresh drinking water is thought to be one of the potential factors that has led to the groups characteristically patchy distribution (Lillywhite et al. 2008).

This dependence of freshwater for drinking also lends this group highly susceptible to impacts of climate change. As mentioned above, all sea kraits are oviparous, except for *Laticauda crockeri* which could potentially be viviparous this has not been confirmed. Average clutch sizes for *Laticauda* are 4–19 eggs. The thin shelled eggs are laid on land and have a high permeability to both oxygen and water. Hatchlings mature rapidly, and sexual maturity is reached in approximately 18 months in males and eighteen to thirty months in females (Heatwole et al. 2005). Courtship can occur on water or land and can involve many males courting a single female at once. However, unlike other species who can engage in polygyny (including *Thamnophis, Natrix,* and *Eunectes* referenced in this book) male sea kraits do not show signs of engaging in combat to fend off other suitors. While in other species body pushes or tail wrestling may be employed, sea krait males seem to not directly compete with one another. Instead males seem to have scamble competition for mating without a influence of male body size on mating success (Sheet and Shine, 2002c). All members of the group are venomous and of medical significance to humans, though generally perceived to be mild mannered in nature. While their venom is highly toxic, Rasmussen et al suggested *Laticauda* might also use their tails as a defense mechanism against predators, twisting them to look like a second head, while their head can continue to forage for food in cracks and crevices (Rasmussen et al. 2009).

Natural predators can include tiger sharks sea eagles, and larger fish. The placement of the sea kraits has been a topic of much discussion over the years. While once classified as their own family Laticaudidae, they were later put into the marine Elapidae subfamily Laticaudinae. With improvements in gene sequencing the close relations of these marine elapids has been more clearly revealed and they have most recently been placed in the monophyletic group Laticaudini (Kishida 2020; Pyron et al. 2011). Less debated than the taxonomic placement of this clade is the ecological categorization with in it. Laticaudini have been divided into three closely related complexes, though the complexes ranges include large overlap, their habitat usage (land versus water) and relation is distinct. The first group is the "*Laticauda colubrina* complex" and includes *L. colubrina, L. frontalis, L. guineai,* and *L. saintgironsi.* Members of this group are notably more terrestrial. The second group is "*L. semifasciata* complex" which includes *L. semifasciata* and *L. schistorhyncha*, which are the most aquatic of the sea kraits. The third group, the "*L. laticaudata* complex" includes *L. laticaudata* and *L. crockeri* and is an intermediate group between the *colubrina* and *semifasciata* complexes, spending less time on land than *colubrina,* but more than *semifasciata* (Brischoux, et al, 2013). The sea kraits are found in both tropical and subtropical coastal waters in the eastern Indian Ocean, south-east Asia, and the western Pacific Ocean. They are found as far north as Ryukyu Islands, as far South as Vanuatu, as far East as the Solomon Islands and as far west as the Andaman Islands (Figure 12.1). While *Laticauda colubrina* and *Laticauda laticauda* have very expansive ranges, other members of the group like *Laticauda schistorhynchus* and *Laticauda saintgironsi* are isolated to single islands (Gherghel 2016; Kishida et al. 2020). There are unconfirmed sightings on the western coasts of Mexico, El Salvador, and Nicaragua, but no records have been presented to back this finding. Sea kraits face many threats including habitat loss, and under regulated harvest. Currently five of the eight species in the genus are considered vulnerable or near threatened by the IUCN.

Figure 12.1. The distributiuon of Laticaudini.

Yellow-lipped Sea Krait

Laticauda colubrina (Schneider, 1799)

Distribution and Habitat. *Laticauda colubrina* has the largest distribution of any species in the Laticaudini group, and while there is a degree of morphological variance throughout the species range, it is still regarded as a singular species (Lane and Shine, 2011). In the Indian Ocean it is found in East India, Sri Lanka, Myanmar, the Andaman Islands, the Nicobar Islands, Western Vietnam, Western Malaysia, and Western Indonesia. In the Pacific it is found in Eastern Vietnam, Eastern Malaysia, Micronesia, Polynesia, Solomon Islands, Vanuatu, Thailand, Philippines, Palau, Taiwan, China, New Guinea, Timor-Leste, Japan's Ryukyu Islands, Australia, New Zealand, Fiji, and New Caledonia. Type locality: not given. Yellow-lipped sea kraits are most often encountered on shallow reef shelfs, small islands, and rocky shores which they utilize for basking and shelter. In the author's experience, sea kraits prefer reef rock lined shores, and can most easily be found sheltering beneath the rocks and in roots by day, or by walking suitable shorelines and islands by night. While this is the most common place of encounter, they can also be found in deep waters many kilometers away from the nearest islands while foraging for prey or floating on the surface at night. Shine et al observed that Yellow-lipped sea kraits exhibit philopatry and return to specific home islands even when relocated distances of more than 5 kilometers (Sheety and Shine 2002a).

Figure 12.2. The distributiuon of *Laticauda colubrina.*

Identification. Head is black, with a characteristic yellow mask that typically encompasses the snake's labial, nasal, prefrontal, and ocular scales. The yellow mask typically terminates at the frontal scale on the top of the head. On the sides of the head the yellow mask divides into two yellow stripes separated by black at the temporal scales just behind the eyes. These stripes are variable in length and can continue just a few scales or to the back of the head

Figure 12.3. Yellow-lipped Sea Krait, *Laticauda colubrina*.
Photography by Yu Sing Lin.

terminating before the first light colored band. While this is the most common coverage of the yellow mask, regional variation can occur in terms of hue and saturation of the yellow, as well as quality of yellow coverage. The body is banded with black and blue alternating bands, often having a darker blue tone dorsally and gradually shifting to a lighter blue or white ventrally. The tail can at times have a yellow tint to it, as can the first band after the head, however coloration of this species does vary throughout its range as does saturation levels of the blue bands. The tail is laterally flattened with the end tip often being a white, blue, or light-yellow color. Ventrals are sizable, averaging one third or larger than half the body width. Rostral is undivided, with a prefrontal shield usually present. As with all *Laticauda,* pupils are round, nostrils lateral and nasals are separated by inter nasals. The mid body has 21–25 longitudinal rows of scales and the average animal has 213–243 ventral scales. *Laticauda colubrina* have 37-47 subcaudals in males, and 29-35 in females. Average snout to vent length on males is 875 mm, and 1420 mm for females. The average tail length for males is 130 mm, and 145 mm for females (Leviton, 2003).

Figure 12.4. This is likely a mating aggregation of *Laticauda colubrina*. **With a large female and many smaller males. Taken on Malapascua Island, Philippines Photography Tony Gerard.**

Natural History. Like all sea kraits, Yellow-lipped Sea Kraits are amphibious in nature, and are most active at dusk and at night. They are not considered fully nocturnal, due to occasional diurnal activity and thermoregulating on land (Heatwole, et al, 2005). This species spends much of its time

Figure 12.5. The terrestrial habitat of *Laticauda colubrina.* A small satelitte island off the coast of Sabah, Malyasia. At low tide it was possible to walk to the pile of rocks. About six sea kraits were on the top in the vegetation. Photography by JCM.

at sea foraging for moray eels (Muraenidae) and conger eels (Congridae). While eels make up most of this species prey, other bony fish have also been observed in stomach content studies (Gorman, et al, 1981). Yellow-lipped Sea Kraits are active hunters, using chemoreceptors to locate eels hidden in rocks and crevices. Like other *Laticauda* this species has a unique saccular lung allowing for deep dives up to 60 m in the search of food. Shine observed sexual dimorphism in this species, like that seen in the Acrochordidae. Large females will search for a single large conger eels in deep water, whereas the males forage for multiple prey consisting of smaller moray eels. Prey are subdued rapidly by a potent neurotoxic venom with an LD50 of 0.1 mg/g IV in mice (Tan, et al, 2017). This corresponds to the morphological differences between the smaller males and larger females with disproportionally larger heads (Shetty and Shine, 2002b). Conversely it was found males have stronger terrestrial locomotion than females yet decreased swimming ability. This could correspond to the fact that males spend more time searching for mates, than females. Increased land mobility in males comes at a cost, decreased aquatic mobility in comparison to the females (Shine and Shetty, 2001). As the most terrestrial of the sea krait groups, the *L. colubrina* complex is also the fastest moving on land when compared to *L. semifasciata* and *L. laticauda* complexes (Wang et al 2013). Breeding cycle and clutch size vary greatly thoughout the species range. Mating takes place on shore throughout the entire range, with breeding behavior being polyandrous. Little is known about the behavior of hatchlings (Wright, 2011).

Rennel Island Sea Krait

Laticauda crockeri (Slevin, 1934)

Figure 12.6. The distribution of *Laticauda crockeri.*

Distribution and Habitat. Restricted to Lake Te-Nggano, Rennell Island, Solomon Islands. It is known exclusively from a single brackish lake, (2.8-6.2% salinity) where it is sympatric withthe distantly related *Laticauda colubrina*. Lake Te-nngano is the largest body of enclosed water in the insular Pacific, spanning 155 km2 and reaching depths of 40 meters (UNEP, 2008). The lake has a hard limestone bottom with several meters of fine, anaerobic, muddy sediment layered on top. This fine sediment renders the depths unsuitable for foraging, and restricts both sexes to foraging in the shallow areas on the edges of the lakes or around the many small islands within the lake, as these shores are comprised of pitted limestone, with far less fine sediment than the lake floor (Cogger, et al, 1987). Type locality: Lake Te-Nggano on Rennell Island.

Figure 12.7. Rennel Island Sea Krait, *Laticauda crockeri.*
Photography by Jonathan Q. Richmond..

Identification. The most melanistic of the *Laticauda,* with 22-35 faint, alternating bands on the body, which vary from dark brown to a dark maroon band or a dark muted blue band alternating with black bands. As with all *Laticauda,* pupils are round, nostrils lateral and nasals are separated by internasals, rostral is undivided, with a prefrontal shield usually present. The mid body has 19–21 longitudinal rows of scales and the average animal has 192 – 210 ventral scales. Males have 24-39 subcaudals and females 24 – 30. Snout-vent length averages for males are 615mm and 795 mm for females. The average tail length in males is 91 mm and 90 mm for females. (Uetz et al, 2020)

Natural History. One hypothesis on the origins of this species is that *Laticauda laticaudata* once inhabited the Solomon Islands, and *Laticauda crockeri* descended from this now extirpated population, diverging from the parent population after the formation of Te-Nggano Lake from a former lagoon (Cogger, et al, 1987). Though closely related to *Laticauda laticaudata, L. crockeri* is sympatric with *Laticauda colubrina*. One hypothesis as to how two species of krait could share a relatively small area is prey preferences. *Laticauda crockeri* are only known to eat one of the two native species in Lake Te-Nggano, the Dusky Sleeper Goby (*Eleotris fusca*). The other native fish, Pacific Shortfinned Eel (A*nguilla obscura*) seems to be eaten exclusively by the lake's population of *Laticauda colubrina*. Unfortunately, neither have been documented preying on the lake's invasive species, Mozambique Tilapia (*Oreochromis mossambicus*).

Breeding of this species is presumed to be seasonal, but nothing else is known about the species reproduction. Cogger states that there are local reports of viviparity in the species, but these claims have yet to be confirmed (Cogger, et al, 1987). The species is listed by the IUCN as Vulnerable since its entire extant of occurrence is a single lake. The lake is listed as a World Heritage Site and provides the species some protection (Lane & Guinea, 2010a).

Niue Sea Krait

Laticauda schistorhyncha (Günther, 1874)

Distribution and Habitat. Known only from the small island nation of Niue, where it inhabits and area less than 300 km². Habitat preferences are poorly studied, studies from Niue are absent however the species is quite abundant along the reefs, and numerous sea caves on the island's coast. (Personal comm. Dr. Jessica Cramp). Type locality: Niue Island.

Figure 12.8. The distribution of *Laticauda schistorhyncha*

Identification. The head is black with a thin off-white mask over the eyes. Black bands are wider than the alternating blue bands and this species has an overall lower band count than other sea kraits. *Laticauda schistorhyncha* and *Laticauda semifasciata* can be distinguished from the rest of the genus by the rostral scale, which is divided horizontally in these two species. *Laticauda schistorhyncha* and *Laticauda semifasciata* can most easily be distinguished from one another based on band count, *Laticauda semifasciata* having 30-42 body bands, compared with *Laticauda schistorhynchus* having 18-31 body bands. As with all *Laticauda,* pupils are round, nostrils lateral and nasals are separated by internasals (Cogger and Heatwole, 2005).

Ventral scales 195-205 compared to *Laticauda schistorhyncha* having 187-195 ventral scales (Guinea, et al, 1983). Males average 38–40 subcaudal scales and females 32–35. The average snout-vent length in males is 670 mm and 750 mm in females. The average tail length in males is 100mm and 110 mm in females.

Natural History. Also known as the Flat-tail Sea Snake and locally known as the Katuali, the species is abundant in sea caves around and beneath the island (Jess Cramp per comms). Despite its local abundance, this species is listed as vulnerable by the IUCN due to its restricted range and vulnerability to severe weather events, coral bleaching, and the effects of climate change, all of which reduce habitat complexity and prey abundance, as well as create a loss of ideal refuge sites (Lane and Guinea 2010b). Though an official population study has yet to be conducted, locals have noted a decline in population densities (Personal communication.

Figure 12.9. Niue Sea Krait, *Laticauda schistorhyncha***.**
Photography by Kirby Gonzalo Morejohn.

Dr. Jessica Cramp). The venom of *Laticauda schistorhyncha* is comprised of erabutoxins with an LD50 of 15 mg/g IV in mice (Guinea et al. 1983). Little is known about this species reproduction and natural history since much of Niue's marine environment has not been studied due to its remote location and difficulty accessing due to the lack of safe harbors (Friedlander et al. 2017). The venom of *Laticauda schistorhynchus* and *Laticauda semifasciata* comprise erabutoxins with an LD50 of 15 mg/g IV in mice (Guinea et al. 1983).

New Caledonia Sea Krait

Laticauda saintgironsi (Cogger and Heatwole, 2005)

Figure 12.10 The distribution of *Laticauda saintgironsi.* **Red area marks the breeding population.**

Distribution and Habitat. Predominantly known from New Caledonia where it is locally abundant, with single specimen sightings in the Caroline Islands and New Zealand. Like other members of the *colubrina* complex, this species spends most of its time in shallow reefs and coastal waters. It can be found both at sea, under rocks, within crevices, inside sea caves, and taking shelter under various forms of cover on land. Type locality: Porc-épic Island, New Caledonia.

Identification. Prior to its description, *Laticauda saintgironsi* was often confused with juvenile and subadult *Laticauda colubrina,* not only because of the two species' morphological similarities, but also because the two species can be found in the same together in the same locations including terrestrial aggregations and aquatic feeding sites (Cogger and Heatwole, 2006).

Figure 12.12. *Laticauda saintgironsi.*
Photography by Pauline Fey.

A uniquely colored member of the genus, with 21-30 glossy black bands alternated by burnt orange bands which fade to a pale cream color ventrally. The scales of the light bands have a dark grey tipping to them, as do the margins of the head and lip scales. Like it's closely related *Laticauda colubrina*, *Laticauda saintgironsi* has a yellow or cream upper face mask pattern, and an undivided rostral scale. Average ventral scale count is 211-224 in males and 215-230 in females. Maximum snout to vent length is 817mm in males and 1090 mm in females. The average tail length in males 78.9 mm and 84.2 mm in females. Males average 37–42 subcaudal scales and females 25-34. Average mid-body scale count is 21 rows in both sexes (Heatwole et al 2005). It can be distinguished from *Laticauda semifasciata* and *Laticauda schistorhyncha* by its undivided rostral. It is easily discernible from *Laticauda laticaudata* and *Laticauda crockeri* by its yellow or cream face mask pattern.

Geographic separation makes the species identification simple from *Laticauda colubrina* simple, with no known overlap, however it may also be distinguished by a lower mid-body scale row count, and lower ventral scale counts. Another key difference is the dark body bands on *Laticauda saintgironsi* often do not meet ventrally, or at least narrow ventrally. Coloration is also a notably different, with *Laticauda saintgironsi* most commonly taking on a brown and orange banded color scheme and *Laticauda colubrina* most often coming in a blue and black banded color scheme.

Natural History. This species spends most of its time in shallow waters foraging for eels, with brief periods on shore hiding in litter, under boulders, in crevices, and vegetation. Heatwole and Cogger report this species may travel some hundreds of meters inland on the islands and up to 100m in elevation. This species is often found in aggregations of 30 or more individuals in single refuges and in the hundreds in some lagoon's small islands. Laticauda saintgironsi Females are thought to breed on average every two years with a mean clutch size of 3.3 eggs. (Bonnet et al, 2014)

Guinea's Sea Krait

Laticauda guineai (Heatwole et al 2005)

Figure 12.13. The distribution of *Laticauda guinea.*

Distribution and Habitat. This species is endemic to Papua New Guinea. Habitat preferences are like that of the closely related *Laticauda colubrina.* Shallow reef shelfs, small islands, rocky shores, and at sea, as well as among roots and leaves on shore. Type locality: Bava Island, Papua New Guinea

Identification. Closely related to *Laticauda colubrina* but is identifiable from all other members of the *Laticauda colubrina* complex by having a higher number of black bands (47 or more) which are notably more narrow than the light colored bands and do not reduce towards the venter as much as in the others. The species is sexually dimorphic in size, and tail length (Heatwole, et al, 2005).

Natural History. Given the recent description of this species, not much is known of it's natural history, however it's close relation to *Laticauda colubrina* and the similarities with in the complex, we can extrapolate some presumptions. Other members of the complex use tongue-flicking to forage reefs for their prey, which almost exclusively consists of eels. Land is used to shedding, breeding and egg laying. This species is listed as near threatened by the IUCN. It is associated with coral reefs, and the loss of habitat due to coral bleaching and elevated sea temperatures is likely to pose a threat to the species. As corals bleach, prey abundance and loss of refuge will likely impact this species future success. (Lane and Guinea, 2010d)

Dwarf Sea Krait

Laticauda frontalis (de Vis, 1905)

Figure 12.14. The distribution of *Laticauda frontalis*

Distribution and Habitat. Endemic to the islands of Efate and Espiritu Santo in Vanuatu. Two individuals have been found at the Loyalty Islands in New Caledonia, but these are presumed vagrants and these islands are not considered to be a part of the species range. (Lane and Guinea, 2010c). This species is often found in seaside rock crevices and beneath mangrove trees when on land. At sea it can be found among coral reefs, and sea caves like the sympatric *L. colubrina.* Type locality: New Guinea.

Identification. A small *Laticauda* with a SVL of 293–717 mm, and a tail length of 34-88 mm with no notable sexual dimorphism in this species. The species has 28-36 dark bands on the body and 3-4 dark bands on the tail. There is no difference in the width of the bands with the sympatric *Laticauda colubrina* (Heatwole et al 2005).

It can be distinguished from *Laticauda semifasciata* and *Laticauda schistorhyncha* by its undivided rostral. *Laticauda frontalis* can be distinguished from *Laticauda laticaudata* and *Laticauda crockeri* by its yellow upper lip. A characteristic shared with *Laticauda colubrina* based on a lower midbody scale count of 21, lower ventral count and smaller size. Also, on *Laticauda colubrina* there is a lower lateral connection between the black head and the first black band on the neck, which is not present in *Laticauda frontalis*. Furthermore, the dark colored body bands on *Laticauda frontalis* do not extend to the middle of the venter anteriorly. (Heatwole and Cogger 2005)

Natural History. It is the smaller sister to *Laticauda colubrina* a larger relative that feeds exclusively on eels. This species is listed as Near Threatened by the IUCN due to continuing decline in the area, extent, and quality of habitat. Other major threats include anthropogenic disturbances such as coastal development, which disturbs nesting. This species predominantly uses the intertidal zone. Rising sea levels and coastal development will impact its survival (Lane and Guinea 2010c).

Blue-lipped Sea krait

Laticauda laticaudata (Linnaeus, 1758)

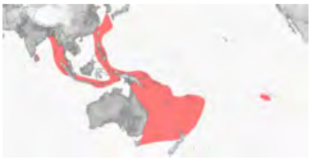


Figure 12.15 The distribution of *Laticauda laticauda.*

Distribution and Habitat. This species inhabits a notably large range, occurring from northeastern India (including the Andaman Islands, and the Nicobar Islands), Malaysia, Indonesia, New Caledonia, the Loyalty Islands, Papua New Guinea, the southwestern Pacific islands, China, Taiwan, and Japan. (Lane et al 2010). Type locality: Indiis. Habitat included coral reefs, on small coral islands, in coastal mangroves and the open ocean. It is usually found at a depths of 0-15 m (Cogger 2007). It has been recorded to dive to depths greater than 80 m (Brischoux et al. 2009).

Figure 12.16 *Laticauda laticauda.* **Photography by Jens Petersen**

Identification. The upper lip of this species is dark brown to black with no pale yellow lip, helping distinguish it from members of the *colubrina* complex. Colors in the species vary across the range from a rich royal blue and black to a muddled dark brown and tan, or even a dark black and beige. Total length for the epics is 910 mm in males and 1070 mm in females with an additional 110 mm in tail length for both sexes. Ventral scales are notably enlarged ranging from third to more than half the width of the body. Nasal scales are separated from intranasal scales, rostral is undivided, and no azygous prefrontal scales are present. The species has 225-243 ventral scales, and 30-47 subcaudal scales, 38-47 in makes, and 30-35 in females (Leviton et al 2018).

Natural History. *Laticuada laticauda* are less terrestrial than members of the *L. colubrina* complex, yet more terrestrial than the *L. semifasciata* complex, however it is slower moving than both on land and water (Wang et al 2013).

Black-banded Sea Krait

Laticauda semifasciata (Reinwardt, 1837)

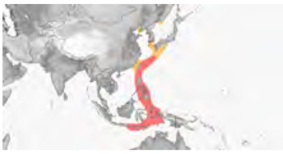


Figure 12.17. The distribution of *Laticauda semifasciata.*

Distribution and Habitat. This species is found in the Philippines, Taiwan, China, Japan, and Palu Api in Indonesia and inhabits shallow tropical seas and coral reefs, as well as rocky shores. Type locality: Moluccas.

Identification. Colors range from dark grey, or black bands alternating with varying saturation levels of blue bands, including some very bright blue examples in parts of the species range. Body bands notably narrow ventrally. This species average SVL is 805 mm for males, and 1190mm for females. It has an average tail length of 115mm for both males and females. Ventral scales 195-205 and 32-43 subcaudal scales. (Uetz et al 2020).

Natural History. *Laticauda semifasciata* is a fish specialist preying primarily on rovers (Emmelichthyidae), tangs (Acanthuridae), and damselfish (Pomacentridae). Prey items are subdued by the species venom, which is contains Erabutoxins

Figure 12.18 *Laticauda semifasciata*.
Photography by by Yu Sing Ling.

On the next page. A Turtle-headed Seasnake, *Emydocephalus annulata.* **Photography by Pauline Fey.**

13. Seasnakes

13. Seasnakes

Myke Clarkson

The true sea snakes of the sub-family Hydrophiinae compose about 60 species of poorly studied marine snakes with paddle tails and front fangs. While more scientists have been examining specimens and diving with snakes to observe their behavior in the last few decades, there is still much to learn. These are the only living snakes to have successfully colonized the oceans, but, of these species, most are restricted to the waters of the continental shelf near sources of freshwater. All the species studied to date are live-bearing and females produce relatively small litters, usually with less than 17 young and often as few as one to three young.

Megan Kerford and colleagues studied the movements of the Bar-bellied Sea Snake (*Hydrophis elegans*) at Shark Bay in Western Australia. Bar-bellied Sea Snakes are specialist predators on snake eels (Family Ophichthidae) that live in burrows on open sand flats. During high tides, Tiger Sharks have access to most of the areas of Shark Bay, and Keford and co-workers discovered *H. elegans* move into adjacent sea grass beds at high tide. The dense grass cover provides few opportunities to forage on eels but does provide cover for the snakes to avoid sharks.

Photoreceptors are usually associated with the head of vertebrates, but Kenneth Zimmerman and Harold Heatwole found photoreceptors on the tail of the Olive Sea Snake (*Aipysurus laevis*). They observed the Olive Sea Snake's tail was more often concealed during the day than at night, and that the tail will be pulled out of the light when it is exposed. By masking parts of the tail with tape so they could not be stimulated by light, they determined the photoreceptors were located mostly on the dorsal portion of the tail. The nature of the photoreceptors was not determined but the snake's behavior revealed their presence.

Only one sea snake has become truly pelagic, drifting with open ocean currents, the Yellow-bellied Sea Snake (*Hydrophis platura*). This is not to say that it does not occur over the continental shelf, because it occasionally gets washed up on beaches from Africa's east coast to the coastlines of western North and Central America. The Yellow-bellied Sea Snake aggregates along slicks or drift lines. Floating debris accumulates in the slicks, and it may remain for days or weeks before a change in wind speed or current direction breaks them up. Aggregations of snakes in these drifts numbered from five to several thousands and are composed of juvenile and adult snakes. Other animals inhabiting the drifts are jellyfish medusa, fish, porpoises, and sea turtles, with sea birds often following the lines of floating debris. Snakes aggregated here because the slicks are a useful place to locate food and mates. The degree to which these snakes have adapted to the marine environment is significant given they represent a recent evolutionary radiation.

Sanders et al. (2008) used mtDNA as well as nuclear genes to examine the relationships of the Australasian elapids and the sea snakes and estimated the time sea snakes diverged from the other elapids. They found the sea kraits to be the sister to all other hydrophiines, and the Melanesian Small-eye Snake (*Micropechis*) the sister to the remaining species. They also recovered a clade containing the true sea snakes, the black swamp snakes (*Hemiaspis*), and the Tiger Snakes and their relatives (*Notechis* group).

Which of these groups form the sister to the sea snakes was unclear? However, of interest is that tiger snakes are known to eat frogs and forage in water or along shorelines, and the black swamp snakes are semi-aquatic. Pre-adaptations to life in the water are widespread in this clade. The time the ancestral sea snake diverged from the terrestrial or freshwater members is estimated at 6.2 Ma (7.9–4.7Ma) and the authors write that this is, "...an extremely brief interval to generate ~60 species of great ecological and morphological diversity."

Short-nosed Seasnake

Aipysurus apraefrontalis (Smith, 1926)

Distribution and Habitat. Ashmore Reef, Hibernia Reef, Ningaloo Reef, Exmouth Gulf, Barrow Island, and Shark Bay, Australia (D'Anastasi et al 2016). This species occurs in the shallow waters around coral reefs, and in subtropical seagrass beds with a maximum estimated depth of 10 meters. They are associated with sections of reef with sparse coral and sandy bottoms (D'Anastasi et al 2016, Voris 1972). Type locality: Ashmore Reef

Identification**.** A medium size snake of 108cm, SVL is 985mm (Storr et al 1986). Body is slender and cylindrical in shape and color is a dark olive to purplish brown in base color with variable faint olive-brown cross bands. In some specimens these bands are rather conspicuous, with scattered olive tipped cream-colored scales creating a speckled like appearance. Body scales heavily overlap, and the anteriorly facing edges are pointed and are loose from the body. They may be smooth or possess tubercles or a short keel posteriorly. Dorsal scale count at mid-body is 17. The head is small and pointed with large symmetrical head shield present with some fragmentation. Parietal shields are divided and larger than the neck scales. Prefrontal scales are absent with the nasal coming in direct contact with the frontal shield. The eye of this species has a small black pupil with a cream-colored iris. Throat scales are small and off white in color anteriorly and dark brown posteriorly. Ventral is most often uniform grey-brown with occasionally scattered white or white blotched scales. Ventral scales are deeply notched with a median keel and often worn hind margins. Ventral scale count is 140-155. Subcaudals are all single with a count of 18-25 and cloacal scale is divided (Wilson and Swan 2013) (Cogger 1975). *Aipysurus apraefrontalis* can be distinguished from *Aipysurus foliosquama* by lacking prefrontal scales and having 17 midbody rows as opposed to 19-21 in *A. foliosquama* (Storr et al 1986).

Figure 13.1. The distribution of *Aipysurus apraefrontalis*

Natural History**.** This species actively searches sparse coral and sandy bottoms for fish with an affinity for eels and gobies (Voris 1972). They are commonly encountered on reef flats hiding in dead coral rubble at low tide or along the shallow waters of the reef's edge or resting beneath coral overhangs 1-2 meters below the surface during the daylight hours (Lukoschek et al 2010a) (Cogger 2000). Once feared extinct until the species 2015 rediscovery by Sanders et al, this critically endangered species has a very restricted range in Western Australia and is in decline. While the cause of the severity of the decline remains unclear, climate change induced degradation of shallow coral reef habitats resulting in bleaching events have a significant impact on this species and its future as do trawling fisheries (Lukoschek et al 2010a).

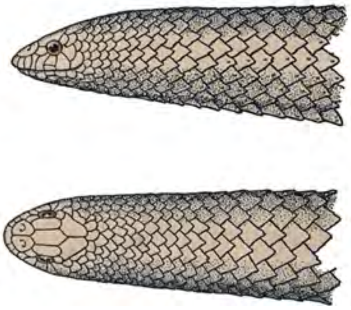


Figure 13.2 The Short-nosed Seasnake, *Aipysurus apraefrontalis***. From Smith 1926.**

Reef Shallows Seasnake

Aipysurus duboisii (Bavay, 1869)

Distribution and Habitat**.** In Australia the species is known from Northern Territory, Queensland and Western Australia, Timor Sea in Indonesia, New Caledonia, and Southern Papua New Guinea. (Uetz and Hosek 2020) This species occurs in reef adjacent shallow waters, including sandy bottoms, sea grass beds, gorgonian coral fields, and among dead broken corals. While it is typically a shallow water dweller, they have been recorded as deep as 80 m although this is a rare exception (Lukoschek et al 2010b). Type locality: Life, Loyalty Islands, New Caledonia.

Figure 13.3. The distribution of *Aipysurus duboisii*

Identification**.** This is a medium sized species with an average total length of 114 cm, SVL 1010 mm (Stor et al 1986). Body color is variable, most often with a purplish-brown base color with pale scale edges, giving the snake a reticulated or net like appearance. Triangular blotches often form bands down the dorsal of the snake, becoming narrower towards the ventral. With exception to the rostral and nasal scales, all scales on this species have a shallow posterior notch and a mild median keel. Scale are imbricate, and smooth with keeled tubercules. Midbody scale row count is 19 (Wilson and Swan 2013). Ventrals number 154-181 and are approximately half as wide as the body. Subcaudals number 25-30 and cloacal plate scale is divided (Storr et al 1986).

Natural History**.** This snake is commonly encountered with a great deal of biofouling made up of algae, bryozoans, tube worms, and polychaetas (Lukoschek et al 2010b). Their diet is comprised of small reef fish including members of the families Muraenidae, Blennidae, Scaridae, Acanthuridae, scorpaenid, and the toxic Tetrarogidae as well as eels (McCosker 1975)**.** This species is the third most toxic known snake known to science when the venom is administered subcutaneously with an LD50 of 0.044 mg/kg (Fry 2002). Reproduction occurs every four years with gestation lasting six to seven months, and with the birthing of 4–6 offspring occurring between March and June (Fry et al. 2001). While this species is currently listed as Least Concern by the IUCN, populations are in decline. Its patchy distribution, and low densities do leave it vulnerable to future threats including climate change and pressures from prawn fisheries (Lukoschek et al 2010b).

Marbled Seasnake

Aipysurus eydouxii (Gray, 1849)

Distribution and Habitat**.** This species is known from the South China Sea, Borneo, Western Malaysian, Vietnam, Gulf of Thailand, Cambodia, Singapore, Papua New Guinea, and Thursday Island in Australia. This species frequents turbid waters from 0-50 meters in shallow bays and estuaries and is associated with muddy substrate but may be found along hard sea floors as well. It is speculated this species may also swim upstream into rivers (Guinea et al 2010). Type locality**:** Indian Ocean.

Identification**.** This is a small snake with a length averaging around 60 cm but up to 91cm long, SVL is up to 790mm (Stor et al 1986). Body is an even diameter throughout and cylindrical in shape with imbricate scales. The body color is brownish or olive green dorsally fading to a paler color ventrally, with 30–42 irregular yellow or brown bands (Sanders et al 2012). Banding and band count is highly variable, but often narrows ventrally. Scales within bands usually with dark margins. Dorsal scales number 17 on the neck and narrow down to

Figure 13.4. Reef Shallows Sea snake, *Aipysurus duboissi* from Anse Vata, Nouméa, New Caledonia. Photography by Jean Roger.

Figure 13.5. The distribution of *Aipysurus eydouxii.*

15 by the vent. Six lower and upper labials are presents, with the fourth bordering the eye. The frontal scales of this species are longer than the tip to snout length. Prefrontals are divided and range in count from two or occasionally four, with two sets one preocular and one post ocular. 10-11 Maxillary teeth behind the fangs. Males possess 129–137 ventral scales, 135-146 for females. Subcaudal count is 30–32 in males 23–27 on females. Both male and female possess a median keel, however in males these develop into spinous tubercles across their body (Leviton et al 2014). *Aipysurus eudouxii* be distinguished from *Aipysurus mosaicus*, based on a higher band count, *Aipysurus eydouxii* having 29 or more and *Aipysurus mosaicus* having 22 or less body bands (Sanders et al 2012). Body row count distinguishes *Aipysurus eydouxi* from *Aipysurus duboisii*, *Aipysurus fuscus*, *Aipysurus laevis*, and *Aipysurus pooleorum* which all have more than 17 scale midbody rows. This species can be distinguished from *Aipysurus apraefrontalis* and *Aipysurus foliosquama* due to its lack of deep median notches on the posterior edge of the ventral scales. It can be distinguished from Aipysurus tenuis by ventral count, having a ventral count of 129–146 scales as compared to *Aipysurus tennis* having more than 170 ventral scales (Sanders et al 2012) (Storr et al 1986).

Figure 3.6. The Marbled Seasnake, *Aipysurus eydouxii.* **The snake was on the sand bar of Chek Jawa Singapore in the early morning. It lmay have been stranded there at low tide. Photography by Ria Tan, Wild Singapore,**

Natural History**.** While many members of the genus *Aipysurus* possess some of the most potent venoms known among snakes, *Aipysurus eydouxii* has evolved away from venom in a similar evolutionary fashion to *Emydocephalus annulatus.* This is believed to be because Aipysurus eydouxiii is a fish egg specialist, searching its habitat for benthic fish eggs, which do not require venom to be subdued. With seasnake venom believed to have evolved for predation and not defense, the dietary shift to fish eggs has led to highly atrophied venom glands with reduced and ineffective fangs resulting in a species that is essentially harmless (Fry et al 2005). This species is listed as Least Concern by the IUCN, however a recent survey in Shoalwater Bay, Australia indicates regional population decline, and the species does face threats including climate change and as by catch in fisheries throughout its range (Guinea et al 2010).

Leaf-scaled Seasnake

Aipysurus foliosquama (Smith, 1926)

Distribution and Habitat**.** Ashmore Reef, Hibernia Reef, Scott Reef, Shark Bay, and Barrow Island Australia. This species is associated with tropical reefs, sub-tropical sea grass meadows, sand over limestone, silt, and sponges (D'Anastasi et al 2016). Type Locality. Ashmore Reefs, Australia (Uetz and Hosek 2020).

Identification**.** A small seasnake measuring 55 cm long, with an SVL of 465 mm (Storr et al 1986). Body color is a light brown to pinkish tan with a variable pattern that can include faint bands or scattered spots. The head shields of this species are large and symmetrical, with some fragmentation occurring around the parietal region with prefrontal scales present. Body scales are smooth to tuberculate and have notable overlap. The edges of the body scales have one to two points on each and are extensible free posteriorly creating the leaf scale like appearance. Mid-body scale row count is 19-21. Ventral scales are nearly half as wide as the body, notably keeled, and notched posteriorly, with a count of 139-153 (Storr et al 1986). Subcaudal count is 20-29. Cloacal scale is divided. (D'Anastasi et al 2016) (Wilson and Swan 2013). *Aipysurus foliosquama* appears similar to *Aipysurus apraefrontalis* but can be distinguished by having prefrontals and 19-21 midbody scale rows as opposed to 17 as in *A. apreafrontalis* (Storr et al 1986).

Figure 13.7. The distribution of *Aipysurus foliosquama*

Natural History**.** This species is an active predator of small reef fish, poking its head into crevices and holes, and then striking at fish hiding with in them. The species is thought to usually inhabit depths of no more than 10 m and as such the populations have limited gene flow between them due to deep water barriers surrounding the localities they are known by (Lukoschek 2010c). Once abundant at Ashmore reef and Hibernia reefs, this species went missing from 2001 despite several dedicated surveys in search of them. With these small locals comprising their entire known geographic range the species was believed extinct until Sanders et al rediscovered the species at Barrow Island in 2015 (Sanders et al 2015). Today it is listed as Critically Endangered by the IUCN, and while the causation of the species initial decline is still not fully understood, impacts from climate change including increased sea temperatures, coral bleaching, and coral reef habitat degradation are suspected threats.

Figure 13.8 *Aipysurus foliosquama* **from Ashmore Reef. Photography by Scott Eipper.**

Dusky Seasnake

Aipysurus fuscus (Tschudi, 1837)

Distribution and Habitat**.** Ashmore, Hibernia, Cartier, Scott, and Serangipatan Reefs in the Timor Sea Western Australia. This species prefers reef and reef edge habitats ranging from 0-12 m, but up to 30 m deep (Lukoschek et al 2010d). Type Locality. Celebes.

Identification**.** A short and stout member of *Aipysurus* with a typical length of 60cm (though up to 96cm has been recorded), and an SVL of 250-823mm. *Aipysurus* can superficially resemble its sister taxon *Aipysurus foliosquama*, with a shorter more punctuated snout. Coloration is brown to dark brown or purplish-brown. Pattern is most often uniform, although faint cross bands can be observed towards the lower dorsal scales. Some individuals feature a darkening in the center of each lateral scale, causing a longitudinal striation pattern. This species has some variable head scales including occasional prefrontals, and most often having frontal scales, but not all. Additionally, this species usually has a single preocular though occasionally there can be two and labial scales vary between 6-9. Consistent features on the head includes: the presence of supraoculars and parietals which are divided, and small temporal scales Body scales are smooth and imbricate, with 19-21 rows of dorsal scales at midbody. Ventral scales number 155-180, and have a slight notch, 20-40 undivided subcaudals, and the cloacal scale is divided (Storr et al 1986) (Cogger 2000).


Figure 13.9 The distribution of *Aipysurus fuscus.*

Natural History**.** This species is a shallow water specialist that searches the reefs edge in search of prey items including reef fish like gobies, eels, wrasses, and their eggs. Being a shallow water species, *Aipysurus* fuses is only known from five disjunct subpopulations, with extraordinarily little gene flow suspected between the subpopulations. All these subpopulations have suffered drastic declines in the past few decades, with some estimates putting the population decline at 70% since 1998. This species' decline coincides with overall seasnake declines on the reefs of the Timor Sea, where it is endemic, and it is listed as endangered with the IUCN. While many seasnakes are stereotyped for having a calm disposition, this species is known to bite defensively when threatened, and should be approached with caution as it does possess a potent venom (Dunson 1975).

Olive-Brown Seasnake

Aipysurus laevis (Lacèpéde, 1804)

Distribution and Habitat**.** Northern seas to Exmouth Gulf off Western Australia, Northern Territory Australia, Southern New Guinea, and New Caledonia (Storr et al 1986). Like other *Aipysurus*, this species is commonly associated with coral reefs however, unlike many of its sister taxa can be found in a wide range and depth of habitat including reef slope, reef edge, sandy bottoms, shipwrecks, deep reefs, inter-tidal habitats, and lagoons. While this species may dive as deep as 133 m (Crowe-Riddell et al 2019), it more typically occurs at depths ranging from 10 to 40 m (Lukoschek et al 2010e). Type locality: Locker Island, Western Australia.

Identification**.** *Aipysurus laevis* is the longest and heaviest member of the genus, with a total body length ranging from 1.2 m up to nearly 2 m long and up to 23 cm in girth. Midbody scale count distinguishes this species from all other *Aipysurus* except for *Aipyrsurus pooleorum,* which it can be distinguished from by the lack of tubercles in males, its larger size and its lighter coloration. Aipysurus laevis can be distinguished by other members of the genus based on its larger size, lack of tubercles in males and paler coloration. This species is highly variable in color and pattern, ranging from dark brown to purplish-brown, often fading to a lighter pale brown centrally, with a speckling of lighter colored scales often increasing towards the ventral creating a sort of mosaic gradient. In lighter


Fugure 13.10. The distribution of *Aipysurus laevis.*

specimens the ventral can be entirely off-white. Like other *Aipysurus*, the center of each scale is often darker than the edges, creating a lateral striation look. The tail can vary from white to brown, with dark brown along the dorsal ridge. Prefrontals are occasionally present, and frontals are often present. Supraoculars and parietals are always divided, and temporals are small. Preocular scales range from 1–3, though most often 1–2. And upper labial scale counts number 8–10. Dorsal scales are smooth and imbricate, numbering 21–25 at midbody. Ventral scales number 142–152, have slight posterior notch, and about are half the width of the body. Subcaudals number 22–30 and cloacal plate is divided (Storr et al 1986) (Cogger 2000). This species goes through an ontogenetic change, and young individuals are notable lighter in coloration than their adult counterparts (Lukoschek et al 2010e).

Natural History**.** The Olive Seasnake is an active nocturnal hunter, which searches a home range of reef for crabs, prawns, fish eggs, and fish. Olive Sea Snakes are naturally curious and are known to approach SCUBA divers, not aggressively but inquisitively, especially at night (Lukoschek et al 2010e). Individuals of this species maintain often overlapping linear home ranges of about 0.18 hectares for females, and 0.15 hectare for males along the edges of the reef. While there is an documented consistency with home ranges, their daytime shelters do not appear to be consistent (Marsh et al 1993) (Lukoschek et al 2010e). While naturally curious, and inclined to approach divers for closer investigation, this species is known to bite when it feels threatened or is restrained. This large species possesses the second most toxic known snake venom when injected intramuscularly, with an IM LD50 of only 0.09 mg/kg and human fatalities are known from *Aipysurus laevis* (Fry 2002) (Dunson 1975). While this species is believed to be in decline, its large geographic range and wide variety of habitats have resulted in a Least Concern listing by the IUCN (Lukoschek et al 2010e).

Figure 13.11. *Aipysurus laevis. Baie de magenta, Nouméa, New* **Caledonia. Photography by Pauline Fey.**

Mosaic Seasnake

Aipysurus mosaicus (Sanders et al, 2012)

Distribution and Habitat**.** This species is known from the Coburg Peninsula, the Gulf of Carpentaria, Thursday Island, Townsville, Swain Reefs, subtropical Queensland, and Shoal Water Bay Australia, as well as West Papua (Figure 13.12) This species is associated with offshore waters, estuaries and tidal rivers where it is often found among soft sand bed and mud bottom substrates. It is most often encountered between 2-22 m, with a maximum known depth of 50 m. Type locality: Gulf of Carpentaria, Weipa, Australia.

Figure13.12. The distribution of *Aipysurus mosaicus*

Identification**.** This species is named for its dark and light scales arrangement which creates a mosaic-like pattern of irregular cross-bands. The body is a yellowish cream to salmon color, with brown to olive green incomplete bands, tampering dorsally, numbering 17-22 in males and 15-12 females. Scale row count at mid-body is 17, ventral scales number 140–154, subcaudals 25-38, and cloacal plate is divided. Head dark brown above and below. *Aipysurus mosaicus* can be distinguished from *Aipysurus eydouxii*, based on a lower band count, *Aipysurus mosaicus* having 22 or less body bands and *Aipysurus eydouxii* having 29 or more. *Aipysurus mosaicus* has a concave front parietal suture compared to Aipysurus eydouxi where it is flat and a crescent-shaped nasal rather than triangular in *Aipysurus eydouxi. Aipysurus mosaicus* also has a larger premaxilla, and a smaller maxilla than sister taxon *Aipyrsurus eydouxi*. *Aipysurus mosaicus* can be distinguished from *Aipysurus apraefrontalis* and *Aipysurus foliosquama* due to its lack of deep median notches on the posterior edge of the ventral scales.

Figure 13.13. *Aipysurus mosaicus* **from Cooloola Qld, Australia. Photography by Josh Jenson**

It can be distinguished from Aipysurus tenuis by ventral count, having a ventral count of 140-154 scales as compared to *Aipysurus tennis* having more than 170 ventral scales. Body row count distinguishes *Aipysurus mosaicus* from *Aipysurus duboisii*, *Aipysurus fuscus*, *Aipysurus laevis*, and *Aipysurus pooleorum* which all have more than 17 scale midbody rows (Sanders et al 2012).

Natural History**.** Like its closest relative, *Aipysurus eydouxi*, *Aipysurus mosaicus* is a benthic fish egg specialist and as such has highly reduced venom glands and delivery. With this species being new to science, much of what is known about it based on prior studies of *Aipysurus eydouxi*. Although other seasnake species in its range are in decline, this species has not been assessed by the IUCN.

Shark Bay Seasnake

Aipysurus pooleorum (Smith, 1974)

Distribution and Habitat**.** Endemic to Shark Bay Australia with strays occurring as far south as Perth, Australia (Wilson and Swan 2013) (Figure 13.14). This species is associated with limestone reef, seagrass meadows, stromatolite, macroalgae fields, sand bottoms, rocky rubble, and artificial human made structures like jetties and rock walls (D'Anastasi et al 2016). Type locality: Shark Bay, WA.

Figure 13.14. The distribution of *Aipysurus pooleorum*

Identification**.** A moderately sized member of the genus at 114 cm long and 19 cm in girth. Females are a dark brown to purplish brown with oblique pale bars, and males are brown tone which radiates to a lighter brown to tan on the flanks (Storr et al 1986). Prefrontals are rare, frontals occasional, 1-2 preocular present, 2-3 post oculars present, 8-10 labial scales, typically 3 primary temporal scales, supraoculars and parietals divided. Dorsal scales are imbricate and smooth in females, but males possess tubercles, increasing in size on the lower rows. Midbody scale row count is 20-23, ventral scale count is 146-159. Ventral scales have a median keel and posterior notch and are approximately half as wide as the body. Subcaudals number 25-33 and cloacal plate is divided (Storr et al 1986).

Natural History**.** *Aipysurus pooleorum* are active foragers, taking advantage of areas with

Figure 13.15. *Aipysurus pooleorum.*
Photography by Scott Eipper.

high structural complexity which provide an abundance of prey and numerous sites for sheltering within. *Aipysurus pooleorum* has not been assessed by the IUCN, however conservationists do believe studies on this small ranging species should be of the highest priority (D'Anastasi et al 2016).

Arafura Seasnake

Aipysurus tenuis (Lönnberg and Anderson, 1913)

Distribution and Habitat**.** The true geographic range of this species is poorly known, but is thought to include the Northwestern coast of Australia from Broome to the Dampier Archipelago on the Pilbarra Coast though recent data suggests it can occur as far out as Ningaloo Reef and Exmouth Gulf (Figure 13.16). It is associated with sandy bottom, seagrass meadows, coastal rock outcroppings, reef, and marine man-made structures (Guinea et al 2010b; D'Anastasi et al 2016). Type locality: Cape Jaubert, Broome, Australia.

Figure 13.16. The distribution of *Aipysurus tenuis*

Identification**.** A large member of the genus, up to 1.3 meters long. Body color is light brown with dark brown scale tips that create longitude lions down the dorsum and/or faint cross bars on the sides. This species has smooth imbricate dorsal scales that number 19 at midbody. Males possess tubercles, increasing in size on the lower dorsal scales (Cogger 2000). Preocular scale is single, however the frontal, supraocular, and parietal scales are all divided. Two postoculars are present, and the labial scales number 7-6. Ventrals number 185-194, with a medium notch and a keel, which is stronger in females than males. Subcaudals number 36-27 and the cloacal plate is divided (Storr et al 1986).

Natural History**.** Very little is known about this poorly studied species, due to it's rarity, and often misidentification with its sister taxon. By 2010 it was only known by four specimens (Guinea et al 2010b), though more recent studies by D'Anastasi et al found 11 during surveys. *Aipysurus pooleorum* has not been assessed by the IUCN, however conservationists do believe studies on this small ranging species should be of the highest priority (D'Anastasi et al 2016).

Figure 13.17. *Aipysurus tenuis.* **Photography by Rick Stuart-Smith.,www.reeflifesurvey.com**

Turtle Headed Sea Snakes - *Emydocephalus*

There are three members of the genus *Emydocephalus* all of which are diurnal, medium sized, heavy bodied hydrophiini elapid snakes which feed exclusively on the eggs of small demersal spawning fish found through chemosensory foraging (Shine et al, 2020). Due to their exclusive diet of fish eggs, the species in this genus lack palatal, maxilla, and dentary teeth, though they do have small teeth on the pterygoid. Members of this genus also have unique fangs which face inward toward the midline, rather than the traditional vertical positioning pointing downward making them ineffective (Voris, 1966). With a specialized diet of eggs, *Emydocephalus* have evolved away from having fangs and a venom apparatus, making them the only marine elapid virtually harmless to humans due to their degenerated venom system (Minton, 1983). *Emydocephalus* do have a high quantity of scale sensilla compared to terrestrial snakes, which are thought to act as a form of tactile mechanoreceptors, as well as potentially functioning as hydrodynamic receptors which sense water displacement (Crowe et al 2016). Males of this genus possess a rostral spine, which was initially suspected to be used for the consuming of fish eggs, but later revealed to be used in mating by the males, utilizing the spine to prod potential mates in courtship.

Instead of using the rostral spine to scrape eggs off surfaces as was previously suspected, *Emydocephalus* use their consolidated upper labial scales to scrape eggs off surfaces (Guinea, 1996). While *Emydocephalus* is closely related to *Aipysurus* and placed within the *Aipysurus-Emydocephalus* clade with in Hydrophiini, *Emydocephalus* have not been shown to possess the light sensing phototactic tail that is present in *Aipysurus laevis*, *Aipysurus duboisii*, and *Aipysurus tenuis*. All members of this genus are dimorphic, with females attaining a larger total size than males, and males possessing the before mentioned rostral spine, which is absent in females (Shine et al 2020).

While members of this genus are mostly banded or blotched, Goiran et al found that individuals living in polluted urban adjacent waters tend to be melanistic. Gorian and his team concluded that the darker skin allows the snakes to excrete the trace elements by binding these elements to the melanin and disposing of them when shedding their skin. In turn animal inhabiting these polluted waters slough more frequently than those in cleaner waters, as mechanism for expelling pollutants (Gorian et al 2017).

Members of this genus occur in the shallow marine waters of Australia, New Caledonia, the Philippine, Vietnam, and Japan. Two of the three species are strongly associated with coral reefs, with the recently described *Emydocephalus orarius* being more closely associate with (Shine et al, 2020) soft bottomed trawl grounds. There is no range overlap between the species in this genus, making identification between the three species simplified (Crowe et al 2019).

Foraging in the genus is conducted in an unusual slow and continuous browsing fashion in a small, restricted home range (Gorian et al 2020). Gorian et al studied the effects tides had on this behavior and found the genus alters where it forages based on the tides, but tides do not make a significant impact on activity Levels. In this study, the authors found that this species is more likely to be associated with rocky or coral habitats during high or medium tides and sandier habitats during low tides (Gorian et al 2020).

Reproduction is seasonal, ovulation and mating occurring September- October, with young born in May, accounting for an 8-month gestation. Neonates grow rapidly with sexual maturity in males occurring at two years and three years for females. *Emydocephalus* only reproduces every two to three years and their litter size is two offspring (Shine et al 2020).

Currently no members of this genus are threatened with extinction, however the most recent assessment by the IUCN has noted that populations of *Emydocephalus annulatus* are decreasing (Lukoschek et al, 2010).

Banded Turtle Headed Seasnake

Emydocephalus annulatus Krefft, 1869

Distribution and Habitat**.** Timor sea, New Caledonia, the Loyalty Islands Vietnam, Philippines, and Australia (Lukoschek et al 2010). This species has a highly disjunct range, however only slight mitochondrial and nuclear divergences occur across the range (Nankivell et al, 2020). Type locality: Unknown, but probably the Australian Seas (Uetz and Hošek, 2020). This species is associated with shallow clear ocean waters and coral reefs, usually seen in water less than 40 meters in depth (Lukoschek et al 2010).

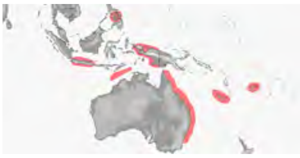


Figure 13.18. The distribution of *Emydocephalus annulatus*

Identification**.** Members of the genus is characterized by having three upper labials, with the second one being very long. This feature alone can distinguish them from other members of the Hydrophiini group. As mentioned, prior, the species only has rudimentary teeth. Adult males posses a rostral spine used in courtship which is absent in females. This species coloration is highly variable and can range from banded patterns of off white to yellow, alternating with dark rings or a patternless dark grey to black. The scales of this species are smooth and overlapping with 15–17 rows at the mid-body. This species has 125–145 wide slightly keeled ventral scales and 20–33 subcaudal scales. Cloacal scales are undivided. Adult males have small tubercles on their ventral scales. Average adult size is 75 cm (Department of the Environment, 2021).

Natural History**. F**orages slowly over coral reefs and rocky environments, searching cracks and crevices for fish eggs using scent to locate their prey, which is exclusively fish eggs from the fish genus Gobiidae, Pomacentridae and Blenniidae. This species uses modified labial scales to break the fish eggs from the surfaces they are adhered to (Department of the Environment, 2021). During low tide *Emydocephalus annulatus* can become dangerously entrapped in shallow pockets, leaving them suscecptible to overheating, and as such most individuals leave the reef flats during low tide, and travel through drainage channels to reach the deeper waters at the edges of the reef (Department of the Environment, 2021).

Ijima's Turtle Headed Seasnake

Emydocephalus ijimae Stejneger, 1898

Distribution and Habitat**.** This species is associated with shallow clear ocean waters and coral reefs but known from waters as deep as 40 meters (Lukoschek & Sanders 2010). China, Taiwan, Japan. Type locality: Ryuku Islands, Japan

Identification**.** Members of the genus are characterized by having three upper labials, with the second one being exceptionally long. As mentioned, prior, the species only has rudimentary teeth. Adult males possess a rostral spine, which is absent in females. This species has an average of 141.7 ventral scales, 32.3 subcaudal scales, and an average of 18 dorsal scales at the midbody. When present the species has 24–29 bands, however coloration and pattern is highly variable, and ranges from alternating light tan to yellow bands against a black to dark grey background, or partially banded, or solid black in color (Nankivell et al, 2020).

Figure 13.19. The Turtle-headed Sea Snake, E*mydocephalus annulatus*. (A) a banded morph from Baie des Citrons, Nouméa, New Caledonia, (B-C) a black morph from Baie de Magenta, New Caledonia. Photography by Pauline Fey.

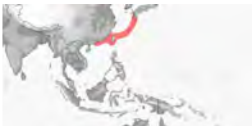


Figure 13.20. The distribution of *Emydocephalus ijimae*

Natural History**.** Both *Emydocephalus ijimae* and *Emydocephalus orarius* share similar natural histories, preying specifically on fish eggs. Their primary diet is goby and blenny fish eggs. These are often laid attached to sandy surfaces, and as such many animals were found to have sand in their colons (Voris, 1966). Masunga et al noted seasonal weight fluctuation in this species, which could be attributed in part to both prey availability and sea temperatures with males attaining higher body weight early spring to late summer (November to March or April), when fish spawning is at its peak. Conversely, body weights lessen in the winter, though more dramatically in females, which could be attributed in part to parturition (Masunaga & Ota, 2003).

Figure 13.21. *Emydocephalus ijimae.* **Photography by Patrick Davis**

Western Turtle Headed Seasnake

Emydocephalus orarius Nankivell, et al. 2020

Distribution and Habitat**.** Endemic to Western Australia, confirmed from Shark Bay, Exmouth Gulf, Pilbara coast and Broome (Nankivell et al, 2020). Type locality: Shark Bay, WA, Australia. Unlike other members of this genus which are mostly associated with rocky and coral areas, *Emydocephalus orarius* is associated with shallow ocean water with soft sandy bottoms (Nankivell et al, 2020).

Figure 13.22. The distribution of *Emydocephalus orarius*

Identification**.** Members of the genus is characterized by having three upper labials, with the second one being long. This feature alone can distinguish them from other members of the Hydrophiini group. As mentioned, prior, the species only has rudimentary teeth. Males possess a rostral spine, absent on females. The males of this species also possess ventral tubercles on adult individuals.

This species has an average of 144–145 ventral scales, an average of 32.3 subcaudal scales, and an average of 17 dorsal scales at the middy. *Emydocephalus orarius* can be distinguished from *Emydocephalus ijimae* and *Emydocephalus annulatus* based on the first upper labial scale. In *Emydocephalus orarius* the first upper labial scale is elongated and contacts the preocular, where as in *Emydocephalus ijimae* or *Emydocephalus annulatus*, it is usually the second upper labial that is elongated. Some specimens may also have an elongated first upper labial, in which case comparing ventral counts. *Emydocephalus orarius* has an average of 144.7 compared to an average of 136.9 in *Emydocephalus annulatus.* This species can be distinguished by neighboring *Emydocepha-*

lus ijimae in having two prefrontal scales compared to the three to four prefrontal scales found in *Emydocephalus ijimae*. Adult males of this species possess tubercles on their ventral scales, absent on *Emydocephalus ijimae* (Nankivell et al. 2020).

Natural History. *Emydocephalus orarius* diurnally forage for small demersal spawning fish eggs which it finds through chemosensory foraging (Shine et al 2020) in an unusual slow and continuous browsing fashion (Gorian et al. 2020). Their primary prey, goby and blenny fish eggs, are often laid attached to sandy surfaces, and as such many animals were found to have sand in their colons (Voris 1966).

Figure 13.23. The Western Headed Seasnake of *Emydocephalus orarius.* **Lighthouse Bay, Exmouth, WA, Australia Photography by Alex Hoschke.and Glen Whisson.**

Arafura Smooth Seasnake

Parahydrophis mertoni (Roux, 1910)

Distribution and Habitat. Papua New Guinea in the Arafura Sea, and Northern Territory, Queensland, Australia. This species occurs in the coastal mangrove, estuarial mangroves, and mudflats (Heatwole 1999). Type locality: Sungei Waskei, Wokam, Aru Island, Indonesia .

Identification. Blue gray, to olive brown dorsal patter with 40-50 irregular darker cross bands joined at the midline, with a lighter center in each band. Head shields have yellow spots except for on the rostral and labials which are black (de Rooij N 1917). The average length is 50 cm. The body scales are smooth and imbricate. Dorsal scale count is 36 to 39 rows at the mid-body, ventral scale count is 153 to 161, subcaudal scales count is 29 and 35, and the cloacal scale divided. Ventral scales are characteristically large in this species. Adults grow to a total length of 50 cm (Cogger 2000). No sexual dimorphism in SVL or tail length seems present (Parkin and Schembri 2011).

Figure 13.24. The distribution of *Parahydrophis metoni.*

Natural History. *Parahydrophis* is a monotypic genus closely related to *Ephalophis* and sister to *Hydrophis* (Sanders et al 2013). Both monotypic genera represent early lineages in the subfamily Hydrophinae and as such retain many of the more primitive traits of land snakes such as a cylindrical head and widened ventral scales. Unlike its other close relative *Hydrelaps* which forages terrestrially at the waters edge on mudflats, *Parahydrophis* forage in mangroves and tidal creek banks for small fish. The species has also been cited as foraging the mudflats at night, when submerged at high tide. Average litter size is three, though it is undetermined if breeding occurs throughout the year or is seasonal (Parkin and Schembri 2011).

Figure 13.26. *Ephalophis greyae.***Photography by Victoria de Bruyn © Broome Community Seagrass Monitoring Project**

North-western Mangrove Seasnake

Ephalophis greyae (Smith, 1931)

Distribution and Habitat**.** Endemic to Australia's Northwestern coast from the Kimberley region to Shark Bay and is associated with mangroves, estuarine mudflats and coastal shallow flats, found at depths from 0-10 meters. (Lukoschek et al. 2010) (Heatwole 1999) Type locality**:** Cape Boileau, Western Australia.

Identification**.** The body scales have a median keel forming 19 to 21 dorsal scale rows at mid-body, 159 to 171 ventral scales, and 27 to 33 sub caudal scales with the cloacal scale divided (Cogger 2000).

Natural History**.** *Ephalophis* is a monotypic genus closely related to *Parahydrophis* and a sister to *Hydrophis* (Sanders et al. 2013). Both monotypic genus represent one of the earliest lineages in the subfamily Hydrophinae and as such retain many of the more primitive traits of land snakes such as a cylindrical head and widened ventral scales. This species forages the waters edge at high tide, and the out of the water on the sand flats at low tides in search of mudskippers (Oxudercidae), its primary prey. Voris also includes gobies (Gobiidae) as a prey. The snakes will consume both the mudskipper and its eggs and has been observed entering the mudskippers burrows in its search. It has also been observed entering crab burrows in search of hiding gobies (Voris & Voris 1983; Lukoschek et al 2010).

Figure 13.25. The distribuition of *Ephalophis greyae*

Port Darwin Seasnake

Hydrelaps darwiniensis (Boulenger, 1896)

Distribution and Habitat**.** Endemic to Australia occurring in the coastal waters of Queensland, Northern Territory and Western Australia. Type locality: Port Darwin, Northern Territory, Australia

Identification**.** Twenty-five to 30 dorsal scale rows at mid body 163 to 72 ventral scales,

Figure 13.27. The distribution of *Hydrelaps darwiniensis*

and 27 to 39 subcaudal scales which may be single but occasionally divided anteriorly. Cloacal scale is divided. (Cogger 2000)

Natural History**.** This monotypic genus and a sister lineage to *Hydrophis* (Sanders et al 2013). Guinea et al. observed specimens crawling onto mud flats and into crab burrows in search of prey, during high tide at 15:00 h. This indicates this species feeds diurnally, and likely feeds on land where its movement is adept for a sea snake. Guinea also observed specimens drinking from shallow upper tidal freshwater pools indicating that like *Laticuada, Hydrelaps* may use these rainwater pools as a water source (Guinea et al 1993).

Figure 13.28. *Hydrelaps darwiniensis*. **From Boulenger 1896.**

Bighead Seasnake

Hydrophis annandalei (Laidlaw, 1901)

Distribution and Habitat**.** Found in the Gulf of Thailand in Cambodia south to Indonesia, including Peninsular Malaysia, Singapore, Java and Sumatra in Indonesia and Vietnam. A record from Brunei however is suspected to have potentially been a washed-up vagrant and may not be a part of the species extant range. Throughout its range the species is associated with shallow muddy coastal waters with one freshwater record in the Pattani region in Thailand (Rassmusen et al 2010). Type locality: Patani Bay, Thailand.

Identification**.** As the common name indicates, this species possesses a notably large head for a sea snake, with irregular head shield and a stout body (Lim 1991). Some noteworthy squamation detail includes a W-shaped rostral scale which is longer than it is wide, a triangle shaped mental scale, and a large scale beneath the eye between super labials 5 and 6. Small distinct ventrals are present which number 363 plus 65 subcaudal scales Body scales are small and highly irregular with a high body scale count of 62-82 scale rows at the neck, and 74-97 body scale rows. The body has 46 dark body bands against a more pale gray backdrop, which narrow on the sides, and can fade with age to a darker dorsal, lighter ventral gradient pattern (Uetz and Hosek 2020) (Das 1993).

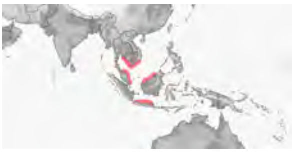


Figure 13.29. The distribution of *Hydrophis annandalei*

Natural History**.** This species is known from shallow muddy coastal waters. Prey includes members of the family Clupeidae which includes herrings, shads, sardines, hilsa, and menhadens, based on stomach content studies (Voris and Voris 1983).

Anomalous Seasnake

Hydrophis anomalus (Schmidt, 1852)

Distribution and Habitat**.** Found in the South China Sea including Malaysia, Vietnam, Sumatra, Java, and Borneo (Uetz and Hosek 2020). Type locality: Listed as "Rhede von

Samarang", Java.

Identification. This species has a light whitish base ton with 30-36 darker bands which taper dorsally creating a triangular shape. A pair of elongated shields separate the nasals, the rostral is divided into 4-5 scales. rostral divided into four or five scales. Dorsal scale rows at mid body are 31–35 and ventrals number 210– 256 (Chan et al. 2015).

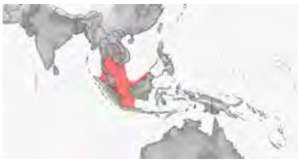


Figure 13.31. The distribution of *Hydrophis anomalus.*

Natural History**.** Formerly place in the monotypic genus *Thalassophios,* little is known about this species ecology and behavior, outside of it's association with estuaries (Chan et al. 2015). Stomach sample studies have shown Conger eels (Congridae) to be one of the prey items of this species (Voris & Voris 1983).

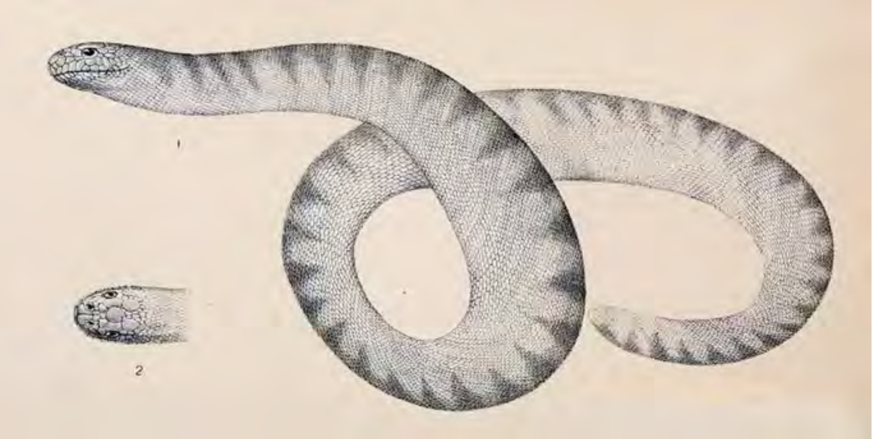


Figure 13.32. *Hydrophis anomalus***. From Schmidt 1852.**

Black-Headed Seasnake

Hydrophis atriceps (Günther, 1864)

Figure 13.33. The distribution of *Hydrophis atriceps.*

Distribution and Habitat. This species is known Indonesia, Malaysia, Vietnam, Thailand, Singapore, China, Taiwan and the Philippines, and Papua New Guinea, Northern Territory and Western Australia. Older literature includes Myanmar and India in this species distribution; however these records should actually be referred to as *Hydrophis fasciatus*. It is associated with turbid off shore waters over sandy bottoms 5-10 km from shore at depths of 20-30 m (Rasmussen et al 2010a; Leviton et al 2003). Type locality: Thailand.

Identification**.** This species head is small, with a long body that becomes slender anteriorly. The body is a light yellow with black banding that narrows dorsally and may or may not connect at mid body. In juveniles the bands may be complete the length of the body, becoming less complete with age. Beneath incomplete bands at mid body, darker spots may be found. The head and neck are a dark olive or black color. Dorsal scales at the thickest part of the body are hexagonal in shape and maybe be juxtaposed or slightly imbricate. Dorsal scale

Figure 13.34. *Hydrophis atriceps.* **From Cao et al. 2014.**

row count is 25-30 at the neck, and midbody scale row count is 39-49. Ventral scales count is 323-452. This species is slightly size dimorphic with the total length in males coming in at 1100 mm and females 990 mm (Leviton 2003).

Natural History. Little is known about the natural history of this species. Their prey is primarily comprised of eels that hung along sandy sea bottoms at depth of 20-30m (Sherratt et al. 2018). Smith reported this species is also commonly associated with the mouths of rivers (Smith 1926).

Faint-Banded Seasnake

Hydrophis belcheri (Gray, 1849)

Distribution and Habitat. Known from south east Asia (Cambodia, Indonesia, Malaysia, Philippines; Singapore; Thailand; Vietnam), Papua New Guinea, and questionably in Australia, where only the type specimen was found. It is presumed to occur in waters over soft bottoms of depths between 0-15 meters (Rasmussen & Sanders 2010; Cogger, 2000). Type locality: Listed as New Guinea, though some authorities question this locals validity.

Identification. This species pattern consists of 52-70 olive-gray bands over an off-white/yellowish backdrop. Bands widen dorsally and fade ventrally ventrally with an off-white to white ventral coloration. This species has a medium sized head, narrow neck and elongate body which is compressed posteriorly, and two to four times the diameter of the neck. The head pattern is an olive green with a yellow hotshot shaped spot running through e prefrontal scales and around the eyes. The fourth supralabial borders the eye, though in rare occasions two supralabials can contact the eyes, either 3 and 4 or 4 and 5. Dorsal scale count rows are 24-27 at the neck and 32-37 at mid body. Ventrals number 278-313 (Kharin & Cheblukov 2007).

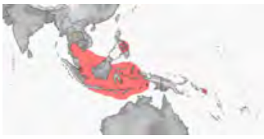


Figure 13.35. The distribution of *Hydrophis belcheri*

Natural History. *Hydrophis belcheri* is an eel specialist, primarily feeding on worm eels (Moringuidae) and other eels (Anguilliformes). Though errantly rumored to be the most lethal snake on the planet, the actual LD50 when tested intramuscularly is 0.07 mg/kg which does make this species the fifth most toxic snake when tested intramuscularly (Voris & Voris 1983; Rasmussen & Sanders 2010; Tamiya and Puffer 1974; Steinhoff, 2018).

Figure 13.36. *Hydrophis belcheri.* **From Boulengeri 1896.**

Peters' Seasnake

Hydrophis bituberculatus (Peters, 1872)

Distribution and Habitat. Known from Phuket harbor in Thailand and Colombo in Sri Lanka. It is thought to live over sandy gravel bottoms, but little is known of its actual habitat

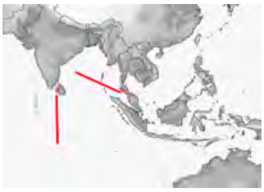


Figure 13.37. **The distribution of** *Hydrophis bituberculatus*

preferences. (Rassmussen & Lobom 2010a) Type locality: Colombo, Sri Lanka.

Identification**.** The head of this species is blackish above, with a lighter whitish grey color at the supralabials, and a light grey color around the eyes. The body is banded with black bands and significantly narrower light colored (grey/white) interspaces. Males have 37-51 bands on the body, 6-10 on the tail and females 38-50 bands on the body, 6-8 on the tail. These interspaces are wider ventrally than dorsally, where they average 1-1.5 scales where they join at the top. Interspaces are narrow anteriorly, widen through the body, and narrow once more posteriorly. Banding continues on to the tail where the interspaces become thinner, approximately one scale wide. The first two interspaces from the head are often not joined. Embryos showed a higher color contrast than their adult counter parts (black bands with white interspace), and the holotype showed almost not pattern, though it is unclear whether this was an older animal showing high ontogenetic shift, or if alcohol bleaching was to blame. Dorsal scales feature a two crested median keel across the entirety of the body, with 25-29 scale rows at the neck and 43-50 scale rows at midbody. Ventral scales are distinct, approximately twice as wide as the adjoining scales, narrowing posteriorly, and number 247-290. Average total length is 110 cm in both males and females, with only slight size variance between the sexes, with the largest recorded male having 1 cm longer tail than the longest recorded female (Rasmussen 1992).

Natural History**.** From its initial description in 1872 by Peters, until Rasmussen's rediscovery of the species in Thailand in 1992, the holotype was the only known specimen. Rasmussen examined 25 specimens caught by trawl from 1987-1989 (8 females, 17 males), though the fisherman did not disclose exact positions of their fishing grounds, so despite the additional specimens, little is still known about this species habitat preferences. Stomach contents of the examined specimens showed five potential species of eels (Anguilliformes), though contents were to digested to determine which species of eels. One of the eight females contained three full term embryos. Four females in total were collected after, and none of others with embryos, indicating November may be the end of the species birthing period (Rasmussen, 1992).

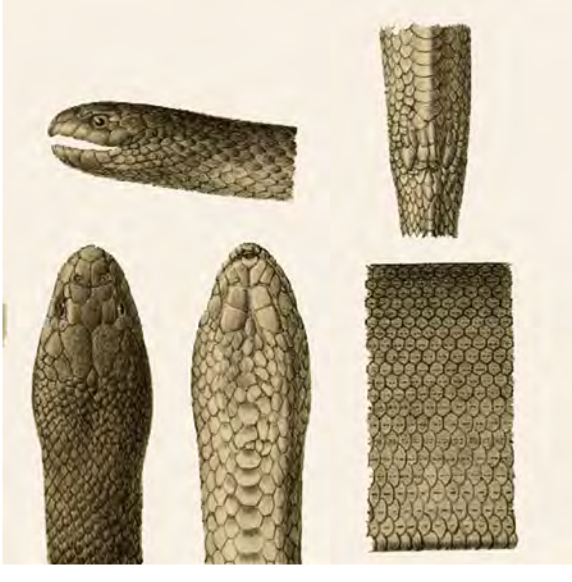


Figure 13.38. *Hydrophis bituberculatus.* **From Peters 1873**

Brook's Small Headed Seasnake

Hydrophis brookii (Günther, 1872)

Distribution and Habitat**.** This species is known from Indonesia, Malaysia, and Thailand known from subtidal muddy regions and estuaries. It is also reported from a freshwater lake in Thailand (Rasmussen et al 2010g). Type locality: Sarawak, Malaysia (Uetz and Hosek 2020).

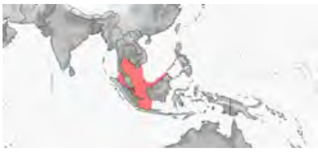


Figure 13.39. The distribution of *Hydrophis brookii* Below. Figure 13.40.

Identification. The head of this species is very small, black in color, with a yellow hotshoe mark on top. The body is long and slender anteriorly which compresses posteriorly becoming to three times the diameter of the neck. The body is bluish white with 60-80 dark grey to black bands which are complete anteriorly and twice the width of the interspace, but become incomplete ventrally down the posterior of the body. Body scales are slightly imbricate, and hexagonal in shape often showing a median tubercle. There are 23 to 31 scale rows at the neck, and 37-45 at midbody. Light colored ventrals are distinct and number 328-414. Adult size is 104cm (Leviton et al. 2014; Rasmussen et al. 2011b).

Natural History. Little is known about this species. Stomach content studies reveled prey items to include gobies (Gobiidae), worm eels (Moringuidae), and snake eels (Ophichthidae). (Rasmussen et al. 2010f; Voris and Voris 1983)

Figure 13.40. *Hydrophis brookii* **.Photography by JCM (left) Figure 13.41 A Vietnamese stamp with an artistic representation of** *Hydrophis brookii* (right)

Dwarf Seasnake

Hydrophis caerulescens (Shaw, 1802)

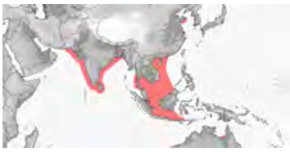


Figure 13.42. The distribution of *Hydrophis caerulescens*

Distribution and Habitat. This species is wide spread, common in South East Asia it is known from Myanmar, Malaysia, Indonesia, Singapore, and Vietnam, but rare in south Asia including Pakistan, India, and Bangladesh. To the north it is known from the South China Sea as well as the coasts of Shandong and Guandong in China. It is also known from Queensland Australia, and New Caledonia. It is known from depths from 0-25 meters above seagrass beds and muddy subtidal regions (Rasmussen et al 2010e). Type locality label cites as "Indian Ocean: Vizagapatam."

Identification. As the name indicates this is a smaller species of sea snake with the average reported length being 0.6cm. The head of this species is black with enlarged head shields. The third and fourth supralabials contact the eyes. The body of this species is is blue-grey above, with 41-43 black blotches or transverse bands, with 7-9 bands at the tail.

These bands taper ventrally and can become indistinct in older adults. Body scales are feebly imbricate and number 37-39 at midbody. At the thickest part of the body, these scales are quadrangular or hexagonal in shape. Ventral scales are barely wider than adjacent body scales and the ventral scale count is 266-287 (Cogger, 2000).

Natural History. Voris and Voris found prey to include true gobies (Gobiodidae), worm eels (Moringuidae), and burrowing gobies (Trypauchenidae) in stomach content. Little is known about the life cycle of this species. Fry et al reported a single brood containing seven young. (Voris & Voris 1983; Fry et al. 2001)

Figure 13.43-44.*Hydrophis caerulescens*. **Photography by Prathamesh Ghadekar**

Cantor's Narrow Headed Seasnake

Hydrophis cantoris (Günther, 1864)

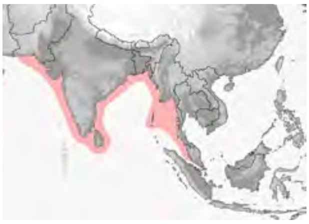


Figure 13.45. The distribution of *Hydrophis cantoris.*

Distribution and Habitat. Pakistan, India, Sri Lanka, Myanmar, to the western Malay Peninsula and Iran (Heatwole 1999; Rezaie-Atagholopour et al 2016). This species habitat includes shallow coastal waters with soft floors (Leviton *et al.* 2003). Type locality: Penang, Malaysia.

I**dentification.** A former member of the genus Microcephalis, this species pointed head and slender neck are considerably smaller than the rest of their body. The head is yellow in color, and the neck is a darker black color with 20-28 faint yellowish incomplete bands that fade towards the body to a darker olive color dorsally graduating to a yellow to off white ventrally. The notably slender neck has 23–25 to scale rows, but as little as 21 have been reported, with a midbody scale count of 41 and ventrals numbering 404-468. Average total length is 1450 mm for males and 1880 mm for females. (Leviton et al. 2003; Rezaie-Atagholipoir et al. 2016)

Natural History. Very little is known about this species, and it is considered rare (Rassmussen et al. 2010d).

Slender-necked Seasnake

Hydrophis coggeri (Kharin, 1984)

Distribution and Habitat. This species is know from Western Australia, Vanuatu, Fiji, the Philippines, Indonesia, and New Caledonia. It is associated with shallow coastal waters, shallow mangroves, coral sea beds, sea grass beds, mudflats, inner reef beds, sea grass fields, coral reef floors, mangroves and ocean floors with sediments and loose organic materials in the 1-40 m depth range. (Palomares and Pauly 2021; Ineich and Laboute 2002). Type

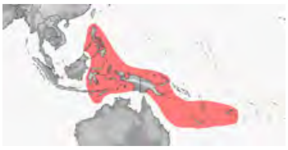


Figure 13.46, The distribution of ***Hydrophis coggeri,***

locality: Port Suva, Fiji.

Identification**.** *Hydrophis coggeri* is a banded sea snake with a thin cylindrical body, a black tail tip, and no spots or markings between the darker colored bands. *Hydrophis coggeri* is differentiated from all other *Hydrophis* species except *Hydrophis donaldi*, *Hydrophis sibauensis* and *Hydrophis torquatus diadema* based on ventrals that are not divided by a longitudinal furrow. This species has 29-30 scale rows the neck, 33-35 scale rows at midbody and 246-288 ventral scales. It can be distinguished from *Hydrophis donaldi* based on having 30-42 bands around the body rather than 47-56 in *Hydrophis donaldi*, and the lack of strongly spinous body scales as is present in *Hydrophis donaldi*. Average adult length is 1 m, with a maximum recorded length of 1.364 m, and females being larger and heavier than males (Cogger 2002).

Natural History**.** *Hydrophis coggeri* is a highly nocturnal species which forages the seafloor in search of its main prey which includes eels of the families Ophichthidae and Congridae. In Fiji the preferred prey includes moray eel species (*Callechelys melanotaenia, Leiuranus semicinctus*, and *Myrichthys colubrinus*). A specimen feeding on eel tail catfish (*Plotosus anguillaris*) has been observed and this may also be common prey. This species gives birth to 1 to 8 live offspring. *Hydrophis coggeri* is a highly venomous species, and it's venom has an intramuscular LD50 of 0.24 mg/ kg. There have been reports of this species quickly pursuing those that provoke it and can be considered dangerous to swimmers, divers, and those who disturb it (Palomares and Pauly 2021; Ineich and Laboute 2002).

Figure 13.47. *Hydrophis coggeri* **from Baie des Citrons, Nouméa, New Caledonia. Photography by Pauline Fey.**

Spine-bellied Seasnake

Hydrophis curtus (Shaw, 1802)

Distribution and Habitat**.** This species is very widespread with one of the most extensive distributions of all sea snakes, *Hydrophis platurus* being one of the only species more widespread. *Hydrophis curtis* range includes the Arabian Gulf (Oman, United Arab Emirates, Iran, Kuwait, Iraq, Qatar, and Saudi Arabia) all of south Asia (India, Sri Lanka, Pakistan, and

Bangladesh), South East Asia (Indonesia, Philippines, Malaysia, Thailand, Myanmar, Brunei, Singapore, and Vietnam) and south east to Papua New Guinea and northern Australia. The furthest southeast recorded specimen was found in New Caledonia, but it is uncertain if this specimen represents a vagrant individual or a breeding population. This species in known from waters between 4-55 m, and is adapt to a wide variety of tropical shallow water habitats including: gulfs, bays, estuaries, and occasional entries into rivers and freshwater habitats. It is associated with waters over soft-sediments, including sands, muds, and seagrass beads adjacent to coral reefs (Rassmussen et al 2021). Type locality: None given.

Identification**.** The presence of large hook like keels on the ventral and lower dorsal scales, but absent on the upper dorsal scales easily distinguishes this species from most others. These large hook-like spines are more prominent in males than females and may play a role in breeding. The spines in males are most prominent during breeding season, meaning the rugosity of the scales maybe hormonally controlled as seen in many species of frogs and fish. This is a short stout sea snake, with three known pattern variations. Color and pattern are variable. The most common pattern is a darker grey dorsally graduating to a grey-whitish ventrally, with lighter grey bands. The two less common pattern and color forms include a yellowish body with blackish bands or a blackish grey body with darker black dorsal bands. In all three-color forms, the dorsal bands are typically fused laterally, creating a zigzag pattern with a black tip of tail. This species has a large head, with a notably tridentate rostral scale, with two notches or groves where the tongue protrudes, rather than a singular notch. The parietal scales on this species are divided into small shields with 7–9 supralabials with the second supralabial contacting with the prefrontal scale and the third and/or fourth touching the eye. Body scale rows number 28– 38 at the neck and 32–43 at the mid-body. Ventral scales are present and distinguishable, number 147–201. Ventral scales are larger (half the body width) and hexagonal shape anteriorly and becoming smaller posteriorly. The average total length for this species is 80-110cm in total length, with no sexual dimorphism in total length. *Hydrophis curtus* can superficially resemble *Hydrophis ornatus*, but can be easily distinguished from *Hydrophis ornatus* in having in having a zigzag pattern form, rather than the even bands in *Hydrophis ornatus*. Another distinguishing distinction is *Hydrophis curtus* has divided parietal forming small shields not present in *H. ornatus* (Buzás et al 2018; Avolio et al 2006; Rezaie-Atagholipour et al 2016).

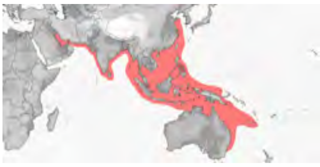


Figure 13.48. The distribution of *Hydrophis curtus,*

Figure 13.49. The "Great Hydrus, *Hydrophis pelamidoïdes*" **is a synonym of** *Hydrophus curtus.* **The illustration is from Iconographia Zoologica - Special Collections University of Amsterdam .**

Natural History. The diet includes a wide range of prey items including amphipods, cuttlefish (sepia), squids, and over 33 families of fish ranging from bottom dwelling benthic fish, near bottom dwelling demersal fish, and even open water pelagic fish. The ability to be both a habitat and prey generalist has allowed this species to occupy a considerable range. It is believed that deep waters act as a barrier for dispersal in this species, with an average known depth of 40 m, and a maximum known depth of 55 m. Genetic studies indicate *H. curtus* expansion into Australia and South Was Asia is recent or sudden. Studies in Australia indicate annual breeding with a 6–7-month gestation period resulting in an average of 4.3 young being born between March and June. In Australia females select shallow, sheltered areas such as the

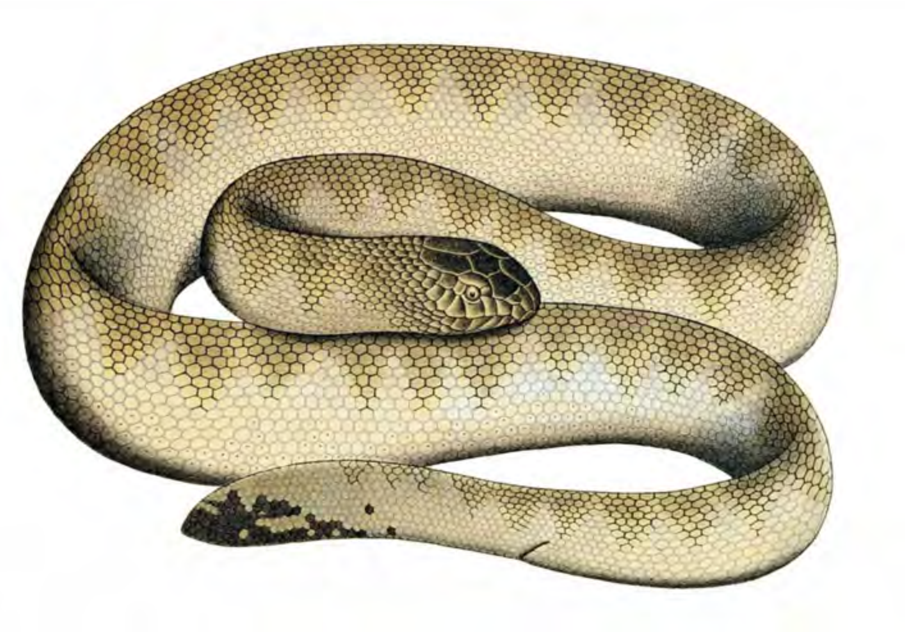


Figure 13.50. *Hydrophis curtus.* **Art work from Soedirman(1916).**

mouths of bays, estuaries, and sea grass beds during the summer months prior to birthing, indicating these habitats could be critically important nursery grounds to the species (Udyawer et al. 2016). While there is anecdotal evidence this species is in decline in Asia, due to the widespread spread nature of it as range, it is listed as least concern by the IUCN. Buzás et al. found the species in the United Arab Emirates, and that it is "generally inoffensive" except for one specimen that "jumped" out of a transport box to attempt to bite the handler's glove. Heatwole reported this species to be "very aggressive if provoked or handled". The venom contains postsynaptic nuertoxins and likely myotoxins and should be treated as a potentially lethal snake (Voris and Voris 1983; Buzás et al 2018; Rassmussen et al 2021; Rezaie-Atagholipour 2012; Heatwole 1999). Taxonomic note: A review of a large number of specimens of *Hydrophis curtus* and *Hydrophis harwickii* did not support speciation based on morphological analysis, and while molecular data does show a deep divergence of the Indian Ocean (*H. curtus*), and South East Asia Australiasia (*H. hardwickii*) clades, the authors will defer to Rassmussen et al's 2021 determination that *Hydrophis curtus* be viewed as a single species until further studies are conducted (Rasmussen et al. 2021).

Annulated Seasnake

Hydrophis cyanocinctus (Daudin, 1803)

Distribution and Habitat**.** This species has a wide range extending west from the Arabian Gulf (Iran, Iraq, Kuwait, Oman, Qatar, United Arab Emirates, and Saudi Arabia), throughout south India (India including Andaman Islands and Nicobar Islands, Sri Lanka, Pakistan, and Bangaladesh) east to south east Asia (Philippines Indonesia, Cambodia, Thailand, Vietnam, Palua), north east to the South China Sea (China, Taiwan, and possibly Japan), and south to northern Australia and Papua New Guinea. It was originally reported present in Solomon Islands, but the author of this finding later retracted this. This species is associated with shal-

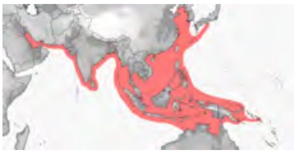


Figure 13.51. The distribution of ***Hydrophis cyanocinctus***

low seas over muddy bottom with depths ranging from 0-30 m. In Pakistan they have been seasonally found in shallow mangrove swamps during monsoons (Minton 1966; Rasmussen et al 2010f). Type locality is listed as "Coromandel" (Uetz and Hosek 2020). *Authors note: Coromandel Coast likely refers to East India.*

Identification**.** *Hydrophis cyanocinctus* is a long and very slender banded sea snake, with a dark olive or gray body which lightens ventrally. The darker body bands number 50–75 which are broader dorsally, tampering to a point ventrally, with widening interspace at the body, which narrows at the head and tail. This species has juveniles presenting a black head with a yellow horseshoe-shaped marking on top of the head with the horse-shoe marking fading with age. The head of this species is slightly enlarged, and the body is elongate but not markedly slender anteriorly. Dorsal scales are imbricate and at the thickest part of the body present round or bluntly pointed tips, and number 39–41 scale rows at mid-body and 25–31 scale rows at the neck. Ventral scales are only slightly distinguishable and number 300–359. Average total length is 1243mm, though exceptionally large specimens, as large as 1495 mm have been recorded (Rezaie-Atagholipour et al 2016). Juveniles of *Hydrophis cyanocinctus* and *Hydrophis lapemoides* can be easily confused, however, the mid-body scale shapes are distinct between these two species. *Hydrophis cyanocinctus* having bluntly pointed scales, and *Hydrophis lapemoides* having hexagonal or quadrangular scales. (Voris and Voris 1983; Rezaie-Atagholipour et al 2016; Egan 2007).

Figure 13,52. *Hydrophis cyanocinctus.*
Photography by Anslem da Silva.

Natural History**.** This species is often seen basking on the surface during the days of warmer months. A 2013 stomach content study in Pakistan's Hara Protected area revealed members of the goby family (*Boleophthalmus, Parachaeturichthys, Periophthalmus, Scartelaos, Taenoides*) comprised 77% of the stomach contents, with all but one species belonging to the mudskippers (Ocudercinae) group. Other known prey items include conger eels (Congeridae), pike conger (Muraenesocidae), gobies (Gobioididae), eel catfish (*Plotosus lineatus*), and unidentified eels (Anguilliformes). This species produces between 3-16 live young, with birthing seasons varying through out their range. Like many sea snake species, it is not uncommon to find this species with heavy barnacle infestations of the sea snake specializing barnacle *Platylepas ophiophila*. This species has a potent myotonic venom and has caused human fatalities. While inoffensive in the water may bite if restrained. (Buzás et al 2018; Voris and Voris 1983; Rezaie Atagholipour et al 2013; Egan 2007).

Fine-Spined Seasnake

Hydrophis czeblukovi (Kharin, 1984)

Distribution and Habitat**.** This species is only known from North and North West Australia with a single record from Bam Island on the north coast of Papua New Guinea. This species has been found as bycatch in deep water trawls and is thought to occur in deep waters over soft substrate up to 110 m deep (Rasmussen & Lukoschek 2010). Type locality: Arafura Sea.

Identification**.** As the common name of the now synonymized Geometrical sea snake (formerly *Hydrophis geometricus*) would indicate, specimens of this species can feature an elaborate and distinctive pattern consisting of two rows of pentagonal like dark grey spots separated by thin lighter colored interspaces creating a very distinct geometrically webbed like appearance. The spots consist of 37 large hexagonal spots running down the back, with a second row of 36 spots, that are smaller and less distinct than the upper row. This patterning becomes much less pronounced and indistinct ventrally, as well as along the base of the tale. The head is brown in color, with large sublingual, with.a moderately sized triangular mental scale. The body scales anteriorly are imbricate, but gradually become hexagonal and without overlap posteriorly. The scales also graduate from smooth at the neck progressing anteriorly to a weak keel consisting of 2-4 tubercles, and by midbody the weak keels transition to stout spines. The neck of this species has 33 scale rows, and 57 scale rows at mid-body. The 306 ventral scales and 45 subcaudal scales are clearly pronounced, being twice the size of the surrounding scales, with 1-2 slight tubercles present anteriorly. There are four cloacal shields adjacent to each other with the posterior shield after the cloacal opening being the largest of the four (Kharin & Hallerman 2010).

Figure 13.53. The distribution of *Hydrophis czeblukovi*

Natural History**.** This species is considered rare, with very little known about their natural history. To date, only eight specimens of this species have been found. (Rasmussen & Lukoschek 2010; Kharin & Hallerman 2010)

Taxonomy Note: Kharin described *Hydrophis czeblukovi* in 1984, based on two female specimens which had been collected by Professor V. P. Shuntov in 1968. In 1986, two *Hydrophis geometricus,* based on three specimens from Western Australia, however upon review, *Hydrophis geometricus* was found to be synonymous with *Hydrophis czeblukovi*, and thus not recognized here as a valid taxon by the authors. Due to the extreme rarity of this species, little is know about its conservation status or population trends and is listed Data Deficient by the IUCN (Kharin & Hallerman 2010; Rasmussen & Lukoschek 2010).

Rough-scaled Seasnake

Hydrophis donaldi (Ukuwela, Sanders, and Fry 2012)

Distribution and Habitat**.** Endemic to the Gulf of Carpenteria, Queensland Australia, where it is commonly associated with estuarine habitats consisting of shale, mud, and/or seagrass bottoms. The species has been found at the mouths of the Mission River and Hey Creek at the connection to the Albatross Bay in Weipa, Queensland. Specimens have been found via spotlighting from a boat traveling at low speeds in the early evening over water 10 m or less deep (Ukuwela et al 2012). Type locality**:** Gulf of Carpentaria, Weipa, Queensland, Australia.

Identification. *Hydrophis donaldi* is a recently described, smaller sea snake with a total length between 92-101 mm. The pattern of this sea snake consists of 47-64 dark brown bands over a lighter yellowish brown interpsace, that are wider than the interspaces. These bands are broad dorsally which narrow latterally, and do not connect ventrally. The bands are also darker in coloration in the first third of the body. The head is brown in color in adults, but one juvenile specimen was found with a black head and a more highly colored body, with turquoise blue interspaces rather than light grey and black and bands. There are 33-35 scale rows at midbody and 29-30 at the neck. The 246-288 ventral scales are distinct and bear two strong spines on each. *Hydrophis donaldi* is distinguished from all other *Hydrophis* species except *Hydrophis coggerii*, *Hydrophis sibauensis* and *Hydrophis torquatus* by having ventral scales that are not divided by a longitudinal keel or furrow, having 29-30 costal scale rows around the neck and by having 246-288 ventral scales. From *Hydrophis coggeri, Hydrophis sibauensis* and *Hydrophis torquatus* it can be identified, by having stronger spines on the body scales, as well as other morphological variances. *Hydrophis donaldi* can be distinguished from *Hydrophis coggeri* based on *Hydrophis donaldi* having more body bands (37-56 compared to 30-42), a larger head blunter head, and a lower average ventral scale count (246-288 compared to 280-360). *Hydrophis donaldi* can be differed from *Hydrophis sibauensis* based on having a higher number of scale rows at the neck and more scale rows around the neck (29-30 in *Hydrophis donaldi* compared to 25-26 in *Hydrophis sibauensis*). *Hydrophis donaldi* can be differed from *Hydrophis torquatus diadema* in having a lower scale row count at the neck, (33-35 compared to 35-42) (Ukulele et al 2012).

Figure 13.54. The distribution of *Hydrophis donaldi*

Natural History. This species was first found by Bryan Fry, and formally described in 2012. It is named after Dave Donald, who was the skipper on the boat at the time of its initial discovery in 2000. From 2000-2012 only nine specimens were found, making it one of the more uncommonly seen species in its poorly surveyed range. As such little is known about its ecology (Ukuwela et al 2012).

Elegant Seasnake

Hydrophis elegans (Gray, 1842)

Figure 13.55. The distribution of *Hydropis elegans.*

Distribution and Habitat. *Hydrophis elegans* is endemic to the waters around Northern Australia, Indonesian West Papua, and Papua New Guinea. The species ranges into Australia's temperate waters as far south in Australia as Kalbarri on the western coast and Gold Coast on the eastern coast giving it one of the furthest south distributions of any sea snake species. In terms of habitat this species is a generalist, inhabiting waters above sand, and mud, coral reefs, seagrass beds, subtidal rock, subtidal gravel, subtidal sand, rocky reef, estuaries, and even up rivers and into freshwater habitats where it has been found by beam trawlers 12 km upstream from the sea on the Burnett River in Queensland. This species is believed to prefer depths between 3.7-26 m, however it has been found in water as shallow as 2 m, and as deep as 250 m. However, Limpus noted the upriver occurrences have only been recorded between December and January and may be seasonal in nature. The discovery of *Hydrophis elegans* 250 m deep in Browse Basin, Australia, marked the first known records of a sea snakes' presence in the dark cold deep waters known as the mesopelagic or "twilight" zone, though the frequency and importance of this deep water behavior is yet unknown and merits more study (Limpus 1975; Milton et al 2010; Crowe et al 2019; Department of the Environment, 2021). Type locality: Port Essington, N. T.

Identification**.** *Hydrophis elegans* is the longest of all sea snakes, with a maximum recorded length of 2.6 m. The body pattern consist of 39-44 blackish bands over a grey or yellowish body, which are widest along the spine and constrict ventrally. Between each bands within the yellowish interspace lies a row of smaller black dots that can produce a secondary black band when joined. This species has an elongated body compressing posteriorly. The body scales are imbricate, with 37-49 rows at the mid-body. The 345-432 ventral scales are only slightly wider than the adjacent scales. Females are generally larger than males, with males attaining an average SVL of 120 - 160 cm and females an average SVL of 140-180 cm. Female *Hydrophis elegans* also have larger heads than males, and as such females prey on larger food items than their male counterparts. *Hydrophis elegans* can be deciphered from the sympatric *Hydrophis major* by having more bands (39-44 in *Hydrophis elegans* compared to 31-40 in *Hydrophis major*), a longer overall length, and a smaller head (Kerford 2005; Department of the Environment, 2021; Milton et al 2010).

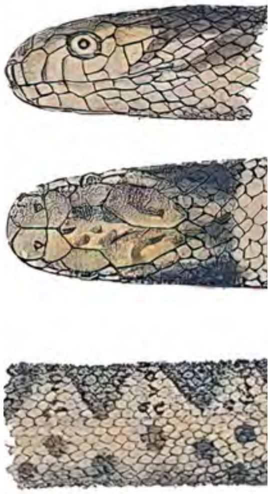


Figure 13.56, *Hydrophis elegans* **from Kretf 1869.**

Natural History**.** *Hydrophis elegans* is a generalist feeder with a diet including a variety of bottom-dwelling fish such as Catfish (*Euristhmus*), moray eels (*Muraenidae* and *Nettastomatidae)*, snake eels (*Ophicthyidae)*, gobies (Gobiidae), Sillago (Sillaginidae), snake eels (Ophichthidae), and squid (*Teuthoidea*). Known predators include tiger sharks (*Galeocerdo cuvier*), of which *Hydrophis elegans* account for 50% of young tiger sharks prey within their range. *Hydrophis elegans* reaches sexual maturity around 2 years old, with the oldest known specimen being 10 years old. This species can reproduce every year or every 2-3 years, with recorded clutch sizes of 12-13 offspring in the Norther Prawn Fishery and Great Barrier Reef. Studies have shown the size of the litter, and size of the resulting offspring vary with the length of the female, with larger females producing larger quantities of bigger offspring (Voris and Voris 1983; Fry et al 2001; Kerford 2005; Milton et al 2010; Department of the Environment, 2021)

Striped Seasnake

Hydrophis fasciatus (Schneider, 1799)

Distribution and Habitat**.** This species is mainly known from southeast Asia where it occurs in Cambodia, Malaysia, Myanmar, Thailand, and Vietnam, but absent from Borneo. It also occurs in south Asia where it is considered rare, known from Eastern India and Bangladesh, but absent in Sri Lanka. It is associated with soft bottom coastal waters ranging from 0-12 meters in depth (Rasmussen & Lobo 2010c; Uetz and Hosek 2020). Type locality: None given.

Identification**.** The head of this species is a dark olive to black color with yellowish triangular-oval saddles forming a banded appearance of dark inverted triangles which fade to gray ventrally. Posteriorly the body is grayish dorsally and a whitish color ventrally. Juveniles

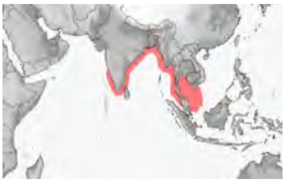


Figure 13.57. The distribution of *Hydrophis fasciatus*

spots appear rhomboidal and can form concentric circles. This is a microcephalic snake, with a small head, slender anterior and long body. Scales on the thickest part of the body are hexagonal in shape, and slightly imbricate, with a mid-body scale count of 47-58 rows, and a neck scale count of 28-33 rows, noting a dramatic scale count increase posteriorly. Ventral scales number 414-514. Males of this species are larger than females, males having a total length of 1100 mm of which 100 mm makes up the tail and females a total length of 990 mm, with 75 mm comprising the tail. (Leviton et al 2003).

Natural History**.** This microcephalic snake is a nocturnal, shallow water, eel specialist, feeding on snake eels (Ophichthidae), worm eels (Moringuidae), burrowing (eel like) gobies (Trypauchenidae), moray eels (Muraenidae), and false moray eels (Xenocongriae) (Voris and Voris, 1983; Glodek and Voris 1982; Rasmussen & Lobo 2010c; Leviton et al. 2003).

Narrow-Headed Seasnake

Hydrophis gracilis (Shaw, 1802)

Distribution and Habitat**.** This species is widespread known from the Arabian and Oman Gulfs (Oman, Iran, Iraq, Kuwait, Bahrain, Qatar, and United Arab Emirates), in south Asia (Pakistan, India, Sri Lanka, and Bangaladesh), and southeast Asia (Indonesia, Malaysia, Myanmar, Philippines, Thailand, and Vietnam), north Asia (China, Hong Kong, and Taiwan), south to Australia and Papua New Guinea. It is known from waters 0-30 meters deep and associated with mangrove swamps, intertidal muddy bottom coasts, and coastal reefs. This species appears to be rather common around eastern India, Borneo, and Northern Java (Indonesia), but uncommon near Pakistan (Guinea et al. 2010b). Type locality: None given.

Identification**.** A microcephalic snake, a long slender body anteriorly which becomes laterally compressed posterior. This species goes through a significant ontogenetic change.

Figure 13.58. *Hydrophis curtus*. Photography Anslem da Silva.

Juveniles have dark lateral spots over a lighter whitish body anteriorly, which become less distinctly defined posteriorly. These blotches form a band like pattern with the lighter colored interspace, creating a count of 40-60 bands. However, this pattern fades posteriorly with age and the pattern become indistinct, creating an almost uniformly grey dorsal graduating to a whitish ventral side anteriorly, with a faintly banded body anteriorly. The body scales are imbricate, numbering 30-36 rows at mid-body, and 12-21 rows at the neck. The scales become keeled with dark brown or black tubercles ventrally. Ventral scales are divided by a longitudinal fissure and number 220-228. Females grow larger than males, females attaining a total length of 1025 mm, 95 mm of which is tail, and males reach 950 mm, 80mm of which is tail (Rasmussen et al 2011; Leviton et al 2003).

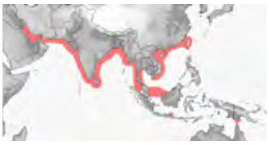


Figure 13.59. The distribution of ***Hydrophis gracilis.***

Natural History**.** *Hydrophis gracilis*, like many microcephalic species, is an eel specialist, foraging sand beds in search of its prey (Guinea et al. 2010b).

Figure 13.60. *Hydrophis gracilis.* **Photography by JCM.**

Hardwicke's Spine-bellied Seasnake

Hydrophis hardwickii Gray 1834

Distribution and Habitat. Persian Gulf, Indian Ocean, South China Sea north to the coasts of Fujian and Shandong Strait of Taiwan, Singapore; Indo-Australian Archipelago; North coast of Australia; Philippines; Pacific Ocean from Myanmar, Thailand, Vietnam, Indonesia, China, Japan, New Guinea (no map). Type locality: India.

Identification. Hardwicke's Spine-bellied Seasnake has long been confused with *Hydrophis curtus*. The following has been take from Leviton (2003:436). Body short, stout, neck region not less than half as thick at midbody; head large; scales squarish or hexagonal, juxtaposed, outer 34 rows larger than others, scale rows: & 23-31 around neck, 27-35, around midbody, 3 25-27, 2 33-41; ventrals small, usually distinct anteriorly, not so posteriorly, in ¢ 114-186, in 2 141-230; head shields entire, parietals occasionally divided; nostrils superior, nasals in contact with one another; prefrontal usually in contact with second upper labial; 7-8 upper labials, 3-4 bordering eye; | pre- and 1-2 postoculars; 2, rarely 3, anterior temporals; greenish or yellow-olive above, whitish below, 35—SO olive to dark gray dorsal bars, tapering to a point laterally, occasionally encircling body, a narrow dark ventral stripe or broad irregular band occasionally present; adults often lack any pattern and are uniform olive to dark gray; head pale olive to black, yellow markings on snout present or not. Total length 860 mm, tail length 85 mm.

Natural History. Diet. Glodek and Voris (1982) found this species has a diet that is more diverse than any other sea snake that it occurs with. *H. hardwickii* had 48 prey species in 21 families of fish as well as squid and cuttlefish (Cephalopoda) , while the other sea snakes it occurred with had 4-7 prey species.

Relative abundance. Ward (2000) found the catch rates of *Hydrophis hardwickii* were highest in the eastern part of the Gulf of Carpentaria at depths of <20 m. Species that represented ≥20% of specimens from one or more areas were: *Hydrophis hardwickii, H. ornatus*, *H. major* and *Aipysurus eydouxii*. Catch rates were highest for *H. elegans.* Catch rates of all species of snakes combined did not differ significantly between 1984–86 and 1989–90 and were moderately high around Groote Eylandt where the fishery is centered. Most by-catch species occur in areas that are not subjected to extensive trawling, and there are no data to suggest that this fishery seriously threatens any population of sea snake. However, sea snakes may be more vulnerable to trawler-induced effects than most other by-catch species, and formal assessment of the status of populations is needed.

Reproduction. The reproductive cycle of *H. hardwickii* reported by Ward (2001) found copulation occurs between early May and the end of July; ovulation during August–September; and gestation during September–December. Females produce approximately 8.5 offspring per clutch. Females breed annually. Average litter swize is is 8.4 offspring per year.

Rangoon Sea Snake

Hydrophis hendersoni Boulenger 1903

Figure13.61 The distribution of *Hydrophis hendersoni*

Distribution and Habitat. Myanmar. Type locality: Rangoon, Burma.

Identification. This species was long considered part of *H. nigrocinctus*. Rasmussen et al (2011c) removed it from *H. nigrocinctus* based on it having 2-3 maxillary teeth behind the fang (0-1 teeth in *H. nigrocinctus*), seven supralabials (eight in *H. nigrocinctus*), 30-33 scale rows on anterior body (27 rows in *H. nigrocinctus*)

Plain Seasnake

Hydrophis inornatus (Gray, 1849)

Distribution and Habitat**.** This species is only known from it's type specimen which was listed as merely "Indian Ocean". It is presumed to live as far east as the Philippines and as far south as the Arafura Sea (Rassmussen 2010). Type locality: "Indian Ocean" (Rassmussen 2010). [no map or photo]

Identification**.** Body is a bluish grey dorsally and dorsally transitioning to white on the ventral. The tail is white light black bands with a black or dark grey end of tail. Body is uniformly wide. Dorsal scan rows are 44 at midbody with 253 ventral scales which are distinct and twice as wide as adjacent anteriorly, narrowing posteriorly. It is distinct from the similar *Hydrophis lamberti,* and *Hydrophis ornatus* based externally on color pattern, and internally by several physiological traits (Rassmussen 1989).

Natural History. Prey include old world silver sides (Atherinidae) and gobies (Gobioididae), with little else known of the natural history of this species (Voris and Voris 1983; Rassmussen 2010).

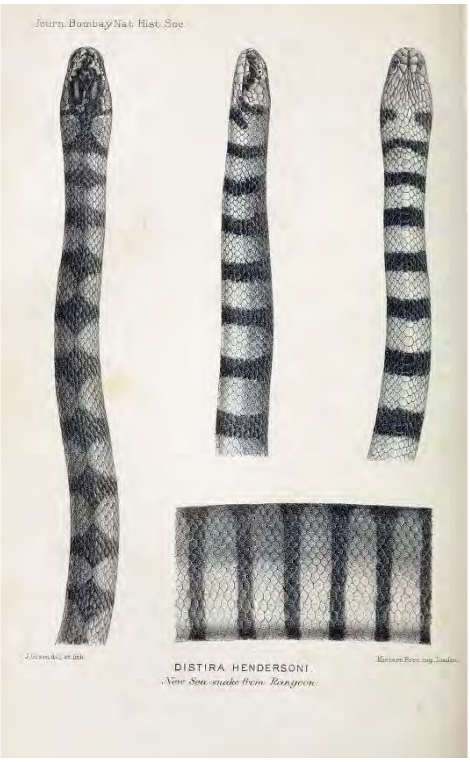


Figure 13.62. *Hydrophis hendersoni* from Boulenger (1903).

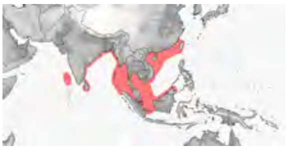


Figure 13.63. The distribution of *Hydrophis jerdonii*

Sadle-Backed Seasnake

Hydrophis jerdonii (Gray, 1849)

Distribution and Habitat**.** Occurs in the Indian Ocean including Sri Lanka, India and Myanmar, Southeast Asia including East Malaysia, and Vietnam, and in the South China Sea including southern China and Taiwan. Despite being known from India's east coast, there have been no records of this species occurring there since 1977 and it is uncommon in the Andaman Sea. This species is associated with gravel and sandy muddy bottoms and has been found between 0-30 m deep (Rasmussen & Lobo 2010; Uetz and Hosek 2020). Type locality: Madras, India.

Identification**.** This species has a short head which is gray or greenish in color on top and white or yellow below. The body is a lighter olive to gray with 30-38 wide black bands which narrow laterally and encircle the entire body. The body is nearly an equal diameter throughout it's length, with keeled and imbricate scales. The scale count at middy is notably low, less than 23 scale rows. The ventral scale count varies regionally from 225–278. Total length for this species is reported at 1000 mm (Chan et al 2015.)

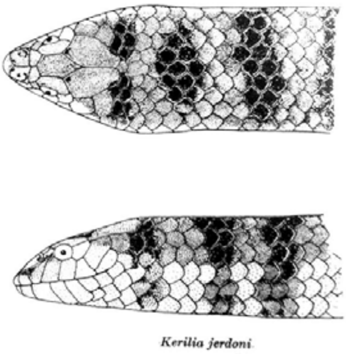


Fig.13.64. *Hydrophis jerdonii.* **From Smith (1943.)**

Natural History. Formerly in the monotypic genus *Kerilia*, this species forages the sea floor peaking its head into crevices and holes in search of prey items which include lizardfish (Synodontidae) and anguilliform or eel like fishes. (Chan et al 2015; Rasmussen & Lobo 2010).

Spectacled Seasnake

Hydrophis kingii (Boulenger, 1896)

Figure 13.65. The distribution of *Hydrophis kingii*

Distribution and Habitat**.** This species is known from northern Australia, West Papua, and Papua New Guinea. It is associated with depths ranging from 0-22 meters over soft sandy and muddy substrates, as well as reef habitat (Milton et al 2010b). Type Locality. Listed as North Australia .

Identification**.** *Hydrophis kingii* has a black head and throat which is followed by banding which becomes a dorsal pattern of 45-50 darker grey to black round to rhombic shaped saddle markings with an yellowish to cream base color forming the innerspaces. The interspace between these rhombic like saddles can have black lining to each scale, most prominent dorsally, but fading on the flanks. The lateral sides have smaller dark spots. Ventrally the coloration becomes cream to pale brown with a black mid-ventral stripe and a series of dark mid lateral triangular markings which are pale grey. The head shields are enlarged, symmetrical and unfragmented, with a large anterior chine shield bordering the mental groove. The body scales are keeled and imbricate, with 37-39 dorsal scale rows at midbody. The ventral scales are notably larger than the dorsal scales and number 324-342. Average total length of adults is 1.5 m (Per obs; Cogger, 2018).

Natural History**.** Little is known of this species as it is considered rare. Most have been found in deeper waters with varying seabeds. Prey include benthic fish including catfish (*Euristhmus nudiceps*), and eels from the family moray eels (Muraenidae). Females give birth annually in September after a six to seven months, producing five young on average, with a maximum recorded litter size of eight (Cogger 2018; Milton et al 2010b; Fry et al 2001; Voris and Voris, 1983).

Kloss' Seasnake

Hydrophis klossi (Boulenger, 1912)

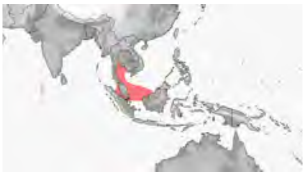


Figure 13.66. The distribution of *Hydrophis klossi.*

Distribution and Habitat. This species is restricted to the Gulf of Thailand, occurring in Thailand, Cambodia, Malaysia, Singapore and Indonesia. Nothing is known of the habitat preferences of this species (Sanders & Rasmussen 2010). Type Locality. Thuala, Selangor, Malay Peninsula.

Identification**.** This species pattern consists of a greyish to dark green dorsally, graduating to yellowish ventrally with 50-75 darker crossbones, with a grayish to greenish head, adorned with a yellow horseshoe marking. The head scallion includes 1 preocular scale, 1 post ocular scale, and 1 anterior temporal plate. Supralabials number 5-6, the second being the larges and the 3rd and 4th scales contact the orbit. There are 607 infra labials. Body scales are smooth or with a slight keel and number 23-27 at the neck and 31-19 at midbody. Ventrals have two tubercles, and number 360-430. Adult length ranges from 975-1190 mm. (Kharin, 2004)

Natural History. Nothing is known of this species habitat preferences or ecology.

Laboute's Seasnake

Hydrophis laboutei (Rassumussen & Ineich, 2000)

Figure 13.67. The distribution of *Hydrophis laboutei.*

Distribution and Habitat. This species is endemic to the waters surrounding New Caledonia and associated with depths from 0-62 meters in depth. Nothing is known about the species habitat preferences, the holotype was caught on a trawl at a depth of 62 m (Rasmussen 2010b). Type Locality. Chesterfield Reefs, New Caledonia (20°21.98'S, 161°04.87'E) (Rasmussen & Ineich 2000).

Identification. This sea snake species has a black head with a weak lighter line over the eyes, with 45-46 black bands with white interspaces, and 7-8 more dark bands on the tail. One noteworthy pattern feature for this species is that the first two or three black bands melt together with the black head dorsally. The white interspaces are widest on the body flanks, narrowing dorsally, and interrupted ventrally by a black ventral surface compressed of 265-280 ventral scales. Dorsal scale rows number 26-28 at the neck and 44-46 midbody. This species can be distinguished by five allopatric species (*Hydrophis atericeps, Hydrophis elegans, Hydrophis kingii, Hydrophis pacificus,* and *Hydrophis vorisi*) on its notably low ventral count (265-280), with the other five allopatrics having a ventral count greater than 311. *Hydrophis laboutei* can be distinguished from *Hydrophis belcheri* 34-37 dorsal scales at the neck, and the first bands do not fuse together as in *Hydrophis laboutei* (Rasmussen and Ineich 2000).

Natural History. This species was only recently described (2000) and is only known from three specimens. Nothing is known about this species ecology, though it is presumed to be rare (Rasmussen 2010b).

Figure 13.68. *Hydrophis laboutei.* **A specimen at MNHN Photographed by Antoine Fraysse - 2017, MNHN Project:RECOLNAT (ANR-11-INBS-0004)**

Lambert's Seasnake

Hydrophis lamberti (Smith, 1917)

Distribution and Habitat. This species occurs through out south east Asia including Cambodia, Vietnam, Thailand, China, Taiwan, Malaysia, Indonesia, Singapore, and the Philippines. It is associated with coastal waters with sandy bottoms (Rasmussen & Gatus 2010). Type locality: Mouth of the Mekong River.

Identification. This species has a large robust head which is grayish to brown colored and mildly patterned above and whitish below. The body's base color is an off-white to pale grey which lightens ventrally, covered with dark bands which are widest dorsally and lighten and narrow ventrally in an upside-down triangular shape. Males have 26-36 bands on the body and 4-6 on the tail, and females have 26-31 bands on the body and 5-6 on the tail. Ventral scales are distinct, about twice as wide as the adjacent scales anteriorly and number 258-395 in males and 237-306 in females. Males have 37-50 subcaudals whereas females have 34-44. Dorsal scale rows number 37-45 at the neck and 45-56 at the midbody. *Hydrophis ornata* has a similar appearance but has fewer than 42 bands on the body and tail (Rasmussen 1989; Chanard et al 2015; Leviton et al 2014).

Natural History. Little is known about this species natural history; it is said to prey on marine catfish. While this species is caught as by-catch in trawling activities, harvested in the Philippines for export to Japan as smoked sea snake, and harvested in Thailand and Vietnam for their skin, it is a widespread species and listed least concern by the IUCN (Das 2010; Rasmussen & Gatus 2010).

Arabian Gulf Seasnake

Hydrophis lapemoides (Gray, 1849)

Figure 13.69. The distribution of *Hydrophis lamberti*

Distribution and Habitat**.** This species is known from the Arabian Gulf including Bahrain, Iran, Iraq, Kuwait, Qatar, Oman and the United Arab Emirates. In south Asia it is found in Pakistan, India, Bangladesh, and Sri Lanka. In South East Asia it is known from Myanmar, Thailand, Malaysia, and Singapore. It is associated with shallow warm waters over sandy bottoms, seagrass beds, and reefs and is often seen basking at the surface. It has also been occasionally found in freshwater or brackish estuaries and as close to shore as rocky sea breaks less than 3 meters deep. As such this species is frequently found washed up on beaches. This species is abundant in the Arabian Sea, however uncommon to rare throughout the remainder of its range (Rasmussen et al 2010i; Egan 2007; Garner 2013; Buzás et al 2018). Type locality: Ceylon, Madras.

Figure 13.70. *Hydrophis lamberti.* **https://www.snakes.ngo/By Franco Colnago - https://www.inaturalist.org/photos/63668789, CC BY 4.0, https://commons.wikimedia.org/w/index.php?curid=92604323**

Identification**.** *Hydrophis lapemoides* has a variable pattern consisting of 33-64 black or dark grey bands over a pale light grey to yellow background. These bands are widest dorsally and taper ventrally, narrowing down the flanks. The rings face ventrally and maybe faded or completely absent in older specimens. The black head has a yellow or off-white horseshoe pattern. This species is a stout Seasnake with a moderate sized head with the widest part of the body 2-3 times wider than the neck. The body scales are keeled and hexagonal in shape, with each scale being as broad as it is long. Towards the tail the scales become more distinctly keeled and widen, in males these posterior keels becoming spike like tubercles. This species could be confused with *Hydrophis ornatus*, however the banding on *Hydrophis ornatus* terminate in a sharp point. This species also could be confused with *Hydrophis cyanocinctus,* however *Hydrophis cyanocinctus* is much thinner and longer than *Hydrophis lapemoides* (Egan 2007; Garner 2013; Buzás et al 2018)

Natural History**.** This species is commonly found near to shore (0-9.7km out to sea) during the day and at dusk in the Arabian Sea, and is one of the most abundant Seasnakes in the region. This species feeds on a wide variety of fish including flat fish (Perciformes), cardinalfish (Apogonidae), gobies (Gobiidae); snake eels (Ophichthidae) and other unidentified eels (Anguilliformes) wrasses (Labridae), goat fish (mullidae), *Pseudochromis* (Pseudochromidae), worm eels (Ophichthidae). Eels, flatfish, and gobies are presumed to comprise the bulk of their diet due to ease of capture. This species actively forages for food by day and forages on the sea floor. One was observed outside of a goby's burrow. Mating takes place in May, with the birthing of 1-5 offspring occurring in November. Like many seasnake species, it is not uncommon to find this species with heavy barnacle infestations from the sea snake specializing barnacle species *Platylepas ophiophila*. This species is considered generally placid, however some reports claim they can be aggressive when removed from the water. The venom of this species contains postsynaptic neurotoxins and possibly myotoxins and is considered relatively dangerous to humans. This species is wide ranging and relatively abundant and listed least concern by the IUCN (Egan 2007; Buzás et al 2018; Voris & Voris, 1983; Rasmussen et al 2010i).

Figure 13.71. The distribution of *Hydrophis lapemoides*

Small-headed Seasnake

Hydrophis macdowelli (Kharin, 1983)

Figure 13.73. The distribution of *Hydrophis mcdowelli*

Distribution and Habitat**.** Northern Australia (including Northern Territory, Queensland, Western Australia), Loyalty Islands of New Caledonia, Papua New Guinea (Uetz and Hosek 2020) Type locality: Northern Australian shelf (Uetz and Hosek 2020)

Identification. As implied in the common name, this snakes head is much smaller in comparison to its body. Its body is slender anteriorly and compressed posteriorly. The base coloration of the body is a beige to cream color becoming more of a lighter yellow to white color ventrally, with a series of 30-40 black or dark grey blotches running along the top of the body, which extend one third of the way down the body. The side of the body also has three longitude series of small grey spots with occasional black outlining. Body scales are imbricate having a median keel, with 35-42 rows at mid-body and 252-274 ventral scales with a double keel, one keel

Figure 13.74. *Hydrophis mcdowelli*
Photography by Hugues Debeyser

on each side of the median line. This species is sexually divergent, with both the body and ventral keels being more obvious in male specimens. The average length is around 80 cm. (Ineich and Laboute 2002; Cogger 2018; Storr et al 1986).

Natural History**.** Australian continental shelf in water up to 50 m deep, in river estuaries and other turbid (muddy) inshore waters. More specifically, Small-headed Seasnakes produce around two or three young in a litter. Gestation lasts six to seven months and young are born in September. Females appear to reproduce every year. (Cogger 2018; Fry et al. 2001).

Olive-headed Seasnake

Hydrophis major (Shaw, 1802)

Figure 13.75. The distribution of *Hydrophis majori.*

Figure 13.76 *Hydrophis major,* **From Anse Vata, Nouméa, New Caledonia Photography by Josh Jensen**

Distribution and Habitat. This species is known from Indonesia in the Arafura sea, Northern Australia, New Caledonia, and southern Papua New Guinea. Exact habitat preferences are poorly known, however it is associated with turbid waters, offshore coasts with soft bottoms including mud and sand, and can also be found in some tidal creeks. In New Caledonia it is thought to be associated with coral flagstones and areas with an abundance of seaweed species including *Sargassum*, *Halimeda* and *Caulerpa* algae. It is often found by trawlers in deeper waters with depths ranging from 1.4-106 m (Ineich & Laboute 2002; Cogger 2018; Guinea et al 2010c; Courtney et al. 2010). Type locality**:** Indian Ocean per Cogger.

Identification. The head of this species is bulky colored dark brown with black flecks, the body is a yellowish to beige color with 25-30 dark blotches or saddles dorsally, that do not form complete bands ventrally and decrease in size towards the tail. The inner spaces between these saddles have small bars about a scale wide. Just below each dorsal saddles, are two rows of smaller round lateral blotches or spots. The ventral scales are barely wider than the adjacent scales and are dark grey with darker tips. The head shields are unfragmented, large, and symmetrical and this species usually lacks an anterior chin shield or one is barely present and the rostral scale is barely noticeable from above. Body scales are imbricate with a single low blunted keel and number 37-43 at midbody. Ventral scales have a double keel and number 230-266 with an enlarged cloacal scale. This species is sexually divergent, with both the body and ventral keels being more obvious in male specimens. Average total length for this species is 1.3 meters. This species superficially resembles *Hydrophis macdowelli*, however its head is much notably larger and wider and there are only two rows of smaller lateral spots in *Hydrophis major* compared to three in *Hydrophis macdowelli* (Ineich & Laboute 2002; Cogger 2018).

Natural History. Despite it's abundance in portions of its range, there is still a lot unknown about this species. Stomach content studies revealed prey to include pearlfish (*Carapidae* sp.), and eeltail catfish (*Plotosidae* sp.). Ineich and Laboute also observed a juvenile foraging on cardinalfish (*Apogon* sp.) and Gon's cardinalfish (*Archamia*) in pinnacle reefs and gulf weeds at depths of 6-15 meters. Reproduction occurs year-round, though slowing in the colder months, with 6-12 live young being produced. This species should be approached with caution as it is considered aggressive compared to many other sea snakes, and human fatalities have been recorded (Ineich & Laboute 2002; Voris and Voris 1983).

Bombay Seasnake

Hydrophis mamillaris (Daudin, 1803)

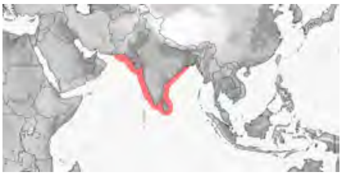


Figure 13.77. The distribution of *Hydrophis mamillaris.*

Distribution and Habitat. Known from Pakistan, India and Sri Lanka waters. (Heatwole 1999) It is known to occur over soft bottom sand or mud (Lobo and Rassmussen 2010). Type Locality. Visakhapatnam, Andhra Pradesh, India.

Identification**.** Alternatively known as the broad banded sea snake, due to the species 44-55 black body bands which are approximately twice as wide as the interspace between then which is a yellow or grayish color. The bands expand slightly dorsally, and are connected at ventrally. The head is entirely black with occasional yellow markings around the temporal region. Body scales are hexagonal in shape, with a tubercules and are feebly imbricate. Dorsal neck scale count is 25-29 scale rows, and 35-43 at midbody. Ventrals are distinct and bicarrinate with a scale count of 302-309.

Natural History**.** There are only 13 reported sightings of this species since it's description, the most recent being in 1926 by Malcolm Smith (Smith, 1926; Lobo and Rassmussen 2010). With the type specimen lost, there has been some debate about the validity of this taxon, considered to be a synonym of *Hydrophis fascaitus* however Rassmussen and Lobo believe it to be a legitimate species. It is presumed this species travels large distances in surface and tidal currents, like *Hydrophis platurus* (Lobo and Rassmussen 2010; Somaweera,2009).

Slender-necked Seasnake

Hydrophis melanocephalus (Gray, 1849)

Distribution and Habitat. While the type specimen is labeled Indian Ocean, this species seems to be restricted to northeast Asia including China, Japan, Taiwan, Korea, Philippines, and Vietnam. It is potentially the most abundant sea snake in Japan's Ryukyu Archipelago. This species is associated with inshore waters. (Rasmussen 2010c; Goris & Maeda 2004; Masunaga et al 2005). Type locality: Indian Ocean.

Identification**.** As the Latin name implies, this species has a very black head, and slender neck, both of which are black with faint yellow spotting. The body of this species is slender, with the forebody about 1/3 the width of the posterior body. The base color of this species is a

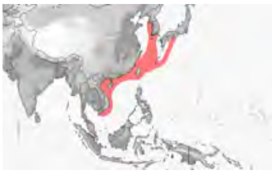


Figure 13.79. The distribution of *Hydrophis melanocephalus*

light yellow with 46-61 dark bands running the length of the body, and 3-8 more dark bands on the tail, which terminates in black. Bands taper ventrally, but usually completely wrapping the body and ventrals. The eyes are notably large, larger than the preocular scale. The frontal scale is longer than it is wide, the parietals are as long as both the prefrontal and frontal scales, and no loreal scale is present. There are nine supralabial scales, with scales 3-4 or 3-5 contacting the orbit, one preocular scale, 1-2 post oculars, and typically one temporal scale, but in rare instances 7 or 8 are present. Body scales are usually keeled, are imbricate anteriorly, but only subimbricate posterity. There are 25-31 scales at the neck, 31-39 at midbody. Ventral scales are larger than the adjacent scales, have two reduced keels, and are sometimes wedged making scale counts difficult. Ventral scale count ranges from 281-353. The average length males of this species is 114 -123 cm in females. (Mao and Chen 1980; Maunaga et al 2005; Goris and Maeda 2004).

Natural History**.** Very little is known about this species. Prey include conger eels (Congridae), worm eels (Moringuidae), and snake eels (Ophichthidae). Goris and Maeda reported this species forages by putting its head in the sand and then holds onto the prey items pulling them from the sand. Females produce 1-8 young, with birthing season varying greatly with locality. The venom of this species is medically significant and has an LD50 of 0.111 mg/kg subcutaneously, with an average yield of 2.1 mg. Due to an overall lack of knowledge on the species, it is listed as Data Deficient by the IUCN. (Rasmussen 2010c; Voris and Voris 1983; Goris & Maeda 2004; Minton 1983).

Robust Seasnake

Hydrophis melanosoma (Günther, 1864)

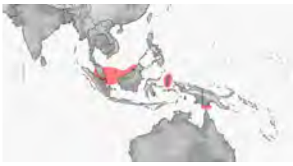


Figure 13.80. The distribution of *Hydrophis melanosoma*

Distribution and Habitat. This species occurs along the east coast of the Malay Peninsula including Malaysia, Indonesia and Singapore. It also occurs along the north coast of Borneo where it is considered rare, along Indonesian Borneo, Malaysian Borneo and Brunei and nearby islands. There is also a disjunct population in Halmahera, Indonesia. It is associated with shallow coastal waters as well as rivers (Sanders 2010b; Stuebing and Inner 1999). Type locality: unknown.

Identification. The body of this species is robust as the common name suggests, grey dorsally that graduates to an off white to yellowish ventrally with 50-70 black cross bands that are complete, and about twice as wide as the interspaces. The neck and head are black with yellow or cream-colored oval shaped pattern that runs over the nasals, prefrontals, preoculars, post ocular and temporal. The head is distinct. The ventral is a cream or yellow color, with two tubercles on each of the 266-368 ventral scales which are slightly less than twice the size of the adjacent scales. The cloacal scale is divided and the end of the tail is black. The dorsal scales are strongly keeled and there are 35-45 scale rows at midbody. Average total length is 1.5 meters. This species can be distinguished from *Hydrophis caerulescens* and *Hydrophis fasciatus,* but both of those species have small heads. *Hydrophis klossi* also appears similar, however the bands are the same width as the interspaces, where as in *Hydrophis melanosoma* the bands are notably wider than the interspaces (Stuebing and Inner 1999; Chan-ard et al

2015; Das 2010).

Natural History. This species forages shallow waters for a variety of prey including conger eels (Congridae), worm eels (Moringuidae), moray eels (Muraenidae) and various other eels (Anguilliformes). The reproductive habits of this species are yet unstudied. Due to a lack of population information, this species is listed as Data Deficient by the IUCN (Voris and Voris 1983; Das 2010; Sanders 2010b).

Figure 13.81. *Hydrophis melanosoma.* **This image is from Boulenger 1898, and is labled** *Hydrophis floweri.* **This species was later placed in the synonomy of** *H. melanosoma.*

Black-banded Seasnake

Hydrophis nigrocinctus (Daudin, 1803)

Distribution and Habitat**.** This species occurs in the Indian Ocean in Bangladesh, India, and Myanmar. Little is known about this species including habitat preferences or ecological niche. The type specimen was found near the tidal zone and lower saline areas near a river in Calcutta (Rasmussen & Lobo 2010d; Rasmussen et al 2011c). Type locality: Sundarbans, Bengal (Leviton et al 2003).

Identification**.** *Hydrophis nigrocinctus* is a banded sea snake species easily distinguished from all the *Hydrophis* in Asia by only having 1-3 maxillary teeth behind the fang. The body is an olive color dorsally graduating to a yellowish on the flanks ventrally. The body of this species is covered in 40-60 thin dark body bands, slightly tapering ventrally on the flanks. The head is black and has a yellow stripe at the supraorbital with a crown pattern that extends to the prefrontals. The mental scale is large and not concealed by the mental grove. There are 27-33 scale rows at the neck and 39-45 scale rows at midbody. Ventrals are distinct, but

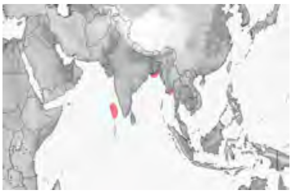


Figure 13.82. The distribution of *Hydrophis nigrocintus.*

not twice as wide as the adjacent scales, and number 296-330. Average total length is 1080 mm (Leviton et al 2003; Rasmussen et al 2011c).

Natural History. Very little is known about this species. It was formerly in the genus *Disteira*, and members of that former genus are diurnal and prefer deep, turbid waters with sandy substrates.Known prey include conger eels (Congridae). Nothing is known about this species reproductive cycle. With very little known about this species, its population size, and ecological preferences, this species is listed data deficient by the IUCN. Rassmusen et al synonymized *Hydrophis walli* with *Hydrophis nigrocinctus* and thus *Hydrophis walli* is not included in this volume. Wallach et al synonymized *Hydrophis hendersoni* with *Hydrophis nigrocinctus* and thus *Hydrophis hendersoni* is also not included in this volume (Voris and Voris 1983; Rasmussen et al 2011c; Rasmussen & Lobo 2010d; Wallach et al 2014).

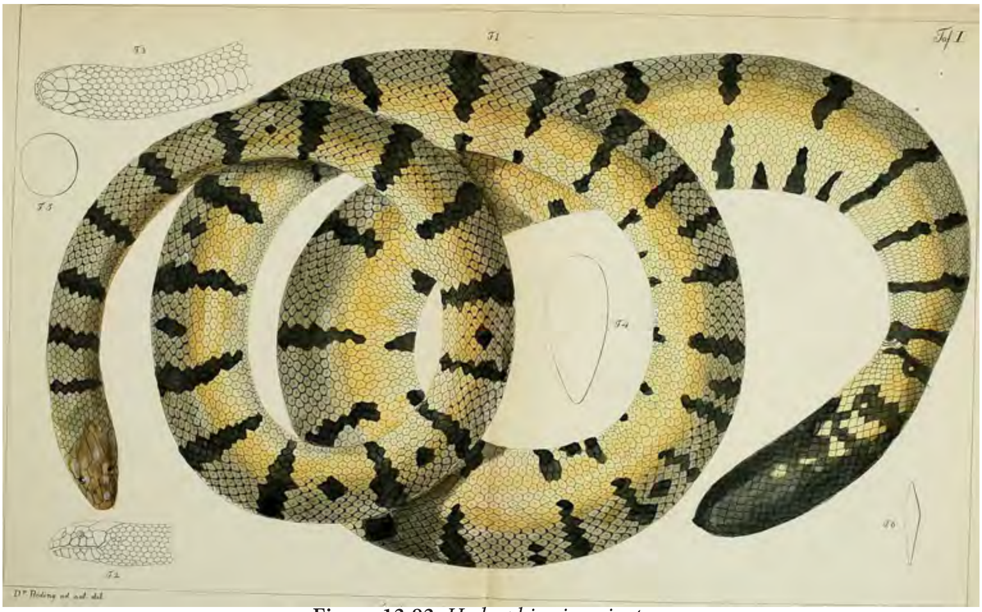


Figure 13.83. *Hydrophis nigrocinctus*
The image is from *Abhandlungen aus dem Gebiete der Naturwissenschaften* **1846.**

Russell’s Seasnake

Hydrophis obscurus (Daudin, 1803)

Distribution and Habitat. *Hydrophis obscurus* is known from east India, Myanmar, Bangladesh, and southern Thailand. It is associated with river mouths, saltwater lakes, and shallow brackish lagoons (Rasmussen & Lobo 2010e; Leviton et al 2003; Das 2010). Type locality: Sundarbans, India (Leviton et al 2003).

Identification**.** This species goes through a significant ontogenetic change, where juveniles are black to bluish grey with 35-55 complete bright yellow to white bands, but adults pat-

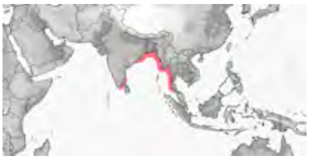


Figure 13.84. The distribuition of *Hydrophis obscurus.*

terns fade to become a completely uniform grey dorsally and yellow ventrally. Juveniles heads are also pattered, with a black base patterned with a curved yellow marking that runs from the snout to the sides of the parietal scales. The body scales are imbricate and have rounded or blunted scale points. There are 19-23 scale rows at the neck and 29-37 at midbody. The ventrals are distinct and number 300-338. Average total length for this species is 1190 mm in males, and 1200 mm in females, with only a slight size variance between the sexes (Leviton et al 2003; Das 2010).

Natural History. This species it is though to inhabit brackish areas including lagoons and river mouths where it searches for prey which are known to include tripodfish (Triacanthidae). Little else is known about this species. (Leviton et al 2003; Das 2010; Voris and Voris 1983)

Ornate Reef Seasnake

Hydrophis ornatus (Gray, 1842)

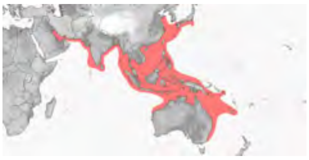


Figure 13.85. The distribution of *Hydrophis ornatus*.

Distribution and Habitat. A very widespread species found west in the Persian gulf, and the Indian Ocean east to South East Asia including Indonesia, Malaysia, Vietnam, Thailand, Phillipines, and Myanmar, North to southern China and Japan, and south to Australia, New Caledonia, and the Solomon Islands. This species prefers waters 30 m or deeper in depth, although it has also been found at coral reefs and mildly turbid inshore water as well as estuaries (Uetz and Hosek 2020; Rasmussen et al, 2010h). Type locality: None given.

Identification. The head color is a dark olive to black above, and off white to yellow below, with a fragmented lighter hotshot pattern and is large and robust. The base dorsal coloration is variable and can include light gray, light olive or off-white with wide black, grey or dark brown bands that come to a point just above the ventral scales. In males 40-55 bands are

Figure 13.86. *Hydrophis ornatus.* from Ponton Méridien, Province Sud, New Caledonia. Photography by Pauline Fey.

present while females have 40-56 bands. Scales are imbricate or juxtaposed, and hexagonal in shape at midbody. Midbody scale count is 33-45 on males, and 39-55 in females, with males having 209-260 ventral scales and 236-312 ventral scales in females. Snout to vent length in males is 950 mm with a tail length of 11 mm Snout length is 860 mm in females, with a tail length of 80mm (Egan 2007; Rasmussen, 1989; Leviton et al, 2003).

Natural History. The diet of this species has been shown to vary regionally and includes a variety of fish species that occur close to coral reefs. In Australia *Hydrophis ornatus* appears to specialize in benthic and demersal fish including cardinal fish (Apogonidae), cusk eels (Sirembo), gobies (Yongeichthys), bigeyes (Priacanthidae), goatfish (Mullidae), and threadfin breams (Nemipteridae). In Thailand six fish families have been found in stomach content studies including cardinal fish (Apogonidae), squirrel fish (Holocentridae), wrasse (Labridae), ponyfish (Leiognathidae), parrot fish (Scaridae), and threadfin breams (Nemipteridae). Because this species diet is known to include free swimming species, there is speculation they may prey on sleeping fish at night. Sexual maturity is reached around 800 mm in females with litter sizes ranging from 1-17. This species' venom contains potent myotoxins and has caused human fatalities (Voris and Voris 1983; Fry et al, 2001; Gardner 2013; Rasmussen, 1989).

Ocellated Sea Snake

Hydrophis ocellatus Gray 1849

Distribution and Habitat. The Northern Territory, Queensland, Western Australia, and Tasmania.[No map.]

Identification. Long confused with *H. ornatus*, however Rasmussen et al. (2014) found no evidence that *H. ornatus* occurs in Australia waters. (no map) but found it in New Caledonia. (see figure 13.87).

Figure 13.87. *Hydrophis ocellatus* **from Cable Beach WA, Australia Photography by Sharmaine Donnelly.**

Fischer's Sea Snake

Hydrophis pachyceros Fisher 1855

Distribution and Habitat. Indian Ocean, South Chinese Sea, and Vietnam. Neotype was obtained from a fish market at Phat Thien, Vietnam the specimen was taken from a trawler catch by Rasmussen et al. (2007).

Identification. Diagnostic characters: Scale rows around neck 26–31; scale rows around body 39–45; ventrals 247–297. Maxillary teeth behind fangs 7–8. Coloration: Body pale yellow above, white below, with pale brown transverse bands fading on the upper part of the flanks. Head white below, black/dark above with pale supralabials and a pale ring around the eyes.

Small-headed Sea Snake

Hydrophis parviceps Smith 1935

Distribution and Habitat. South Chinese Sea -Vietnam. Type locality: coast of Cochin China (no map).

Identification. Head small, body slender anteriorly. Scale rows around neck 19–21; scale rows around body 31–34; ventrals 329–348. Maxillary teeth behind fangs 6–. Coloration: Body olivaceous above, greyish below, with 65–0 blackish bands. Head black with no or only a few faint paler marks.

Pacific Seasnake

Hydrophis pacificus (Boulenger, 1896)

Figure 13.88. The distribution of *Hydrophis pacificus.*

Distribution and Habitat**.** This species is known from southern Papua New Guinea and Northern Territory and Queensland in Australia. It is associated with continental shelf waters, inter-reef waters, as well as soft sediment estuaries and tidal rivers, with a known from depths ranging from 0-50 meters. Most of the records for this species come from shore wash-ups, trawler by-catch, or surface captured animals basking in shallow continental shelf waters (Milton et al 2010c; Cogger, 2013). Type locality**:** New Britain, Papua New Guinea.

Identification. *Hydrophis pacificus,* which is also known as the large-headed sea snake, has a large-head compared to other members of the genus, with a relatively slender body that is notably compressed laterally. Juveniles present 49-72 pronounced black bands against a lighter foreground that are complete and from the black head to the tail. The throat in juveniles is also black with light-yellow spots behind each eye and pale spots on the snout. Pattern becomes less distinct in adult specimens, with a darker grey dorsal side with a mid-body lightening ventrally. Bands in adults may be faded, the bands on the neck are usually, but not always connected by black ventrals. Adult bands maybe divided or displaces on the vertebral line. Thread on adults is park grey above, lighter beneath, and has pale flecks. Head shields in this species are distinct and regular. Body scales are imbricate and number 45-49 rows at midbody. Ventral scales are mostly undivided, not much broader than adjacent scales, and number 320-430. Average adult length is 1.4 m. (Wilson and Swan, 2013; Cogger, 2013)

Figure 13.89. *Hydrophis pacificus.* **From Boulenger 1896.**

Natural History**.** This fish specialist is slow to mature and reproduce, with the approximate age of maturation occurring at eight years, yet a total longevity estimate of only twelve years. Litter size is reported to be 17 live young. Due to this species slow reproductive rate, and the pressures from being captured as by catch from trawling, it is listed as vulnerable by the IUCN and is thought to be in decline. While generally considered non-aggressive this species may bite when restrained and does posses postsynaptic neurotoxins which are considered potentially lethal to humans. (Milton et al 2010c; Wilson and Swan, 2013; Tangella, 2019)

Horned Seasnake

Hydrophis peronii (Duméril, 1853)

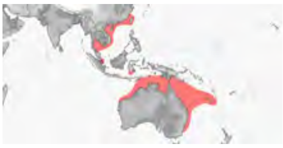


Figure 13.90. The distribution of *Hydrophis peroni.*

Distribution and Habitat. This species is known from northern Australia, southern Papua New Guinea, the Solomon Islands, the Loyalty Islands, southern Indonesia, and New Caledonia in the southern hemisphere. The northern and southern hemisphere populations are notably disjunct, with no known occurrence in the Philippines or Central Indonesia. This species distribution picks up again in the northern hemisphere where it is known from Cambodia, China, Malaysia, Singapore, Taiwan, Thailand, and Vietnam. *Hydrophis peronii* is associated with soft sandy bottoms adjacent to coral reef and is found in depths from 0-60 m (Lukoschek et al 2010). Type locality: New Holland (Modern day Australia)

Identification. This species is easily distinguished from all other *Hydrophis* by having pronounced spines on its head. The head is short, and small, with very broad shallow nostrils,

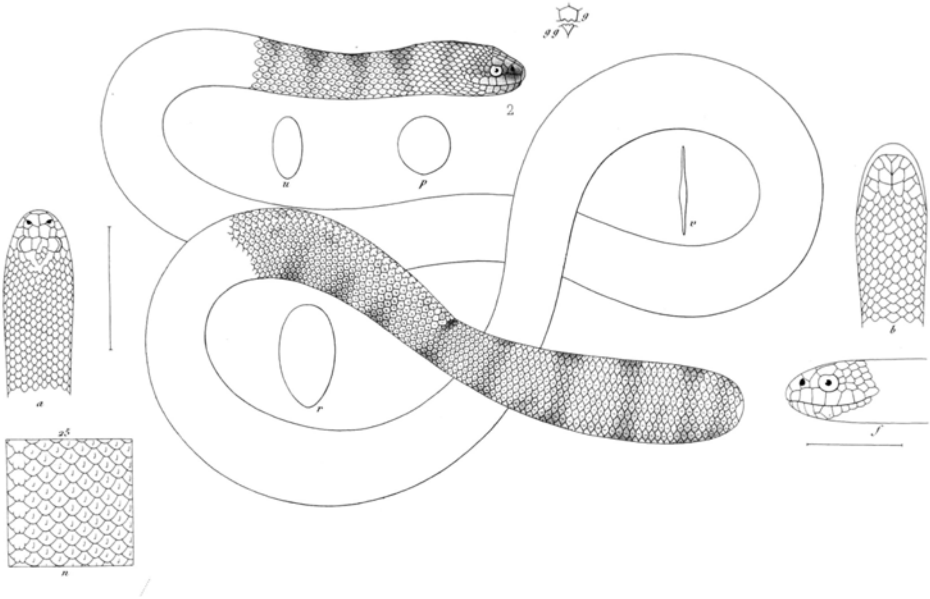


Figure 13.91. Shows *Hydrophis peroni.* **From Jan and Sordelli 1872.**

and distinct eye color of off-white, with a black ring encircling a slightly darker shade of white with black pupils. The body color is off-white to gray, lighter below than above with 25-30 brown or black bands which taper ventrally, which can become obscure in older specimens. On some specimens, there is a second set of smaller incomplete dark bands, between the primary bands. This pattern may be obscured by biofouling, with reports of some specimens found covered in algae and seaweed. The supraocular, postocular, and adjacent scales are raised and pointed along the posterior border with projecting spines in adults, that present as still present, yet less distinct tubercles in juveniles. Parietal and frontal shields are indistinct, fragmented into smaller scales, and the prefrontal scales are absent. This species' neck is slender, and only one-third to two-thirds the width of the diameter of the body. The body scales of this species have a strong dorsally facing spine shape, with short keels, more distinct in males than females. This banding becomes faded and less distinct on the tail. Ventrally narrow bands or spots may be present. Dorsal scale count is 18-24 scale rows at the neck, 21 to 31 rows at the mid-body, ventral scale count is 140-210, subcaudal scales count is 29 and 35, and the cloacal scale divided. The average adult total length is 1.1-1.3 meters. (Cogger 2014; O'Shae, 2005; Leviton et al 2014; Fry et al 2001)

Natural History**.** *Hydrophis peronii* is reported to go through an ontogenetic prey shift, with juveniles specializing in shrimp and adults hunting the ocean floor looking for burrowing gobies (*Gobiidae*) in the genus *Trypauchenidae* and Oxyurichythys. This species appears to be active both day and night, though Retfield et al. had greater success collecting specimens on trawl by day than night. Hunting consists of prodding their smaller head and narrow necks into the burrows of gobies, which are comprised of mud, sand, gravel, and broken coral. The prey is quickly subdued with the species' potent post-synaptic neurotoxic venom, with an LD50 of 0.125 ug/g when tested intravenously in mice, and a total yield of 18.3 mg. While incredibly toxic, the snake has a small yield and no human bites or fatalities have been recorded. This species appears to reproduce annually giving birth to up to 10 live young. In Australia gestation lasts six to seven months with birthing in March to June. (Cogger, 2014; Voris, 1972; Voris and Voris 1983; Fry et al. 2001; Mori and Tu, 1988; Leviton et al 2014)

Yellow Bellied Seasnake

Hydrophis platurus (Linnaeus, 1766)

Distribution and Habitat. *Hydrophis platurus* possess the largest natural range of any living squamate (Rasmussen et al 2011). In the New World, in the Pacific Ocean, they have been spotted as far south as Coastal Chile (Donoso, 1966), and as far north as Ventura County, California (Nafis, 2020). It should be noted, that though this species can occur in these far limits of its presumed "extended" range, due to the species low tolerance of cooler water temperatures (Graham, 1974). These occurrences are often attributed to accidental current drift, and likely do not represent known breeding populations. Type locality Unknown.

H. p. platurus populations with year-round breeding are likely limited from Mexico to Ecuador, where occurrence of the species is far greater. There have also been four sightings of the species in the Caribbean Sea, off the coast of Colombia, though these sightings are presumed to be due to human introduction, be it via the Panama Canal or other means (Hernández-Camacho et al. 2006). In the Old World this species ranges throughout the greater part of Southeast Asia and Australia, south into New Zealand and Tasmania and as far North as Southern Japan. *Hydrophis platurus* also inhabits all the Indian Ocean includ-

Figure 13.92. The distribution of *Hydrophis platurus.*

ing the entire East African coast, the adjacent Persian Gulf and the Red Sea. Their range in the Indian Ocean occurs all the way south to South Africa, where their occurrence is considered rare. They have on two occasions been spotted across into the Atlantic Ocean in South Africa and Namibia (Branch, 1998), though this occurrence is considered likely an accidental current displacement and does not represent a breeding population (Visser, 1967). Should climate change continue to warm these waters, it is the authors opinion that this species could see significant range expansion, as cold waters appear to be their main barrier to further dispersal. As the alternate common name, the pelagic sea snake implies, this species is entirely pelagic. They are most often seen off tropical shores, where rain is plentiful and ocean temperatures stay between 36-18 C. While the species is capable of surviving temperatures below 16 C, feeding has been documented to cease from 18-16 C, and thus areas in this range are not common places for them to occur (Dunson and Ehlert, 1971; Graham, 1974). Though the species does inhabit the open ocean, as its movements are largely dictated by currents, they are mostly found within 1-20 km from shore throughout their range. Due to their "drifting" lifestyle, they can most easily be located in "debris slicks" where currents converge along shorelines. These slicks can be identified by the large number of debris, and an obvious flatness. Some have described them as looking like "small roads" on the surface of the ocean, a description the author finds fitting for the general width and appearance. (Per obs)

Identification**.** *Hydrophis platurus* is one of the most distinct looking of all the snakes in the subfamily Hydrophiinae. It's laterally compressed body, side by side semi-hexagonal to quadrangle shaped scales, flattened head, and distinctive bicolor (though variable) patterning all contribute to the relative ease of this species identification. The common pattern is a black colored dorsal side, yellow colored ventral side, down to the tail, which is an aberrantly spotted and highly variable mix of white and black, though on some individuals the white is not present, and instead the yellow coloration front he ventral side continues to the tail. Juveniles' tails may be yellow instead of white, and tail coloration could be an ontogenetic change. The bicolor arrangement is most common, though colors may vary including brown and yellow bi-color, black with a lateral strip and yellow, aberrant, and fully melanistic. The recently described subspecies *Hydrophis platurus xanthos* lacks the black and is instead solid yellow with occasional black dots. Scales are irregular in shape varying from sub-quadrangular to hexagonal. These scales become very small along the body with 49–67 rows around thickest part of body and a ventral scales count of 264–406. Their head is narrow, with an elongated snout and large head shields. nasal shields in contact with one another; prefrontal in contact with second upper labial; 1–2 pre- and 2–3 postoculars; 2–3 small anterior temporals; 7–8 upper labials, 4–5 below eye but separated from border by subocular. Species snout to vent length is dimorphic, Female reaching 880 mm and males reaching 720 mm (Leviton et al. 2014).

Natural History**.** *Hydrophis platurus* is a truly pelagic species, occurring off tropical shores around the world. Like other Hydrophiinae, the species is reliant on rainwater for fresh drinking water, and as such is most densely populated in areas with heavy rain fall. Some unique characteristics of the species include their "knotting behavior" employed for ecdysis, and their ability to swim backwards or forwards with equal ease. While the species can dive, they are mostly encountered floating on the surface of the water. The species is primarily diurnal, and most encountered in the morning hours. Upon approached carefully, the snakes rarely dive, unless there is a significant water disturbance. While adept swimmers in the water, this species is almost incapable of locomotion on land due to their complete lack of

Figure 13.93. A *Hydrophis platurus* from Birubi Beach, Newcastle, New South Wales, Australia Photography by Scott Eipper.

ventral scales. The species feeding behavior is quite unique. The bicolor camouflage underneath looks like the leaf and debris they hide in while in debris slicks. As fish approach the snake, they prey upon them using a lateral striking method, and often consume them without the aid of venom. Heatwole proposed the snake may use small sensory organs on the scales to feel the presence of prey items, similar to the predation tactics employed by acrochordids. They can often be found among washed out leaves and sticks in these slicks. As small fish approach the debris in search for food, they become prey items for the Hydrophis platurus. *Hydrophis platurus* breed year-round, with gestation lasting about six months, giving live birth to 1–10 offspring. There is some speculation that the offspring may stay with their mother for the first few days of life, which would be a unique maternal behavior among sea snakes. While human deaths are rare, the venom of *Hydrophis platurus* is highly potent nuerotoxin (with other unique isotoxins) with a subcutaneous LD50 0.055 mg/kg, making it the seventh most toxic snakes on earth when tested subcutaneously. This said the species is hesitant to bite in the water, and the species average yield is only. (Bolaños et al 1975; Pickwell et al 1972; Steinhoff, 2018). While a lethal bite is possible, it is unlikely due to the species hesitancy to bite unless restrained. However, in the author's experience this species will in fact attempt to bite if restrained, and as such handling by an untrained professional should be avoided unless necessary.

Taxonomy. In 2017, Brooke L. Bessesen, and Gary J. Galbreath described the Golfo Dulcean Sea Snake (*Hydrophis platurus xanthos)*, as the first subspecies in the long-standing monotypic species. They described the subspecies as having a notably smaller body, and nearly solid yellow pattern. They also noted that this subspecies is most active at night, and not associated with drift-lines as *Hydrophis platurus platurus* is. This subspecies is endemic to the Golfo Dulce in Southern Costa Rica (Bessesen, Galbreath 2017).

Beaked Seasnake

Hydrophis schistosus (Daudin, 1803)

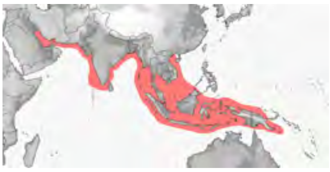


Figure 13.94. The distributuion of *Hydrophis schistosus.*

Distribution and Habitat. A very widespread species found as far west as the east coast of India, east to Southeast Asia, north to southern China and south to northern Australia. The species also appears to be a habitat generalist occurring in deep sea locations with rocky or sandy bottoms, tidal creeks, shallow open sea, river mouths, lagoons mangrove forests and estuaries. It has also been found in freshwater lakes in Cambodia and India, as far up as 7l km in the Goa River in India (Rassmussen et al 2018). The species prefers depths between 5 m and 30 m (Rassmussen et al 2018). Animals are active night and day and night, and most seen in marine environments with soft bottoms. This is the most encountered sea snake by humans (Karithkeyan and Balasubramanian 2007). Type locality**:** Tranquebar, India.

Identification. *Hydrophis schistosus* is distinct from most other sea snakes other than based on its beak shaped rostral. It shares this shape with *Hydrophis zweifeli,* which it can be distinguished from based on its 1-2 preoculars which are lacking in *Hydrophis zweifeli*, and instead are fused with the supraoculars. Juveniles are darker on top and lighter below, with bands that fade with age to a uniform dark dorsal gradient to a lighter ventral side. Dorsal scales are somewhat imbricate or juxtaposed with a short central keel. Midbody scale count in males is 43-52 and in females 48-55. Ventral count is 262-322, with a maximum total length of 1400 mm, though average adults rarely surpass 1100 mm total length (Rezaie-Atagholipour et al 2016; Ukuwela et al 2013).

Natural History. The beaked sea snake is active day and night, and forages for prey including crustaceans and fish, larger specimens feeding mainly on fish, with an apparent preference for catfish. Voris and Voris found a large variety of prey items in their 1983 stomach content study including eels (Anguilliformes), catfish (Ariidae), anchovy (Engraulidae), lizard fish (Harpadontidae), ponyfish (Leiognathidae) eeltail catfish (Plotosidae), drums (Sciaenidae), and even the toxic pufferfish (Tetraodontidae), and shrimp. Mating occurs March to April. Males combating other males for mates, such as seen in some terrestrial species, has been observed in this species. Female mature rapidly at 18 months, producing first offspring at 24 months. Offspring are large 21-24 cm and numerous (up to 30 or more in larger females), though only 6% of females survive to a reproductive age. Ernst and Zug's book, Snakes in Question: The Smithsonian Answer Book errantly declared *Hydrophis schistosus* as the most toxic snake in the world, and with an LD50 of 0.1125 mg/kg SC, it is certainly one of the more lethal snake species, but not the most toxic by any route of injection. While human fatalities are rare, they have occurred, and the species should be treated with caution. (Voris and Voris, 1983; Karithkeyan and Balasubramanian, 2007; Rassmussen et al 2018; Rezaie-Atagholipour et al. 2016; Fry 2012)

Lake Taal Seasnake

Hydrophis semperi Garman, 1881

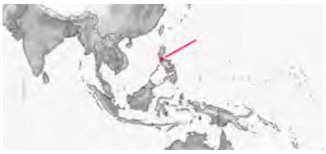


Figure 13.96. The distribution of *Hydrophis semperii.*

Figure 13.97. The Lake Taal Seasnake, *Hydrophis semperi.* **Photography by Vhon Oliver S. Garcia.**

Distribution and Habitat. Lake Taal, island of Luzon, Philippines is freshwater lake and the type locality for this sea snake. The lake is a deep meso-eu¬trophic lake in a volcanic caldera. Taal Lake was once a navigable inlet to Balayan Bay. A series of eruptions in the early 18th century culminated in 1754 with the largest eruption that blocked the Pansipit River, blocking the lake's outlet to the sea. This caused the waters to rise, Since the 1754 eruption, the surface elevation had risen from sea level to 5 m above sea level. Lake Taal became freshwater after centuries of precipitation. Taal Lake was declared a national park, Taal Volcano National Park, in 1967, it covers 62,292 hectares. When Garman (1881) described this snake, he considered it similar to *Hydrophis fasciata* and *H. fisheri* (presumably *Platurus fischeri* which is now in the synonymy of *Laticauda laticauda)*. However, Voris (1977) considered it similar to *Hydrophis cyanocinctus* that is not present in the waters surrounding Luzon.

Other endemic species have evolved and adapted to the desalination of the lake's waters. The lake has a freshwater-adapted population of the fishes, *Caranx ignobilis* and *Sardinella tawilis*, Two other endemic fish are the gobies *Gnatholepis volcanus* and *Rhinogobius flavoventris*. The Bull Shark, *Carcharhinus leucas,* was part of the lake's ecosystem but were extirpated by the local people by the 1930s.

Identification**.** Head slightly larger than the neck, crown convex, snout broad, rounded

Figure 13.95. *Hydrophis schistosus* **from Sri Lanka.**
Photography by (a) Paul Freed (B-C) by Anslem da Silva.

; tail about one eighth of the total length, moderately broad. Body not compressed anteriorly, greatest diameter about twice that of the neck. Maxillary teeth behind fangs six to eight; scales on body imbricate and with short keel, 29–21 around neck, 37–43 around body (increase of 10–12); ventrals 314–356, distinct throughout, bicarinate, about twice as broad as adjacent scales; precloacal scales enlarged; head black, body black with 50 to 60 narrow whitish bands of annuli, ventral scales usually black (Garman 1881; Leviton et al. 2014).

Natural History**.** Analysis of gut contents found gobies and eels are primary prey items. Halfbeaks (Family Hemiramphidae) were recorded as one of the Lake Taal Sea Snake's prey which is considered a new prey record for sea snakes (Garcia et al. 2014).

Garcia et al. (2017) reported a distinct surfacing behavior. As the snake approaches the surface to ventilate its lungs it arch's its body. The motion begins with a nearly vertical, ascent to the sur-face. The sea snake appeared to drag its body with its head as it ascended, with the momentum causing its head and neck to break the water surface. Its head briefly remained above the surface (1–2 s). It then formed an arch by diving back into the water as it swam towards the bottom, as opposed to simply descending in reverse motion. This type of biomechanics is like other sea snake species that ascend to the water surface to respire. The authors recorded the behavior 2–3 times day and night. They also observed the behavior of captive *H. semperi* was limited to moving from crevice to crevice and surfacing to breathe.

Threats to the species come from aquaculture and fishing. While they may avoid aquaculture by staying in open water their surfacing behavior makes them susceptible to gillnets.

Kalimantan Seasnake

Hydrophis sibauensis (Rasmussen et al., 2001)

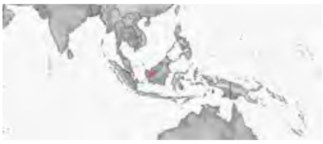


Figure 13.89. The distribution of *Hydrophis sibauensis*

Distribution and Habitat. This species is known from only three specimens which were found in the freshwater river habitats of the Sibau River in Kalimantan, Indonesia, 1000 km upriver from the coast (Rasmussen et al 2001). Type locality: Sibau Kecil, Putussibau (Kalimantan, Indonesia) (Rasmussen et al 2001).

Identification**.** *Hydrophis sibuaensis* appears to occur alone in the Sibua river, with no conspecifics. This species head is black dorsally and ventrally with light yellow dots or lines below creating a forward-facing arrow and dots or blotches behind the arrow. Base color of the body is dark grey to black and dark anteriorly than posteriorly. The ventral surface is black ventrally, but grayish yellow from midbody back. The body is patterned with 49-58 yellow bands that do not connect ventrally. The coloration of the bands transitions with the shade of yellow being brighter anteriorly and transitioning to a dark yellow to light orange posteriorly. The tail is patterned in 8-9 elongated blotches. There is one postocular scale, The dorsal scales have a long median keel and number 15-26 scale rows at the neck and 35-37 scale rows at the midbody. This species ventral scales are twice as wide as the adjacent scales, unfurrowed, and number 257-264. Total length is 45.5-73.5 cm (Rasmussen et al 2001).

Natural History**.** This species is known only from three specimens from a single isolated location. All specimens were collected during the regions two rainy seasons (July to August and November to December). As such the river was flooding, with estimated depths of 2 to 3 meters. The holotype was gravid with seven unborn young collected in December, indicating this species may give birth in December, however if the breeding is seasonal or year-round remains unknown (Rasmussen *et al.* 2001).

Yellow Seasnake

Hydrophis spiralis (Shaw, 1802)

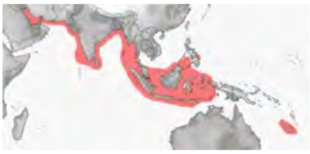


Figure 13.99. The distribution of *Hydrophis spiralis*

Distribution and Habitat. This species is widespread occurring in the Arabian Sea in Bahrain, Kuwait, Iran, Iraq, Oman, Saudi Arabia, United Arab Emirates, and Qatar. In south Asia it is known from Pakistan, India (including the Andaman and Nicobar Islands), Sri Lanka, and Bangladesh. In southeast Asia it is known from Indonesia, Malaysia, Myanmar, Philippines, Singapore, and Thailand. There is also a disjunct range in New Caledonia. This species is associated with both deep-water habitats over sand muddy bottoms up to 50 meters deep, as well as shallow waters over coastal reefs and sandy bottoms (Gardner 2013.) Type locality: Indian Ocean.

Identification. This species head is moderately sized, only slightly wider than the neck and mostly indistinct from the body. the head color is black with a yellow horseshoe pattern in juveniles, but in adults this head pattern fades and lends the head to be typically mostly yellow with some black markings. The long slender body has a yellow to mustard brown base color, which fades to a paler yellow or white on the flanks. The body is patterned in 30-60 narrow bands (normally less than 50), which are usually complete, and thinner than the wider interspaces. The tail often has black blotching, with the end tip being black. The complete narrow black bands on a long and slender yellow body help distinguish this species from others. There are 6-8 upper labials with the 3rd and 4th or 4th and 5th contacting the eye. One preocular scale is present, as well as 1-2 postocular scales.

Figure 13.100. *Hydrophis spiralis*.
Photography by Anslem da Silva

The dorsal scales are imbricate and smooth with a small tubercle and nearly hexagonal in shape, though longer than they are broad. There are 29-39 dorsal scale rows at midbody, and 282-373 dorsal scales. This is the longest of all known sea snakes, and can reach up to 2.75 m, though 1.6-1.9 meters is more common (Egan 2007; Garner 2013; Buzás et al 2018).

Natural History**.** Very little is known about the life history of this species, despite its wide distribution. This species is encountered both during the day, and at night, with some reports associating it with deeper water, while others shallow waters. It is occasionally seen at the surface basking when the water is calm. Known prey items include eels including conger eels (Congridae), and snake eels (Ophichthidae), as well as small hole dwelling fish. Clutch sizes range from 5-15, though little else is known about their reproductive cycle. There are vastly contrasting reports as to this species disposition, some stating it is rather aggressive, and others stating it is placid, however this species has led to human fatalities, and its venom contains potent myotoxins. This species is widespread, and though it is found as bycatch by trawl fisheries, is listed as Least Concern by the IUCN (Egan 2007; Garner 2013; Buzás et al 2018; Voris and Voris 1983; Rasmussen et al 2010j).

Stoke's Seasnake

Hydrophis stokesii (Gray, 1846)

Figure 13.101. The distribution of *Hydrophis stokesi*

Distribution and Habitat**.** A widespread species occurring in UAE, Pakistan, Oman, Pakistan, India, Sri Lanka, China, Taiwan, Thailand, Malaysia, Vietnam, Indonesia, New Guinea, Eastern Australia, and the Phillipines. In the Strait of Malacca it is reported too have been observed in the thousands floating along sea slicks, similar to reports of *Hydrophis platurus* by Lillywhite et al. in Costa Rica. *Hydrophis stokesii* is a habitat generalist, inhabiting reefs and harbours over mud and sand substrates found in depths ranging from 0-50 m (Uetz and Hosek 2020; Lillywhite et al 2015; Sanders et al 2018). Type locality**:** Australia.

Identification**.** *Hydrophis stokesii* is the heaviest of all the true sea snakes often reaching a weight of 2 kg, with a record weight of 5.144 kg. with a notably large head, stout body, and thick neck. It is also notable for having the longest fangs of any marine snake, up to 6.7 mm, making it capable of penetrating neoprene wetsuits. The juvenile pattern includes alternating dark blotches along the vertebral line and narrow incomplete dark bands against a yellow-brown, to light yellow foreground. Two series of dark spots flank the lateral surfaces alternating from the lower lateral line to the mid-dental line. Pattern fades with age, and alternating bands can diminish to narrow rows of spots. Adult color ranges from off-white to dark grey, obscuring the reticulate pattern. Unfragmented large head shields are present and are symmetrical. One preocular and two postoccular scales are present, 10-12 lower labial scales are present, as are 8-10 upper labial scales of which the second and third may meet the prefrontal scales, and upper labial scales 4-6 contact the eyes. Body scales possess a median keel or series of tubercles and are imbricate, numbering 46-63 at mid-body. Ventral scales at the throat consist of single rows. Posteriorly the ventral scales become broken up and are often cryptic with the remainder of ventral scales consisting of reduced, strongly keeled, elongated pointed scales with dentate tips which number 226-286. The notable ventral points may be absent in juveniles. This is a large species that can reach a maximum adult length of nearly two meters. (Wilson and Swan, 2013; Sanders et al 2018; O'Shea 2005; Cogger, 2013).

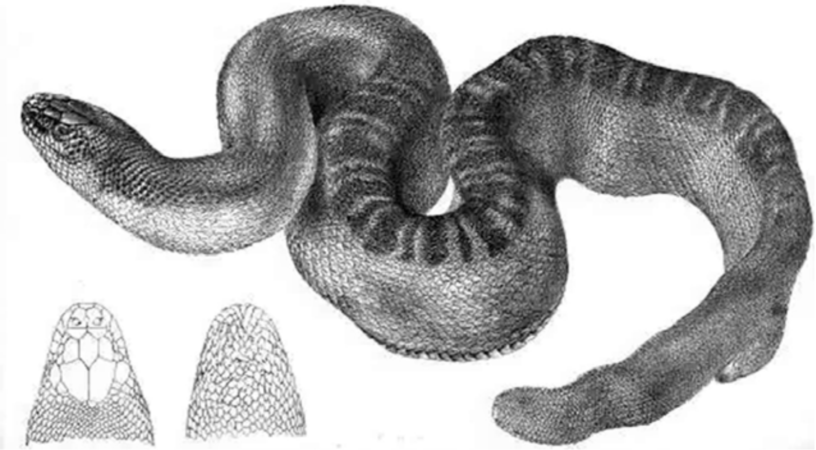


Figure 13.102. *Hydrophis stokesii.*
From from John Lort Stokes (1846) book Discoveries in Australia, volume 1.

Natural History**.** This species forages among reefs for fish including venomous juvenile stonefish, venomous toadfish (Batrachoididae), jawfish (Opisthognathidae), gobies (Gobiidae), and similar fish. This species is one of the few sea snakes stereotyped with having aggressive behavior towards humans, reportedly pursuing them with repeated bites. Coupled with a potent post-synaptic neurotoxin and fangs long enough to penetrate 5 mm wetsuits, it should be approached with caution, though no human fatalities have been reported (Voris and Voris, 1983; Sanders et al 2018; O'Shae 2005; Williamson, 1996).

Collared Seasnake

Hydrophis stricticollis Günther, 1864

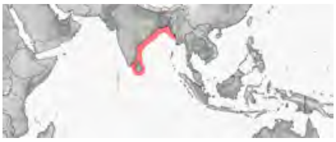


Figure 13,103. The distribution of *Hydrophis stricticollis*

Distribution and Habitat**.** *Hydrophis stricticollis* is endemic to the Indian Ocean and adjacent bodies of water, including India, Sri Lanka, Bangladesh, and Myanmar. Little is known about the habitat preferences of this species. It is associated with muddy bottoms, turbid waters, and is known to into rivers (Rasmussen & Lobo 2010). Type locality**:** India (Uetz and Hosek 2020).

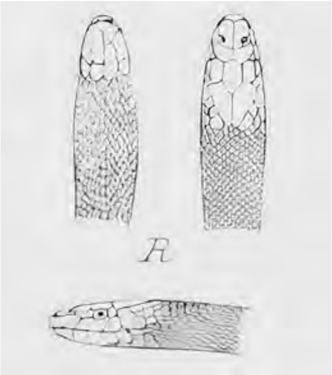


Figure 13.104. *Hydrophis striicticolis.* From Günther 1864)

Identification. *Hydrophis stricticollis* is a long and slender banded sea snake with a small head, with the posterior portion of the body being 2.5-3 times thicker than the anterior portion. This species is commonly patterned with 45-65 dark bands which are widest dorsally and narrow ventrally, but these bands may fade entirely with age. The body color is grey to olive dorsally and yellowish ventrally. Head color ranges from olive to black with yellow markings on the head and snout. One anterior temporal scale is present, and rarely divided, as are 7-8 upper labial scales of which the second one contacts the prefrontal scales and scales 3-4 border the eye. Scales at the thickest part of the body are hexagonal in shape, mildly imbricate or juxtaposed, and number 45-55 at midbody. Ventral scales number 374-452, and are less than twice as large as the adjacent scales though they are distinct down the length of the body. Total length in both males and females is 1050 mm, of which 140 mm is tail in males and 90 mm is tail in females (Leviton et al 2003).

Natural History. Little is known about the natural history of this species. They are thought to produce a viviparous brood of ten or fewer offspring measuring approximately 350 mm at birth. Specific prey is unknown, but it is suspected to hunt near-shore environments for fish. (Rasmussen and Lobo 2010).

West Coast Black-headed Seasnake

Hydrophis torquatus Günther, 1864

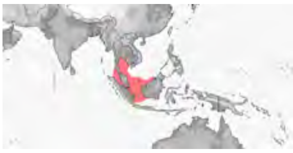


Figure 13.105 The distribution of *Hydrophis torquatus.*

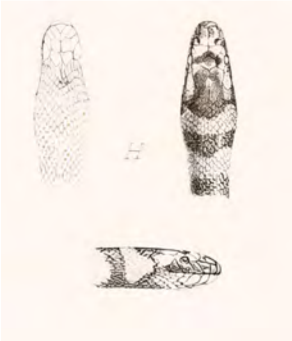


Figure 13.106. *Hydrophis torquatus* **from Gunther 1864, plate 25.**

Distribution and Habitat**.** This species is known from the Straits of Malacca, as well as the Gulf of Thailand including Thailand, Vietnam, and Cambodia. It is noted as particularly abundant at the mouths of the Mekong and Chanthaburi rivers and is unique among the genus for being one of the few known species to travel up rivers. One interesting, confirmed record of this species includes Cambodia's inland lake, Tonle Sap, well known for its abundance of Homalopsidae. This specimen likely traveled up the Mekong River, where the species is notably abundant, which breaks into the Tonle Sap and Mekong Rivers in Phnom Penh, and continued up the Tonle Sap river to arrive at the lake. There is a single record of this species in Borneo, though this is suspected to be a vagrant. There are also several museum specimens labeled as China, though the locality here is suspected to be incorrect. *Hydrophis torquatus* is associated with shallow coastal waters, estuaries, brackish waters, and freshwater rivers mouths, and has been documented in freshwater rivers and freshwater lakes (Rasmussen 2010; Ineich 1996; Das 2010). Type locality**:** Penang, Malaysia .

Identification**.** *Hydrophis torquatus* has an elongated body that compresses posteriorly with a moderate size head. Color and pattern typically consist of 55-68 dark grey to black bands or saddles 3-5 scales wide which are complete across the ventral scales anteriorly. Juvenile color and pattern are more pronounced with 46-63 well-distinguished black bands over a white body. The body coloration consists of a greenish-grey to greyish-tan dorsally and a yellowish cream color ventrally. The head pattern consists of a dark grey, dark olive, or black forehead with a yellowish horseshoe-shaped pattern often present across the snout and sides of the head. Yellow spots may also sometimes be present on the frontal and parietal shields. A single preocular scale, and 1-2 postocular scales are present, as well as 7-8 supralabial scales, of which scales 2-3 contact the eye. Scale rows number 35-42 at midbody, and the dorsal scales are squarish in shape at the thickest portion of the body. Ventral scale count is 242-343 with preanal scales enlarged (Chan-ard et al 2015; Murphy et al 1999; Das 2010).

Natural History**.** Little is known about the natural history or behavior of this species, other than its ability to inhabit both freshwater and marine environments. It is reported to search crevices for prey (Chan-ard et al. 2015; Das 2010).

Viperine Seasnake

Hydrophis viperinus (Schmidt, 1852).

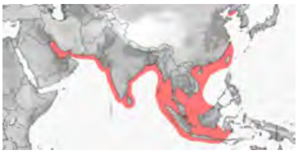


Figure 13.107. The distribution of ***Hydrophis viperinus*****.**

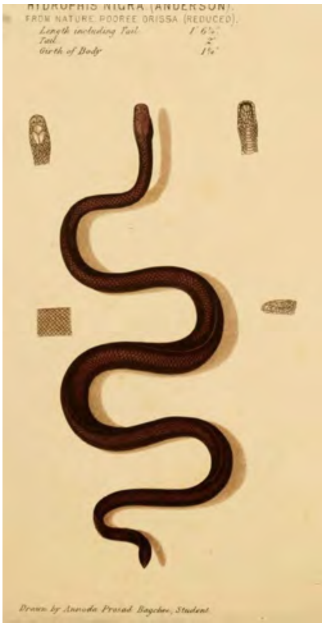


Figure 13.108. ***Hydrophis viperinus*****. Art work from Ewart (1869).**

Distribution and Habitat**.** This species is widespread and is found in Bahrain, Bangladesh, Cambodia, China, India (Andaman Is., Nicobar Is.), Indonesia, Iran Iraq, Japan, Kuwait, Malaysia, Myanmar, Oman, Pakistan, Philippines, Qatar, Saudi Arabia, Singapore, Sri Lanka, Taiwan, United Arab Emirates, and Vietnam. This species is notably absent from Phillipines, and only one record off the island of Phuket exists in Thailand. This species is associated with muddy bottoms, warm coastal waters, lagoons, estuaries, creeks, and deeper waters (15 - 30m). It's enhanced ventral scales allow this species to be slightly more mobile on land than other members of *Hydrophis,* and can crawl across dry areas, though feebly and with great effort (Rassmussen et al 2018; Uetz and Hosek 2020; Egan, 2008). Type locality**:** Java, Indonesia.

Identification**.** *Hydrophis viperinus* is a relatively stout-bodied, heavily-built snake sea snake, with wide anterior ventrals, and ventrals clearly present along the length of the body, making it fairly distinguishable from other members of the genus. The species has a variable body pattern often consisting of 25-34 rhomboidal spots running along the dorsal side with a bicolored body of grey dorsally transitioning in a straight line to white on the lateral flanks and white ventrally. Color and pattern are variable, and animals in some localities are more commonly plain grey dorsally, creams white ventrally with rhomboidal pattern indistinct or diminished entirely. The head is large, wide, and distinct from the neck, with complete head shields. Nasal shields contact each other. Prefrontal scales are longer than they are wide, and not in contact with the upper labials. The iris of this species is pale with a dark round pupil. Post and pre-ocular scales number 1-2, with 7-9 upper labial scales of which 3-5 border the labial scales. Body scales are juxtaposed and hexagonal in shape with 27-34 scale rows on the neck and 37-50 scale rows at the mid-body. Adult males have spinose protrusions on the distal edges of the body scales and the anterior edges of the ventral scales. Ventral scales are notable wide anteriorly, as wide as the body, which helps distinguish this species from the often-sympatric *Hydrophis schistosus*. These ventral scales narrow anterior to twice the size of adjacent dorsal scales posteriorly and number 226-274. The average total adult length in males is 925 mm, of which 100 mm is comprised of the tail, and 820 mm in females of which 80 mm is comprised of the tail. (Leviton, 2003; Egan 2008).

Natural History. Little is known about the natural history of this species. It is known to forage shallow warm waters for prey, which has been documented to include flatfish (*Kumococius*), gobies (*Gobiidae*), and eels. This species gives birth to 3-5 live young in early summer to notably large young (Rassmussen et al 2018; Egan, 2008).

Estuarine Seasnake

Hydrophis vorisi (Kharin, 1984)

Figure 13.109.The distribution of *Hydrophis voirsi.*

Distribution and Habitat. This species occurs in the Torres Strait, the Timor Sea, and the Arafura Sea between Australia and Papua New Guinea, and is associated with estuarine and shallow inshore waters (Cogger, 2018; Kharin 1984). Type locality: New Guinea (Kharin 1984).

Identification. This species head is very small, with an elongate body that is slender anteriorly, and compressed posteriorly. The body is a grayish white with 70-80 light black bands which are twice as wide as the patternless interspaces dorsally and taper ventrally. On some specimens the bands break or are displaced along the ventral line. The body scales imbricate, smooth anteriorly. But keeled posteriorly, and there are 29-35 scale rows at midbody. Ventrals are small, not much larger than the adjacent scales posteriorly, though slightly larger anteriorly and number 330-350 (Cogger, 2018; Kharin 1984; O'Shea 1996).

Natural History**.** This species is rarely encountered, and only known from two specimens. There is little known about their natural history, but they are presumed to feed on eels, and are viviparous. With almost nothing known about this species, it is listed as Data Deficient by the IUCN (Rasmussen & Guinea 2010; Cogger 2018; O'Shae 1996).

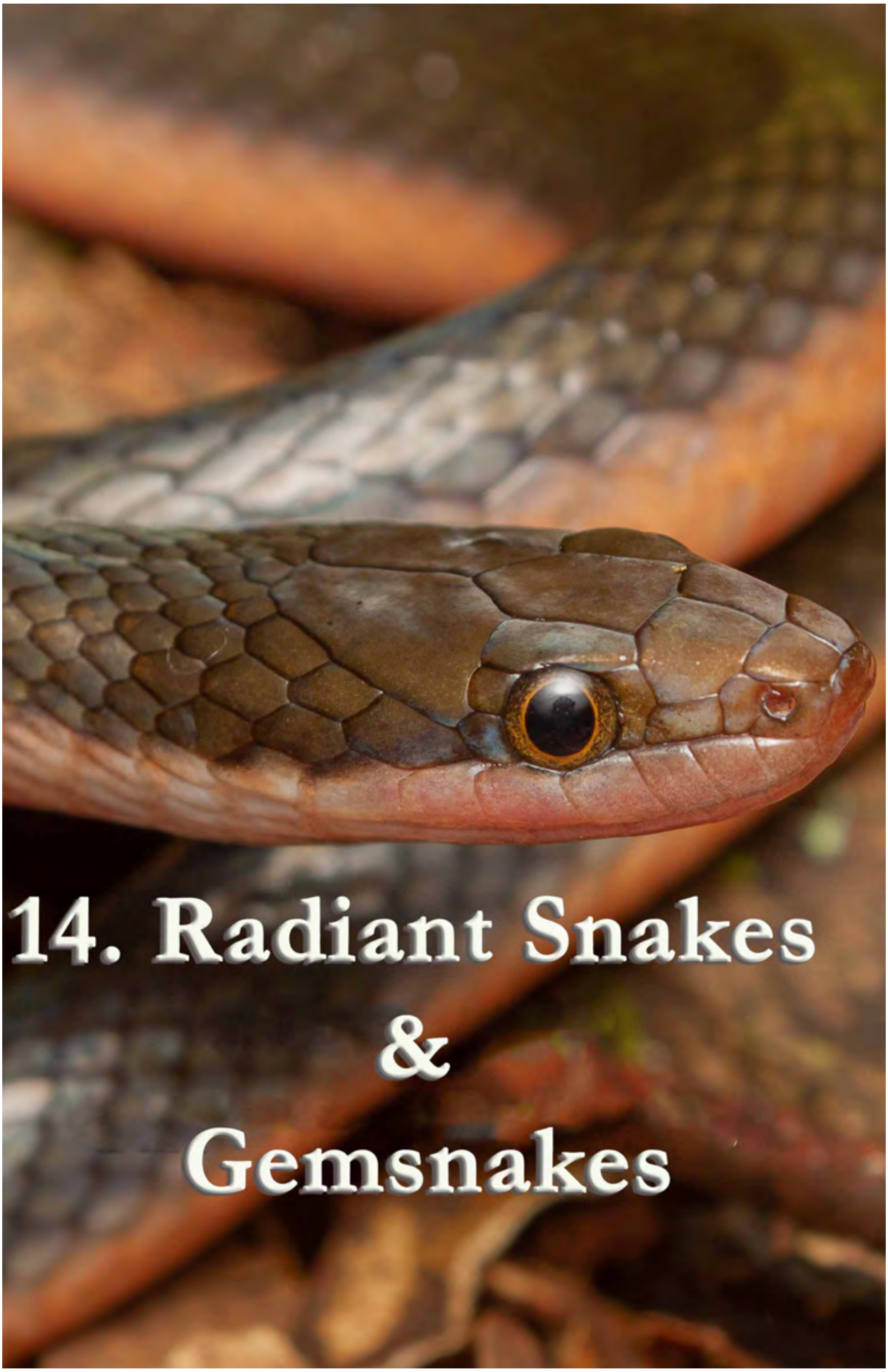
Sepic Beaked Seasnake

*Hydrophis zweifeli (*Kharin, 1985)

Distribution and Habitat**.** Papua New Guinea, Australia (Queensland, Northern Territory). Habitat is only known from one specimen which was at the mouth of the Sepic River, leaving he assumption it has a preference for gulfs. Type locality: "Off mouth of Sepik River, PNG."[No map.]

Identification**.** This species is very similar in appearance to *Hydrophis schistosus*, but distinguishable based on the lack of preocular, which are fused with the supraocular in *Hyrdophis zweifeli*. Another distinguishing trait between these two species is the presence of a split fourth supralabial in *Hydrophis zweifeli* which is absent in *Hydrophis schistosus*. *Hydrophis zweifeli* is distinguishable from all other sea snakes due to its beak like head. This species has 36 body bands that taper ventrally, which are gray in color over and off-white background. Midbody scale count is 48, ventrals number 271 (Ukuwela et al. 2013).

Natural History**.** This species is only known from a single specimen collected in 1966 off the mouth of the Sepik River and as such virtually nothing is known about its ecology. Population size and population trends remain unknown (Rassmussen, 2018).



14. Radiant Snakes & Gemsnakes

14. Radiant Snakes and Gemsnakes

. The Radiant Snakes, the lamprophiids (Lamprophidae) are diverse, most are terrestrial, others are fossorial or arboreal, and members of the genus *Lycodonomorphus* are semi-aquatic. Family members occur in deserts, grasslands, and forests in temperate and tropical regions. Radiant Snakes are part of the Elapoidea. They take vertebrate and invertebrate prey. Some genera subdue prey with venom, others use constriction. Dental morphology is also diverse and reflects the variety of prey they eat. Most species are oviparous. Lamprophiid distribution is primarily in Africa and Madagascar with some representation in the Middle East and Europe. Nine subfamilies are recognized, some of these are given family status by some authors (Aparallactinae, Atractaspidinae, Atractaspidinae, Cyclocorinae, Lamprophiinae, Prosymninae, Psammophiinae, Pseudaspidinae, Pseudoxyrhophiinae)

Radiant Water Snake Clade,

Lycodonomorphus

The African Water Snake Clade is known from the countries of Angola, Belgian Congo, Botswana, Congo, the Democratic Republic of the Congo, Malawi, Mozambique, Republic of South Africa, Rwanda, Tanzania, Zambia, Zimbabwe.

Figure 14.1. Olive Snake, *Lycodonomorphus inornatus* from Overberg, Western Cape, ZA Province, South Africa. from Western Cape, ZA Cape Town, Western Cape, ZA, South Africa. Photography by Alex Rebelo. Arebelo23@gmail.com

Lycodonomorphus is diagnosed by the following combination of characters (following Kelly et al. 2011): body cylindrical and moderately elongated; tail moderate to short; head moderate to small, slightly broader than neck and distinct from it; eye moderate, with vertically elliptical or sub-circular to round pupil; midbody scale rows 19–23 (rarely 25), vertebral row not enlarged; dorsal scales smooth, without apical pits or with two pits; ventrals 152–196, without lateral keel; subcaudals paired, 37–89; cloacal plate entire (exceptionally divided); maxilla with 18–25 teeth, subequal or slightly smaller or larger posteriorly, diastema absent**.**

While most members of the genus are aquatic - *Lycodonomorphus inornatus* seems to be mostly, if not completely, terrestrial. A photo is provided here for comparison purposes.

Tanganyika Water Snake

Lycodonomorphus bicolor (Günther, 1893)

Distribution and Habitat**.** Endemic to Lake Tanganyika. Diurnal behavior is restricted to the shallow water of the shoreline where they spend their time on a rocky substrate.

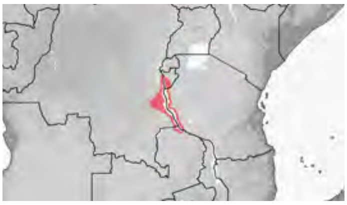


Figure 14.2. The distribution of *Lycodonomorphus bicolor*

Natural History**.** Diet in composed entirely of cichlid fishes of the genera *Leprologist, Chalinochromis*, and *Xenotilapia*. They are actively forage in the evening, but moonlight depresses activity. Females were found gravid throughout the year. The smallest gravid female was 50 cm in total length. Clutch sizes of 4, 5, and 8 eggs have been reported. The only predators observed were crabs. Population densities of 9000 to 29,000 individuals per square kilometer were reported but estimates suggest that as many as 38,000 snake per square kilometer are possible (Madsen and Osterkamp 1982). Barbault (1970) had reported a density of 3390 snakes per square kilometer.

Figure 14.3. Tanganyika Water Snake, *Lycodonomorphus bicolor* **from Lake Tanganyika, County Nkasi, RU, TZ District. Photography by Hubert A. Szczygieł.**

Dusky Bellied Water Snake

Lycodonomorphus laevissimus (Günther, 1862)

Distribution and Habitat**.** The eastern Cape from Transkei and Natal to the southeast Transvaal. In Swaziland it is restricted to the highveld region. It in habits pools in forested streams. Type locality: "East Indies" in error.

Figure 14.4 Distribution of *Lycodonomorphus laevissmus*

Natural History**.** More aquatic than *L. rufulus*, often seen swimming, completely submersed, along the beds of streams and rivers. Diurnal in the wild captives may be more active at night. Highly susceptible to dehydration and soon die without water. Diet includes frogs, tadpoles (*Rana, Phrynobatrachus,* etc.), and fish (*Tilapia*). Large animals are constricted but small ones are merely seized and rapidly swallowed while still struggling. Prey caught underwater are eaten without the snake surfacing for air unless swallowing is prolonged when the snake will drag its prey to a position above the surface before resuming (Raw 1973). Females lay 8-17 eggs in the Southern Hemisphere's summer.

Figure 14.5. To the right. Dusky Bellied Water Snake, *Lycodonomorphus laevissimus*. **Photography by Kirsty Kyle.**

Mulanje Water Snake

*Lycodonomorphus leleupi (*Laurent, 1950)

Distribution and Habitat**.** Southern Democratic Republic of the Congo (Zaire), eastern Zimbabwe, western Mozambique, Malawi, and Zambia. Uses small streams, pans and vleis (vegetated wetlands).

Figure 14.6. Distribution *Lycodonomorphus leleupi.*

Natural History**.** It is diurnal. Feeds on frogs and their larvae. Two species have been recognized. Females lay clutches of up to nine eggs. Broadley and Coterill (2004) wrote, "This endemic water snake was described from the Kundelungu plateau and also occurs on the Kibara plateau in the P.N.U. between 1250 and 1810 m (Witte 1953). It was described as a subspecies of *L. whytei* (Boulenger) of northern Malawi and adjacent Tanzania, but was later thought to be conspecific with *L. rufulus mlanjensis* Loveridge of southern Malawi and eastern Zimbabwe (Broadley 1967). These are now considered to be sister species, distinguished by ventral colouration:

dark with yellow patches and a dark tail in L. leleupi and yellow with a few dark spots and a dark median stripe on the subcaudals in *L. mlanjensis*. The nearest populations are separated by a gap of 1000 km."

Mlanje Water Snake

Lycodonomorphus mlanjensis Loveridge, 1953

Distribution and Habitat**.** Eastern Zimbabwe, southern Mozambique, and Malawi. Inhabits swamps, pools, and rivers in montane grassland and savanna. Local name of the Mlanje Water-Snake: Chirumi (Manganja). Type locality: Ruo River, Mlanje Mountain, Malawi.

Natural History**.** Feeds on fish, frogs, and tadpoles.

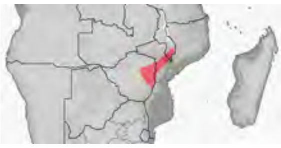


Figure 14.7. Distribution of *Lycodonomorphus mlanjensis*

FitzSimons Flood-plain Water Snake

Lycodonomorphus obscuriventris Fitzsimons, 1963

Distribution and Habitat**.** The flood plains of the Lower Shire Valley in southern Malawi in the north, through Mozambique and Zimbabwe, into Kruger National Park through Eswatini (Swaziland) in the east and southward into the Isimangaliso World Heritage Site, South Africa (Kyle et al. 2021).

Natural History**.** A nocturnal, but sometimes diurnal species that hunts frogs on floodplains. Kyle et al. (2021) reported a large gravid female laid a clutch of eight eggs in early December 2012, confirming speculations of oviparity in the species. Average egg length was 27.3 mm (23.1–30.9 mm) and the average width was 15.9 mm (range 15–17 mm). All eggs hatched in early February after approximal 60 days of incubation, and neonates were released at the capture site of the mother. Average total length of neonates was 147 mm (range 138–160 mm; N = 6) and average ventral scale count was 173 (range 167–176; N= 5).

Figure 14.8. Distribution of *Lycodonomorphus obscuriventris*

Common Brown Water Snake

Lycodonomorphus rufulus (Lichtenstein, 1823)

Distribution and Habitat**.** includes Zimbabwe, S Mozambique, Republic of South Africa (Eastern Cape), Swaziland (it occurs throughout the country in the highveld, middleveld, low veld Lesotho, Natal, Botswana, Malawi. Type locality: South Africa.

Natural History**.** Feeds on tadpoles (probably *Rana angolensis*). Taylor (1970) reported one of these snakes swimming toward the bank in a stream in Rhodesia's eastern highlands. The snake swam with the first few inches of its body out of the water and had a tadpole in its mouth. It shifted the tadpole in its mout several times while swimming (Taylor, 1970). and Lubombo regions, more common in the highveld.).

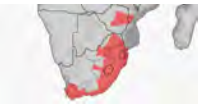


Figure 14.9. Distribution of *Lycodonomorphus rufulus*

Figure 14.10. Common Brown Water Snake, *Lycodonomorphus rufulus* **from Umgungundlovu, KwaZulu-Natal, South Africa. Photography by Gus Benson.**

Congo White-bellied Water-Snake

Lycodonomorphus subtaeniatus Laurent, 1954

Distribution and Habitat. Northern Angola to the Democratic Republic of the Congo (Zaire) Congo (Brazzaville). Type locality: Keseki, near Kwamouth, Belgian Congo. Restricted to lake Upemba.

Figure 14.11. The distribution of *Lycodonomorphus subtaeniatus*

Natural History**.** A skink was found in the stomach of one of these poorly known snakes.

Taxonomy**.** Branch (2018) wrote the following about this snake. "Laurent (1954) described *Lycodonomorphus subtaeniatus* based on a specimen from Keseki (DRC) and a series of 12 paratypes, including four from Dundo, which remain the only Angolan material. At the same time Laurent (1954) also described the subspecies *L. s. upembae* from Nyonga (DRC). The type series for both taxa included material previously identified as *Boaedon*, i.e., *B. virgatus* and *B. lineatus,* respectively (Laurent 1952; De Witte 1933). It was thus not unexpected that when preparing a molecular phylogeny of house snakes of the description of their new species *B. radfordii*, Greenbaum et al. (2015) found *L. s. upembae* embedded within *Boaedon*, to which it was transferred. No new material was available to assess the generic relationships of *L. subtaeniatus,* but the current placement within *Lycodonomorphus* is problematic and its relationship to *B. virgatus* with which has previously been confused should be investigated."

Whyte's Water Snake

Lycodonomorphus whytii (Boulenger, 1897)

Distribution and Habitat**.** Inhabits small montane streams in southwest Tanzania, Mozambique, Republic of South Africa (Transvaal. Swaziland). Type locality: Fort Hill, (Chipata), Malawi.

Natural History. Associated with upland streams and preys on anuran larvae and adults (J.B. Rasmussen 2004). Loveridge (1955) wrote the following, "Its stomach contained the hind legs of a frog (*Rana fuscigula*) and the entire digestive tract was riddled with worms. These have been identified by J. T. Lucker as *Oxyuroidea*, both sexes of a *Kalicephalus*, probably *K. micrurus*. In the mesentery were two *Dracunculus* sp. and numerous encapsuled larvae of one of the Physalopteridae."

Figure 14.12. Distribution of ***Lycodonomorphus whytii*****.**

Figure 14.13. Whyte's Water Snake, *Lycodonomorphus whytii*..
Photography by John Valentine Lyakurwa

White-bellied Water Snake

Boaedon upembae (Laurent, 1954)

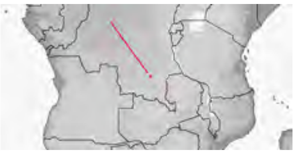


Figure 14.14. Distribution of *Boaedon upembae.*

Distribution and Habitat**.** Democratic Republic of the Congo (Zaire, Katanga; near Lake Upemba). Type locality: Nyonga, Katanga, Belgian Congo. Laurent described this snake as a subspecies of *Lycodonomorphus subtaeniatus.* Greenbaum et al. (2015) moved it to the genus *Boaedon* based on molecular evidence. Laurent (1954) commented on this species noting that *Lycodonomorphus s. subtaeniatus* and *L. s. upembae* bear a superficial resemblance to *Boaedon.* This is why they were both confused with *Boaedon lineatus,* a common species often determined by sight, without examining the number of scales. For the typical form, this examination led to confusion with *B. virgatus*, whose numbers of scales are similar, but which is nevertheless very different due to its characteristic ventral coloration. (Laurent 1954)

Natural History. One specimen contained a catfish so it seems likely to be partly aquatic (Greenbaum et al. 2015).

The Gemsnakes, Pseudoxyrhophiidae

The Pseudoxyrhophiinae was included in the family Lamprophiidae (Vidal et al. 2007), but Zaher et al. (2029) raised it to family status, the Pseudoxyrhophiidae. About 88 species in 21 genera compose the endemic Madagascar subfamily Pseudoxyrhophiinae.

Burbrink et al. (2019) found the Pseudoxyrhophiinae, the sister to a clade composed of East African genera *Amplorhinus* and *Duberria*. Sister to all other pseudoxyrhophiines was the Socotran Island (Yemen) endemic *Ditypophis*. Burbrink et al. (2023) found that the Pseudoxyrhophiidae originated in the early Miocene. Aquatic habits have evolved in at least two genera of Gemsnakes, but they are poorly known.

The Pseudoxyrhophiinae was included in the family Lamprophiidae (Vidal et al. 2007), however Zaher et al. (2029) upgraded it to family rank, the Pseudoxyrhophiinae. Pseudoxyrhophiidae is an indigenous clade to Madagascar, made up of about 88 species in 21 genera.

Pseudoxyrhophiinae is the sister group to the East African taxa *Amplorhinus* and *Duberria*, according to Burbrink et al. (2019). Sister to all other pseudoxyrhophiids was the Socotran Island (Yemen) endemic *Ditypophis*. According to Burbrink et al. (2023), the early Miocene is when the Pseudoxyrhophiidae first appeared. It is poorly recognized that at least two genera of gemsnakes have adopted aquatic habits.

It appears that two other genera of Malagasy snakes, *Thamnosophis* (Cadle 2003; Glaw & Vences 2007) and *Madagascarophis*, have semi-aquatic lifestyles (Rosa et al. 2016). Foraging along streams has been documented for *Madagascarophis meridionalis* (Neaves et al. 2019). There is only one known instance of *Thamnosophis mavotenda*, and it was caught in the Tsingy de Bemaraha National Park. It was swimming in a river when it was caught. implying that it is a semi-aquatic species as well. (Glaw et al. 2009). The most aquatic species are the three listed below, and some documented observations substantiate their frequent usage of aquatic environments.

Closer examination will likely show more aquatic or semi-aquatic species in this family. The genus *Thamnosophis* Jan 1863 is part of another radiation of Malagasy snakes. Currently, six species are included in the genus: *Thamnosophis stumpffi, T. lateralis, T. infrasignatus, T. epistibes, T. martae,* and *T. mavotenda* These species have 19 rows of dorsal scales and minimal sexual dimorphism in tail length. During a recent survey in the Tsingy de Bemaraha in western Madagascar, a single individual of a new *Thamnosophis* species strongly resembles *T. martae* in scale arrangements but *T. epistibes* in live coloration. The adjacent vegetation was disturbed by dry forest on calcareous ground. The snake probably tried to escape by swimming, having been disturbed by people walking in the river. Jovanovic et al. (2009) report a successful predation event on the Malagasy poison frog *Mantella aurantiaca;* the observations were made in Torotorofotsy Wetlands, one of the few known sites where *M. aurantiaca* occurs. The predation event was believed to be carried out by this snake. After 30 minutes of observation on the frog *Thamnosophis* (probably *T. lateralis,* but it could be confused with *T. epistibes,* a similar species that also inhabits this area.), as the snake started to swallow the frog, it did not seem bothered by the taste. The toxins from the frog may not bother this species. After ingestion, the snake showed no signs of intoxication.

Six-lined Water Snake
Liopholidophis sexlineatus (Günther, 1882)

Figure 14.18. The distribution of *Liopholidophis sexlineatus.*

Distribution and Habitat. Madagascar (elevations up to more than 2500 m). close to water including anthropogenic bodies of water (rice paddies) as well as swamps, and marshes. Type locality: "Eastern Betsileo, Madagascar." North Fianarantsoa Province, in central Madagascar. Widespread in the central highlands and south-east of Madagascar. Additionally, there are records from Toamasina and Mangindrano on the north end of the island.

Liopholidophis Mocquard, 1904 is a genus endemic to Madagascar. The genus was recently revised by Cadle (1996, 1998) whorecognized nine species in two species groups. The *Liopholidophis sexlineatus* group contains *L. sexlineatus L. varius L. dolicocercus, L. grandidieri* and *L. rhadinaea.* These species have 17 rows of dorsal scales and are characterized (with the exception of *L. varius)* by an extreme sexual dimorphism in tail length, the tails of the males being much longer. Accordingly, the number of subcaudals is much higher and the total length is longer in males than in females.

Natural History**.** A semi-aquatic, diurnal snake that inhabits open areas near water (Glaw and Vences 2007). Diet includes frogs in the genera *Ptychadena Heterixalus*, and *Boophis* and the skink *Trachylepis madagascariensis.* It is viviparous with litters of 4-10 young reported in December.

Figure 14.19 *Liopholidophis sexlineatus.*
Photography by Konrad Mebert.

Lateral Water Snake

Thamnosophis lateralis Duméril, Bibron and Duméril, 1854

Distribution and Habitat**.** Widespread in Madagascar [No map.] Mostly terrestrial but also found in water, including rice paddies. Cadle (1996) examined 20 specimens and found the largest male 729 mm total length, 212 mm tail length (29% of total; tip of tail missing). The largest females was 820 mm total length, 234 mm tail length (29% of total). Natural History**.** Diet is mostly frogs. Clutches of 6-13 eggs.

Figure 14.20. The distribution of *Thamnosophis lateralis.*

Yellow-striped Water Snake

Thamnosophis stumpffi (Boettger, 1881)

Figure 14.21. *Thamnosophis lateralis.*
Photography by Gonçalo M. Rosa.

Distribution and Habitat. Forests of northeast Madagascar. The type locality is the island of Nossi-Bé (no map).

The *stumpffi* group contains *T. stumpffi* , *T. lateralis, T. infrasignatus,* and *T. epistibes.* These species have 19 rows of dorsal scales and do not show an extreme sexual dimorphism in tail length. They are distributed throughout eastern Madagascar from Montagne d'Ambre in the north to Andohahela in the south, ranging from sea level to about 4700 ft. In addition, *T. lateralis, T. stumpffi*, and *T. epistibes* are also known from less humid localities in western Madagascar.

Natural History. A diurnal, mostly terrestrial snake inhabiting low elevation forests. It uses primary closed canopy forests and forests that have been disturbed (Blumgart et al. 2017). It is threatened by habitat fragmentation, deforestation, and agricultural expansion.

Figure 14.22. *Thamnosophis stumpffi*
Photography by Paul Freed.

The Dipsadidae Section

The Dipsadidae Section

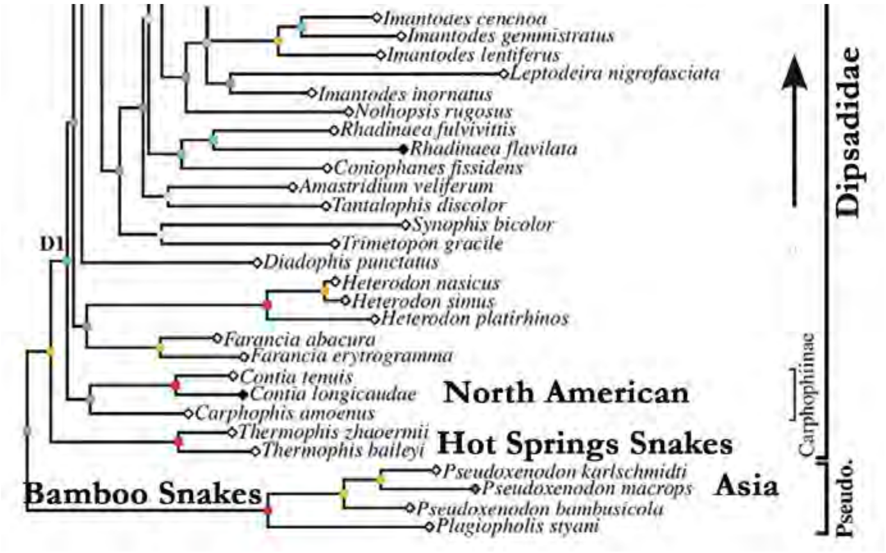
The snake on the previous page is an arboreal *Imantodes* from Peru - its not aquatic. I use it to mark the begining of the chapters on the dipsadids.

The Dipsadidae (or Dipsadinae) are ecologically and morphologically diverse; some are arboreal, others are terrestrial, fossorial or aquatic. Most are oviparous, but some *Helicops* appear to be facultatively viviparous. Many prey on vertebrates, yet others feed on soft-bodied invertebrates such as earthworms, snails, and slugs.

The clade contains 843 species that are mostly restricted to the neotropics, but some occur in North America.

However, the sister clades to the dipsadids are the bamboo snakes of the family Pseudoxenodontidae (genera *Pseudoxenodon* and *Plagiopholis)* following Zaher et al. (2019). They found the immediate sister to the bamboo snakes was the Tibetian hot springs Snakes of genus *Thermophis*. Surprisingly. the sister to *Thermophis* was the North American clade Carphophiinae that includes the genera *Carphophis* and *Contia*. This section covers the next eight chapters each discussing one or more subclades.

Figure 1. Modified from Zaher et al. (2019) shows the position of the Bamboo Snakes as the sister to the dipsadids and the basal position of Asian *Thermophis* and North American *Carphophis Heterodon,* and *Farancia,* in the Dipsadidae



Next page.
***Pseudoxenodon bambusicola.* Photography by Konrad Mebert**

15. Bamboo Snakes, Pseudoxenodontidae

15. Bamboo Snakes, Pseudoxenodontidae

Pseudoxenodontidae contains 10 species in two genera. Several species are polytypic. They are found in South and Southeastern Asia, from northeast India to southern China (including Taiwan) and south into Indonesia as far east as Wallace's Line. Little is known about them. Bamboo Snakes spread a small hood as part of their defense behavior they are commonly referred to as false cobras.

They are small to medium-sized oviparous snakes. *Pseudoxenodon* occurs along streams in wet forests (Rahadian and Das 2012; Stuart and Heatwole 2008). *Plagiopholis* are more terrestrial (Zhong et al. 2015). The two genera (*Pseudoxenodon* and *Plagiopholis*) have similar hemipenes morphology and molecular data confirmed their close relationship (McDowell 1987; Pyron et al. 2011). They were recovered as the sister to the Dipsadidae by Zaher et al. (2019). The degree to which these snakes are semi-aquatic is not known. The literature suggests that some of them are semi-aquatic.

Common Bamboo Snake

Pseudoxenodon bambusicola Vogt, 1922

Figure 15.1. The distribution of *Pseudoxenodon bambusicola*.

Distribution and Habitat**.** Leaf litter and moist ground under large objects they are generally found in inland wetlands, or close to permanent water from southern and southeastern China, central Laos, northern Thailand, and northern and central Vietnam.

Natural History**.** Diet includes frogs of the genus *Microhyla.* This has an impressive threat displays, including flashing boldly banded ventral patterning and bright yellow coloration, spreading a hood, and death feigning (Pope 1935).

Figure 15.2. *Pseudoxenodon bambusicola.*
Photographed by greenlapwing@gmail.com

Baramen Bamboo Snake

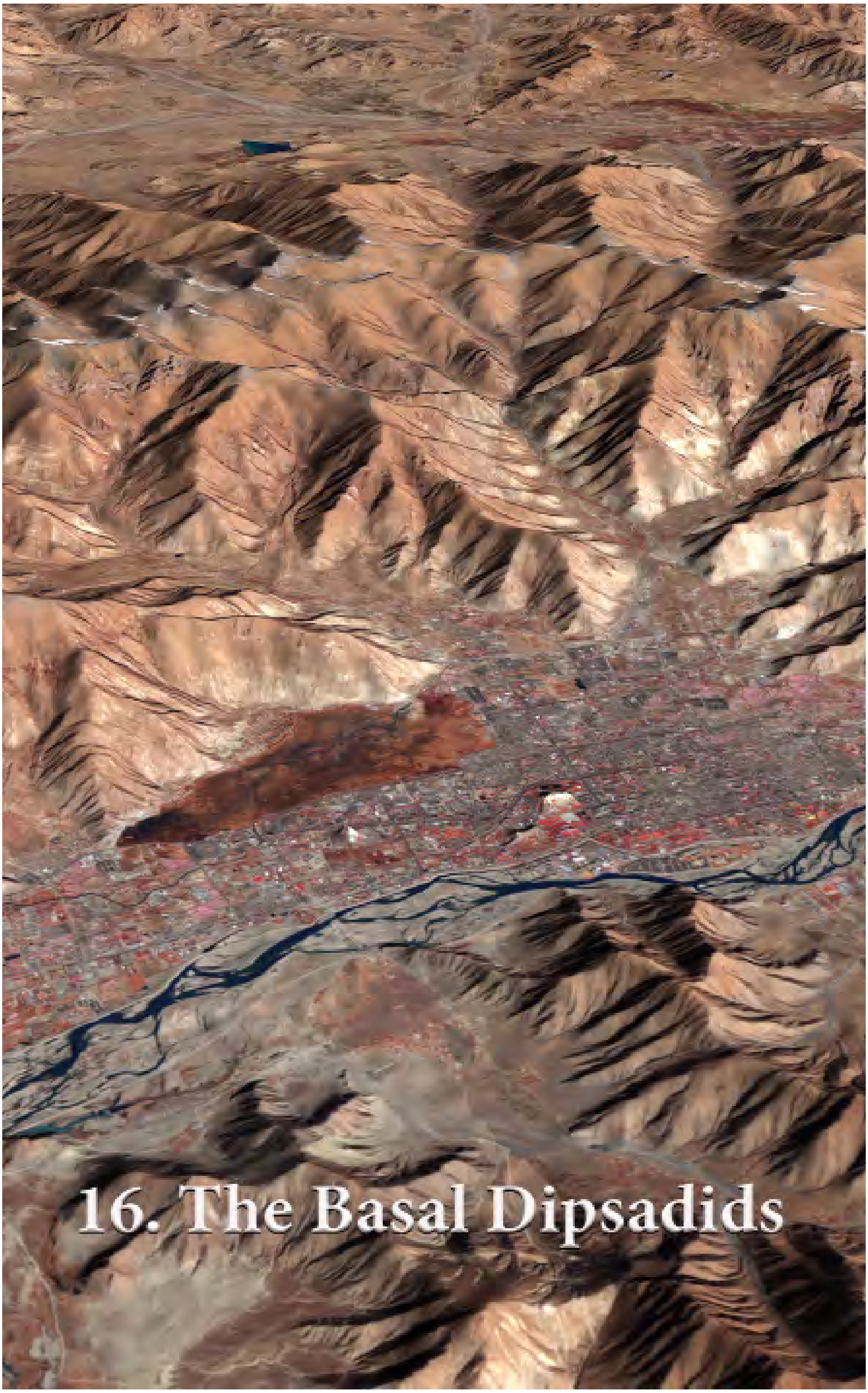
Pseudoxenodon baramensis (Smith, 1921)

Figure 15.3. The distribution of *Pseudoxenodon baramensis*

Distribution and Habitat. Malaysia (Borneo, Sarawak). Type locality: "Mount Dulit, Sarawak, North Borneo, at 1,000 metres." [=Banjaran Dulit, 3rd Division, Baram District, northern Sarawak, central East Malaysia, 1000 m, 3˚15'N, 114˚15'E]. Stuebing et al. (2014) notes the species is known from a few submontane sites in Sabah, Sarwak, and Kalimantan at elevations above 1000 m ASL

Figure 15.4. Baramen Bamboo Snake *Pseudoxenodon baramensis.* Photography by Fenoy Xavier.

On the next page. Lhasa, Tibet. This three-dimensional view of Lhasa, Tibet that illustrates how the city fills a flat river valley nestled in the ranges of the Himalaya Mountains in southern China.This image originally appeared in the NASA Earth Observatory story Lhasa, Tibet. NASA image created by Jesse Allen, using data provided courtesy of NASA/GSFC/METI/ERSDAC/JAROS, and U.S./Japan ASTER Science Team. Caption by Holli Riebeek.



16. The Basal Dipsadids

16. The Basal Dipsadids

It is unexpected to find the closest ancestor of New World dipsadid snakes that are mostly tropical exist in a landscape that looks like the one to the left. Yet, the Tibetan hot springs snakes in the genus *Thermophis* represent a lineage that moved from Asia into the Western Hemisphere. The literature suggests that at least some dipsadid species are semi-aquatic, while others are more terrestrial. The only other Asian dipsadid is the gastropod-eating *Stichophanes ningshaanensis* formerly consider a member of the genus *Oligodon (*Wang et al. 2014). Messenger and Wang (2015) found *Stichophanes* to be terrestrial and oviparous. Basal dipsadids also contain the Carphophiinae (the North American fossorial genera *Carphophis* and *Contia*) neither are semi-aquatic. Zaher et al. (2019) found these snakes to be the sister to the highly aquatic mud snakes of *Farancia*.

Bailey's Hot-spring Keelback

Thermophis baileyi (Wall, 1907)

Distribution and Habitat**.** China (Tibet = Xizang, Lhasa region), 3000-4000 m elevation or higher. Type locality: Tibet. Dorge et al (2007) surveyed locations that offered suitable habitat and found it closely associated with hot-springs. Altitudinal distribution is 3600 to 4900 m asl. The species occurred in glacial refugia associated with hot-springs during the uplift of the Tibetan Plateau and during the cooler periods of the ice ages.

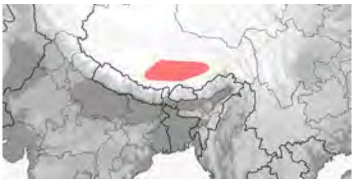


Figure 16.1. The distribution of *Thermophis baileyi*

Natural History**.** Diet appears to be restricted to metamorphs of the frog *Nanorana parkeri* and fishes of the genus *Schizopygopsis.* The areas around hot springs are used for basking on the warm ground between rocks or along riverbanks. They are particularly active after rain. Some individuals were observed in the warm pools of hot springs and in adjacent rivers. The water temperatures of the hot springs were relatively constant over the season and ranged from 29 to 33°C. River temperatures were much lower (8–11°C) and did not vary during a given day. At ground level, temperatures rose to 35°C as early as March. Low-sulfur sites along rivers provide food and basking sites for thermoregulation. However, the temperature of such thermal sites plays no role, or only a secondary role, in determining the species' presence. (Dorge et al. 2007, Hofmann et al 2014).

Yunnan Hot-spring Keelback

Thermophis shangrila Peng et al, 2014

Distribution and Habitat. Shangri-La County, Yunnan, China. The holotype was in a grassland at the forest edge near a hot spring about 500 m in Shangri-La, Northern Yunnan, China, at 12:30 on 23 August 2011, when it was moving towards the forest. The authors (Peng et al. 2014) considered this snake terrestrial – but based on a limited observation.

Natural History. A diurnal and possibly terrestrial snake. The temperatures recorded at the mouths of hot springs at the 31 known sampling sites of *Thermophis* exceed 40°C. There are 229 hot springs with the temperature hotter than 40°C in the area, raising the questions why only a few hot springs are utilized by *Thermophis* and why did snakes sympatric with

Figure 16.2. *Thermophis baileyi* **Photography by Sylvia Hofmann.**

Thermophis in earlier geologic periods fail to survive in these regions?

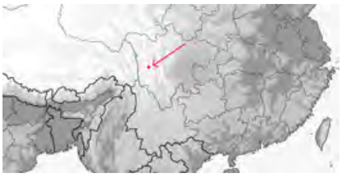


Figure 16.3, Distribution of ***Thermophis zhaoermii.***

Sichuan Hot-spring Keelback

Thermophis zhaoermii Guo, Liu, Feng & He, 2008

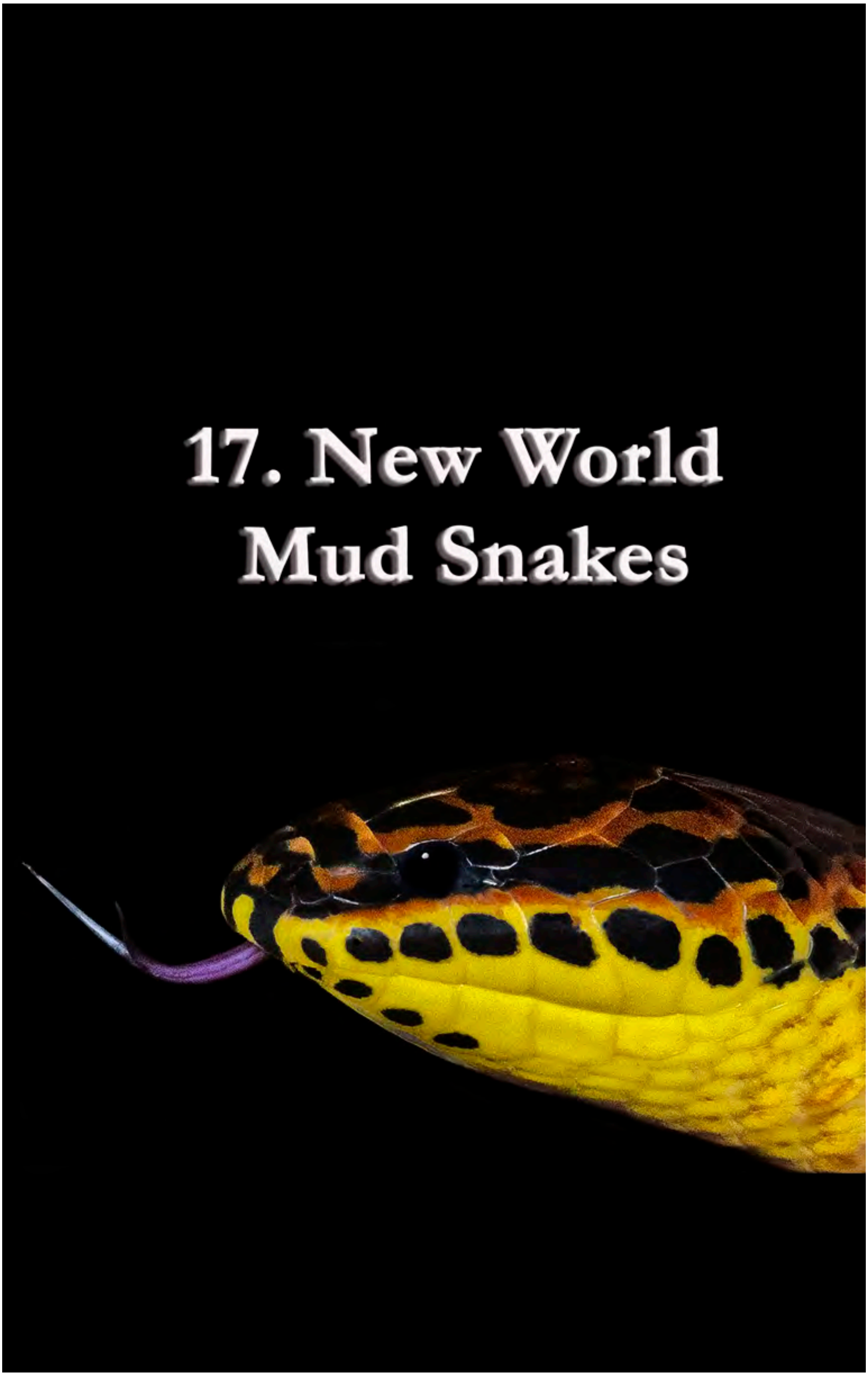
Distribution and Habitat**.** Found at high elevations in the Hengduan Mountains of China. Recent investigations show the Sichuan Hot-spring Snake is restricted to geothermal zones above 3000 m ASL. The type locality, Litang County, Suchuan, China, elevation 3700 m.

Survival of hot-spring snakes is seriously threatened. The exploitation of geothermal resources and the construction of hydropower stations are the major threats to its survival.

This is especially the case for the Sichuan hot-spring snakes. The development of hot-spring tourism in Sichuan may encroach on *T. zhaoermii* habitat, resulting in habitat degradation, water pollution, and limited access to food resources (Ren et al. 2022). *Thermophis zhaoermii* only occurred in about one-quarter of the investigated hot-springs. Before the construction of hydropower stations and exploitation of geothermal resources, Ren et al. (2022) propose detailed population surveys should be conducted to guide policy decisions.

Figure 16.4. *Thermophis zhaoermii.* **Photography by Sylvia Hofmann.**

17. New World Mud Snakes



17. NEW WORLD MUD SNAKES

The two species that compose the genus *Farancia* are considered some of the most aquatic snakes in North America, but both species are known to wander overland (Steen et al. 2013). Droughts may trigger their movement from a wetland, and excessive rainfall may also trigger their movement. Females will also move overland to nest. Both species take aquatic prey. Semlitsch et al. (1988) have described juvenile emergence in both the Fall and Spring and note that hatchlings may benefit from Fall emergence by feeding prior to their first winter. However, Fall emergence may present the hatchlings with dried or reduced aquatic habitats while spring emergence would have abundant habitat and food (larval salamanders).

The members of the genus are known to have maternal attendance of eggs; a highly specific diet of elongated prey; American eels (*Anguilla rostrata*) and the eel-like salamanders of the genera *Siren* and *Amphiuma*. Knowledge about even basic aspects of their biology may be subject to revision. For example, relatively recently both species but were found to make overland movements far from water (Steen et al. 2013).

Red-bellied Mud Snake

Farancia abacura (Holbrook, 1836)

Distribution and Habitat**.** The Coastal Plain of the southern United States from southern Virginia southward throughout Florida; follow the Mississippi drainage as far north as Southern Illinois and west to eastern Texas and the occur the Coastal Plain and range into the Piedmont of western Georgia. They occur in seasonal wetlands, ditches, Carolina bays, cypress swamps, marshes, slow-moving streams, and the heavily vegetated lakes and ponds margins. Type locality: South Carolina. This is a polytypic species, with an eastern race and a western race and a zone of intergration between them. The Western Mud Snake, *F. a. reinwardtii* has fewer than 52 red bars.The nominate race has more than 53 red bars

Natural History**.** These are highly aquatic and spend much of their lives in submerged vegetation and debris. They seldom bask out of the water and are seen on rainy nights when they may traverse roads into adjacent aquatic habitats. Prey is usually the giant aquatic salamanders in the genera *Amphiuma* and *Siren*; young snakes consume other amphibians (usually larval anurans and salamanders). However, *Farancia abacura* feeds heavily on mole salamanders, *Ambystoma,* in wetlands without fishes, despite giant salamanders being relatively common in those habitats (Durso et al. 2013). Eggs are laid in summer (July-August) and hatch in September-October, often in sandy upland habitats near water, and females may attend the eggs until hatching. Eggs are sometimes laid in American Alligator nests and the distribution of mud snakes is similar to, and overlaps that of alligators. The eight-week incubation fits well with a strategy of commensal nesting with alligators, whose eggs have about a nine-week incubation period. Several turtles have also been found to have commensal nesting with alligators. This strategy may provide nesting snakes and turtles, as well as their eggs, with a degree of protection from egg predators and provide an excellent medium for egg incubation, thus decreasing maternity costs. This is particularly true if the nest is actively defended by an adult crocodilian, because depredation

Figure 17.1. The distribution of *Farancia abacura.*

On the previous page. *Farancia erytrogramma*
Photography by William W. Lamar.

rates are markedly higher in undefended nests (Metzen, 1977; Crawshaw, 1991).

Large females may lay more the 100 eggs; but the average clutch size is about 25 eggs. Hatchlings have total lengths of 158-231 mm.

Figure 17.2. *Farancia abacura*
Photography by Jake Scott

Rainbow Snake

Farancia erytrogramma Palissot De Beauvois, 1801

Distribution and Habitat**.** There is an isolated population in southern Florida. Otherwise, the distribution is from the Potomac drainage of southern Maryland southward through the Coastal Plain into north-central Florida, westward into eastern Louisiana. *Farancia erytrogramma* inhabits streams that are alkaline (calcareous) to pH neutral waters. Type locality: "l'Amerique septentrionale." Restricted by Harper, 1940, to "the lower Cooper River, in the vicinity of Charleston, S. C."

Natural History**.** Mostly nocturnal. Adults prey almost exclusively on the common fresh-

Figure 17.3. The distribution of *Farancia erytrogramma.*

water eel, *Anguilla rostrata* but they will also eat salamanders. This species was included in the study done by Durso et al. (2013) but the sample size was too small to include in their analyses. They observed this species feeding heavily on *Ambystoma* at one fishless wetland site. Eggs are laid in early summer and hatch in mid-August with 75-80 days of incubation. Females may attend the nest. They do not spend the winter in the water at the northern edge of their distribution while they do so in the southern portion of the range (Neill 1964, Steen et al. 2013). Durso and Laverick (2021) discovered a dead specimen entangled in plastic mesh that had been placed to reduce soil erosion. The same plastic mesh had also trapped a cottonmouth which was dead.

Figure 17.4. *Farancia erytrogramma* **Photography by William W Lamar.**

18. Wetland *Coniophanes*

18. Wetland *Coniophanes*

About 17 species of Black-striped Snakes of the genus *Coniophanes* range from Texas to Peru. They are venomous with rear fangs, and have long fragile tails – presumably to aid in escaping predators. *Coniophanes* snakes typically reach a maximum length of 31–46 cm with a brown body and black stripes running down the sides and center of the back, as well as a red or orange ventral scales. However, some species have no stripes. They spend much of their time in burrows beneath decaying plants, in loose soils, or in leaf litter on the forest floor. They are nocturnal and forage on the surface for small vertebrates. *Coniophanes* are oviparous, depositing clutches of up to ten eggs in loose soil. Depending on the humidity and relative temperature, the eggs hatch in about 40 days. Hatchlings are about 17 cm in length. Most are terrestrial, leaf-litter dwelling species, at least two are semi-aquatic (Lee 1996).

Two-spotted Snake

Coniophanes bipunctatus Günther, 1858

Figure 18.1. The distribution of *Coniophanes bipunctatus.*

Distribution and Habitat**.** Moist lowland forest, including swampy areas, has also been taken in ciénegas (stagnant standing water bodies) from southern Mexico to northwest Panama. Dry forest (Köhler 2008) and disturbed forest (McCranie 2011) are also used. Henderson and Hoevers (1977) considered this species aquatic in the Orange Walk area of Belize. McCoy (1969) considered both species aquatic and present in the mangrove forests and coastal lagoons of the Yucatan. Type locality: Unknown.

Natural History**.** Crepuscular and nocturnal. Feeds on fish, frogs, and lizards. Nahuat-Cervera and Barrao-Nobrga (2021) report a specimen attempting to eat the frog *Lithobates brownorum.*Clutches of up to six eggs were reported in June.

Five-striped Snake

Coniophanes quinquevittatus Duméril, et al. 1854

Figure 18.3. The distribution of *Coniophanes quinquevittatus.*

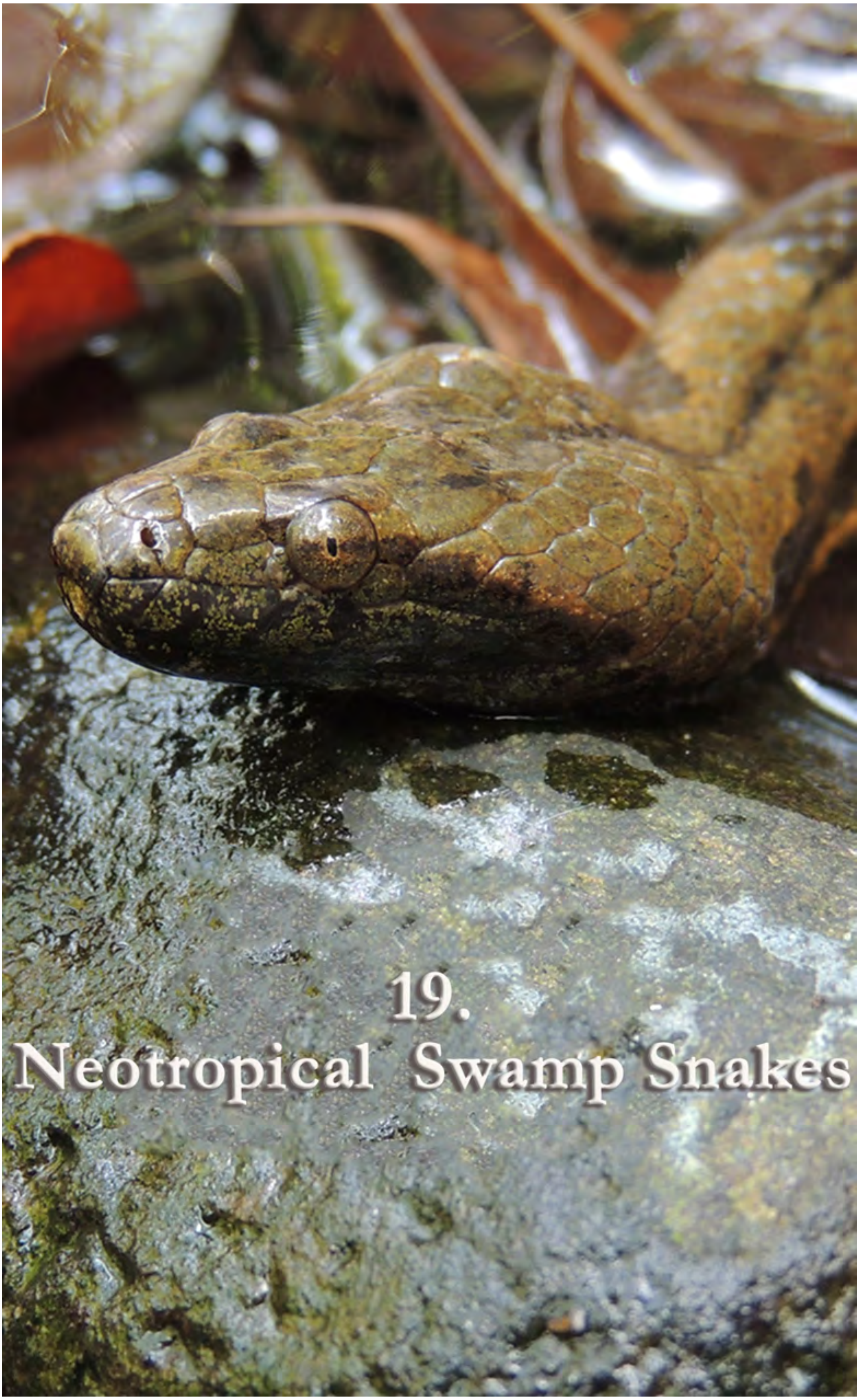
Distribution and Habitat**.** Inhabits mangrove forests and coastal lagoons in Mexico (Chiapas, Tabasco, S Veracruz, Yucatan, Campeche), and northern Guatemala. The distribution seems to be discontinuous. Type locality: Unknown.

Natural History. Poorly known. Conant (1965) found this species and its congener *C. bipunctatus* in the same *Typha-Pontederia-Thalia* marsh southwest of Coatzacoalcos, Veracruz. The Tiger Heron has been reported as a predator on this species

On the previous page. *Coniophanes quinquevittatus*
Photography by Andrew @ Journeys in Conservation,.

Figure 18.2. *Coniophanes bipunctatus* **from Selva Lacandona, Chiapas, Mexico. Photography by Ruth Pecino Daniel**

Figure 18.4. *Coniophanes quinquevittatus* **from Tabasco Mexico. Photography by Chris Harrison.**



19.

Neotropical Swamp Snakes

19. Neotropical Swamp Snakes

This chapter discusses two clades of dipsadid snakes the poorly known Prawn Snakes of the genus Hydromorphus and the Swamp Snakes of the genus *Tretanorhinus*. A related clade consists of the arboreal-terrestrial *Imantodes* and *Leptodeira* (Zaher et al. 2019). While *Leptodeira* is considered semi-aquatic by some authors my (JCM) experience with them is that they are much more arboreal and terrestrial, and are dietary specialist on frogs, tadpoles, and frog eggs from non-aquatic foraging sites.

Perhaps the most interesting aquatic dipsadids, are the snakes in the genus *Tretanorhinus*. Four species are known from Ecuador, Central America, Cuba, and the Bahamas. The long head, square muzzle, and long tail suggest this snake may be convergent with the Tentacled Snake (*Erpeton tentaculatus*) from Southeast Asia. Few herpetologists have examined these snakes since Wilfred Neil observed them in Cuba in 1949 and reported them hunting at night in shallow water and described them as highly aquatic. They move very slowly, use freshwater, brackish water, and possibly full-strength sea water. Neill observed them snapping at small fish in shallow pools stating that they were quite successful in capturing prey.

Prawn Snakes, *Hydromoprhus*

Hydromorphus are medium-sized snakes (males to 690, females to 797 mm TL) with rounded heads barely distinct from the neck, and moderately short tails (13-19% of TL). Eyes are small, with a round pupil. Nostrils are directed dorsally. Head scales are typically except for having 1 or 3 internasals and 1 or 3 prefrontals. Nasals are usually entire but may be partially or entirely divided below the nostrils. A loreal bordering the orbit usually present. A single, upper preocular may be present (the lower preocular is usually fused to the loreal) but two or more may be found Two pairs of chin shields with a mental groove variably developed or absent. Dorsal scales are smooth (except for supra-cloacal keels in one species), in 15- 17 rows at midbody, 13-15 near the vent. Cloacal plate and subcaudals are divided. Ventrals number 157-186, subcaudals 33-54. Dorsal color is dark gray to dark brown or olive green somewhat paler on rows 1-2. The venter is yellowish or cream-colored with variable dark smudging along the edges and the center of the ventrals, more abundant on the body's posterior portion (Villa 1990).

Peter's Prawn Snake

Hydromorphus concolor Peters, 1859

Figure 19.1. The distribution of *Hydromorphus concolor*

Distribution and Habitat. Atlantic lowlands and premontane slopes from Guatemala to Panama (Honduras, Nicaragua, Costa Rica, Panama); Colombia; reaches 900 m elevation in Honduras. Inhabits streams and the adjacent forest floor in wet forests. Type locality: Not given, presumably, Costa Rica.

Natural History. Diet may include prawns as well as other aquatic prey. Active day and night. When in the water, often at the bottom in debris. Active on land after heavy rains. Clutches of four and seven eggs in June and hatch in November and December.

Previous page. A *Tretanorhinus variabilis wagleri*
Photography by Tomás Michel Rodríguez Cabrera.

Figure 19.2. *Hydromorphus concolor.*
Photography by Twan Leenders (upper two) Fabio Hidalgo (bottom)

Dunn's Prawn Snake

Hydromorphus dunni Slevin, 1942

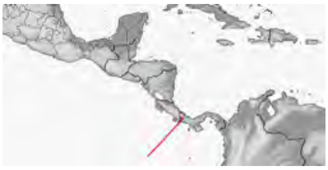


Figure 19.3. The distribution of *Hydromorphus dunni*

Known from a single specimen from Chiriqui, Panama at 1250 m in premontane forests. Total length of 482 mm.

Swampsnakes, *Tretanorhinus*

The Neotropical Swampsnakes are nocturnal and highly aquatic. Currently, four species are recognized, and the genus remains poorly studied. *Tretanorhinus* is exclusive to the Neotropics where it inhabits fresh and brackish water bodies such as rivers, streams, lagoons, estuaries, mangroves, and cow wells. They seem to require a muddy or rocky substrate with aquatic vegetation where they can hide and rest. But there are reports of individuals found out of the water, usually, after flooding, that forces the snakes to search for another water body. The distributions imply the ability of these snakes to disperse and survive in across saltwater barriers (Barbour and Amaral 1924; Neill 1958) since they have colonized several islands.

Dunn (1939) described the generic traits as: "Dorsal scales keeled, striate, pitless, reducing by dropping the paravertebrals, 21-17; subcaudals double; cloacal plate double; head scales normal with at times two loreals and at times one or three prefrontals; internasals small; pupil circular to slightly oval; maxillary teeth about 27, subequal."

Zaher et al. (2019) found this genus to be paraphyletic with *T. variabilis* and *T. nigroluteus* separated by quite a few nodes, thus some generic changes may be expected.

Mocquard's Swampsnake

Tretanorhinus mocquardi Bocourt, 1891

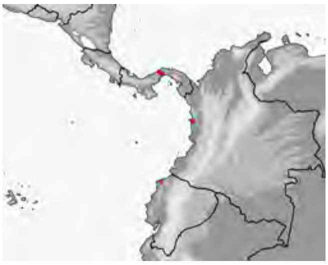


Figure 19.4. The distribution of *Tretanorhinus mocquardi*

Distribution and Habitat. Lowland forest swamps on the Pacific coasts from Panama to Ecuador. Type locality: "Belize" in error. Dunn (1939) states that it is Panama City. There is apparently one record from eastern Panama that may be the result of dispersal along the Canal.

Natural History. Presumably, fish and amphibians are the prey of this species.

Orange-bellied Swampsnake

Tretanorhinus nigroluteus Cope, 1861

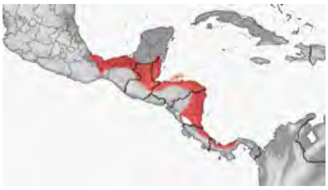


Figure 19.5. The distribution of *Tretanorhinus nigroluteus*.

Distribution and Habitat. Pacific and Caribbean slopes of Mexico (Chiapas, Oaxaca, Tabasco, Quintana Roo, Campeche), Guatemala, Honduras (Islas de la Bahia and Utila), Nicaragua, Belize, El Salvador uncertain, Costa Rica, Panama. Records of this species in Colombia are controversial (Barquero and Arguedas (2019). Inhabits streams in the Chocó Tropical Humid Forest and rivers and coastal lagoons in Quintana Roo, Mexico (Cedeno-Vazquez et al. 2021).

Natural History. Diet. Known to feed on poecilid fish (*P. sphenops* and *P. mexicana*) (Cedeno-Vazquez et al. 2021).

Striped Swampsnake

Tretanorhinus taeniatus Cope, 1861

Distribution and Habitat. The Pacific coast of Colombia and Ecuador. In Colombia reported from the Valle del Cauca**.** In Ecuador it is only known from Esmeraldas Province, at an altitude of approximately 140 m. Type locality: River "Sapayo", Esmeraldas Province, Ecuador.

Natural History. Aquatic in fresh water, black water, and salt water. When threatened they dive for concealment.

Caribbean Swampsnake

Tretanorhinus variabilis Duméril, et al., 1854

Distribution and Habitat. Swamps, streams, including coastal situations with brackish water. Cuba, Isla de la Juventud, Cayman Island. Type locality: Unknown.

Figure 19.6. *Tretanorhinus nigroluteus* **Cahuita, Costa Rica. Photography by Daniel Jablonski.**

Natural History. Diet. López-Hurtado et al. (2020) document fish, frogs, and freshwater crabs in the diet of this species. The diversity of the prey suggests this snake uses a variety of foraging strategies. Petzold (1967) reported a captive female laid eight eggs on 31 August, on

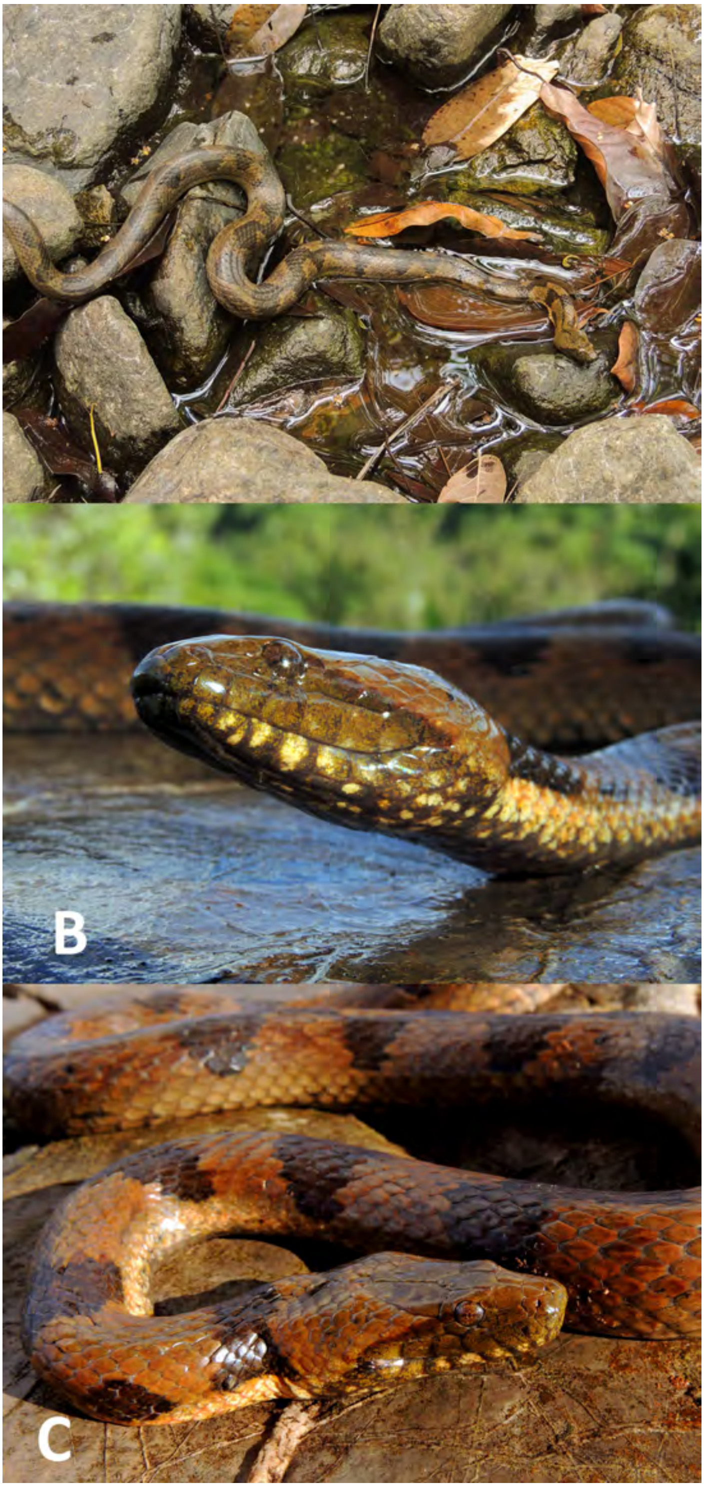


Figure 19.7. *Tretanorhinus variabilis.* **(A-C)** *T. v. wagneri*. **Photography by Tomás Michel Rodríguez Cabrera.**

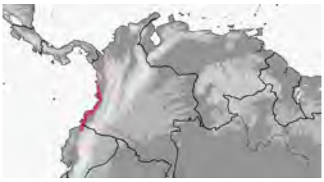


Figure 19.8. Distribution of *Tretanorhinus taeniatus*

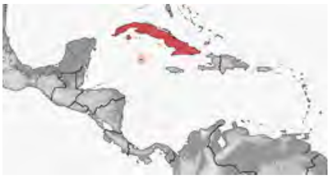


Figure 19.9. The distribution of *Tretanorhinus variabilis.*

wet moss on the border of the water basin in the terrarium. Four eggs were saved, and the temperature was 30-32 C during the day, 20-25 C at night). Egg sizes were: 33 x 18, 35 x 16, 36 x 16, and 36 x 17 mm.; the average weight was 5.4 grams. After an incubation period of 35 days. The total length of the newborn ranged from the pattern of the young snakes resembles that of the adults, but in the young, there is greater contrast between the spots and the ground color. Males possess tubercles on the shields of the lower side of the head-on the mental, the anterior chin shields, and the first lower labials (here very clearly). The females lack these tubercles (Petzold 1967). When disturbed the body is rolled up like a ball with the head hidden in the middle (Petzold 1967).

This is a polytypic species that needs further investigation using molecular data.

Tretanorhinus variabilis variabilis Duméril, Bibron & Duméril 1854. Distribution: Cuba, from La Habana Prov. in the west, east into Guantánamo Prov. (except for region about Sierra Maestra, Granma Prov.). Type locality: Unknown.

Tretanorhinus variabilis binghami Schwartz & Ogren 1956. Distribution: Cuba, Granma Prov., lowlands, and lower foothills of Sierra Maestra. Type locality: Finca Bucares, 22 km S Bueycito, in the Rio Yao, Granma Province, Cuba.

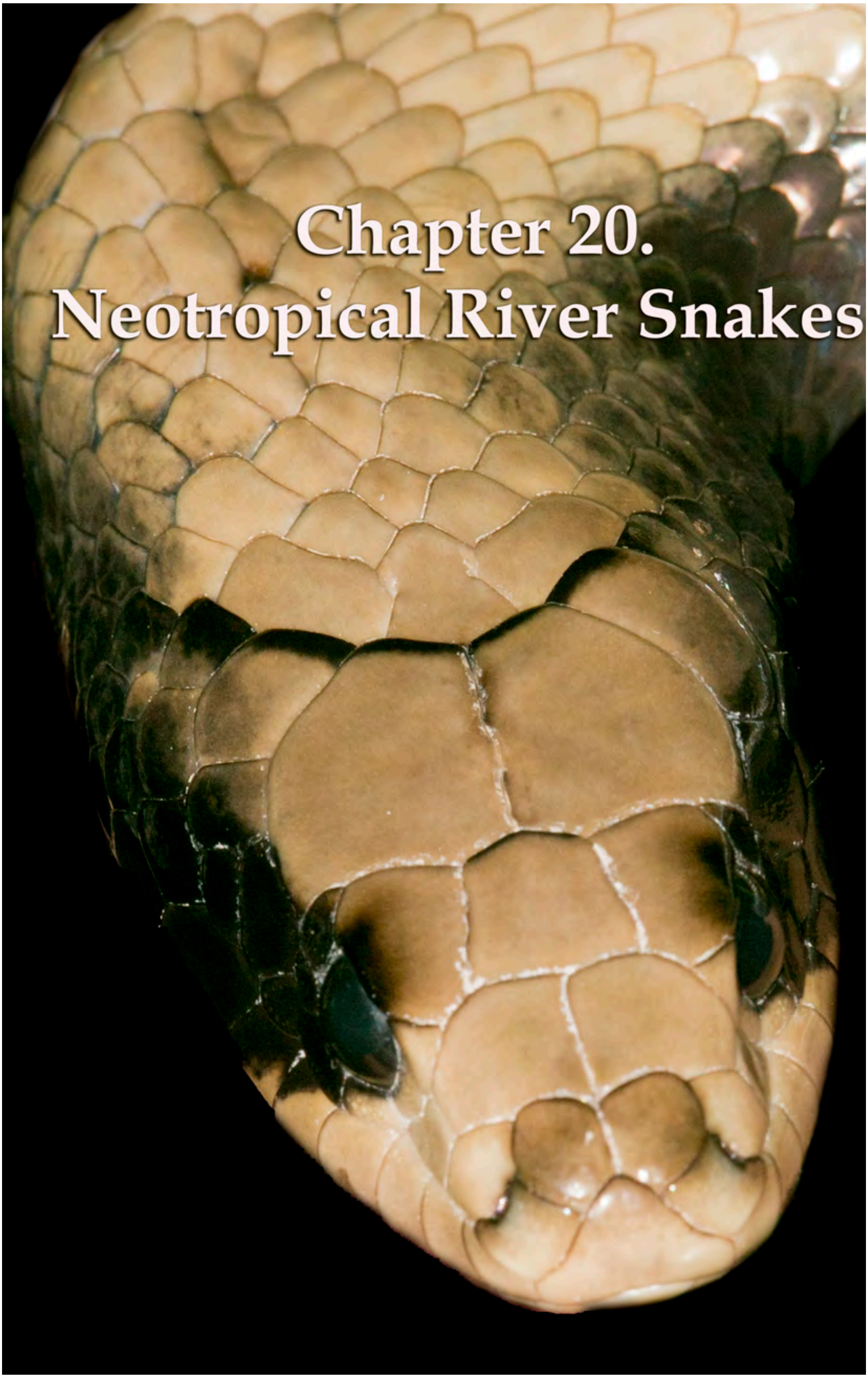
Tre*tanorhinus variabilis insulaepinorum* Barbour 1916. Distribution: Isla de la Juventud; Type locality: Isla de la Juventud.

Tretanorhinus variabilis lewisi Grant 1941 Type locality: North Side, Grand Cayman Island, Cayman.

Tretanorhinus variabilis wagleri Jan 1863. Distribution: Cuba, Pinar del Rio Province. Type locality: Brazil (in error)

On the next page. *Hydrodynastes giga***s, Photography JCM**

Chapter 20.
Neotropical River Snakes



20. Neotropical River Snakes

Zachary J. Loughman and John C. Murphy

Two snakes, Herman's Water Snake (*Hydrodynastes bicinctus*) and the False Water Cobra (*Hydrodynastes gigas*) constitute the dipsadid tribe Hydrodynastini. Both snakes are aquatic, with *H. bicinctus* rarely being found outside of forests streams, and rivers. *Hydrodynastes gigas* are among South America's largest colubroid snakes. Specimens in excess of 2.5 m weighing more than 5 kg are frequently encountered. Like most xenodontines, both species occur over a wide portion of northern and central South America. *Hydrodynastes bicinctus* occurs primarily in Amazonia and portions of the Cerrado, while *H. gigas* have a wide distribution across several South American biomes. Ecologically, both species could be considered habitat specialists given their habitat associations with wetlands, streams, and rivers. *Hydrodynastes bicinctus* is piscivorous and a feeding specialist. *Hydrodynastes gigas* have a much more generalized diet and will readily eat any vertebrate small enough to be consumed. Both species have enlarged opisthoglyphous teeth in the posterior portion of their upper jaw. Several bioactive peptides have been retrieved from both species Duvernoy's glands. Due to this, most herpetologists consider *Hydrodynastes* to be rear-fanged venomous snakes.

Natural History & Diversity

Hydrodynastes bicinctus and *H. gigas* have both similar and different ecologies. While both species are aquatic, *H. bicinctus* appears to have stronger affinities for a truly aquatic existence. The majority of *H. bicinctus* found in the field are found in water. Furthermore, *H. bicinctus* is frequently encountered in lotic waterways, often under rocks and in woody snags. Wetland environs are the preferred haunts of *H. gigas*, particularly those choked with macrophytes. Unlike *H. bicinctus*, *H. gigas* is often encountered outside of water, though aquatic habitats are never far away. While both species have these preferences, it is possible to encounter *H. bicinctus* and *H. gigas* in any aquatic environment across their respective distributions. Both species' populations decline in lentic and lotic systems with moderate to heavy anthropogenic presence (Loughman 2023).

Both *Hydrodynastes* are diurnal and are rarely encountered in the open after dark. *Hydrodynastes gigas* often is observed basking on mats of aquatic vegetation during morning hours; *H. bicinctus* rarely is encountered outside of water. *Hydrodynastes gigas* diel activity is strongly associated with morning and evening hours. Refuge is sought during the heat of the day, especially during dry seasons. During transitional months between dry and wet seasons *H. gigas* is active during all hours of the day (Giraudo et al. 2014). *Hydrodynastes gigas* activity declines as the dry season reaches its zenith. During this time, activity is limited to early morning hours, overcast days, and evening hours (Giraudo et al. 2014).

Little is known about *H. bicinctus* dietary habits other than they consume fish and amphibians. The feeding ecology of *H. gigas* has been studied extensively (Lopez and Giraudo, 2014). *Hydrodynastes gigas* are feeding generalists, and readily consume vertebrates they encounter (Lopez and Giraudo, 2014; Ballini et al. 2015). Specifically, amphibians and fish are consumed by all demographics (Giraudo et al. 2014; Lopez and Giraudo, 2014). As *H. gigas* mature and increase in size, snakes and mammals are added to their dietary repertoire. By the time they reach adulthood, *H. gigas* diets include any moderate to small sized vertebrate they encounter. Ballini et al. (2015) studied the feeding habits of a South American snake community in eastern Argentina. *Hydrodynastes gigas* were part of this community and had the evenest prey selection of any species studied. Amphibians, reptiles, fish and birds were all consumed in this respective order – all vertebrate classes were consumed.

Hydrodynastes gigas predatory behavior is similar to other aquatic snakes. Prey when encountered in water is captured by *H. gigas* waving its head, mouth agape, until contact occurs. Prey is grasped, and depending on prey size, either rapidly consumed, or constricted, dispatched, and then consumed. Duvernoy's secretions and envenomation seem to serve little to no role in prey acquisition. *Hydrodynastes gigas* is an enthusiastic feeder and will often consume multiple prey items at once if the opportunity presents itself. Strussman and Sazima (1970) noted a unique *H. gigas* feeding behavior. Large *H. gigas* were observed using the posterior portion of their bodies to flush fish and tadpoles from macrophyte beds out to deeper water. Hydordynastes gigas were observed using the first third of their bodies, which were held in an arc, to corral flushed fish into their open mouths.

Several other unique behaviors are exhibited by these snakes outside of prey aquisition. *Hydrodynastes gigas* when disturbed are well known for flattening the anterior portion of their bodies, producing hoods similar to cobras. Interestingly, *H. gigas* can flatten the entire body, not just the cervical region, and will do so if a threat is perceived. During these displays, the head is often lifted off the ground and the tongue flicked slowly and deliberately. If the perceived threat advances, *H. gigas* will use the last two-thirds of their bodies as a whip, and bludgeon their attackers (Loughman, 2023). If this does not dissuade the attacker, thanatosis may occur. Both adults (Marques et al. 2013) and neonates (Loughman, 2023) play dead. Variation in thanatosis frequency occurs at the population level – some *H. gigas* populations readily employ thanatosis while others rarely do (Marques et al. 2013).

Hydrodynastes are opistyghlyphous. Both species have enlarged teeth in the posterior portion of their mouths (Loughman 2023). Bites from *H. bicinctus* are rare. The effect of *H. bicinctus* Duvernoy’s secretions on mammals is poorly understood. *Hydrodynastes gigas* Duvernoy’s Gland secretion have been studied and are well understood. *Hydrodynastes gigas* Duvernoy’s secretions have high concentrations of proteins, specifically azocasinases, caseinases, and metalloproteinases (Hill and Mackessy, 1997). The latter enzyme is responsible for the frequent comparison of *H. gigas* to Timber Rattlesnakes (*Crotalus horridus*). Metalloproteinases are primary components in several viper venoms. They are powerful enzymes that target fibrinogen, which is used to hold cells together. While *H. gigas* possess metalloproteinases, venom delivery is very inefficient. Most people who have reactions to H. gigas bites experience localized edema. Bigger snakes deliver more venom and often produce the most virulent reactions.

Reproductive information for *H. bicinctus* is lacking, though a specimen brought into captivity laid 17 eggs. The reproductive biology of *H. gigas* is well understood. *Hydrodynastes gigas* frequently produce clutches of 30 or more eggs in human care (Loughman, 2023). In nature, *H. gigas* clutches normally number from 15 to 25 eggs. Vitellogenesis occurs in September, and oviductal eggs were present in northeastern Argentina populations from October through December (Giraudo et al. 2014). *Hydrodynastes gigas* is considered a discontinuous breeder. Males are always willing to mate, and like other aquatic snakes will form breeding balls around receptive females (Loughman, 2023). Follicles were present year-round in road-killed animals indicating the possibility of multiple clutches being laid in a single year (Giraudo et al. 2014). In human care, *H. gigas* have produced as many as 63 eggs in a single 10-month period (Z.J.L. personal observation).

Taxonomic History

Both *Hydrodynastes* species have a tumultuous taxonomic history. Hermans Watersnake was described by Herman in 1804 as *Coluber bicinctus*. A type specimen was not denoted, and the initial description was based on specimens that were lost. Wagler and Spix (1824) described *Elaps schranki* from Amazonia, which ultimately was determined to be Herman's *C. bicinctus*. Schlegel (1837) transferred to *E. schranki* to *Xenodon*. Fitizinger (1843) determined *X. schranki* was worthy of generic recognition and described and placed Herman's Watersnakes into *Hydrodynastes*. When Dumeril, Bibron, and Dumeril (1854) described the False Water Cobra, they initially placed the species in *Xenodon* as *X. gigas*. Jan (1863) placed both species in *Lejosophis*, a genera that contained several obscure South American snakes. Cope (1854) described *Cyclagaras* to house South America's Water Cobras, and removed them from *Lejosophis*. Over the next century, Hermans Watersnake would be split from False Water Cobras two more times, and placed in *Urotheca* (Dunn, 1894) and then the monotypic genera *Dugandia* (Dunn, 1944). Hoge (1958) determined that the then *D. bicinctus* should not be recognized due to name priority, and moved *D. bicinctus* back into *Hydrodynastes.*

In 1966 Hoge somewhat unceremoniously moved *L. gigas* to *Hydrodynastes* and described *Hydrodynastes bicinctus schultzi*. *Hydrodynastes bicinctus* subspecies were differentiated by Hoge (1966) based on the extent of the postocular stripe, ventral scale patterning, and distribution. *Hydrodynastes b. bicinctus* was limited to Amazonia, while *H. b. schultzi* occurred in the Cerrado. Murta-Fonesca (2015) demonstrated morphologically that characters overlapped extensively between both Amazonia and Cerrado populations, and relegated *H. b. schultzi* to be a single nominate taxon. Carvalho et al. (2023) supported these results with molecular phylogenetic data.

Hydrodynastes gigas was moved back to *Cyclagaras* by Peters and Orejas-Miranda in 1970. At the time, apical pits were thought to hold significant taxonomic validity. *Hydrodynastes bicinctus* lacked pits, while *H. gigas* possessed them. Later work determined that apical pits were not taxonomically significant for certain groups of snakes, leading Dowling and Gibson (1970) to place *C. gigas* back into *Hydrodynastes*. By 1970, both *H. bicinctus* and *H. gigas* were in *Hydrodynastes* where they have remained until today. *Hydrodynastes melanogigas* was described from the Tocantins River basin in East-Central Brazil in the early 2000's by Franco et al. (2007). The only characteristic used to differentiate *H. melanogigas* from *H. gigas* was the extreme melanism observed in the taxon. Carvalho et al. (2020) dissolved this taxon by showing that meristically and genetically there was nothing that could be used to differentiate *H. bicinctus* from *H. gigas* other than coloration. Carvalho et al. (2023) determined that though both species have rather extensive ranges over South America, they are closely related to each other, evolved in the mid-Pleistocene, and display little population variation.

Biogeography

Both hydrodynastinins occur in South America, and in certain portions of their range are syntopic. *Hydrodynastes bicinctus* prefers more forested environments compared to its more ecologically cosmopolitan relative. As currently understood, *H. bicinctus* occurs in riverine habitats and riparian corridors in central, eastern, and northern Amazonia in Brazil, Venezuela, French Guiana, and Guyana. *Hydrodynastes bicinctus* has also been recorded in the central and southern portions of the Cerrado and along the junction of the Atlantic Coast Forest and Cerrado in Brazil.

Hydrodynastes gigas has a larger distribution than *H. bicinctus*. *Hydrodynastes bicinctus* and *H. gigas* occur syntopically in central and eastern Amazonia, a small portion of the Pantanal (Fischer et al. 2018) as well as central and southern portions of the Cerrado (Noguiera et al. 2019). *Hydrodynastes gigas* also occur in the Chaco of northeastern Argentina, eastern Bolivia, and western Paraguay, the Caatinga of Northeastern Brazil, and throughout the Brazilian Pantanal wetlands. Across their respective distributions, both *Hydrodynastes* species are strongly associated with lotic environments (Giraudo et al. 2014; Carvalho et al. 2023; Loughman 2023). *Hydrodynastes bicinctus* appears to be more aquatic than *H. gigas* and are rarely encountered outside of water. While encounters with *H. gigas* have occurred outside of water, aquatic habitats are almost always nearby. *Hydrodynastes gigas* utilize a wider array of aquatic habitats and are frequently encountered in lentic as well as lotic systems.

Carvalho et al. (2023) investigated the phylogeography of both *Hydrodynastes* species. Both are relatively young species and diverged from each other within the past 1.7 million years in the Pleistocene. Genetic evidence points towards *Hydrodynastes* originating in the Tocantins River of east-central Brazil roughly 1.5 mya. By the last glacial maxima, both species had likely reached all watersheds and habitats they currently occur in. Genetic evidence suggests that *H. gigas* populations have declined slowly over the last 20 thousand years; *H. bicinctus* populations have remained stable.

Often animals with distributions strongly associated with river corridors have genetic divergence and population structure allied to specific basins and watersheds. Given their extensive range, one would expect *H. bicinctus* and *H. gigas* to have haplotypes associated with specific river systems. This, however, is not the case. Both *Hydrodynastes* species exhibit little to no population variation across their rather extensive range. Carvalho et al. (2023) attributed a lack of genetic distinctiveness to life history and ecological attributes. Both species are large and capable of expansive movements over their lifetimes. Given their generalized feeding habits, emigrating populations likely have little problem finding habitat, refugia, or prey. Vicariance is not likely to occur under these conditions, explaining the lack of population distinctiveness observed in *Hydrodynastes* populations.

Conservation

Hydrodynastes bicinctus and *H. gigas* appear to be stable across their expansive ranges. The International Union for Conservation of Nature lists both species as Least Concern. *Hydrodynastes gigas* is a CITES II species, which eliminates its exportation from any country of origin without an import permit. Both species currently occur in herpetoculture. *Hydrodynastes bicinctus* is rarely maintained, though a stable captive *H. gigas* population exists in both North America and Europe eliminating the need for importation (Loughman 2020, 2023). Habitat destruction is the most pressing concern for H. bicinctus and *H. gigas*. Pollution, degradation, and destruction of riparian and riverine habitats, as well as wetlands, eliminate populations of both species at a local level. Given their cantankerous nature when disturbed, *H. gigas* is often killed on-site when encountered by humans. Throughout its distribution *H. gigas* is referred to as Nacanina which translates as Evil River Snake in Spanish and Portuguese respectively. Climate change will likely impact both species negatively. Extensive drought conditions followed by expansive fires have become much more common in the Chaco, Pantanal, and Amazonia over the past two decades. Destruction of habitat by fires likely displaces *Hydrodynastes* populations.

Herrmann's Water Snake

Hydrodynastes bicinctus Herrmann, 1804

Figure 20.1. The distribution of *Hydrodynastes bicinctus.*

Distribution and Habitat. Guiana, Suriname, French Guiana, Brazil (Amazonas, Rondonia, Pará, Maranhão, Goiás, Mato Grosso do Sul, São Paulo, Amapa, Tocantins), Colombia, Venezuela. Type locality: None given. Neotype locality: municipality of Novo Progresso, about 240m ASL, state of Pará, Brazil. The species is polytypic with two subspecies. *H. b. bicinctus*: Colombia, Venezuela, Guianas, Brazil (Amazonas). Type locality: "none given; Rio Japurá, Brazil" (fide Kornacker 1999); *H. b. schultzi*: Brazil (São Paulo, Goias: HR 33: 226, Tocantins, Mato Grosso do Sul) .

Figure 20.2. *Hydrodynastes bicinctus.*
Photography by William W. Lamar

False Water Cobra

Hydrodynastes gigas (Duméril et al, 1854)

Figure 20.3. The distribution of *Hydrodynastes gigas*

Distribution and Habitat. French Guiana (along the coast), Suriname, southern Brazil, Piauí, São Paulo, Tocantins, Minas Gerais, eastern Bolivia, Paraguay, N Argentina (Misiones, Corrientes, Entre Rios, Santa Fe, Chaco, Formosa), Venezuela, Colombia, Guyana, possibly Peru. Type locality: Corrientes, Argentina. A polytypic species with two subspecies. *H. g. gigas*, and *H. g. melanogigas*: Tocantins, Brazil. Type locality: Municipality of Palmas State of Tocantins, Brazil. Habitat ranges from wet savannas and grasslands to subtropical dry forests, gallery forests, shrublands and a wide variety of wetlands (rivers, streams, marshes, swamps).

Natural History. The diet reported by López and Giraudo (2004) included, amphibians (30%), colubrid snakes (26%), fish (22%) and mammals (22%). One specimen contained fish eggs, and representatives of two fish families were identified, Synbranchidae and Callichthyidae. Two adults regurgitated four swamp eels (*Synbranchus marmoratus*). The shape and behavior of swamp eels are similar to those of aquatic snakes. Swamp eels breath air and may leave the water to move overland.

Figure 20.4. *Hydrodynastes gigas* **photographed near Filadelfia, Paraguay. Photography by Mike Pingleton.**

Venom. *Hydrodynastes gigas* is rear-fanged snake with poorly known venom. An adult male human was bitten on the fourth digit of the left hand and the snake was attached to the digit for approximately 30 seconds. Within 5 minutes intense local pain developed, and at 4 hours post bite the entire dorsal aspect of the hand was significantly edematous. The local effects progressed and involved the entire forearm, and the local pain referred to the axillary region. Mild paresthesia and local blanching ("pallor") were noted in the affected digit but resolved within seven days. Thus, moderate localized symptoms may result from the bite of a juvenile *H. gigas*.

21. Neotropical Fishing Snakes

21. Neotropical Fishing Snakes

The genera *Helicops*, *Hydrops*, and *Pseudoeryx* form a widely distributed clade in the Amazon basin. They have small dorsal eyes and narrow ventral scales and are found in many aquatic habitats where they feed on fish including synbranchid eels. Species that reproduce by oviparous and viviparous modes are present in this clade as well as species suspected of being facultatively viviparous.

Schöneberg and Köhler (2021) provide distributions and identification diagnoses for all the species of *Helicops*. *Helicops* contains 20 species and more are likely to be described. *Helicops angulatus* probably contains multipe cryptic species.

Neotropical water snakes in the genus *Hydrops* Wagler, 1830 (Serpentes, Dipsadidae, Hydropsini) are distributed across the northern two-thirds of South America and have been reported from Colombia, Venezuela, Trinidad (not present on Tobago) Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia, Paraguay, and Argentina. Three species are currently recognized: *Hydrops caesurus*, *Hydrops martii*, and *Hydrops triangularis*.

The eel snakes of the genus *Pseudoeryx* are widespread in South America east of the Andes. They seem to prefer shallow water habitats where the search for synbranchid eels. Two species are currently recognized with one polytypic species (*P. plicatilis*).

Water Mapepire

Helicops angulatus (Linnaeus, 1758)

Figure 21.1. The distribution of *Helicops angulatus*

Distribution and Habitat. A widespread species: Venezuela and Trinidad, Colombia, Brazil, Bolivia, Peru, Ecuador, French Guiana. It is almost exclusively aquatic, using shallow water habitats (ponds, rivers or swamps, canals, flooded fields (Murphy, 1997; Martins and Olivera, 1998; Ford and Ford, 2002). It is mostly nocturnal. Henderson et al. (1976), found activity starts about 20 minutes after dark. *Helicops angulatus* seems to show site fidelity at least in the short term. The size of the area in which *H. angulatus* utilizes in a period of about three days has been found to be approximately 30 square meters squared (Henderson et al., 1976).

Natural History. It forages for fish at night but has also been observed foraging during the day (JCM observation, Martins and Olivera, 1998). Prey includes tadpoles, frogs, fish, and aquatic lizards. I (JCM) observed young trailing each other in a flooded ditch at night – the snakes in the lead may startle prey into moving and allow the individuals behind to discover the prey more easily. Strüssmann et al. (2013) report earthworms as prey and reports *H. angulatus* feeds on the giant earthworms of the genus *Rhinodrillus*.

Reproduction. On Trinidad and at scattered locations in Brazil it appears to be facultatively viviparous (Braz et al. 2016; Murphy et al. 2020), that is, they can give birth to live young as well as lay eggs. Eggs and young are likely produced year-round (Martins and Oli-

On the previous page is *Helicops angulatus* **Photography by JCM**

Figure 21.2. *Helicops angulatus* Photography by Photography by Luis Alejandro Rodriguez J.

vera, 1998; Ford and Ford, 2002; Murphy et al. 2020). Clutch and litter size ranges from 2-20. *Helicops angulatus* does not appear to be territorial (Ford and Ford, 2002).

Apiaka Watersnake
Helicops apiaka Kawashita-Ribeiro et al, 2013

Distribution and Habitat. Known from southern Pará and Mato Grosso State, Brazil: Alta Floresta, Guaranta do Norte, Paranaíta, and Peixoto de Azevedo municipalities. These localities are situated in the southern Amazon Basin along rivers in the drainages of the Teles Pires River, all are tributaries of the Tapajos River. Type locality: Teles Pires River. municipality of Paranaíta, Mato Grosso, Brazil.

Figure 21.3. The distribution of *Helicops apiaka*

Natural History. Sympatric with *H. angulatus* and *H. polylepis*. It is nocturnal in small and large streams and flooded areas. It is nocturnal and frequently observed at the type locality, in small streams and major branches of the Teles Pires River. It is active, from 1830 to 2330 h, along the margins of the Teles Pires River, or partially submerged in small streams and flooded areas. When handled, they may attempt to bite (Kawashita-Riberio et al. 2013).

Figure 21.4. *Helicops apiaka.* **Photography by Ricardo Alexandre Kawashita-Ribeiro**

Fire Watersnake

Helicops boitata Moraes-da-Silva et al, 2019

Figure 21.5. The distribution of *Helicops boitata*

Distribution and Habitat. Mato Grosso, Brazil. Known only from the type locality- the Municipality of Poconé, Mato Grosso state, Transpantaneira Road, municipality of Poconé, Mato Grosso state, Brazil Brazil at the northern limit of the Brazilian Pantanal.

Natural History. Known only from the holotype. It has been found in mid-afternoon and may be diurnal. The holotype was found in a flooded area at the edge of an unpaved road in the Panatal. The location corresponds to a tributary of the Bento Gomes River..

Figure 21.6. The distribution of *Helicops carinicaudus*

Rough Tail Watersnake

Helicops carinicaudus (Wied-Neuwied, 1825)

Distribution and Habitat. The distribution extends from the estuary of the Rio de La Plata along the shoreline of Brazil to the province of Pernambuco.

The name *Helicops baliogaster* Cope 1885 was listed as a synonym of *Helicops carinicaudas* by Boulenger 1886.

Natural History. Active during the day and at night. It is often found along the Serra do Mar Range. Diet includes fish and amphibians. The reproductive mode is viviparous with a vestigial shell membrane. Reproduction is seasonal with vitellogenesis occurring from September to December, embryos present from November to March and young present from the end of the rainy season to the beginning of the dry season (Marques 1998, Nogueira and Marques 1998).

Cope's Watersnake

Helicops cyclops Cope, 1869

Known only from the type specimen. Type locality Bahia, Brazil. It has a remarkably short snout and head compared to *H. angulatus*. Murphy et al. (2020) removed it from the synonymy of *H. angulatus*.

Figure 21.7 *Helicops carinicaudus* **from the Guandu River, City of Seropedica, State of Rio de Janeiro. Photography by Adam Carvalho**

Daniel's Watersnake

Helicops danieli Amaral, 1938

Figure 21.9. The distribution of *Helicops danieli*

Distribution and Habitat. Shorelines of large swamps and lakes, and mangroves in Colombia west of the Andes. There is a report from the lowland in the east near the Brazilian border which may be in error. Type locality: Colombia, Santander, Carare.

Natural History. Sea level to 1500 meters ASL. It is abundant in the Magdalena River basin. Activity is nocturnal and it uses aquatic plants as a refuge. Young feed on tadpoles; switch to fish with age. Viviparous.

Amaral's Keelback

Helicops gomesi Amaral, 1921

Figure 21.10. The distribution of *Helicops gomesi.*

Distribution and Habitat. Streams and rivers in the vicinity of Sao Paulo Province to the Mato Grosso do Sul and Gorias, Brazil. Type locality: Costa Pinto Station, Railway Sorocaba, São Paulo, Brazil.

Natural History. Occurs under rocks along the edges of streams. Oviparous, a clutch of three eggs has been reported; originally reported as viviparous, may be facultatively viviparous. Braz (2020) found a three-barbeled catfish, *Pimelodella* sp. (Heptapteridae) in a female that also contained 14 pre-ovulatory vitellogenic follicles on 5 November. This suggests the snake reproduces in the wet-warm season (November-December).

Figure 21.11. *Helicops gomesi.* **From Amaral, 1926.**

Hagmann's Keelback

Helicops hagmanni Roux, 1910

Figure 21.12. The distribution of *Helicops hagmanni*

Distribution and Habitat. It occurs from the Amazon estuary to the Brazilian province of Amazonas and the Venezuelan province of Amazonas. There is a single record from northern Rondônia, Brazil. Type locality: Santarem, Brazil.

Natural History. The diet appears to be composed exclusively of fish and it forages in the medium and upper strata of the water column in the lentic zone (de Carvalho Teixeira, 2017). de Lima Moraes and Fraga (2015) found an adult perched about two meters above the ground, on the vegetation adjacent to a small first order stream, in a sunny clearing.

Sturaro and Gomes (2008) observed an adult *Helicops hagmanni* 5`16 mm SVL, weight 162 g) preying on the catfish, *Rhamdia muelleri* (215 mm total length and 70 g) in the field at 2300 h. The water was 20 cm deep. The snake seized the fish biting the prey's posterior body between the anal and post-anal fins, maybe to avoid the fish's pectoral spines. The snake held the prey with anterior, horizontal coils, similar to what has been observed in other colubrid snakes. Subsequently, the snake extended constriction

until the opercula area of the catfish. Thereafter, the snake examined the prey's body and swallowed it, starting ingestion head first.

Jan's Keelback

Helicops infrataeniatus Jan, 1865

Distribution and Habitat. Southern Brazil, Uruguay, Argentina, possibly Paraguay. Type

Figure 21.14. The distribution of ***Helicops infrataeniatus.***

Figure 21.13. *Helicops hagmanni* **(A) From Presidente Figueiredo, Amazonas, Brazil. Photography by Jairmaia (B) from Beruri, Amazonas, Brazil. Photography by Marco Aurelio de Sena.**

locality was given as "Mexico" in error; other type material from Brazil.

Natural History. The diet is composed of fish (70%) and frogs (30%). Foraging behavior likely occurs at the water's edge and at multiple depths in the water column. The reproductive cycle is longer than other oviparous colubrids from subtropical and temperate zones of Brazil. Vitellogenesis occurred from September to February. Oviductal embryos were found from September to May. Births took place in September, January, February, and March, and occurred in two peaks. Litter size ranged from 5 to 22 offspring. The differences between the number of vitellogenic follicles and embryos, and between embryos and newborns were not significant, thus practically all follicles were generally converted into embryos and embryos into neonates.

Spotted Keelback

Helicops leopardinus Schlegel, 1837

Distribution and Habitat. The distribution is peripheral to the central Amazon basin and the species is known from the northwestern Argentina to the Amazon estuary and from Ecuador to the Brazilian state Bahia. Wetlands of Guiana, Suriname, French Guiana, Brazil, Bolivia, Paraguay, Ecuador, Peru, and possibly Colombia. It is abundant in the Pantanal. Type locality is unknown.

Natural History. Diet includes mostly fish (and the fish are often Gymnotiformes) and

Figure 21.15. The distribution of *Helicops leopardinus*

about 30% anurans, most of which are hylids. The mean litter size is 6.6 and a range of 4–11. The reproductive cycle is seasonal, with parturition occurring late in the wet season (simultaneous with the flooding of the Paraguay River). Young snakes disperse on floating vegetation and the floating vegetation may be a critical habitat for *H. leopardinus*, and management plans for their maintenance need to be developed (Ávila et al. 2006). Ruiz-Garcia et al. (2020) found the Crab-eating Fox is a predator on this snake.

Figure 21.16. *Helicops leopardinus*. **(A) Photography by Wolfgang Wuster (B) from Gral Paz, Corrientes, Argentina Alfredo Sabaliauskas**

Olive Keelback

***Helicops modestus* Günther, 1861**

Distribution and Habitat. Distributed in the Brazilian province Minas Gerais, Distrito Federal, Goias, Bahia, and Pará, Brazil

Natural History. A diurnal and nocturnal snake with a diet of fish and small anurans. A juvenile *H. modestus* preyed on a small leiuperid frog, *Physalaemus cuvieri.*

Live fish fed to *modestus* in captivity were taken while the snake was submerged (Oliviera et al. 2016). After tongue-flicking the snake faced and approached the fish. Using repeated lateral undulations, resulting in irregular sinusoidal flexions that pushed the body forward, typical of pre-striking behavior. Strikes were followed by immediate bites on the fish's head, mid-regions or tail. Prey was sometimes pinned against the terrarium wall. Ingestion began headfirst, with the fish either dead or alive but always immobilized. The mean swallowing time was 16 minutes. The Duvernoy's glands are connected to the ungrooved, blade-like maxillary fangs by a vestibule from which the secretion is drained.

Figure 21.17. The distribution of *Helicops modestus.*

Observations of prey-handling suggests *H. modestus* strikes and holds fish in its mouth while repeatedly carrying out bilateral raking motions with both maxillae. Fish are swallowed alive but are immobilized, suggesting that the venom is associated with the immobilization of the fish prey Oliveira et al. (2016).

One female gave birth to 20 young in March. Another 590 mm (SVL) female gave birth on 31 January to a litter of 24 neonates. The relative clutch mass (RCM) was 0.34, a high value but like the values reported for other *Helicops*. Neonates have SVLs 120-160 mm, and weigh 1.1-2.5 g. The reproductive cycle is seasonal with vitellogenesis occurring from September to December, embryos from November to March and recruitment from the end of the rainy season to the beginning of the dry season (Maia et al. 2015). Da Costa et al. (2021) observed the leaf cutter ant *Atta opacieps* attack and kill one of these snake crawling across a trail.

Figure 21.18. *Helicops modestus*
Photography by Wolfgang Wuster

Quenya Keelback

Helicops nentur Costa, et al., 2016

Figure 21.19. The distribution of *Helicops nentur.*

Distribution and Habitat. In southeastern Brazil it is known from the eastern half of Minas Gerais, Brazil. It inhabits the Bahia Interior Forest ecoregion (Tropical and Subtropical Moist Broadleaf Forests biome), its border with the Cerrado ecoregion (Tropical and Subtropical Grasslands, Savannas, and Shrublands biome), and the ecotone between the Atlantic Dry Forest and the Caatinga ecoregions (Tropical and Subtropical Dry Broadleaf Forests biome and Deserts and Xeric Shrublands biome). The type locality is a swamp in Fazenda Papa Capim São José da Safira, in the state of Minas Gerais, Brazil.

Natural History. Inhabits lentic water bodies such as swamps. The holotype was collected while active at 0300 h, partially submerged. After collection, it gave birth to two stillborn specimens not measured nor preserved. One specimen has an umbilical scar on ventrals 91–95. Date of collection of these two specimens suggest that reproduction in *H. nentur* may occur during the rainy season (October–March) (Costa et al. 2016).

Shreve's Keelback

Helicops pastazae Shreve, 1934

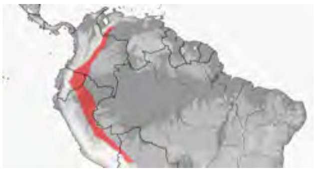


Figure 21.20. The distribution of *Helicops pastazae.*

Distribution and Habitat. Ranges from eastern Venezuela to eastern Ecuador – unknown from Colombia. The type locality is on the Río Pastaza, between Canelos and the Marañon River, Ecuador.

Natural History. The diet includes fish and anurans. Garcia-Cobos and Gomez-Sanchez (2019) collected a clutch of 11 eggs on 20 December (early dry season). The eggs were buried under a substratum composed of sand, small rocks and decomposing material located under a large rock separated about two meters from the edge of the river. After 46 days of incubation, on 4 February, the eggs started to hatch, and hatching continued until 7 February.

García-Cobos et al. (2020) studied the reproductive cycle of this species in a montane river in the Andean foothills of Colombia. They sampled 212 snakes from 2013 to 2017 and classified the monthly reproductive stages of the adult snakes. Females showed a marked seasonal reproductive cycle, with secondary vitellogenic individuals mainly clustered during the high precipitation months, ovigerous stages found throughout low precipitation months, and egg-laying occurred at times of low precipitation at the end of the wet season to the early dry seasons. Males produced spermatozoa throughout the year indicating year-round reproduction at a population level. They found sexual dimorphism in tail length, with both juvenile and adult males showing significantly longer tails than females, while adult females were larger than males and showed greater midbody width, head length, and head width. The reproductive activity of *H. pastazae* is highly seasonal in females, driven by regional rainfall patterns, whereas males are reproductive thorough the year, being a permanent resource for females. Defense behavior of this species includes striking with the mouth open and flattening the head and body. Predators include other snakes, birds, and carnivorous mammals.

Peter's Water Snake

Helicops petersi Rossman, 1976

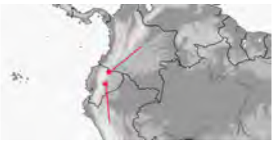


Figure 21.22. The distribution of *Helicops petersi.*

Distribution and Habitat. is known only from a very small area in the Ecuadorian province Napo. The type locality is on the east bank of Rio Misahualli, 1 mile northeast of Tena, Napo, Ecuador.

Identification. *Helicops petersi* can be distinguished from all its congeners except *H. pastazae* by the combination of 21–23 dorsal scale rows at midbody, reduced to 16 rows anterior to cloaca, and 135–150 ventrals.

Natural History. Arteaga (2021) states that it inhabits lentic waters in areas of evergreen lowland and foothill forest. It occurs in tributaries of large lakes and rivers, including small

Figure 21.21. *Helicops pastazae.* **Photography by Mario Yanez Munoz**

streams and fast-flowing whitewater rivers, but it is also present in flooded habitats altered by humans. This species occurs in open and forested areas with various degrees of human disturbance. Peter's Watersnake is nocturnal but can occasionally be seen moving during the day. During the day, individuals have been found buried in the sand besides rivers. They are sit-and-wait predators that feed on fish. Individuals have been captured in fish nets. Faced with a potential threat, individuals make an S-coil, flatten the body and head dorsoventrally, open the mouth, and strike. When manipulated, they rotate the body, bite, and produce cloacal discharges. This species is probably oviparous. One female contained 12 small ova.

Ghost Water Snake

Helicops phantasma Moraes-da-Silva et al, 2021

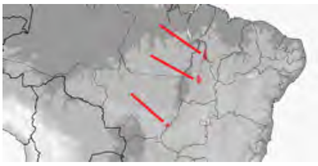


Figure 21.23. The distribution *Helicops phantasma.*

Distribution and Habitat. The species is only known from the Tocantins-Araguaia River Basin in the provinces Toncantins, Mato Grosso and Maranhão in northern Brazil. The type locality is Barra do Garças, Mato Grosso, Brazil, at 840 m ASL.

Norman's Keelback

Helicops polylepis Günther, 1861

Distribution and Habitat. Ranges from Brazil (Amazonas and Pará), Colombia, Peru, and Bolivia. The type locality is the upper Amazon.

Natural History. The diet includes *Synbranchus* eeland other fishes (Flores et al. 2010; de Carvalho Teixeira C et al. 2017)), Females have a larger body size than males, consistent with most viviparous snakes (Carmago et al. 2021)

Figure 21.24. *Helicops phantasma* **from Barra do Bugres-MT, eastern of Mato Grosso. Photography by Ricardo Alexandre Kawashita-Ribeiro.**

Figure 21,25. The distribution of *Helicops polylepis.*

Figure 21.26. *Helicops polylepis.* **The top image is an adult, bottom is a juvenile. Photography by (top) Mike Pingleton; (bottom) Paul Freed.**

Hog's Keelback
Helicops scalaris Jan, 1865

Distribution and Habitat. Known only from a small area in the northern border area between Colombia and Venezuela, western and northern of Lake Maracaibo in Venezuela. The type locality is Venezuela.

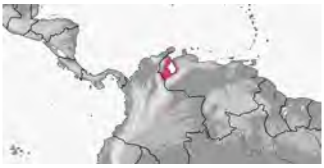


Figure 21.27. The distribution of *Helicops scalaris.*

Figure 21.28. *Helicops scalaris*. **Photography by Raul Carmona.**

Cobra-D'água

Helicops tapajonicus Da Frota, 2005

Distribution and Habitat. Shallow water with muddy substrates at two localities on the Tapajos River close to its confluence with the Amazon in the Brazilian state Pará. The type locality is the community of Parauá, on the right bank of the Tapajós river, in the municipality of Santarém, Pará, Brazil.

Natural History. The specimens were found at night, near the mouth of the streams on the Tapajós River. At the time of collection, the specimens were in the water, in a muddy area with grasses, fallen branches and roots (Da Frota 2005)

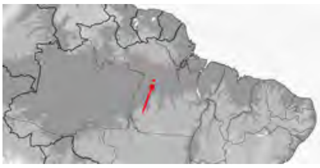


Figure 21.29. The distribution of *Helicops tapajonicus*

Equatorial Keelback

Helicops trivittatus (Gray, 1849)

Distribution and Habitat. Forested streams in eastern Pará, in northern Brazil. The type locality was given as "India ?" in error.

Natural History. Active day and night, in streams of forested areas or near residences of riverside residents. Diet: fish (*Acaronia nasa*, *Plagioscion squamosissimus*). Reproduction: female with 26 follicles in advanced vitellogenesis in March; and oviducts with marks of recent spawning in August and November; parturition in March; litters of seven to nine offspring.

Figure 21.30. The distribution of *Helicops trivittatus.*

Peruvian Keelback
Helicops yacu Rossman, 1975

Figure 21.31. EquatoriaL Keelback, *Helicops trivittatus.* From Belém, Pará, Brazil Photography by Gisele Cassunde.

This is the most poorly known member of the genus. The type locality is Moropon, Departamento de Loreto, Peru. Natural History. Unknown.

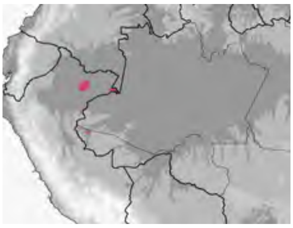


Figure 21.32. The distribution of *Helicops yacu.*

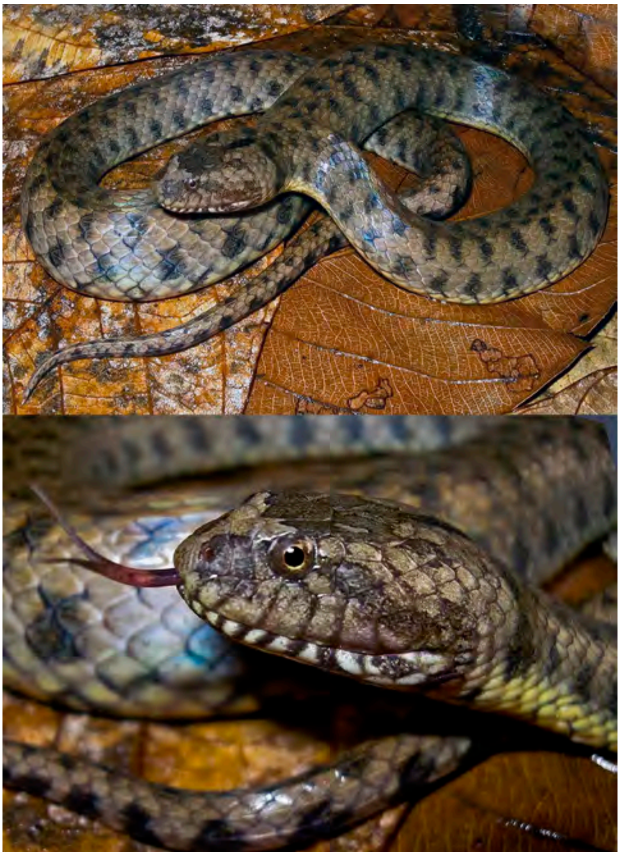


Figure 21.33. To the right.This snake is most likely *Helicops yacu,* It is from the Rio Morpon in Peru. Photography by William W. Lamar.

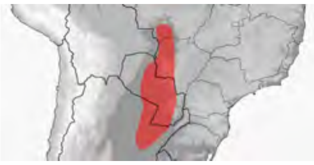


Figure 21.34. The distribution of *Hydrops caesurus.*

Southern Water Snake

Hydrops caesurus Scrocchi et al. 2005

Distribution and Habitat. Northeast Argentina and Paraguay. The distribution is disjunct from other members of the genus. It inhabits temperate and subtropical latitudes from the Paraná and Plata River basins, from Pantanal in Mato Grosso do Sul, Brazil, through Paraguay and Paraná rivers Type locality: Departamento Itapúa, Isla Paloma, Canal de los Jesuitas, Paraguay.

Natural History. Information on this species is limited. Clutches of nine and 12 eggs have been reported (Álvarez et al., 2003, Etchepare et al. 2012). The clutch of 12 had calcareous shells, they were found on 15 November Puerto Tala, Isla Apipé Grande, Corrientes province, Argentina. The nest was on the border of the embankment of a rural road that crosses a marsh. An embryo examined was in Zehr stage 26. It measured 40.7 mm body length (from the snout to the tail tip).

Figure 21.35. *Hydrops caesurus* **Photography by (A-B) Stephen Barten, (C) Ricardo Alexandre Kawashita-Ribeiro.**

Triangle Water Snake

Hydrops triangularis Wagler, 1824

Distribution and Habitat. Aquatic habitats of tropical and subtropical moist broadleaf forest, though it also occurs in tropical and subtropical grasslands, savannas and shrublands in the Amazo-

Figure 21.36. The distribution of *Hydrops triangularis.*

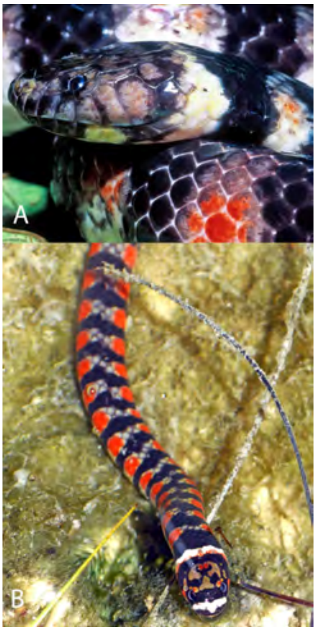


Figure 21.37. *Hydrops triangularis*. **Photography by (A) Nuevo, Peru William W. Lamar; (B) Trinidad, Renoir Auguste.**

nas, Orinoco and Guyana drainages includes Bolivia, Venezuela, Guyana, Surinam, French Guiana, Trinidad, E Peru, Ecuador, Brazil, Colombia, and Argentina. Type locality: Ega (= Tefé) Lago Tefé, at confluence with Rio Amazon, Brazil.

Natural History. An aquatic specialist. It is relatively common in streams found in open forests and savannas (Rivero- Blanco and Dixon 1978; Hoogmoed 1982; Murphy 1997) and they often use shady, lentic environments. Activity usually after dark when fish, especially synbranchid fish (which have eel-body forms) are active. Females produce clutches of 8- 34 eggs.

Figure 21.38. The distribution of *Hydrops martii.*

Amazon Water Snake

Hydrops martii (Wagler, 1824)

Distribution and Habitat. Aquatic habitats in tropical and subtropical moist broadleaf forest. East of the Andes in the Amazon basin from Colombia and eastern Peru to Maranhao, Brazil. Known from tributaries of Rio Amazonas, the Rio Ucayali and Rio Marañon, Peru. Roze (1957) reported a specimen from Rio Cairary, near Jurupary waterfall, on the boundary between Colombia and Brazil. Type locality: Provincia Maranhao, Rio Itapicuru, Brazil.

Natural History. Pinheiro et al. (2020) found the stomach contents of the piranha, *Serrasalmus rhombeus*, containing a partly digested *Hydrops martii.* A hatchling found in November. De Carvalho Teixeira et al. (2017) reported active specimens during the day, in a stream traversing primary forest. They considered the snake primarily aquatic, and suggest it will eventually be found active on the ground, foraging during day and night. Dietary information was reported by Cunha and Nascimento (1993) as fish (*Callichthys callichthys*, *Pimelodella cristata*, *Hoplias malabaricus* and *Erythrinus erythrinus*) and

Figure 21.39. *Hydrops martii* **from Momo, Peru. Photography by William W. Lamar.**

Bartlett and Bartlett (2003), reported Synbranchidae in its diet, confirming the ichthyophagous habit. Reproduction is poorly known. One offspring was found in November in Ecuador (Dixon and Soini, 1977).

Amazonian Eel Snake

Pseudoeryx plicatilis (Linnaeus, 1758)

Distribution and Habitat. It occurs east of the Andes in marshy areas and dense reedbeds as well as in streams, ponds, and flooded areas in the northern region of the Amazonian rainforest, including the Orinoco River basin and drainages of Guyana area. It occurs in the Amazonas River basin and its major tributaries to the east of the state of Pará and west of the state of Maranhão. It also occurs along the Prata River basin (restrict to the Paraguay River basin), in the states of Mato Grosso and Mato Grosso do Sul in Brazil (in flooded areas of the Pantanal region), to the east of Bolivia, north of Argentina, and southwestern Paraguay. Type locality: Ternataeis.

Figure 21.40 The distribution of *Pseudoeryx plicatilis.*

This is a polytypic species: *Pseudoeryx plicatilis plicatilis* (Linnaeus 1758) occurs in Colombia, Venezuela, Ecuador, Peru, Guyana, Suriname, French Guiana, Paraguay, N Argentina, Brazil. *Pseudoeryx plicatilis mimeticus* Cope 1885 occurs in Bolivia. Type locality: Bolivia, Rio Mamoré.

Natural History. The diet is composed of fish with eel-like bodies Reproductive mode is oviparous, and available evidence suggests that females remain with eggs throughout incubation.Facultative viviparity maybe present in this snake. Defensive behaviors are shared with other water snakes and include: dorso-ventral flattening, hiding the head, and cloacal discharge. *P. plicatilis* flattens the whole body making the snake look bigger than it is, and may intimidate visual predators, such birds. Many snakes hide the head as anti-predator mechanism. *Pseudoeryx* may hide the head and tail at the same time. *Pseudoeryx* also inverts the body and knots the body (Cavalheri et al. 2021).

Figure 21.41. *Pseudoeryx plicatilis* **Bottom photo shows death feigning behavior Photography by Konrad Mebert.**

Maracaibo Eel Snake

Pseudoeryx relictualis Schargel et al, 2007

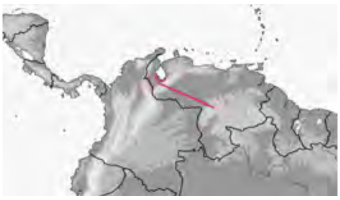


Figure 21.45 The distribution of *Pseudoeryx relictualis.*

Distribution and Habitat. Irrigation canals, swamps, flooded pastures of the Maracaibo Basin in northwest Venezuela. Known from three locations when it was described in 2007.

Natural History. The holotype was found in an irrigation channel that provides water from the Catatumbo River to crops and pastures in the area. The channels have herbaceous and aquatic vegetation, especially water hyacinths. The type locality is on a farm where patches of the original vegetation, ombrofilous evergreen forest, persist. This area undergoes periodic flooded by the Catatumbo River. The original forests in this region, have been called "Humid Forests of the Catatumbo" and are currently considered critically endangered. The specimen from Bobures, was collected in flooded pastures used for cattle farming and where most of the original forest has been cleared. This locality is only about 100 m from Lake Maracaibo. The specimen from Ensenada El Congo comes from a wildlife reserve consisting of extensive swamps where the natural vegetation of flooded pastures and forests remains almost pristine (Schargel et al. 2007).

Figure 21.46. *Pseudoeryx relictualis.*
Photography by Luis Alejandro Rodriguez J.

22. Neotropical Bush Snakes

22. Neotropical Bush Snakes

Bailey (1967) first recognized the Tachymenini grouop. Today it contains 37 species. However Zaher et al. (2019) found the morphologically diverse clade was only moderately supported. It contains arboreal, terrestrial, fossorial, and aquatic species in seven genera: *Calamodontophis, Gomesophis, Pseudotomodon, Ptychophis, Tachymenis, Thamnodynastes, Tomodon.*

Calamodontophis contains two poorly known species from southern South America. They appear to be terrestrial. *Pseudotomodon* – monotypic genus from western Argentina, is not aquatic. *Tachymenis* has about six species distributed from Peru to Chile, that are not aquatic. *Tomodon* are specialized slug and snail-eating species that are terrestrial and arboreal.

Thamnodynastes is composed of 20 small to medium size species with an enlarged pair of fangs at the back of the maxillae. These fangs are grooved to transport venom into the bite punctures. They are viviparous snakes, with elliptical pupils, single nasal scales (which may be semi-divided). Some may be best regarded as semi-aquatic and terrestrial snakes, that forage in or near the water for anurans. The semi-aquatic *Gomesophis* is the sister to the other members of the clade (Vidal et al. 2010).

The two highlt aquatic Tachymenini species are both in monotypic genera. The most recent discussion of these poorly known snakes is Gonzalez et al. (2014).

Brazilian Burrowing Snake

Gomesophis brasiliensis Gomes, 1918

Figure 22.1. The distribution *Gomesophis brasiliensis*

Distribution and Habitat. Slow-flowing water, muddy wetlands, and the margins of streams and ponds in cold-water environments of Minas Gerais, Sao Paulo, Parana, Rio Grande do Sul, and Santa Catarina, Brazil. Type locality: Pindamonhangaba, São Paulo, Brazil. *Gomesophis* occurs in aquatic habitats. Two specimens were collected at night in an area that was originally ombrophylous Mixed Forest (Brazilian pine forest). One collection site was a pond with a muddy bottom and turbid water, 80 cm deep. Herbaceous aquatic macrophytes (emergent and floating) are often present. It often hides in burrows dug into the mud of wetlands and banks of streams and ponds. (Gomes 1918, Franco 2000, Prudente and Brandão 1998; Lema 2002; França and Araújo 2007; Fortes et al. 2010).

Most of the distribution of *G. brasiliensis* is associated with the Plata Basin, the second largest river basin in South America, The Plata Basin is threatened by hydroelectric impoundments. The species is restricted to elevations of 427–1235 m ASL, (mean = 808 m ASL.) with high rainfall levels and a cool climate (Prudente 1993), although it can also be found at lower elevation in Rio Grande do Sul with a cooler subtropical climate.

Natural History. G*omesophis* are specialized earthworm-eaters, including the giant earthworms (family Glossoscolecidae) (Marques 1996, Oliveira et al. 2003, Pereira et al. 2007, Strussmann et al. 2013). Giant earthworms occur at many groundwater upwelling sites found along riparian systems belonging to the Rio Verde sub-basin. It is sympatric, but not syntopic, with *Ptychophis flavovirgatus* in most parts of its geographical range.

Previous Page. *Thamnodynastes ramonriveroi* **. southwest Trinidad**
Photography JCM

Figure 22.2. *Gomesophis brasiliensis* **from the Serra do Papagaio, Aiuruoca, MG, Brazil. Photography by Frederico de Alcântara Menezes, Arthur Diesel Abegg, Bruno Rocha da Silva, Francisco Luís Franco, Renato Neves Feio**

Fanged Water Snake

Ptychophis flavovirgatus Gomes, 1915

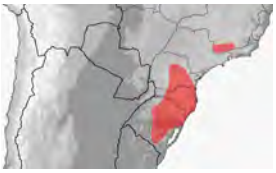


Figure 22.3. The distribution *Ptychophis flavovirgatus.*

Distribution and Habitat. Lotic waters in the Brazilian states of Minas Gerais, Paraná, Santa Catarina, and Rio Grande do Sul. It uses crevices between stones in the water for refuge. It has an elevational distribution between 316–1358 m ASL. Most locations are above 800 m ASL, and the lower elevation localities (316– 687 m ASL) are in the State of Rio Grande do Sul, in a seasonal-subtropical climate where vegetation can be open or Araucaria forests (Porto & Caramaschi 1988).

Natural History. Both sexes reach the sexual maturity at a similar body size. The reproductive cycle of *Ptychophis flavovirgatus* is long (October to June), vitellogenesis is seasonal (August and September). Six females contained between 5 and 10 embryos in the oviducts. The recruitment probably takes place in the winter and early spring (Scartozzoni and Marques 2004).

Thamnodynastes

Most members of this genus feed on anurans and are therefore likely associated with wet habitats. However, many of these species are either terrestrial or are too poorly understood to assess their use of aquatic habitats: *Thamnodynastes* are terrestrial and semi-aquatic. They are viviparous, opisthoglyphous and have elliptical vertical pupils. The genus has

Figure 22.4. *Ptychophis flavovirgatus* **Bottom photo death feigning behavior. Photography by Pedro Bernardo**

21 valid species, 11 of which occur in Brazil.

Thamnodynastes may not represent a monophyletic genus (Franco & Ferreira 2003; Zaher et al. 2009; Vidal et al. 2010; Grazziotin et al. 2012; Zaher et al. 2018), and Franco et al. (2017)have already noted the cryptic diversity associated with its members. The combination of taxonomic issues and the absence of robust diagnostic characters have perpetuated the difficulty to correctly assign individuals to species. The *Thamnodynastes pallidus* group represents an exception to this pattern. Bailey et al. (2005) defined the group based on several scale characters, body shape, color, behavior, and hemipenial morphology. The hemipenes are characteristic of the group, with no enlarged spines.

Chaco Bush Snake

Thamnodynastes chaquensis Bergna and Álvarez, 1993

Distribution and Habitat. Wetlands including the Pantanal of Paraguay, Uruguay, Brazil, Argentina. The type locality is Colonia Las Mercedes, San Fernando Department, Chaco, Argentina. Bellini et al. (2014) found this semi-aquatic species inhabits dry forest (51%), wetlands (16%), wet savannas (14%) and marshes (10%) and (9%) suburban areas. Harrington et al. (2018) found it is also partly arboreal. Akmentins et al (2010) reported a specimen submerged in a small temporary pond in secondary montane forest made up mostly of alders (*Alnus acuminata*).

Natural History. Diet contains hylid, microhylid and leptodactylid frogs as well as other small vertebrates. Frogs compose about 70% of the diet Small frogs seem to be swallowed with the posterior first (Bernarde et al.2000).

Figure 22.5. The distribution *Thamnodynastes chaquensis.*

Argentina Bush Snake

Thamnodynastes hypoconia (Cope, 1860)

Distribution and Habitat. Stagnant and slow-moving wetlands of Brazil, Argentina, Paraguay, and Uruguay. Habitats include wetlands surrounding large rivers. Riparian situations in forests, and wetlands around farmland, urban and suburban areas. Type locality: Buenos Aires, Argentina.

Figure 22.6. *Thamnodynastes chaquensis* **Photography by Dan Riley.**

Natural History. The diet is composed mostly of amphibians (96%) and the occasional skink. Anuran families making up the diet: Hylidae (34%), Leptodactylidae (16%), Leiuperidae (11%), Bufonidae (5%), Cycloramphidae (3%), Scincidae (3%), and unidentified amphibians (29%) (Bellini et al. 2013).

Figure 22.7. The distribution *Thamnodynastes hypoconia.*

Females have vitellogenic follicles from March to May, and oviductal eggs from September to December indicating seasonal reproduction. Births occur in January, litter sizes reported range from 7-13. Neonates with umbilical scars were found from January to March. Females may only reproduce once every two years. Males have continuous reproductive cycle, with no

Figure 22.8. *Thamnodynastes hypoconia.* **Photography by Paul Freed.**

significant difference in testicular volume between months (Bellini et al. 2013).

Snakes are found throughout the year, but encounter frequency was higher in spring and summer (September to March) than in winter and autumn Encounters peak in March. The daily activity maximum occurred from twilight to nightfall, with the greatest number of encounters between 1800 and 2200 h (Bellini et al. 2013).

Mato Gross Bush Snake

Thamnodynastes lanei Bailey, Thomas, and da Silva, 2005

Distribution and Habitat. The larger streams and riparian systems and their flood plains are the usual habitats in Brazil (Mato Grosso do Sul), probably also in Argentina, Paraguay, and northeast Bolivia. Type locality: Salobra, Mato Groso, Brazil. Natural History. Poorly known. A semi-aquatic snake that feeds on frogs of the genus *Leptodactylus* (Eversole et al. 2016).

Figure 22.9 The distribution *Thamnodynastesl lanei*

Linne's Bush Snake

Thamnodynastes pallidus (Linnaeus, 1758)

Distribution and Habitat. Guyana, Suriname, French Guiana, Brazil, Peru, Venezuela, Colombia, Bolivia, Ecuador. Type locality: Indiis [in error]. They are in forests or at forest edges. Also known from old secondary growth. Wetlands, riparian floodplains, swamps, floating islands of vegetation.

Natural History. Usually associated with frog choruses. Diet is composed of mostly hylid frogs. Litters of 2-7 young. Six near-term embryos measured 108 mm and 110 mm SVL for two females and 115-173 mm for four males.

Figure 22.11. The distribution *Thamnodynastes pallidus*

Turimiquire Bush Snake

Thamnodynastes ramonriveroi Manzanilla and Sánchez, 2005

Distribution and Habitat. Streams and wetlands of Venezuela (Turimiquire massiff, elevation 0-1750 m), Suriname, Guyana, Brazil, and Trinidad. The type locality is Cerro La Laguna, Turimiquire massif, Freites, Anzoátegui, Venezuela.

Natural History. On Trinidad often associated with frog

Figure 22.10. *Thamnodynastes lanei.* **Pedro Bernado**

Figure 22.12. *Thamnodynastes pallidus.* **Photography by Dario Jose Alarcon Naforo**

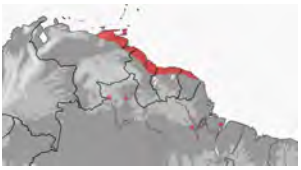


Figure 22.13. The distribution *Thamnodynastes ramonriveroi*

choruses, streams, and flooded ditches. Litters of four and five embryos reported. Defense behavior includes flattening the first half of body and when tormented they opened mouth very widely; death feigning occurred when struck with a light stick (Manzanilla & Sánchez, 2005; personal observation JCM).

Figure 22.14. *Thamnodynastes ramonriverio,* **southern Trinidad. Photography by JCM.**

Gunther's Bush Snake

Thamnodynastes strigatus (Günther, 1858)

Figure 22.15. The distribution of *Thamnodynastes strigatus.*

Distribution and Habitat. In lotic aquatic habitats, such as marshes in Argentina, Uruguay, Paraguay, and southern Brazil. Type locality India (in error).

Natural History. Diet includes fish, frogs, and mammals. Snakes ambush fish from the vegetation. They peering at fishes and use lingual luring to attract them. It will also actively forage at the margins of bodies of water. Proenca et al. (2015) recovered the remains of the fish *Hoplias malabaricus* from the stomach of this species. Reproduction. Four females (407-602 mm SVL) produced 12, 13, and 26 neonates. A fourth female had 22 oviductal eggs. Two of the litters were born in October. The neonates were 130-168 mm in total length (average = 151 mm). The three litters had RCMs of 0.313, 0.609, and 0.309 (Braz and Scartozzoni 2020).

Figure 22.16. *Thamnodynastes cf. strigatus* **Photography by Wolfgang Wüster,**

On the next page. *Erythrolamprus* cf *reginae*. **Photography by Konrad Mebert**

23. The Semi-Aquatic Painted Snakes

23. The Semi-Aquatic Painted Snakes

The Painted Snakes form a tribe level clade, the Xenodontini. Zaher et al. (2019) found unambiguous support for a common ancestor shared by the genera *Erythrolamprus, Lygophis, Xenodon,* and possibly *Umbrivaga*. The 80-plus species tend to be small (less than a meter), feed on small vertebrates, are oviparous, and have continuous reproductive cycles in tropical latitudes and seasonal reproduction in more temperate latitudes (Pizzatto et al. 2008). Members of the genus *Erythrolamprus* tend to have fewer eggs, but larger offspring and *Xenodon merremii* have the largest clutches. Adult females tend to be larger than males, but both sexes reach sexual maturity at the same size. Tail lengths and subcaudal counts in many of these species are not sexually dimorphic.

I have not included species of *Xenodon* here because the evidence for semi-aquatic habits is scarce, although Hoogmoed (1985) suggests they have valvular nares and note they feed primarily on frogs. As these snakes become better known, they may be shown to be semi-aquatic.

The Painted Snake name is derived from the bright colors found in many of them. Frequently the bright coloration is restricted to the ventral surface. A high contrast red, orange, or yellow venter with dark bands or stripes are found in many aquatic and semi-aquatic dipsadids (*Erythrolamprus almadensis, E. reginae, Sordellina, Helicops, Farancia*), natricids (*Lithodytes, Nerodia, Smithophis*), homalopsids (*Enhydris, Homalophis, Homalopsis, Hypsiscopus)*, and cylindrophiids (*Cylindrophis*).

Bright colors and high-contrast patterns, such as stripes or bands, on the ventral surface of aquatic snakes, suggest that this pattern may be aposematic and useful for deterring predators during encounters in aquatic environments (Batista et al. 2020). However, an alternative hypothesis was proposed by Goldenberg et al. (2021). They found brightly colored and patterned ventrals may have evolved for moving heat absorbed by soils to snakes when they are in contact with the ground. Dry soil and rocks convey heat more rapidly than wet soils. Thus, variation in soils' thermal properties could be significant for species that live in continuous and close contact with their substrate. In addition, melanins, a ubiquitous class of multifunctional macromolecules, largely determine the brightness of the integument. Melanins absorb and transform solar radiation into heat and have good electrically conductive properties. Thus, brightly colored ventral surfaces may be more than just aposematic.

Gunther's Striped Snake

Lygophis anomalus (Günther, 1858)

Distribution and Habitat. Humid grasslands in Southern Brazil, Uruguay, Paraguay, and northern Argentina. Type locality the Banks of the Paraná.

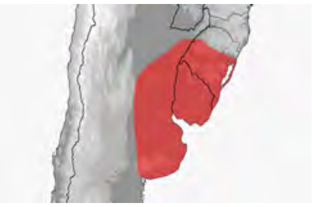


Figure 23.1 The distribution of *Lygophis anomalus.*

Natural History. The diet is composed mostly of anurans, and occasionally reptiles. Prior to swallowing, prey was oriented for headfirst ingestion. Sexual dimorphism in head length, and diet composition was absent suggesting that *L. anomalus* is opportunistic. Its feeding activity seems to depend more on the season that on the day/night cycle (Panzera and Maneyro 2014). Females lay a clutch of about 15 eggs in in December and January.

Figure 23.2 L*ygophis anomalus*
Photography by Alfredo Sabaliauskas

Erythrolamprus

Fifty-five species of *Erythrolamprus* occur in the Antilles and on mainland South America from the slopes of the Andes to northern Brazil and the Chaco of Argentina. The genus comprises one of the most morphologically diverse radiations of snakes found in the New World. Its color patterns range from coral snake mimics to uniform colorations, banded patterns, striped patterns, and complex pigmentation of scales that produce various color and pattern effects. Within the genus are at least 9-13 subclades (Hurtado-Gomes 2026), many of which contain one or more species with aquatic habits. Even though some of these species are widely distributed and locally common they remain poorly studied.

Of interest, Dixon (1983) found no sexual dimorphism in ventral or subcaudal counts, nor did he find sexual dimorphism in tail/snout-vent length (SVL) ratios in the *E. reginae* group. Subcaudal and ventral counts are often sexually dimorphic in snakes with males having more subcaudals (and longer tails) and fewer ventral scales than females (Lindell et al. 1993). These traits are closely associated with body size, locomotion, and reproduction and are thus under continual selection. The absence of sexual dimorphism in these traits makes the *E. reginae* group of ecological and evolutionary interest given that not all members of the genus have these traits. Alencar et al. (2014) found that *Erythrolamprus poecilogyrus* differed in overall body and clutch size between geographic regions. Generally, females attain larger body size than males but do not have a higher number of vertebrae (corresponding with ventral scale counts). They did not find intersexual differences in tail length, which may be related to low intersexual competition among males. Diet composition was very similar throughout the species' range and characterizes *E. poecilogyrus* as an anuran specialist. Eisfeld and Vrcibradic (2019) examined sexual dimorphism of the semi-aquatic *Erythrolamprus miliaris* in southeastern Brazil and detected sexual dimorphism in body size (snout-vent length), with females averaging larger than males, but no sexual dimorphism in the relative length of the tail. Eisfeld et al. (2021) analyzed the diet of *E. miliaris* in five different regions along the Atlantic Forest in eastern Brazil and found the most frequent prey were fishes and frogs. Their data suggest that younger snakes feed mainly on anurans, tending to consume more fish as they grow

In this chapter are some, but not all of the semi-aquatic snakes in this genus. Also, I have placed an account for *Sordellina punctata,* a species not closely related to *Erythrolamprus* at the end of this chapter.

Importantly, many of these snakes hold cryptic diversity that has yet to be resolved. Their morphology is similar but confusing and molecular data will be needed to resolve many of these relationships. The 55 known species of *Erythrolamprus* could easily double in the next few decades.

Military Ground Snake
Erythrolamprus miliaris (Linnaeus, 1758)

Figure 23.3. The distribution of *Erythrolamprus miliaris.*

Distribution and Habitat. Brazil, Uruguay, Paraguay, Bolivia, Peru, Colombia, French Guiana, Guyana, Venezuela, Argentina. The large distribution and polytypic nature of this species suggest it contains cryptic diversity. Terrestrial and aquatic situations including swamps, marshes, streams, floodplains, and coastal habitats are used.

Natural History. The diet includes fish (including the electric eel), amphibians, reptiles, and mammals (Farina et al. 2019, Tpantiza-Tuguminago et al 2019, de Oliveira et al. 2019).The summary of the subspecies that follows is based upon Dixon (1983).

Erythrolamprus miliaris miliaris (Linnaeus 1758). Distribution and Habitat. Guyana, Suriname, and French Guyana. Type locality: South America.

Erythrolamprus miliaris amazonicus (Dunn 1922). Distribution from Santarem, Brazil, south to Rio Itenez, Beni, Bolivia, east and south into Mato Grosso, Brazil. The type locality is Santarem, Brazil.

Erythrolamprus miliaris chrysostomus (Cope 1886). Distribution and Habitat. Dense rainforests of lowland Amazonian parts of Brazil, Colombia, Ecuador, and Peru. Type locality: Upper Rio Amazonas.

Erythrolamprus miliaris merremii (Wied 1821). Distribution and Habitat. Brazil, from Recife, Pernambuco, to Rio de Janeiro; primarily in the Atlantic rainforest and similar wetland sites in eastern Minas Gerais. The type locality is Sao Pedro d'Alcantara, Bahia Brazil.

Erythrolamprus miliaris orinus (Griffin 1916). Distribution and Habitat. The Southern Coastal Atlantic Forest between the States of São Paulo and Paraná on the eastern slopes of the Brazilian "Serra do Mar" covered by rainforest. Southeastern Brazil, from southern Minas Gerais, south through the states of Sao Paulo, Parandi, Santa Catarina, to the northern third of Rio Grande do Sul. Type locality: Sierras of Bolivia; restricted to Sao Paulo, Sao Paulo, Brazil, by Gans (1964).

Natural History. Marques and Souza (1993) reported this snake preys upon the Frillfin Goby, *Bathygobius soporator*, in tide pools. They also cited information from third parties discussing predation on the Sleeper Goby, *Guavina guavina*, in mangroves. Duarte et al. (2014) observed this snake attempting to prey on the Sleeper Goby but the snake in their observation abandons the prey. They also observed the snake foraging in mangrove crab (*Ucides cordatus*) burrows. as well as the surface of the water and the substrate (Farina et al. 2019).

Figure 23.4. *Erythrolamprus sp.*
Photography by Myke Clarkson.

Yellow-bellied Frog Snake

Erythrolamprus poecilogyrus, (Wied-Neuwied 1825)

Distribution and Habitat. A polytypic species, it is present in many forested and open habitats with (or without) wetlands, streams, and rivers in South America from se Venezuela and e Guyana to the Argentinian Pampas and Chaco (Figure 23.3).

Figure 23.5. Distribution of *Erythrolamprus poecilogyrus.*

Erythrolamprus poecilogyrus poecilogyrus (Wied-Neuwied 1825). Distribution and Habitat. Bolivia, Uruguay, Argentina, Paraguay, Brazil (Amazonas, Para, Minas Gerais, Bahia, Goiás, SW Pernambuco, São Paulo, Rio Grande do Sul to coastal Santa Catarina, Mato Grosso, Piauí); Type locality: Barra de Jucú, Rio Espirito Santo, Brazil.

Erythrolamprus poecilogyrus caesius (Cope 1862). Distribution and Habitat. Argentina, Bolivia, Paraguay; Type locality: Santa Fe, Argentina.

Figure 23.6. *Erythrolamprus poecilogyrus.* **Photography by (A-B) Steve Barten, (C) Alfredo Sabaliauskas.**

Erythrolamprus poecilogyrus schotti (Schlegel 1837). Distribution and Habitat. Venezuela, Brazil (Sã Paulo, Bahia). Type locality: South America. Restricted to Estado do São Paulo, Brazil by Hoge (1964)..

Erythrolamprus poecilogyrus sublineatus (Cope 1860). Distribution and Habitat. Uruguay, Argentina; The type locality is Buenos Aires, Argentina.

Natural History. The diet of *E. p. sublineatus* included anurans (54.1%), fishes (42.3%), reptiles (2.7%) and mammals (0.9%) (Correa et al. 2016).

Golden Swamp Snake

Erythrolamprus semiaureus (Cope, 1862)

Distribution and Habitat. Wetlands in savannas, grasslands, and tropical forests in Paraguay, west and south of Iguazfi Falls, northeastern Argentina, southern and eastern Uruguay and the southern one half of the Brazilian state of Rio Grande do Sul. Type locality: Sao Joao de Monte Negro, Rio Grande do Sul, Brazil.

Natural History. Diet is compopsed of mostly fish. Mature females were significantly longer, had higher body weight, and reached sexual maturity at a greater length than males. Males have longer tails than females. The reproductive cycle was seasonal with greater activity in the temperate periods of the year, although prior to the flood season. *Erythrolamprus semiaureus* invested more energy in reproduction than in growth, which allows them to start reproducing at smaller sizes compared to other populations, without delaying their reproduction until they reach larger sizes. This can be an advantageous strategy in seasonal climates.

Figure 23.8 *Erythrolamprus semiaureus.*
Photography by Alfredo Sabaliauskas.

Erythrolamprus cobellus Clade

The *Erythrolamprus cobellus* group, as currently recognized, includes four species: *E. breviceps*, *E. cobellus* (Linnaeus, 1758), *E. frenata* (Werner, 1909), and *E. taeniogaster* Jan, 1863 (Fernandes et al. 2002). *E. breviceps* and *E. cobellus* are distributed only in the northern portion of Amazon basin, while *E. frenata* occurs in central-southwest Brazil, east Paraguay, and north Argentina (Dixon 1989; Giraudo 2001). *Erythrolamprus taeniogaster* is the most widely distributed species of this group, with two disjunct populations, one in northeastern Brazil ranging from south Bahia to Pernambuco and Maranhão, and another one in Amazon Basin until Lomalinda, Colombia, south to Buena Vista, Bolivia, east to the state of Mato Grosso, Brazil (Fernandes et al. 2002). All have dorsal scale rows 17-17-15, smooth, no apical pits.

Cope's Short-headed Watersnake
Erythrolamprus breviceps (Cope, 1860)

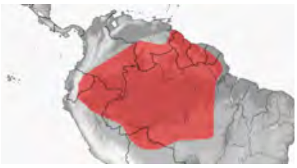


Figure 23.9. The distribution of *Erythrolamprus breviceps.*

Distribution and Habitat. Flood plains, wet agricultural areas such as rice paddies in Suriname, northwest Brazil, Ecuador, Colombia, Bolivia, Peru, French Guiana, Guyana. Type locality: Suriname. Natural History. The diet includes synbranchid eels, frogs, and earthworms. A clutch of eight eggs has been reported.

Figure 23.10. ***Erythrolamprus breviceps.***
Photography by Konrad Mebert

Mangrove Snake
Erythrolamprus cobellus (Linnaeus, 1758)

Figure 23.11. The distribution of *Erythrolamprus cobellus.*

Distribution and Habitat. Widespread in northern South America - Colombia, Venezuela, Trinidad, the Guianas, Brazil, and Ecuador. Semi-aquatic in fresh and brackish water; present in mangroves swamps, herbaceous swamps, rice paddies, and associated streams.

Natural History. Moves overland and may be seen on roads. Active late afternoon and after dark. Diet: includes a variety of small vertebrates but fish and frogs are likely more important in its diet than are lizards . Reported to lay eggs in June, clutch sizes less than six eggs (Beebe 1946; Duellman 1978). This species inhabits swampy coastal areas between 0 and 20 m ASL, ditches along roads in agricultural areas, and secondary-growth vegetation in water, vegetation near water, and occasionally elsewhere. It has been found in irrigated watermelon plantations. It feeds mainly on fish .

Figure23.12. *Erythrolamprus cobellus*, **Trinidad. Photography by Renoir Auguste.**

Werner's Swamp Snake
Erythrolamprus frenatus (Werner, 1909)

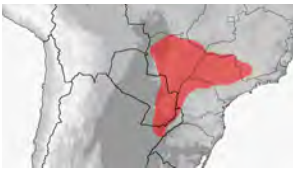


Figure 23.13. The distribution of *Erythrolamprus frenatus.*

Distribution and Habitat. Distributed mainly within Cerrado (tropical savanna) and forested parts of the Amazon Basin in Bolivia, Brazil, Colombia, Peru, and similar areas of French Guiana, Guyana, Surinam, and Venezuela. Type locality: Paraguay. Natural History. Batista et al. (2020) observed five specimens in the water and two on land close to water. Of 120 snakes examined only four had prey, all the were synbranchid eels.

Figure 23.14 *Erythrolamprus frenatus* **Photography credit Bruno Catossirosa**

Jaeger's Ground Snake
Erythrolamprus jaegeri Günther, 1858

Figure 23.15. The distribution of *Erythrolamprus jaegeri.*

Distribution and Habitat. Open habitats near water in Brazil, Uruguay, Paraguay, Argentina. A polytypic species. *E. j. jaegeri* is in Uruguay, southern Brazil. Type locality: Brazil. *E. j. coralliventris* is in Argentina, Paraguay,

southern Brazil. Type locality is the island north of Concepcion, near San Salvador, northern Paraguay.

Natural History. Prey items consisted of anuran amphibians (82.2%), fishes (10.7%) and isopods (7.1%). Anurans in the diet consisted of *Leptodactylus latrans* (35.7%), *Physalaemus gracilis* (28.6%) and *Pseudopaludicola falcipes* (3.6%) and fish prey of *Phallocerus caudimaculatus* (10.7%). Isopods could not be identified at the species level (Correa et al. 2016).

Figure 23.16. *Erythrolamprus jaegeri* **from Corumba, Matto Grosso, Brazil. Photography by Vinicius Carvalho (top). and Konrad Mebert (bottom)**

Figure 23.17. *Erythrolamprus taeniogaster.*
Photography by Ricardo Alexandre Kawashita-Ribeiro.

Jan's Swamp Snake
Erythrolamprus taeniogaster (Jan, 1863)

Distribution and Habitat. Aquatic and terrestrial habitats, including flooded forests south of the Amazon in Brazil, to central Brazil and coastal Bahia, Para, Amapa, Paraiba, Pernambuco, Maranhao, Mato rosso, S Ceara, and Piauí, west to Colombia, south to Bolivia (Buena Vista), Peru, Ecuador. Type locality: Brazil. It is a polytypic species.

Natural History. Diurnal and nocturnal in forest and clearings. Diet composed of fish, including Callichthys callichthys, Rivulus sp., Synbranchus marmoratus, and Gymnotus carapo, as well as frogs. Litter sizes of 7-10 reported in February and October, neonates present in May and June.

Linnaeus Royal Snake
Erythrolamprus reginae (Linnaeus, 1758)

Figure 23.18.The distribution of *Erythrolamprus reginae.*

Distribution and Habitat. *Erythrolamprus reginae* occurs from the Guyana Shield, along the Venezuelan Llanos and Pantepui, as well as in the Amazon basin of Brazil, Colombia, Ecuador, and Peru, on the "Brejos de altitude" rainforests in northeastern Brazil, into the coastal fragments of Atlantic Forest from the Northeastern and Southeastern Brazil (Ascenso et al. 2019). The type locality was given as "Indiis" by Linnaeus but it was restricted to Suriname by Dixon (1983). It is unclear what the exact distribution of this snake is. Cryptic diversity has shown numerous species were previously concealed under this name. Photo on page 357.

Zweifel's Royal Snake
Erythrolamprus zweifeli (Roze, 1959)

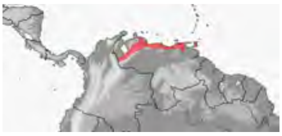


Figure 23.19. Distribution of *Erythrolamprus zweifeli..*

Distribution and Habitat. Venezuela (Trujillo, Falcon, Amazonas, etc.) and Trinidad. This species is associated with streams in premontane and montane humid forest where it forages . The species tolerates some level of disturbance and uses streams in coffee plantations and other agricultue between 400-2000 m ASL. Type locality: Rancho Grande in the state of Aragua, Venezuela, at an elevation of 1100 meters, in a cloud forest. Identification. *Erythrolamprus zweifeli* differs from *E. reginae* in having a salt-and-pepper dorsal pattern (vs dorsum with dense pale and dark paravertebral flecking in *E. reginae*) and in having a higher number of subcaudal scales (69–88 vs 55–78 in *E. r. regina.* On Trinidad this snake hunts along forested streams for frogs, their tadpoles and fish.

Figure 23.20. *Erythrolamprus zweifeli* from Trinidad.
Photography JCM.

Cobra D'água

Erythrolamprus macrosomus (Amaral, 1936)

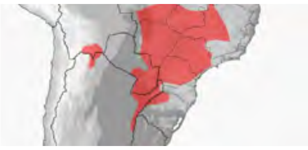


Figure 23.21 The distribution of *Erythrolamprus macrosomus*

Distribution and Habitat. Inhabits semideciduous forests of the Atlantic Forest in Paraná and São Paulo states, in the Brazilian Cerrado in Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, São Paulo, and Paraná states, and in the Chaco from Paraguay and Argentina. The distribution extended to El Palmar National Park, province of Entre Ríos, Argentina, representing the southernmost record (based upon Ascendo et al. 2019).

Figure 23.22 *Erythrolamprus macrosomus*. **Photography by Alfredo Sabaliauskas**

Erythrolamprus melanotus Clade

The status of this clade needs verification. It may belong with the *E. cobellus* clade, or it may be distinct. Murphy et al. (2019) recovered *Erythrogaster pseudoreginae* and *E. epinephalus* as the sister to *E. melanotus*. *Erythrolamprus pseudoreginae* is endemic to Tobago and poorly known. It has been found within several meters of streams. *Erythrolamprus epinephalus* is a widespread mainland species complex associated with marshes and wetlands

Maps and photos of most of these are not presented here.

Green Marsh Snake

Erythrolamprus epinephalus (Cope, 1862)

Distribution and Habitat. Wetlands, marshes, riparian floodplains, and wet forests from Costa Rica southward to Panama and Colombia, Peru, northwest Ecuador and westward to Venezuela. The type locality is Truando, (New Granada) Colombia (no map)..

A polytypic species. Torres-Carvajal and Hinojosa (2020) found the species to be paraphyletic and support recognition of the subspecies *albiventris*, *fraseri* and *lamonae* as distinct species. Leaving the subspecies: *E. e. bimaculatus* from Colombia, Venezuela, Ecuador; with a type locality of Colombia. "Presumably from the vicinity of Bogotá" (Dunn 1944); *E.e. juvenalis* from Costa Rica with a type locality of San Jose, Costa Rica; *E. e. kogiorum* from Colombia (Magdalena), Venezuela (Zulia) with a type locality of Ciudad Perdida,Sierra Nevadade Santa Marta, Departamento de Magdalena, Colombia, 1100 m elevation; *E. e. opisthotaenius* from the Venezuelan states of Merida, Barinas, Táchira, Trujillo, Zulia, Falcón), and Colombia; and *E. e. pseudocobella* from W Colombia (Andes), Ecuador; with a type locality of Angelópolis, Colombia.

White-bellied Marsh Snake

Erythrolamprus albiventris (Jan, 1863)

Distribution and Habitat. West of the Andes in Ecuador and Colombia. The type locality is western Andes of Ecuador and Guayaquil, Ecuador (no m

ap). Diurnal and terrestrial, inhabits evergreen to semi-deciduous forests, cloud forests, and humid montane shrublands. The species also occurs in areas having a matrix of pastures, plantations, and remnants of native vegetation, as well as in gardens in urban areas. They are common in marshes, swamps, artificial ponds, and along streams; they enter caves and abandoned mines. Most active in the morning, crossing roads and trails, basking in open areas, or foraging on leaf-litter, soil, or among grass or shrubs. May climb up to two meters in vegetation. They hide under logs, agave plants, stones, and in crevices.

Natural History. They actively hunt frogs and tadpoles. Lizards are also preyed upon. Often, they rely on crypsis to avoid predation. However, if disturbed, they flatten the body and produce cloacal musk. Predators include snakes and domestic animals.

Breeding congregations have been observed during the rainy season in western Ecuador (December–May). In one hole, five males and one female were coiled into a reproductive ball. Females lay 5–10 eggs in heaps of rotten vegetation (account based on Arteaga 2020a).

Olive Marsh Snake

Erythrolamprus fraseri (Boulenger, 1894)

Distribution and Habitat. Western side of the Andes in Ecuador and Peru. The type locality is western Ecuador.

Natural History. A diurnal and terrestrial snake that inhabits humid to dry montane shrublands, highland grasslands, high evergreen montane forests, and areas having a matrix of pastures, plantations, rural gardens, and remnants of native vegetation. Individuals occur in rural gardens, along roads, and occasionally inside houses. They also use marshes, swamps, and streams. Most active on sunny morning, basking in open areas or foraging on leaf-litter, mud, or in tall grass. Hide under debris on the ground. Hunt amphibians, mostly frogs and tadpoles. Flee when threatened but rely mostly on crypsis. If disturbed, they may flatten their body and produce release cloacal musk (based on Arteaga 2020b).

Lamon's Ground Snake

Erythrolamprus lamonae (Dunn, 1944)

Distribution and Habitat. Colombia (Andean slopes, 1,500 - 2,600 m elevation) and southward to east central Ecuador. The type locality is Sonsón, Antioquia, Colombia at 2410 m.

Shaw's Dark Ground Snake

Erythrolamprus melanotus (Shaw, 1802)

Figure 23.23 The distribution of *Erythrolamprus melanotus*

Distribution and Habitat. Colombia, Venezuela (Cojedes), Isla Margarita, Trinidad, Tobago, and Grenada. The type locality was given as the Cape of Good Hope, Africa in error. A forest and forest-edge snake that is closely associated with streams and ponds, it will also use cacao plantations and other disturbed habitats.

This is a polytypic species with three subspecies: E. m. melanotus, *E. m. neosus* (Trinidad & Tobago), and *E. m. lamari* (Zulia, Venezuela).

Natural History. Diurnal. Diet in the Trinidad and Tobago population includes small vertebrates, mostly frogs (*Engystomops pustulosus*, *Pristimantis urichi*) tadpoles, and lizards (*Bachia trinitatis*, *Gonatodes vittatus*). Clutches of 2–10 eggs have been reported between January and August.

Figure 23.24 *Erythrolamprus melanotus* **from Tobago Photography by JCM**

Sordellina punctata Clade

Sordellina punctata is a poorly known species from Brazil that, until recently, had an uncertain phylogenetic position. Molecular data place this species in the tribe Echinanterini (Miranda et al 2012; Abbeg et al. 2022). There is a single species in the genus. It inhabits the Atlantic Forest wetlands of Brazil.

Yellow-spotted Snake

Sordellina punctata (Peters, 1880)

Figure 23.25. The distribution of *Sordellina punctata*

Distribution and Habitat. Occurs in the Atlantic Forest and southeast Brazil with confirmed specimens from the states of São Paulo, Paraná and Santa Catarina. Pereira et al. (2007) suggest reports of this species from the western Mato Grosso do Sul and all literature citations for Rio de Janeiro are questionable. Pereira et al. also suggest this species is probably associated with water-logged soils than aquatic habitats. Muddy and soaked soils in floodplains were reported as habitat.

Figure 23.26. *Sordellina punctata.*
Photography by Wolfgang Wuster.

Natural History. A species specialized to feed on earthworm and occasionally includes the giant earthworm in its diet (Marques 1996, Oliveira et al. 2003, Pereira et al. 2007). Pereira et al. (2007) found the burrowing caecilian *Chthonerpeton indistinctum* in the stomach of *S. punctata*. The caecilian is common in muddy riparian floodplains and wetlands. They did not consider this a truly aquatic snake writing that, “It seems more associated with wetlands and other soak soils, surrounding lakes or rivers, than water bodies itself.” However, water-soaked soils are indeed an aquatic environment. It is not “open water,” but it is a water-filled micro-habitat. This species is an aquatic burrower.

The Cosmopolitan Watersnake Section

The Cosmopolitan Water Snakes is a family level (Natricidae) clade (Zaher et al. 2009, Burbrink et al. 2020). Other authors consider it a subfamily (Natricinae) of the Colubridae. Here I will refer to the clade as the family Natricidae (natricids). Most species occur north of the equator, and the greatest diversity occurs in Asia and North American and Sub-Saharan Africa have radiations that are monophyletic.

This manuscript was quite far along when Deepak et al. (2021) published their overview of natricids . Ideally, the organization of the next seven chapters would have followed their trees. The text has been adjusted but does not completely follow their results..

The oldest extant lineages found by Deepak et al. (2021) are found today in mainland Asia and India+Sri Lanka (*Amphiesmoides* and *Aspidura*), and their estimation of the ancestral area suggests natricids were likely from one of these two areas. Deepak et al. (2021a, b) also propose a single dispersal event from India plus Sri Lanka to sub-Saharan Africa and from mainland sub-Saharan Africa to the Seychelles. Extant natricids from the Philippines were hypothesized to have originated by dispersal from Sundaland + Wallacea. Extant natricids from Australo-Melanesia were inferred to have evolved from a primarily Philippine clade. The Sundaland + Wallacean, Philippine and Australo-Melanesian natricines were all suspected as originating from an initial dispersal from India plus Sri Lanka. Extant natricids from North and Central America and Europe, Central Asia, and North Africa were reciprocally monophyletic, and the best-fitting model suggested that the dispersal route was from mainland Asia plus Japan to North and Central America to Europe, Central Asia, and North Africa (Deepak et al. 2021).

Natricids are semi-aquatic or aquatic (53%) and terrestrial (28%); aquatic burrowers (10%) or terrestrial burrowers (8%). Deepak et al. (2021) estimated the ancestral habitat of all natricines to be terrestrial (~50%), followed by semi-aquatic/aquatic. Many natricids are dietary generalists (37%) or aquatic generalists (25%). Some feed only on anurans (18%), and others on worms (12%). Most vermivores are also burrowers or aquatic burrowers. A few species (8%) are dietary specialists feeding on fish, mollusks, or crayfish. The ancestral state estimation for all natricines shows a higher proportion of anuran or aquatic generalists than the other six diet categories.

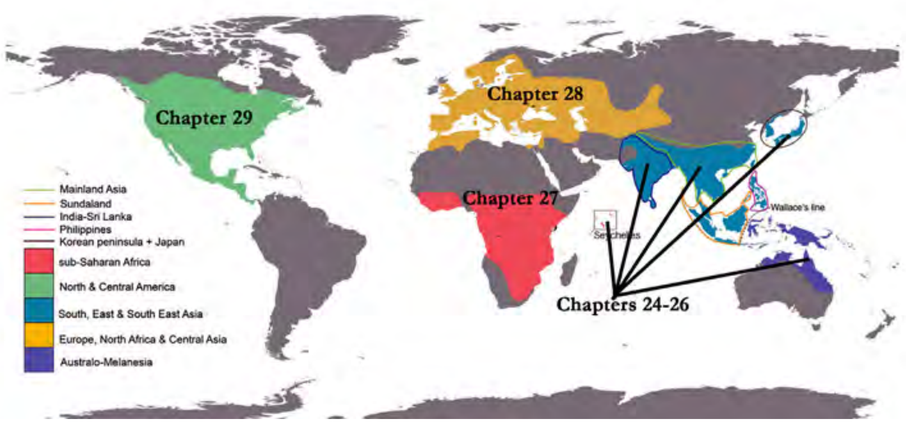
All North American natricids are viviparous. The only non-American viviparous natricids are the Asian *Pseudagkistrodon rudis* and *Trimerodytes annularis*. These two species represent independent origins of viviparity from oviparous ancestors. When testing for associations between habit and reproductive mode, the best-fitting model was one with symmetric transition rates among states. This suggests that there was no association between habitat and reproductive mode (Deepak et al. 2021).

Most extant species are terrestrial or semi-aquatic and are often dietary generalists, yet some have specialized their diet. Fully aquatic species are typically generalists, but some feed only on crayfish or worms, small crustaceans, or fish (Deepak et al. 2021). Natricids range in maximum size from ~115 to 1195 mm SVL, with many of the smallest species being fossorial (Deepak et al. 2021).

Most are harmless to humans, but a few garter snakes (*Thamnophis*) have venom, causing localized symptoms. However, a few species of Asian *Rhabdophis* have venom that is life-threatening to humans.

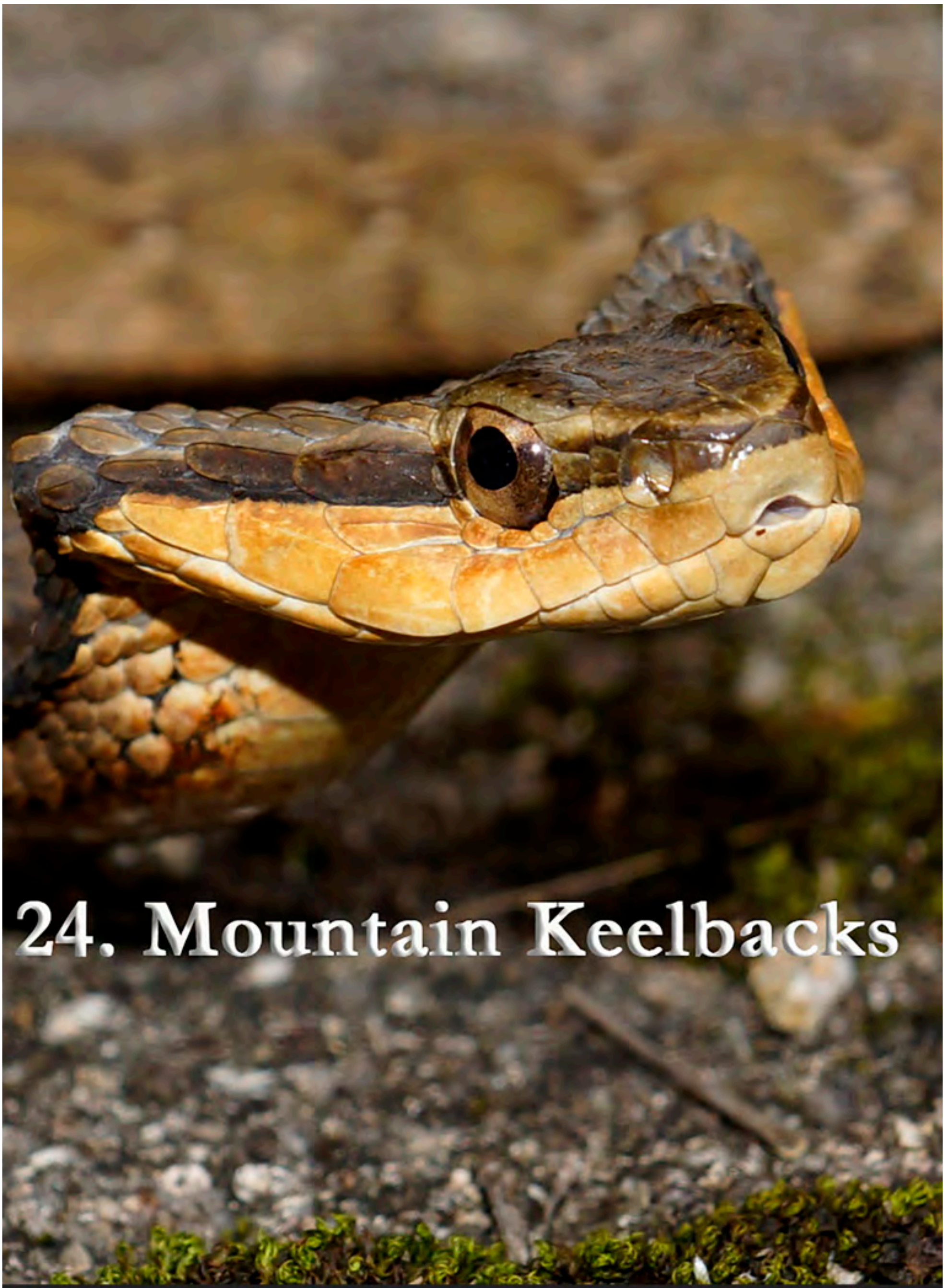
Natricids were present in North American in the early Miocene (Holman, 2000) and by the late Miocene members of the genera *Nerodia*, *Thamnophis*, and *Neonatrix* were present. Mead and Steadman (2017) found *Nerodia* fossils in the late Pleistocene site Sawmill Sink, on Abaco Island in the Bahamas. Georgialis et al. (2019) describe natricids fossils from the Neogene (latest Miocene or earliest Pliocene) locality of Maramena, in northern Greece. *Natrix* aff. *rudabanyaensis*, and another distinct species of *Natrix* probably inhabited nearshore environments. The Cosmopolitan Water Snakes are discussed in the next seven chapters.

The oldest natricid lineage recovered by Deepak et al. (2021) is *Amphiesmoides ornaticeps* (White-eyed Keelback). It occurs along forested streams in southern China (including Hainan) and northern Vietnam. Its type locality is Northern Hainan, China.



Natricid distribution. Modified from Deepak et al. 2021. The chapters covering the various clades are given on the map.

On the next page *Pseudoagkistrodon rudis* **Photography by Konrad Mebert**



24. Mountain Keelbacks

24. Mountain Keelbacks

This chapter discusses the genera *Pseudagkistrodon, Rhabdops Herpetoreas, and Hebius.* Das et al. (2020) recovered these four genera in a clade with the terrestrial-fossorial *Trachischium monticola* and two species of *Blythia*. *Trachischium* are worm-eating, oviparous, fossorial snakes from the Trans-Himalayan region of China, Tibet, and north Vietnam (Ren et al. 2018, Wang et al. 2019). The natural history of *Blythia* is poorly known.

Herpetoreas contains seven species distributed along the southern edge of the Himalayas, into northeast India and adjacent China. Five species of *Herpetoreas* (*H. burbinki, H. platyceps, H. sieboldii, Herpetoreas tpser, H. venningi*) are known only from subtropical and temperate regions above 900 m (up to 3056 m) ASL. The northeast Indian *Herpetoreas xenura* and *H. pealii,*) on the other hand, occur from 30 m up to 1170 m. *Herpetoreas* are semi-aquatic snakes with keeled dorsal scales. The posterior maxillary teeth are the longest, in a continuous series, with the anterior ones. Body and tail slender and compressed. Two nasals, one loreal, one anterior, and two posterior oculars. Dorsal scales are moderately elongated, keeled, and in nineteen rows.

Giri et al. (2017) used molecular data to confirm that the aquatic Indian genus *Rhabdops* also belongs to this clade. Two species of *Rhabdops* inhabit the Western Ghats of peninsular India. These two species are the most aquatic members of the clade.

Snakes of the genus *Hebius* were formerly in the genus *Amphiesma* and were commonly called keelbacks. They are terrestrial to semi-aquatic snakes that are oviparous and widespread in Asia. Currently, 48 species are known – here, I discuss a sample (25%) of the species in the genus.

David et al. (2021) recognized two informal groups among the "dark-bellied" species of Asian natricid snakes. These two groups share: (1) 15, 17 or 19 dorsal scale rows; (2) a very dark dorsum (dark grey, dark brown, or blackish-brown); (3) dark reticulations on the back, often with orange or reddish-brown spots or dorsal blotches; (4) venter at least in part blackish-brown or black; (5) postocular stripe absent or present; and (6) strongly keeled scales at the base of the tail in those species with 17 dorsal scale rows. These groups include species referable to the genus *Hebius*, as currently conceived following Guo et al. (2014), but also the two species formerly placed in the genera *Parahelicops* Bourret, 1934 and *Pararhabdophis* Bourret, 1934 are now placed in *Hebius.*

The 49 species of *Hebius* are on the continuum between terrestrial to semi-aquatic. The color pattern commonly consists of dark dorsolateral spots forming two longitudinal stripes. Many also have a black or very darkly pigmented venter. *Hebius andreae* and *H. leucomystax* are sisters to all the other members of the genus. Here, I have accounts for 12 species, which may or may not be the most aquatic ones. The lack of knowledge on habitat use in these snakes is significant. David et al. (2021) provide detailed morphological descriptions for these snakes - I do not repeat that here

Pseudagkistrodon rudis is common in montane meadows, riparian areas, valleys, and roadsides. It ranges from 600–2,650 m ASL. The species is polytypic, with three recognized subspecies.

Annam Keelback

Hebius annamensis (Bourret, 1934)

Distribution and Habitat. Vietnam and southeast Laos. Type locality: Bana, Annan, Vietnam (now Ba Na Nature Reserve, Da Nang City, Vietnam), 1500 m elevation. Habitat in-

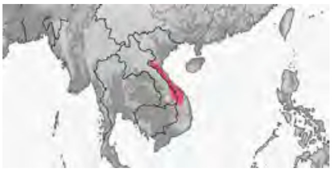


Figure 24.1. The distribution of *Hebius annamensis*

cludes tropical wet evergreen forests and subtropical montane evergreen forests between about 300-1,500 m ASL, although most specimens for which elevation data are available were collected between 1,200 and 1,400 m ASL (Stuart & Nguyen 2012a). All were collected in primary montane evergreen forests and in close association with fast-running, rocky forest streams. It is mostly a nocturnal and aquatic snake, although one specimen was found on the ground. According to Stuart (2006), specimen FMNH 258637 was collected at night (20.30 h) in steep terrain covered by wet evergreen forest between 1,280–1,500 m elevation. The snake was first observed on land 50 cm from a small, swift, rocky stream, then it dove into the water and swam under a rock on the stream bottom. Specimen ZFMK 86457 was captured at night (20.00–21.00h) in the leaf litter of a forest stream at 510 m ASL, with only the snout tip protruding from the surface of the water (David et al. 2015b). The diet and reproductive habits of Hebius annamensis, remain unknown.

Figure 24.2. *Hebius annamensis.* **Hoa Son Quang Binh (A), Kon Tum (B) Vietnam. Photography by Truong Nguyen.**

Vietnam Water Snake

Hebius chapaensis (Bourret, 1934)

Distribution and Habitat. Streams in Laos, northern Vietnam (Lao Cai, Yen Bai) and China (Yunnan). Type locality: Chapa, Tong-King (= Sa Pa, Lao Cai Province, North Vietnam). At elevations of primary forest, at elevations between 1050 - 2046 m.

Natural History. Tropical and subtropical evergreen montane forests between 900 and 2,046 m ASL support this species (Ren et al. 2018). All specimens for which data are available were collected near streams in montane, wet evergreen forests. This species is nocturnal, semiaquatic, and terrestrial; no specimen was collected more than a few meters from water. A specimen from Laos was swimming in submerged vegetation along the bank of a three-meter-wide stream with moderate current; another specimen was seen perched on a tree one meter from a stream. A specimen observed by Ren et al. (2018) was actively preying upon tadpoles of the treefrog *Rhacophorus duboisi* on the edge of a pool. Brakels et al. (2021) found it feeding on the frog *Amalops cremnobatus*. The snake was under a rock in a stream swallowing the frog head first.

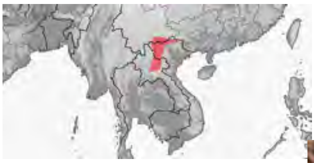


Figure 24.3. The distribution of *Hebius chapaensis.*

Figure 24.4. *Hebius chapaensis* **Photography by Kai Wang.**

Figure 24.5. The distribution of *Hebius craspedogaster.*

Kuatun Keelback

Hebius craspedogaster (Boulenger, 1899)

Distribution and Habitat. Montane forests associated with streams in Southern China and Vietnam. Type locality: Guadun, Fujian Province, China, 500-2000 m elevation or higher.

Natural History. Pope (1935) found this snake common in the Yenping Mountains and extremely abundant about Sanchiang and Kuatim in Chimgan Hsien. It was present in forests 1500-6000 feet ASL and is considered semi-aquatic. Pope recovered young frogs or toads and tiny tadpoles from the digestive systems of this species.

Figure 24.6. *Hebius craspedogaster.* **Photography by Kevin Messenger.**

Chiang Mai Keelback

Hebius deschauenseei (Taylor, 1934)

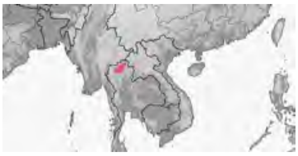


Figure 24.7. The distribution of *Hebius deschauenseei.*

Distribution and Habitat. Semi-evergreen and mixed deciduous submontane and montane forest in Chiang Mai Province, Thailand.

Natural History. Chan-ard et al. (2015), found this species inhabits semi-evergreen and mixed deciduous submontane and montane forest. It is nocturnal and terrestrial and occurs in the vicinity of forest streams. Nothing else is known of the biology of this rare species Nocturnal and terrestrial. The degree of its aquatic habits are unknown.

Figure 24.8. *Hebius deschauenseei,* **Doi Phu Kha National Park, Thailand. Photography by Rushen Bligin.**

Modest Keelback

Hebius modestus **(Günther, 1875)**

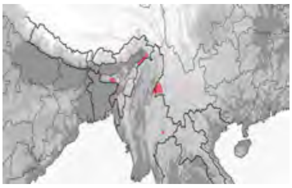


Figure 24.9. The distribution of *Hebius modestus.*

Distribution and Habitat. A semi-aquatic stream dweller known from Myanmar, India, Myanmar, Yunnan, China. Type locality, the Khasi Hills, India. It may be present in Bhutan. There are questionable records from Vietnam. It is unknown from Assam; Mizoram (India); Laos, Cambodia; Guizhou, Guangdong, China; Mizoram, India.

Natural History. A poorly known species. This species inhabits evergreen or semi-evergreen submontane forests up to 1,600 m ASL, and is associated with hill or montane forest streams. It occupies the forest litter in riparian areas. It probably feeds on tadpoles and frogs. Based on the photo from Jian Wang it also feeds on fish. Wall (1926) recorded a female, preserved between June and August, that contained three large eggs in its oviducts. This species is either secretive or rare (David et al. 2021).

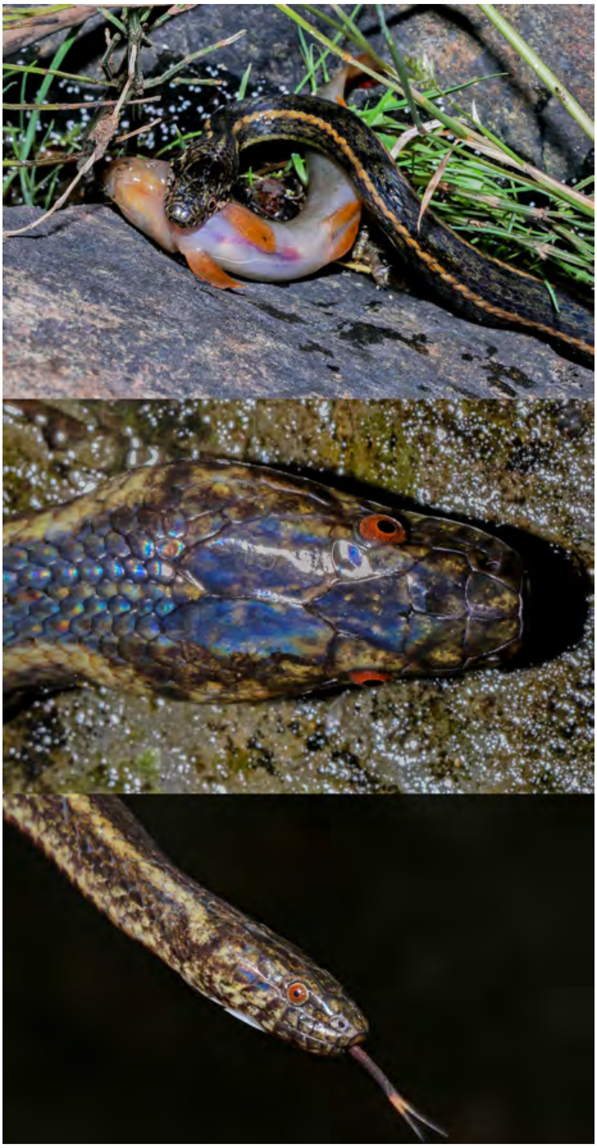


Figure 24.11. ***Hebius modestus*****, (A) is from Mt. Mopan, Xinping County, Yunnan, China; (B-C) is from Mt. Cenwanglaoshan, Tianlin County, Guangxi, China. Photography by Jian Wang.**

Black-bellied Keelback

Hebius nigriventer (Wall, 1925)

Distribution and Habitat. Evergreen or semi-evergreen submontane forest and mixed or deciduous moist montane forest from 350 up to 1,550 m ASL from Myanmar (Kachin State. Bhamo District; Myitkyina District); People's Republic of China (Yunnan Province. Yingjiang County, Dehong Dai and Jingpo Autonomous Prefecture; Gongshan County, Nujiang Prefecture; Mengla County, Jinhong Prefecture.) It may also be present in northern Laos.

Natural History. Wall (1925) noted one had swallowed two large and four small tadpoles. Diurnal and active at dusk and early evening, at air temperatures from about 24 to 27 °C. Mostly aquatic. It occurs in hill and montane streams, between or on rocks in the stream bed. Another one, a female collected in June, contained two large eggs, indicating that egg laying would have taken place at the beginning of the rainy season (David et al. 2021).

24.10. The distribution of *Hebius nigriventer*

Figure 24.12. *Hebius nigriventer*
Photography by Jian-Huan Yang.

Eight-lined Keelback

Hebius octolineatus (Boulenger, 1904)

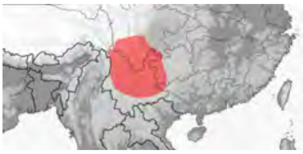


Figure 24.13. The distribution of ***Hebius octolineatus***

Distribution and Habitat. SW China (Yunnan, Sichuan, Guangxi). Type locality: Kunming Shi, Yunnan Province, China; about 2000 m elevation.

Natural History. Mell (1922) and Pope (1935) agree that thisi is the most common snake in cultivated fields from Yunnanfu to Tali and Pope reports small fish and a frog in three stomachs, suggesting that this is an aquatic snake.

Figure 24.14. *Hebius octolineatus* **from Dali Bai, Yunnan, China. Photography by Xavier Rufray**

Pope’s Keelback

Hebius popei (Schmidt, 1925)

Figure 24.15. The distribution of *Hebius popei*

Distribution and Habitat. It inhabits mountain and hill streams in forests at 281–900 m in China (Hainan, west to Hunan and Yunnan) and Vietnam. Type locality: Nodoa, Hainan, China.

Figure 24.16. *Hebius popei* **. Photography by Konrad Mebert**

Figure 24.17. The distribution of *Hebius parallelum*.

Yunnan Keelback

Hebius parallelum (Boulenger, 1890)

Distribution and Habitat. India (Sikkim, Nagaland), Nepal (?), Bhutan. Type locality: Sikkim. To at least 1890 m ASL.

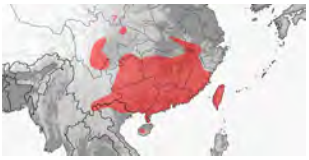
Natural History. Literature states its diet includes tadpoles and fish.

Figure 24.18. *Hebius parallelum* **from Nagaland.**
Photography by Viral K. Mystery.

Kosempo Keelback

Hebius sauteri (Boulenger, 1909)

Distribution and Habitat. Taiwan, southern China (Jiangxi, Guangxi, Guangdong, Fujian, Sichuan, Hubei, Hong Kong), and north Vietnam to elevations of 1200 m. Type locality: Kosempo, Formosa (it is present in the Jiaxian District, Kaohsiung City, south Taiwan).



igure 24.19. The distribution of *Hebius sauteri.*

Natural History. A montane, semi-aquatic, forest dwelling snake that feeds on tadpoles and slugs (Pope, 1935), frogs and earthworms (Mao, 1998). Oviparous (Kuntz, 1963).

Figure24.20. ***Hebius sauteri,*** **China. Photography by Gernot Vogel.**

Kachin Keelback

Hebius taronensis Smith, 1940

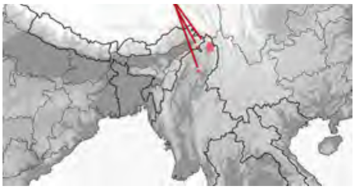


Figure 24.21. The distribution of *Hebius taronensis*

Distribution and Habitat. David et al. (2021) reports this species inhabits semi-evergreen submontane forest and mixed or deciduous moist montane forest from about 1,000 up to at least 1,850 m ASL. The species is thought to be diurnal. Most specimens were obtained from small mountain streams. One was eating a frog, another specimen had eaten tadpoles. Others were found under rocks near a stream.

Figure 24.22. *Hebius taronensis.* **From Lake Indawgyi, Mohnyin Township, Kachin State, Myanmar. Photographic credit Nikolay Poyarkov.**

Chin Hills Keelback

*Hebius venningi (*Wall, 1910)

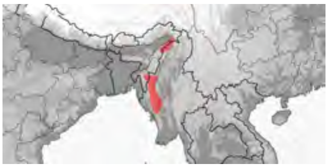


Figure 24.23. The distribution of *Hebius venningi.*

Distribution and Habitat. Hill streams to at least 1040 m. of India (Meghalaya, Mizoram, Arunachal Pradesh), northern Myanmar, China (Yunnan). Type locality: Haka Chin Hills, Myanmar. It occurs berween 900-1800 m ASL.

Diagnosis. Dorsum dark grey, brown with indistinct black checkering with a dorsolateral chain of yellow spots. An incomplete yellow collar may be present. Ventral surface yellow. Dorsal scales in 17 rows, weakly keeled, outer rows smooth. Two preoculars, nine upper labials (4-6 border orbit. Ventrals 158-172, subcaudals 117-140. Total length to at least 680 mm, tail 225 mm. Natural History. The diet includes tadpoles and frogs.

Figure 24.24. *Hebius venningi* **Photography by Ashok Captain.**

Burbrink's Keelback

Herpetoreas burbrinki Guo, et al., 2014

Figure 24.25. The distribution of *Herpetoreas burbrinki* .

Distribution and Habitat. Xizang, China. Type locality: Zayu County, Xizang A. R., China, at an elevation of 1889 m. At this writing this species is known from two specimens from the type locality.

Assam Keelback

Herpetoreas pealii (Sclater, 1891)

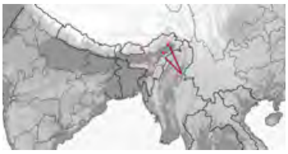


Figure 24.26. The distribution of *Herpetoreas pealii.*

Distribution and Habitat. Small, slow-moving streams with muddy bottoms that transect forests in Assam, Arunachal Pradesh, India. Type locality: Sibsagar district of Assam (Das et al. 2020).

Figure 24.30. *Herpetoreas pealii*
Photography by Abhijit Das

Himalayan Keelback

Herpetoreas platyceps (Blyth, 1854)

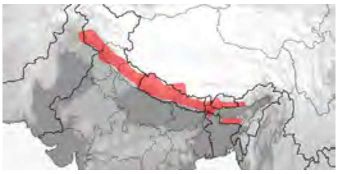


Figure 24 27. The distribution of *Herpetoreas platyceps*

Distribution and Habitat. Kashmir, Sikkim, Punjab, Assam, Darjeeling, Meghalaya, Arunachal Pradesh, Himachal Pradesh,

Jammu and Kashmir, India; Nepal (1040-3657 m ASL), Bangla-desh, Pakistan, Bhutan, Tibet, China. Type locality: Restricted to "Darjiling" by Malnate (1966).

Natural History. The stomachs of specimens examined con-tained the skink *Leiolepisma himalayanum.* Malnate (1966) found three of the four snakes having fed on this lizard had swallowed their prey tail first. One snake contained eight adult and four juvenile specimens of *L. himalayanum.* A female 111 mm in total length, containing two large (25 X 8 mm) eggs.

Figure 24 28. The eastern form of *Herpetoreas platyceps*
Photography by Abhijit Das

Siebold's Keelback

Herpetoreas sieboldii Günther, 1860

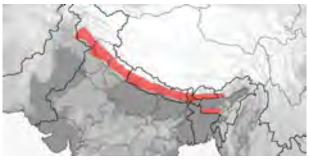


Figure 24 29. The distribution of *Herpetoreas sieboldii*

Distribution and Habitat. Pakistan, India (Uttar Pradesh, Sikkim, Punjab), Nepal, Myanmar, Bangladesh, and Bhutan. Type locality: Sikkim, Himalaya 2500 m ASL).

Natural History. Prey includes frogs, tadpoles, frog eggs, and skinks of the genus *Lygosoma.* A female, 435 mm. in total length, contained five small, undeveloped eggs (Malnate 1966).

Mêdog Himalayas Keelback

Herpetoreas tpser Ren, Jiang, Huang, David and Li, 2022

Distribution and Habitat. Evergreen broad-leaf forest or the moist fields of forest margins covered with dense vegetation close to the water. Known from Beibeng and adjacent Ani Bridge, Hanmi, and 80K, Mêdog County, southeastern Xizang Autonomous Region (Tibet), southwestern China, at an altitude of 1087–2280 m ASL. [No Map.]

Natural History. Diurnal, at least on a cloudy or mildly rainy days. The species has a fierce disposition and bites when handled, often holding the mouth open while on the defensive. The specific epithet *tpser* is the acronym of "Tibetan Plateau Scientific Expedition and Research" of China, which promoted the scientific research of the Qinghai-Tibet Plateau. All *Herpetoreas tpser* were collected during The First and the Second Tibetan Plateau Scientific Expedition and Research.

Wall's Keelback

Herpetoreas xenura (Wall, 1907)

Distribution and Habitat. Forest floor near streams Bangladesh, Myanmar, and Assam, India. Type locality: Cherrapunji, Khasi Hills, Assam.

Natural History. Diet. It is known to feed on anurans and snakes including *Hydrophylax leptoglossa, Ingerana borealis, Rhabdophis himalayanus* (Decemson and Lalremsanga 2021)

Figure 24.31. *Herpetoreas xenura.* **Photography by Abhijit Das.**

Aquatic Rhabdops

Rhabdops aquaticus Giri, et al., 2017

Distribution and Habitat. it is restricted to the Western Ghats region of Goa, on the north at Karnataka and on the south to Maharashtra, at elevations of 750–1000 m. The species is encountered mostly during the monsoon season, when it is predominantly aquatic or semi-aquatic, and can be observed along streams in semi-evergreen forest and waterlogged habitats

Figure 24.33. The distribution of *Rhabdops aquaticus.*

At the type locality, Giri et al. found adults in streams traversing the semi-evergreen forest and juveniles seen mostly on lateritic plateaus during the monsoon; it was also encountered close to a village. Small individuals were seen mostly under rocks, always in moist or waterlogged areas. Larger individuals were encountered primarily on large, seasonal pools, though also during

Figure 24.34. *Rhabdops aquaticus*, **Chalkewadi, Satara, Maharashtra, India. Photography by Christian Langner**

the day in wet soil under rocks.

Natural History. Activity is primarily nocturnal; foraging occurs in lentic or slowly flowing water. Opportunistic observation of five actively foraging individuals in a stream stayed submerged for 4–12 minutes. During the day, *R. aquaticus* was mostly under rocks close to streams or on plateaus. During the day, individuals bask on exposed rocks in the stream. Giri et al. (2017) have no direct observations on the diet of *R. aquaticus. Still,* remnants of arthropod (seemingly crustacean) exoskeletons were observed in the feces of one specimen temporarily kept for observation and photography. Specimens were observed in ephemeral pools under rocks directly alongside remnants of freshwater crabs.

Olive Ghats Keelback

Rhabdops olivaceus (Beddome, 1863)

Distribution and Habitat. Semi-evergreen hill forest Western Ghats region of peninsular India. A total of six individuals were encountered in three different habitats by Bhosale and Joshi (2014). Four were found in the Kaas Region, and two were recorded from Chalkewadi Plateau. A specimen from Kaas Lake was found active during the day, whereas individuals from Chalkewadi and Kaas plateau and forest stream were inactive under medium-sized rocks. Four specimens from plateaus (2 from each Kaas and Chalkewadi) were found in water-logged conditions (>2 inches depth). Our observations suggest that *Rhabdops olivaceus* chiefly inhabit the seasonal pools on the plateaus apart from the hilly forest streams, which can be considered among their preferred monsoon habitats. In all four localities, individuals were found under small to medium-sized rocks in soggy conditions. This habitat was also shared by *Hemidactlyus* cf. *brookii* (geckos were found on lower surfaces of the small-sized boulders under which the snake was encountered), *Monopterus* sp., *Nyctibatrachus* sp., etc. The specimen from Kaas represents the northernmost locality to date. A review of district bution records reveals its occurrence in at least four Indian states: Goa, Maharashtra, Karnataka, and Kerala. Their observations indicate that species are not restricted to perennial hill streams but also occupy seasonal water bodies like the ones that develop post-monsoons on the lateritic plateaus at Chalkewadi and Kaas.

Figure 24.35. The distribution of *Rhabdops olivaceus*.

Bhosale and Joshi (2014) observations suggest that seasonal water pools on the plateaus are one of the preferred habitats of this species. Their observations in the Satara district attest to this.

Figure 24,36. ***Rhabdops olivaceus,*** **(A) Photography by Christian Langner (B) Choraundem, Goa, India Photography by Saniya Chaplod**

The patchy distribution and its small size can lead to its uncommon occurrence, thus enlisting it as a rare species and remaining poorly known. The species seems widespread throughout the Western Ghats data, however, is preliminary, and it is hoped that additional information on natural history, distribution, and variation in habitat will be provided. Indeed, significant fieldwork is required for further studies of this species.(Bhosale and Joshi 2014).

Natural History. It is a nocturnal, semi-aquatic snake found in slow-moving water. The diet of *R. olivaceus* is reported as fish, slugs, earthworms, and soft-bodied invertebrates

(Whitaker and Captain 2004; Radhakrishnan 1997; Srinivasulu et al. 2014). However, Giri et al. (2017) could not find a primary published report to confirm this.

False Habu

Pseudagkistrodon rudis Boulenger, 1906

Distribution and Habitat. Taiwan, southern China (Fujian, Yunnan, Sichuan, Guizhou, Hunan, Jiangxi, Zhejiang, Guangxi, Guangdong). Type locality. Tongchuan, Yunan, China. A polytypic species with two subspecies: *Pseudagkistrodon rudis rudis* Boulenger 1906. *Pseudagkistrodon rudis multiprefrontalis* (Zhao and Jiang 1981) which ranges in China (Sichuan) and has a type locality: Xichang, Sichuan Province, at about 2650 m ASL.

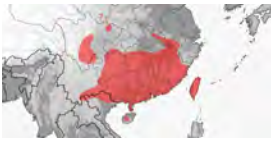


Figure 24.37. The distribution of *Pseudoagkistrodon rudis*

Identification. Stout, brown body with black blotches, and the crown maybe black, blotches separated by narrow brownish-white interspaces; posteriorly the ground-color passes gradually to olive-brown, with a median series of round and a lateral series of longitudinally elliptic blackish spots; blackish brown above, cream-white on the upper labials; venter grey-olive speckled with black anteriorly, blackish speckled with white posteriorly. Rostral one and a half times as long as deep, scarcely visible from above; upper head-shields rugose ; internasals broader than long, nearly as long as the prefrontals ; frontal once and one fourth as long as broad; loreal small, deeper than long ; three preoculars, four post oculars, and three suboculars separating the eye from the labials ; temporals scale-like, strongly keeled ; seven upper labials ; five lower labials in contact with the anterior chin-shields, which are shorter than the posterior. Scales very strongly keeled, in 19-25 rows, 23 rows at midbody. Ventrals 123-156 (Zhao et al., 1998); anal divided; subcaudals 37-65 (Maki, 1931; Zhao et al., 1998). Maximum size in total length respectively male 97.5 cm and female 121.7 cm (Zhao et

Figure 24.38. *Pseudoagkistrodon rudis*
Photography by Konrad Mebert

al., 1998).

Natural History. A diurnal-nocturnal species in mountainous forest floors, bush- and grassland, and near streams. The diet is primarily toads, but frogs, small snakes, lizards, insects, and earthworms are also prey. Viviparous, with litters of 12-27 young in late summer and fall. Neonates 130-200 mm in total length. Defensive behavior includes flattening the head and forebody, or the entire body, it coils up. When flattened, the oval head becomes triangular to mimic vipers. This species has rear fangs that are kinetic and which appears to be the specialisms for toad ingestion (Wu, 2004), and a venom gland may be able to deliver a medically important bite to humans.

25. Keeled Water Snakes

25. Keeled Water Snakes

Nathan Rusli, Gunther Köhler,

Jean-Jay Mao, and John C. Murphy

The keeled water snakes are terrestrial and semi-aquatic species. However, as a clade, they are not well studied. All forms are thought to be oviparous, with clutch sizes small to moderate (2 to 11). Specific data are included in the accounts of the species. Unfortunately, much of the information on *Tropidonophis* here is based upon Malnate and Underwood (1988) a publication badly in need of revision.

Tropidonophis ranges from the central and southern Philippine Islands southeastward to the Moluccas and east through New Guinea and the Bismarck Archipelago to the Trobriand Islands and the Louisiade Archipelago. The genus also occurs in northeastern Australia. Little is known of the life habits of these snakes. The limited collection data available suggest that they are semiaquatic forest dwellers. One form, *brongersmai,* makes an extensive incursion into the savannah region of southeastern New Guinea. Altitudinal distribution is from sea level to 2200 meters. Stomach contents indicate that most species feed on frogs, apparently foraged from the forest floor. The presence of tadpoles and a few small, stream-living fish (gobiids) in stomachs is evidence of semiaquatic habits. Ground skinks (lygosomines) are known to be eaten by two species and geckos by a third.

Rhabdophis is distributed in eastern Asia from southeastern Siberia and Japan south through China, the eastern Himalayas, Ceylon (unknown in peninsular India), the Malay region east to Flores, Borneo, Sulawesi, and the Philippine Islands. These are primarily terrestrial snakes, with some being semi-aquatic. None seem highly adapted to an aquatic lifestyle, although many eat anurans and tadpoles, and some feed on fish and earthworms. They have rear-fangs, and a few have highly toxic venom. Some *Rhabdophis* specialize in feeding on toads and sequester the toad's poisons in nuchal glands to deter predators. They are oviparous.

Figure 25.1 The Red-necked Keelback, *Rhabdophis subminiatus is* one of a subclade of these snakes that has a nuchal gland. The gland stores molecules obtained from toads. The snake usesd those molecules to deter predators.The gland secretions can been in this photo Photography by Konrad Mebert

About 26 species are widely distributed in Asia. Although, most are poorly known, *Rhabdophis subminiatus* is sometimes referred to as a water snake, and while I (JCM) have seen about a dozen specimens in the field none were in water. Instead, they were in small bushes or on the ground. De Lang (2017) reports similar habits.

Natricids of the genera *Fowlea* and *Xenochrophis* are distributed throughout many parts of Asia. They have a cylindrical body, do not exceed 2 meters in length, and have a round pupil. These snakes are oviparous, diur

Figure 25.2. The Checkered Keelback, *Fowlea flavipunctatus* is a semi-aquatic member of this clade. ,It is dirunal and moves in and out of the water in search of food. Photography by JCM

nal, semi-aquatic, and are often found near water. Members of this group are opistoglyphous (rear-fanged), but just a few are considered dangerous to humans.

The snakes now classified under *Fowlea* and *Xenochrophis* have undergone many taxonomic revisions since their respective establishments in 1868 and 1864. The genus *Fowlea* was erected by Theobald (1868), to accommodate a new species, *Fowlea peguensis*. In his *Catalogue of Snakes*, Boulenger (1893) considered *F. peguensis* a junior synonym of *Tropidonotus punctulatus*, based on maxillary dentition and nasal characters. In this publication, all species currently under *Fowlea* and *Xenochrophis* were classified under the genus *Tropidonotus*, except for *X. cerasogaster*.

In his book *Herpetology of Japan and Adjacent Territory*, Stejneger (1907) demonstrated how poor the taxonomic status of *Tropidonotus* was. On that basis, he assigned many to *Natrix,* which were used in many other herpetological works after that. After Stejneger's publication in 1907, Smith (1943) considered *bellula*, *punctulata*, *piscator*, and *trianguligera* to be in the genus *Natrix* and listed *flavipunctata*, *asperrimus*, and *melanzostus* as subspecies of *Natrix piscator*.

During the mid-twentieth century, *X. cerasogaster* was the only species of the genus *Xenochrophis*, which remained monotypic for many years until a revision of the genus *Natrix* (*sensu lato*) by Malnate (1960) split the snakes into five genera: *Macropophis*, *Fowlea*, *Rhabdophis*, *Natrix*, and *Amphiesma*. In 1965, Malnate and Minton found that *X. cerasogaster* was congeneric with *Fowlea* spp., which at the time consisted of the species *piscator*, *punctulata*, and *vittata*. On this basis, they moved these snakes from *Fowlea* to *Xenochrophis* (by priority). In 1988, Malnate & Underwood published another revision of this group, reclassifying what were then known as *Macropophis maculata*, *Sinonatrix trianguligera*, and *Sinonatrix bellula* into the genus *Xenochrophis*.

The *Xenochrophis piscator* complex (comprised of *X. asperrimus*, *X. flavipunctulatus*, *X. melanzostus*, *X. piscator*, *X. sanctijohannis*, *X. schnurrenbergi*, and *X. tytleri*) was revised by Vogel & David (2006), and subsequently by the same authors in 2012. In 2019, Purkayastha *et al.* reallocated the *X. piscator* complex, along with *X. punctulatus*, into the genus *Fowlea*, based on molecular data.

The diagnostic characteristics that distinguish these genera from other snakes are still undefined, and the taxonomy of this group needs further study. In 1864, Günther erected the genus *Xenochrophis* for type *X. cerasogaster*. They share a cylindrical body with a narrow, elongated head, a round pupil, keeled scales in 19 rows, and a divided cloacal plate. The nostrils are laterally positioned on the nasal scales.

Based on the original genera descriptions by Günther (1864) and Theobald (1868), the only differences that could be found were the number of dorsal scale rows (19 in *Xenochrophis* and 17 in *Fowlea*) and the shape of the pupil (round in *Xenochrophis* and vertical in *Fowlea*). However, these characters are no longer diagnostic for the two genera.

The revision of natricids by Malnate (1960) reassigned many snakes previously classified

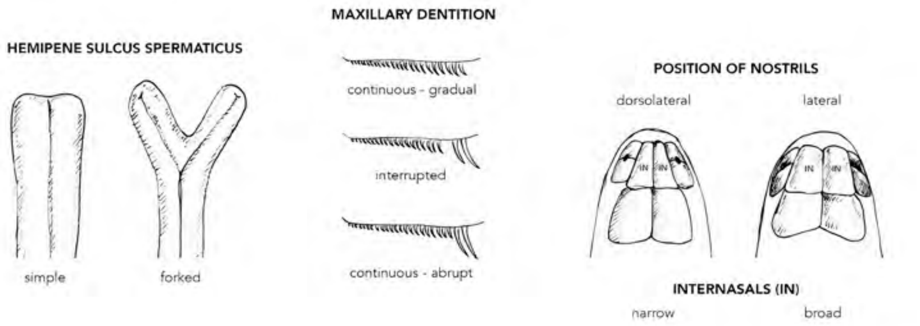


Figure 25.3. Characters used by Malnate (1960) to distinguish the genera of natricid snakes. (Diagrams by Nathan Rusli, adapted from Malnate, 1960).

by Boulenger (1893) as *Tropidonotus*. Malnate divided them into *Macropophis*, *Fowlea*, *Rhabdophis*, *Natrix*, and *Amphiesma*, based on hemipenes structure (sulcus spermaticus simple or forked), maxillary dentition (continuous gradual, continuous interrupted, or continuous abrupt), number of maxillary teeth (more than 33 or less than 30), internasals (narrow or broad), and position of nostrils (dorsolateral or lateral). These characters are illustrated in Figure 25.1, adapted from Malnate (1960).

This group's most recent taxonomic revision (Purkayastha et al. 2019) provided detailed morphological descriptions for *X. cerasogaster*, distinguishing it from all other species of *Xenochrophis* and *Fowlea*. However, the reallocation of many *Xenochrophis* species to the genus *Fowlea* was based on molecular data rather than morphology. In their study, *X. trianguligerus* and *X. vittatus* were found to be more closely related to the genus *Rhabdophis*. However, limited data provisionally kept the species in the genus *Xenochrophis*, along with *X. bellulus* and *X. maculatus* which were not investigated in the study. Therefore, further research is necessary to ascertain the phylogeny of this group, especially for *X. bellulus*, *X. maculatus*, *X. trianguligerus*, and *X. vittatus*. In addition, further research investigating morphological characters to determine diagnostic features of genera and species is also needed.

Twelve species (seven *Fowlea*, and five *Xenochrophis*) are recognized: *Fowlea asperrimus, F. flavipunctata, F. melanzostus, F. piscator, F. punctulatus, F. schnurrenbergeri, F. tytleri, Xenochrophis bellulus, X. cerasogaster, X. maculatus, X. trianguligerus,* and *X. vittatus.* The St. John's Keelback, *Fowlea sanctijohannis,* is not treated here as a valid species, following the taxonomy by Vogel & David (2012), who stated that there was insufficient evidence to support the validity of the species.

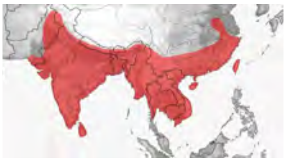


Figure 25.4. The distribution of *Amphiesma stolatum.*

Buff-striped Keelback

Amphiesma stolatum (Linnaeus, 1758)

Distribution and Habitat. Widespread in South and Southeast Asia: Forests and modified human-modified habitats, including agricultural lands in Taiwan, China (Hainan, Hong Kong, Fujian, Jiangxi), Sri Lanka, possibly the Andaman Island, India (Kerala, Tamil Nadu, Andhra Pradesh, Karnataka, Gujarat, Madhya Pradesh, Chhattisgarh, Orissa, Uttar Pradesh, Assam, Bihar, Maharashtra, Arunachal Pradesh, Punjab, Himachal Pradesh, Jammu and Kashmir, Bhutan, Myanmar, Thai-

Figure 25.5a. ***Amphiesma stolatum*****. A. China Photography by Konrad Mebert. Bottom. India. Photography by Daniel Jablonski.**

land, Vietnam (Hoa Binh), Laos, Cambodia, Nepal, Pakistan. Type locality. America (in error).

Identification. The head is distinct from the body. The head and anterior body are orange, red-brown or blue-grey. Upper labials are white, becoming gray posteriorly and edged with black: body olive-green or brown with black spots or reticulated cross bands with two yellow or tan longitudinal stripes. Ventrals are white with some dark spots on the outer edge of each ventral scale and counts 141-151 on males 143-149 on females in Taiwan (Mao, 1998).

Natural History. A mostly terrestrial or riparian zone between wetland to grassland snake, that feeds on a variety of prey (e.g. fishes, frogs, toads, grasshoppers, etc.) (Norval et al., 2005, 2007, 2008) both in and out of the water. Usually close to water and up to 2000 m ASL. It was often associated with human-modified habitats as well as forests. Anurans and lizards form the largest portion of their diet (Baruah et al. 2001). In Sri Lanka, it has been reported eating the Indian Burrowing Frog, *Sphaerotheca breviceps* (Dissanayake and Wellappuliarachchi 2016). Females are known to lay 1-14 eggs in May-September and remain with the eggs. When disturbed, it will flatten its forebody (Pope, 1935)

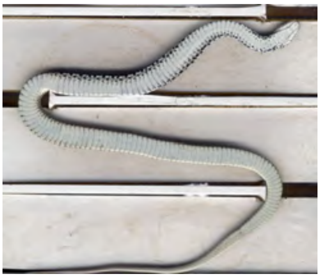


Figure 25.5b Ventral view of *Amphiesma stolatum* in Taiwan (Photographer: Jean-Jay Mao).

Barred Keelback

Tropidonophis doriae Boulenger, 1897

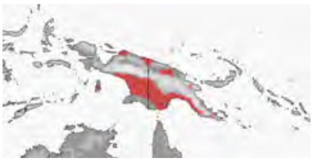


Figure 25.6. The distribution of *Tropidonophis doriae*

Distribution and Habitat**.** Forest streams in New Guinea east of the Vogelkop, absent from higher elevations in the central mountain spine. The species also is present in the Aru Islands. Elevational records for collection sites range from sea level (Western Province, Papua New Guinea) to 1300 meters at Moroka in the Owen Stanley Range (Central Province, Papua New Guinea).

Identification**.** Dorsum brown or gray-brown with darker crossbands that usually are more distinct and broader on the anterior body and narrower and/or less well defined on the posterior body. Bands on the body 31-47, each two to six scales long and are separated by one to three scales. bands may be interrupted into two or four series of dark spots on the posterior third or more of the body length. Occasional specimens have narrow bands anteriorly and a reticulate pattern of darkened scale edges posteriorly or are uniformly brown dorsally. The chin and throat are cream-color or yellow; some lower labials may have dark edges. Juveniles are more boldly patterned. Size. Males to 1049 mm total length, 794 mm SVL; females to 1113 mm, 829 mm SVL. Tail length 24.3% to 28.5% of the total length. Dorsal scales in 17-17-17 rows; ventrals 134-153, subcaudals 71-90. Pits are present on head scales (Malnate and Underwood 1988).

Natural History**.** Inhabits primary and secondary forest, mostly in riparian areas. It is mostly aquatic and mainly diurnal. Diet is mostly frogs but will also take fish, frogs' eggs and tadpoles. It is oviparous with a clutch size of between 2 – 8 (Allison et al. 1998).

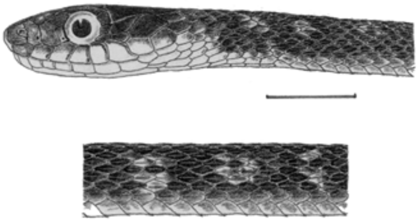


Figure 25.7. *Tropidonophis doriae.* **from Papua New Guinea. From Malnate (1988).**

Elongated Keelback

Tropidonophis elongatus (Jan, 1865)

Figure 25.8. The distribution of *Tropidonophis elongatus*

Distribution and Habitat**.** Inhabits the Moluccas Island Group, Indonesia. Including the islands of Ambon, Irian Jaya, Ceram, Ambon, Halmahera, Salawati, Numfoor and Biak; possibly Buru and Obi). Type locality: Molucca; restricted to Ambon by Malnate and Underwood 1988.

Identification**.** A slender-bodied snake with a long tail. Brown above with vertebral blotches or transverse bands. Ventral surface with brown spots mainly on the outer edges of ventrals. On a pale background. Dorsal scales are keeled in 15-15-15 rows. Ventrals 155-175, subcaudals 72-109 (Malnate and Underwood 1988).

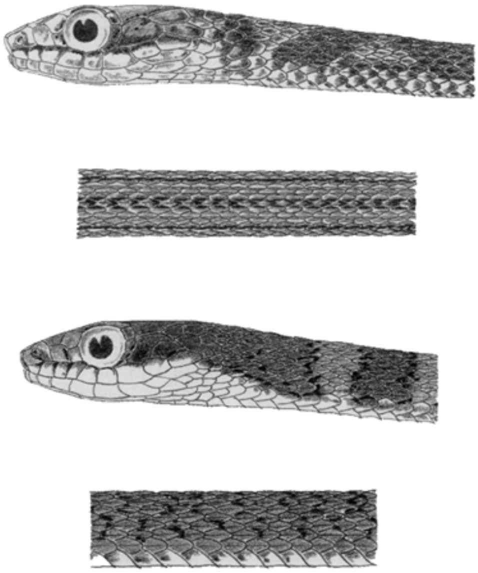


Figure 25.9. *Tropidonophis elongatus*. **Top RMNH 5163, female; Seri, Ambon. Lower: Lateral view of the head and posterior body Bottom. RMNH 18607b, male; Aitinjo, Vogelkop, Irian Jaya. From Malnate (1988).**

Natural History**.** Poorly known species, de Lang (2013) found one in a fast-moving stream at 400 m ASL.

Mair's Keelback

Tropidonophis mairii Gray, 1841

Distribution and Habitat**.** Creeks, swamps, eucalypt forests, heaths, pastures, parks, and suburban gardens are inhabted. In New Guinea it occurs along the east coast of the Gulf of Papua (Central Province). In Australia it is found from the Cape York Peninsula, Queensland, westward through the northern portion of the Northern Territory to the vicinity of Darwin, and southward to the Clarence River in northern New South Wales. Malnate and Underwood (1988) considered this species polytypic and names the New Guinea population west of the Gulf of Papua *T. m. plumbeus* and the Australian population *T. m. mairii.* Type locality: for *T. m. maririi* New Holland (= Australia). Neotype locality: Port Essington, NT; Type locality for *T. m. plumbeus* Katow (now Mawatta), Western Province (Malnate and Underwood 1988).

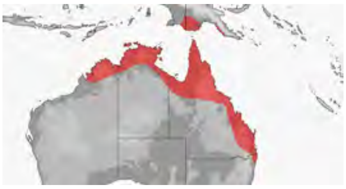


Figure 25.10. The distribution of *Tropidonophis mairii*

Identification**.** The dorsum is a uniform brown or gray, that may have scales with darker edges. A dark gray vertebral stripe or vertebral area with vague lateral definition often is present. A series of small dark spots may be present on the third, fifth and vertebral scale rows. The spots may be enlarged on the forebody. The head and nape. The top of the head may be pale with the plates, especially the parietals, mottled or marbled with dark. Paired light parietal spots may be present. The upper labials are pale with the upper edges of all plates darkened; the last two labials may be dark. A postocular dark stripe is present, often narrow, sometimes prominent, occasionally absent. Dorsal scales keeled and in 15-15-15 rows. Ventrals males 133-166, in females 133-156. Size. Males to 728 mm total length, 585 mm SVL; females to 814 mm, 712 mm s-v. Tail length is 23.2% to 30.8% of the total length (Malnate and Underwood 1988).

Natural History**.** Diet seems to be mostly frogs, will also feed on lizards. Active day and night. Capable of eating the introduced and highly toxic Cane Toad. It will climb into vegetation.

Females lay 2-18 eggs in June. Females the selected substrates with more moisture for egg deposition produced young with larger body size at hatching (Brown and Shine, 2004). Brown and Shine (2005) tested 42 gravid *Tropidonophis mairii* from tropical Australia for preference

Figure 25.11. *Tropidonophis mairii*
Photography by Shawn Scott.

of egg laying sites. Given the choice of laying their eggs in a nest containing empty eggshells of their own species, empty eggshells of their predator, the Slatey Grey Snake, (*Stegonotus cucullatus*), or a control with no eggshells. Six of the females chose the control box (no eggshells), 16 used the box with keelback eggshells, and 20 laid their eggs in nest boxes with the slatey-grey snake implying that the presence of eggshells may prompt the snake to lay eggs there because other successful hatchlings took place at that site.

Many-scaled Keelback

Tropidonophis multiscutellatus (Brongersma, 1948)

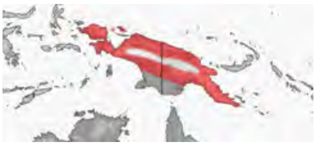


Figure 25.12. The distribution of *Tropidonophis multiscutellatus.*

Distribution and Habitat**.** New Guinea, the islands of Batanta and Salawati off the western tip of the Vogelkop. It is also present on Noemfor and Biak Islands in Geelvinck Bay, and Liki, Manam, and Karkar Islands off the north coast of New Guinea. On the mainland of New Guinea *multiscutellatus* is distributed from the western tip of the Vogelkop to Fife Bay, near the tip of the southeastern peninsula, but absent from the higher elevations of the central massif and the savannah region in the southeast**.** Known from elevations from 15 m to about 1440 m. Type locality: Alkmaar, Lorentz River, Irian Jaya (Malnate and Underwood 1988).

Identification**.** The dorsum uniformly brown or gray, may have dark, edged scales. A pattern of dark spots is common. The spots may be irregularly spaced or linear on the third, fifth and vertebral scale rows; they may be small or large, obscure, or prominent, those on the fifth and vertebral rows and may fuse to form narrow crossbars. The venter is light, gray, or brown at the sides, with short, dark transverse streaks at the outer corners of the ventrals. Dorsal scales keeled and in 15-15-15 rows. Ventral scales 231-253 in males, and 228-254 in females. Size. Males to 808 mm, total length, 583 mm SVL; females to 951 mm, 710 mm SVL. Tails are 25.3-34.2% of the total length.

Natural History**.** Diet includes fish (gobies). Females produce clutches of 2-10 eggs (Malnate and Underwood 1988).

Figure 25.13. *Tropidonophis multiscutellatus* **Photography by Nick Baker.**

Negros Spotted Water Snake

Tropidonophis negrosensis (Taylor, 1917)

Figure 25.14. The distribution of *Tropidonophis negrosensis*

Distribution and Habitat**.** Stream and their vicinity on the central Philippine islands of Mindoro, Masbate, Panay, Sicogen, Pan de Azucar, Negros and Cebu. At altitudes of 411-823 meters. Type locality: Canlaon Volcano, Occidental Negros, Philippines (Malnate and Underwood 1988).

Identification**.** Head and nape are dark gray or black, the snout is lighter. Paired light spots often are present on the parietals. Upper labials are pale, darkened at their upper borders and vertical sutures; the last scale often is heavily pigmented. A black stripe extends from the lowest postocular to the corner of the mouth but may be obscure or absent. The dark area on the nape is followed by three or four dark crossbands enclosing light lateral spots; occasionally, the bands are broken into large dark spots. A narrow, light vertebral stripe sometimes is

Figure 25.15. *Tropidonophis negrosensis,* **Twin Lakes Natural Park, Negros Oriental, Philippines. Photography by Chris Cafer.**

present on the neck, continuing through the anterior quarter of the body. The chin and throat are pale. Two rows of black spots along the sides of the venter. Dark speckling also may be present at the sides. Each subcaudal bears a single bold dark spot; scattered gray flecks may occur along the midline of the scutes. Dorsal scales keeled and in rows 19-19-17. Ventrals in males 252-262, in females 245-261, subcaudals in males 92-100, in females 87-98. Size. The largest male 775 mm total length, 554 mm SVL; the largest female 784 mm, 586 mm SVL. Tail length 24.1-30.5% of the total length (Malnate and Underwood 1988).

Natural History**.** Diet includes frogs and their tadpoles. Clutches of 3-7 eggs (Malnate and Underwood 1988).

Speckled Belly Keelback

Tropidonophis punctiventris (Boettger, 1895)

Figure 25.16. The distribution of *Tropidonophis punctiventris*

Distribution and Habitat. A semiaquatic snake that uses slow-moving shallow streams that transect rainforests. Halmahera, Indonesia. Type locality: Konorra, Halmahera (Subasli 2020).

Identification**.** A brown or olive dorsum with a series of pale spots on scale rows 4-6. Ventral is pale with brown spots. The slender body with a long tail. Dorsal scales keeled in 15-15-15 rows. Ventrals 145-160, cloacal plate divided, subcaudals 74-75. Size. A small snake, 320 and 460 mm long total length for the two known specimens (Malnate and Underwood 1988).

Natural History. Nothing known.

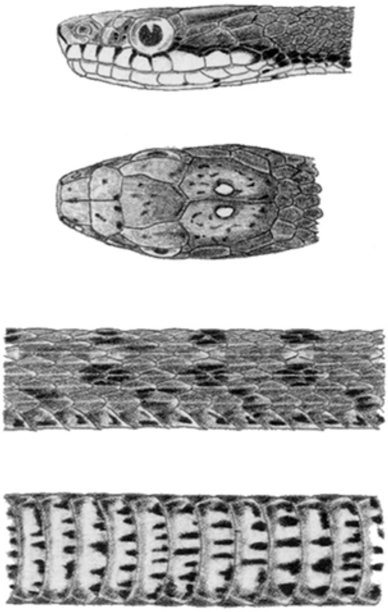


Figure 25.17. *Tropidonophis punctiventris*. **The male, holotype from Soa Konorra, Halmahera. From Malnate (1988).**

Truncated Keelback

Tropidonophis truncatus (Peters, 1863)

Figure 25.18. The distribution of *Tropidonophis truncates.*

Distribution and Habitat**.** Small streams on Salawati, Halmahera, Bacan, and Ternate Indonesia. Type locality: Dodinga, auf der Mitte der Insel Djololo [Halmahera] (Malnate and Underwood 1988).

Identification**.** A slender cylindrical body with a moderately long tail. Dorsum brown or dark grey with a network of black stripes formed by the dark edges on the scales. Maybe a uniform pattern. Venter with a pale background with dark speckling. Dorsal scales in 15-15-15 rows, most rows keeled, except the vertebral and para vertebral rows that are smooth. Ventrals 132-159, cloacal plate single, subcaudals 36-51. Size. Maximum length 560 mm total length. Tail about 0.2 of the total length (Malnate and Underwood 1988).

Figure 25.19. *Tropidonophis truncates* **A female syntype from Halmahera. From Malnate (1988).**

Natural History. Nothing known.

White-lined Water Snake

Rhabdophis auriculatus (Günther, 1858)

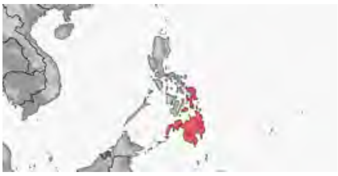


Figure 25.20. The distribution of *Rhabdophis auriculatus*

Distribution and Habitat. Along streams in the Philippines (Basilan, Bohol, Leyte, Samar, Mindanao). Type locality: Philippines. A polytypic species. *Rhabdophis auriculata myersi* Leviton 1970; Type locality Davao Province, Mindanao Island. Differs in subcaudal counts than the nominate subspecies.

Identification**.** A dark brown to olive green dorsum with a pale vertebral stripe on each side of this stripe is a series of dark elongate spots, immediately below those is a series of pale gray spots, followed by another series of dark spots below. The first two scale rows are pale pink. The ventral scales are black with white lateral spots.

Head short, blunt, very distinct from anterior body; rostral visible barely visible from above; parietals longer than frontal, in contact with one postocular; two nasals, the posterior highest; loreal higher than wide, in contact with second and third labials; preocular single, three postoculars; temporals 1+3; eight upper labials, third, fourth, and fifth border the orbit. Five lower labials touching anterior chin shields, which are shorter and broader than posterior. Dorsal scales keeled and in 17 rows. Ventrals 150-158; subcaudals 75-91. Size. To at least

Figure 25.21. *Rhabdophis auriculatus* **from Ormoc, Leyte, Philippines. Photography by Stefanie de Win.**

524 mm total length, tail 145 mm (Taylor, 1922). This seems to be a small snake compared with other members of the genus.

Natural History**.** Diet includes ranid frogs in all life stages (eggs, tadpoles, adults).

Zigzag-lined Water Snake

Rhabdophis lineatus (Peters, 1861)

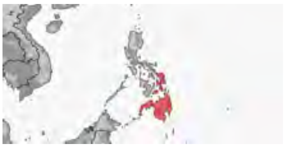


Figure 25.22. The distribution of *Rhabdophis lineatus*

Distribution and Habitat. Coastal freshwater swamp edges in the Philippines (Basilan, Bohol, Mindanao, Samar, Leyte) Type locality: Loquilocun, Insel Samar.

Identification. A red-brown dorsum with scattered black spots that look like smudges of black on scales. A white stripe on the upper labials extends to about the tenth ventral, bordered by black above. Dorsal scales keeled and in 19 rows, ventrals 132-142, subcaudals 64-71. Size. To at least 625 mm total length, tail 159 mm.

Figure 25.23. *Rhabdophis lineatus* **from Taft, Eastern Samar, Philippines. Photography by Jeff Weinell.**

Blueneck Keelback

Rhabdophis rhodomelas (Boie, 1827)

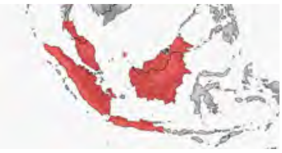


Figure 25.24. The distribution of *Rhabdophis rhodomelas.*

Distribution and Habitat**.** Brunei Darussalam, Myanmar, Cambodia, India, Indonesia, Laos, Malaysia, Singapore, Thailand, Vietnam. Usually occurs in lowland areas but can be found up to 1200m asl. Associated with aquatic habitats, such as rivers and swamps. Type locality: Java, Indonesia.

Identification**.** Body robust and cylindrical, with a long tail. Head distinct from neck. Eye large with round pupil, diameter of eye greater than distance between eye and edge of lip. Loreal present, one preocular, and three or four postoculars. Nine upper labials (rarely 8 or 10), 4th to 6th (rarely 5th-7th) touching eye. Scales in 19 rows on midbody, strongly keeled. Ventrals 130-145,cloacal plate divided, subcaudals 67-99.

Dorsum olive grey or brown, with distinct or indistinct dark triangles. On the posterior half of the body, there are often small, light spots positioned laterally, in the middle of the dark triangles. Juveniles tend to have brighter coloration, and many specimens have bright red markings laterally, alternating with the triangular pattern. The head is olive, with white labials and black sutures on the upper labials. Ventrals pale with no markings.

Natural History**.** Mostly aquatic. It occurs in disturbed areas such as canals, ditches, and fishponds. It is diurnal, actively hunting fish and frogs. At night, specimens have been observed resting on vegetation overhanging small streams and large, fast-flowing rivers. Individuals have also been recorded resting on water hyacinths at night, and twigs emerging from the water in a large man-made lake. When captured, they will often secrete a foul-smelling musk. Oviparous, with a clutch size of about 5-8 eggs.

Figure 25.25. *Rhabdophis rhodomelas.* **Photography by Medi Sanyan**

Japanese Tiger Keelback

Rhabdophis tigrinus (Boie, 1826)

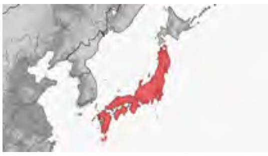


Figure 25.26. The distribution of *Rhabdophis tigrinus.*

Distribution and Habitat. Coastal wetlands to montane streams, including roadside ditches, ponds, and rice paddies on Honshu, Kyushu, Shikoku, and the Satsunan Islands of the Ryukyu group, Japan.

Identification. Dorsal scales are keeled in 19-17-17 rows (sometimes to 15 rows post body). Ventral scales are 148-160 in males and 153-162 in females; subcaudals in males 57-73, in females 52-65. Size. Males reach at least 730 mm SVL; females reach at least 780 mm SVL.

The Japanese populations have prominent geographical variations in coloration. Goris (1971) found populations from Kanto (eastern Honshu), Kinki (western Honshu), and Kyushu have distinct dorsal color patterns. The Kanto population expresses many dark dorsal blotches on a red ground color; the Kinki type has obscure dorsal blotches, and the ground color is not red; and the Kyushu type has large, dark dorsal blotches on red ground color.

Natural History. The diet consists mainly of anurans, most often tadpoles, toadlets (Bufonidae) and froglets. It uses chemical and visual cues to locate prey (Tanka 2002). Home range size showed considerable individual variation, with home range area ranging from 1.3 to 11.0 ha in a temperate forest in Kyoto, Japan (Kojima and Mori 2014).

Figure 25.27. *Rhabdophis tigrinus.* **Photography by Yasunori Koide.**

Venom and Poison. Severe envenomation by this species was reported by Mittleman and Goris (1974); symptoms included delayed, spontaneous, superficial hemorrhaging and profound impairment of normal blood coagulation. Severe internal hemorrhaging and hemolysis were present in two cases. Human deaths have resulted from envenomation by this snake (Mittleman and Goris 1978). Rhabdophis is one of three genera with nuchal glands containing cardiotonic steroid toxins (bufadienolides). Rhabdophis tigrinus (and R. lateralis and R. formosanus) sequesters bufadienolides from its toad prey and stores them in the nuchal glands as a defensive mechanism (Takeuchi et al. 2018). Gravid females with high nuchal gland toxin levels pass the compounds to their offspring. Snake hatchlings thus also benefit from the toad-derived defenses found in their parent.

Taiwanese Tiger Keelback

Rhabdophis formosanus (Maki, 1931)

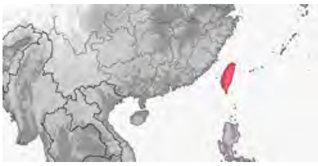


Figure 25.28. The distribution of *Rhabdophis formosanus*

Distribution and Habitat. Montane streams, ponds, and nearby riparian zones, forest edges, and roadside ditches within elevations 1600 to 3000 m in Taiwan (Mao et al., 2012)

Identification. Head is distinct from neck; body is moderately stout. The snake has a pair of nuchal glands and enlarged rear fangs. Crown of head olive at least anteriorly; there is a wide, curved transverse band of yellow on the nape, to which a black cross band adjoins in the front and rear. The upper labials are yellow with black sutures, the black areas along the sutures below eye are broad. Upper body and tail bear green-yellow-orange and black spots arranged in five alternating rows, creating a checkered appearance. Ventral head is white. Ventral scales on body and tail are black with (irregular) posterior margins of light green-yellow. Cloacal scale is divided and subcaudals are paired. Dorsal scales are keeled, in 19-17-17 rows (sometimes to 15 rows post body), Ventral scales are 148-160 in males and 153-162 in females. *Rhabdophis formosanus* has high subcaudal counts (≤ 80 in males, ≤ 77 in females). Thus, subcaudal counts could distinguish *R. formosanus* from *R. tigrinus* and *R. lateralis*, except for the Kyushu populations of *R. tigrinus* with partially overlap of the ranges (Ota & Mori, 1985; Ota et al., 1999). Males reach at least 730 mm SVL, females reach at least 780 mm SVL. Total length up to 100 cm.

Figure 25.29. *Rhabdophis formosanus.* **Taiwan. Photography by Yu Sing Lin.**

Natural History. Diet is primarily anurans but will also feed on fish and other snakes. Females produce 8-47 eggs per clutch in summer; hatchlings measure about 160 mm in total length. Defense behavior includes flattening the anterior body into a narrow hood.

Chinese Tiger Keelback
Rhabdophis lateralis Berthold, 1859

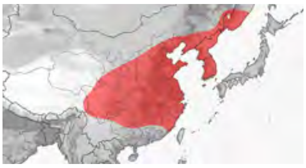


Figure 25.30. The distribution of *Rhabdophis lateralis*

Distribution and Habitat. Coastal wetlands to montane streams, including roadside ditches, ponds, and rice paddies in China, North Korea, Russia, South Korea, and Vietnam.

Identification. Dorsum green ventral surface white anteriorly and dusky green posteriorly. Narrow black bars on the labial scales. Black transverse bands extend down the body and fade on the tail. Spaces between bands are red anteriorly and become green posteriorly. Dorsal scales are keeled, in 19-17-17 rows (sometimes to 15 rows post body). Ventral scales are 148-160 in males and 153-162 in females; subcaudals in males 57-73, in females 52-65. Size. Males reach at least 730 mm SVL, females reach at least 780 mm SVL. Pope (1935) considered the longest specimen to be 998 mm.

Natural History. Li et al. (2008) found hibernation occurs from the middle of October to following April. Most activity occurs from May to August. The diet is composed of anurans. Reproduction occurs from the middle of June to the middle of July in the Beijing area. Clutches contain six to 22 eggs, and the incubation period is 41 to 43 days.

Figure 25.31. *Rhabdophis lateralis* **from Licun Village, Fenghua County, Zhejiang, China. Photography by Jian Wang.**

Olive Keelbacks, *Atretium, Fowlea,* and *Xenochrophis*

The genus *Atretium* contained two species that were not monophyletic. They appear in two different places in a tree with *Xenochrophis* and *Fowlea*. The Yunnan Olive Keelback is the sister to *Fowlea asperrimus and A. schistosum* is the sister to a clade containing both *Xenochrophis* and *Fowlea* (Zaher et al. 2019).

Olive Keelback
Atretium schistosum (Daudin, 1803)

Distribution and Habitat**.** Ponds, marshes, flood agricultural land, and swamps of South Asia, Sri Lanka, India, Bangladesh, and Nepal. Possibly in Bhutan. Peninsular India south of latitude 15 degrees north and along the east coast to Uttarakhand. Up to 1000 m ASL. Absent from most of North India. Type locality: None given.

Identification**.** A uniform olive green to brown above with a yellow to orange venter. It is a small, robust snake with a narrow head, short snout, and slit nostrils placed relatively high.

Figure 25.32. The distribution of *Atretium schistosum*

Figure 25.33. *Atretium schistosum***. Avrajjal Gosh.**

It is sometimes tinged with pink or purplish on the flanks. The tail length is one-third to one-fourth of the total length. Dorsal scales keeled in 19-19-17 rows; ventrals 129-160, cloacal plate divided, subcaudals paired 53-85. Upper labials number eight, third and fourth border the orbit (or nine upper labials with the fourth and fifth bordering the orbit). Specimens from South India have a distinct reddish line along the fifth and sixth or the fourth and fifth scale rows up to the vent. This stripe is brighter in males. The females are between 700 and 750 mm long, and the males are between 500- and 600-mm. Maximum size 870 mm total length (Schleich & Kastle 2002; Wall 1921).

Natural History**.** Diet includes fish, tadpoles, frogs, and mosquito larvae. Oviparous clutches of 12-30 eggs laid between December and March.

Bar-necked Keelback

Fowlea schnurrenbergeri (Kramer, 1977)

Distribution and Habitat**.** Slow rivers and streams, marshes, swamps, ponds, and lakes in Nepal and northern India. Type locality: Devanandpur, Bhairawa, Nepal.

Identification**.** Characterized by a small checkerboard dorsal pattern; a broad, straight crossbar on the nape; two well-defined subocular streaks, the posterior one extending from the eye to the corner of the mouth but not meeting the nuchal crossbar; and ventral and subcaudal scales with broad, dark margins (Vogel & David 2006). Dorsal scales are keeled and in 19:19:17 rows. In males, ventral scales are 132-139, and subcaudals are 71-80; in females ventral scales are 141-152, and subcaudals are 61-79. Males average 600 mm in total length,

Figure 25.34 The distribution of *Fowlea schnurrenbergeri*

and females average 900 mm in average total length. Internasals are narrow anteriorly; upper labials 9-10, 4-5 border the orbit; preocular one; the loreal is single; postoculars 2-3; sometimes a single subocular; temporal 2+2 or 2+3 or rarely 1+2.

Zaher et al. (2019) found this species to be the sister to all the other members of the genus *Atretium* and *Fowlea.*

Natural History**.** A poorly studied species.

Yunnan Olive Keelback

Fowlea yunnanensis Anderson, 1879

Distribution and Habitat**.** Western Yunnan, China. Type locality: Lianghe, Yingjiang County; and Husa, Longchuan County; both in Yunnan Province, southern China. May also be present in Myanmar. To elevations of 1500 m ASL.

Identification**.** Color uniform dark olive-brown above; yellow beneath. Snout rather pointed; internasals triangular and form a short suture with the rostral but may be excluded from the rostral by a small azygos scale which is wedged between them. The prefrontals are broader than long, and about the same width as the internasals. Parietals longer than the vertical, rounded behind, sometimes with a portion separated from their hinder extremities. Loreal subquadrangular, higher than broad. One preocular reaching to the upper surface of the

Figure 25.36. *Fowlea schnurrenbergeri.* **Photography by Avrajjal Ghosh.**

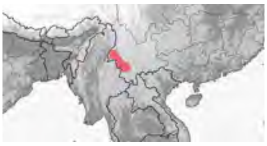


Figure 25.37. The distribution of ***Fowlea yunnanensis.***

head. Three postoculars, the lowest in contact with three labials. Temporals 2+3. Nine upper labials, the fourth and fifth border the orbit. Twenty-three maxillary teeth, increasing in length posteriorly. Ventrals 144- 154; subcaudals 62-85. Dorsal scale rows keeled in 19 rows. Yunnan specimens differ from the Indian species in the narrow suture between the anterior frontals and rostral; in the divided posterior frontals; in the presence of nine upper labials, and in having slightly larger preoculars, and occipitals.

Chen et al. (2021) note that Atretium yunnanensis was originally recognized as a variant of Atretium schistosum. It was subsequently elevated to full species status and has long been assigned to the natricine genus Atretium. They used morphological and genetic evidence and found Atretium yunnanensis nested within the genus Fowlea Theobald, 1868.

Natural History. This species inhabits paddy fields, ponds, and river valleys between 800 m and 1500 m ASL. It is diurnal, preys on frogs, fish, and rats. Defense behavior includes biting repeatedly and violently.

Boulenger's Keelback

Fowlea asperrimus (Boulenger, 1891)

Distribution and Habitat**.** Endemic to Sri Lanka. Occurs in elevations up to 1000m asl, usually living in or near water bodies such as flooded rice fields, lakes, marshes, ponds, and rivers. Type locality: Ceylon.

Figure 25.38. The distribution of *Fowlea asperrimus*

Identification**.** Body robust and cylindrical, tail length moderate. Head distinct from neck. Eye small with round pupil, diameter of eye less than or just reaching greater than distance between eye and edge of lip. Loreal present, one preocular, and three (rarely two) postoculars. Nine upper labials (rarely 10 or 11), 4th and 5th (rarely 5th and 6th) touching eye; 10 (rarely 9 or 11) lower labials. Scales in 19 rows on midbody, strongly keeled. The keels form sharp lines posteriorly, except for the outer rows, which are smooth. Ventrals 127-142, cloacal plate divided, subcaudals 75-92. Maximum total length 890 mm for females; males much shorter (maximum length females / males 1.41), longest male 630 mm. Relative tail length sexually dimorphic: tail 28.3–31.4 % of total length in males, 25.7–28.9 % in females (Vogel and David 2012).

Dorsal color pale with broad, dark, confluent blotches anteriorly, which become separated on the posterior part of the snake. Blotches number 22-32. The anterior part can also be described as dark with incomplete

Figure 25.39. ***Fowlea asperrimus*** **from Kalawana, Ratnapura, Sri Lanka. Photography by Susan Meyer**

crossbands, larger at the base, sometimes forming a triangular shape. The head is dark olive dorsally, with two narrow black streaks on the sides, located under and behind the eye. Light-colored ventrals, outer edges clouded with dark grey (based on Vogel and David 2012).

Natural History**.** Mostly aquatic, presumably diurnal. Has been recorded from a creek near paddy fields and observed swimming in a river during the day. Oviparous.

Yellow-Spotted Keelback

Fowlea flavipunctata (Hallowell, 1860)

Distribution and Habitat. India, Thailand, Myanmar, South China, Taiwan, West Malaysia, Laos, Cambodia, Vietnam, Bangladesh. Occurs in slow-moving streams, rivers, ponds, swamps, and marshes. It is also present in modified habitats such as paddy fields and ditches. Some working rotavator on paddy fields make this species vulnerable to opportunistic avian foragers in Taiwan (Mao and Norval, 2013). Type locality: Canton River, Kwangtung, China (now Guangdong).

Identification. Body robust and cylindrical, tail length moderate. Head distinct from neck. Eye large with round pupil, the diameter of eye greater than the distance between eye and edge of lip. Loreal present, one preocular, and three or four (rarely two) postoculars. Ten upper labials (rarely 8), 4th and 5th (rarely 4th, or 5th and 6th) touching eye; 9-11 lower labials. Scales in 19 rows on midbody, rather weakly keeled anteriorly and more strongly keeled posteriorly. Ventrals 120-143, and present sexual difference on males 124-132 (n=20) and females 138-143 (n=28) in Taiwan (Mao, 1998), anal divided, subcaudals 60-91 (Fig. 25.41b).

Dorsal color varies between different shades of olive, brown,

Figure 25.41a. (to right)_*Fowlea flavipunctatus.* Top: Sakaeret, Thailand. Photography by Harry Ward-Smith Middle: Laos. Photography by Daniel Jablonski. Bottom Hong Kong. Photography by Artur Tomaszek.

orange-red or grey. Clear, dark spots arranged in 6-7 alternating rows, producing a checkered pattern; more distinct anteriorly and larger laterally. Dorsal scales often have pale margins. In life, some specimens have vivid red or orange markings on the flanks.

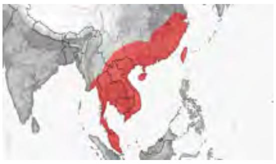


Figure 25.40. The distribution of *Fowlea flavipunctatus*

Natural History**.** Mostly semi-aquatic, diurnal. Like most keelbacks, its diet consists of fish (e.g.: snakehead fish [*Channa asiatica*] and frogs (e.g.: Heymonsi's Narrow-mouthed Toad [*Microhyla heymonsi*]) (Norval et al., 2010). In Taiwan, this species usually shared habitat (sympatric) with *Amphiesma stolatum*, *Hypsiscopus murphyi*, *Myrrophis chinensis*, and *Trimerodytes annularis* but differences in spatial or active time (JJ Mao, unpublish data). Some literature and observations indicated that the krait is an obvious predator of this snake (Mao, 1970; Mao et al., 2006; Mao et al., 2010). Oviparous, clutch size are 23-112 eggs, copulation in Autumn (October to early November), parturition in early May, and then the egg takes two months to hatch (JJ Mao, unpublish data).

Figure 25.41b. (top)_The newly hatchling snake of *Fowlea flavipunctatus* in JJM lab. of Taiwan. (middle) The right side hemipenis of Fowlea flavipunctatus of Taiwan (Photographer: Jean-Jay Mao). (bottom) The ventral view of large female Fowlea flavipunctatus of Taiwan. Photography by Jean-Jay Mao

Javanese Keelback

Fowlea melanzostus (Gravenhorst, 1807)

Distribution and Habitat**.** Endemic to Indonesia, specifically the Java, Sumatra, and Bali islands. It occurs in lowland habitats with varying degrees of disturbance. These habitats often have still or slow-moving bodies of water, such as paddy fields, ditches, or fishponds. Type locality: Batavia, Java (now Jakarta).

Identification**.** Body robust and cylindrical, tail length moderate. Head distinct from neck. Eye average-sized with round pupil, the diameter of eye roughly equal to the distance between eye and edge of lip. Loreal present, one preocular, and three (rarely two) postoculars. Nine upper labials (rarely 10), 4th and 5th (rarely 4th, or 5th and 6th) touching eye; 10 (rarely 9 or 11) lower labials. Scales in 19 rows on midbody, strongly keeled except for the outer 2-3 rows. Ventrals 128-143, cloacal divided, subcaudals 66-83.

Dorsal color varies between shades of yellow, light brown, grey, or olive. There are two forms; blotched and striped. The blotched form has four rows of large black blotches on the neck and one vertebral blotch behind the neck. These are followed by five rows of smaller blotches, which often fade posteriorly. The striped form has four dark stripes starting on the neck and a vertebral stripe

Figure 25.42. The distribution of *Fowlea melanzostus.*

starting behind the neck. Like the blotched form, these markings also fade posteriorly. Some dorsal scales often have dark margins. In life, some specimens have bright red markings laterally. The head is darker than the body, and has dark streaks below and behind the eye. Ventrals are pale yellow or cream, often with black outer edges.

Natural History**.** Mostly aquatic, in rice paddies with shallow water, in ditches, and on the edges of fishponds. It is primarily diurnal but occasionally observed hunting at night. It is an active hunter with a diet consisting of fish and frogs. When captured, this species secretes a strong musk as a defensive mechanism to deter predators. Oviparous.

Figure 25.43. *Fowlea melanzostus.*
Photography by Muhammad Azib

Checkered Keelback

Fowlea piscator (Schneider, 1799)

Distribution and Habitat**.** Pakistan, Sri Lanka, India, Bangladesh, Bhutan, Nepal, Myanmar, Thailand, Laos, Vietnam, Malaysia, Singapore, and China. It occurs in aquatic habitats such as slow-moving rivers, lakes, and marshes. Also common in modified habitats such as canals and fishponds. Type locality "East Indies" (unspecified).

Identification**.** Body robust and cylindrical, tail length moderate. Head distinct from neck. Eyes average size with a round pupil, eye diameter equal to, or greater than the distance between eye and edge of the mouth. Loreal present, one preocular, and three or four postoculars. Nine upper labials (rarely 8 or 10), 4th and 5th (rarely only 4th or 5th) touching eye; 10 (rarely 9 or 11) lower labials. Scales in 19 rows on midbody, weakly keeled except for the outer 2-4 rows. Ventrals 128-154, cloacal divided, subcaudals 68-96 (based on Vogel and

David 2012).

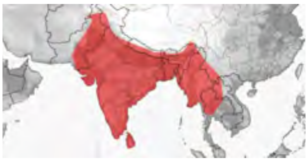


Figure 25.44. The distribution of *Fowlea piscator.*

Base color on dorsum shades of light or dark brown, grey, yellow, or olive. The dorsal pattern usually consists of 5-7 rows of alternating dark blotches, forming a checkered pattern. The dark blotches may vary in size, and sometimes lighter speckling is present. In addition, it has narrow dark streaks below and behind the eye. Ventrals are usually pale yellow or cream, often with lateral cloudy spots.

Natural History**.** Mostly aquatic and diurnal. It is an active hunter with a diet consisting of fish and frogs. Patel et al. (2017) found a specimen that had died trying to eat the fish *Anabas tertudineus*. Presumably, the fishes' spines prevented the snake from swallowing the fish and caused it to suffocate. Kalki (2020) found this snake feeding on the eggs of the Malabar Gliding Frog (*Rhacophorus malabaricus*). When threatened, it flattens its neck, mimicking a cobra. Autonomy of the tail has also been recorded in this species. Oviparous, average clutch size of 30-70 eggs.

White-Spotted Keelback

Fowlea punctulatus (Günther, 1858)

Distribution and Habitat**.** Myanmar, Thailand. It occurs in mangrove habitats and tidal marshes. Type locality: Unknown.

Identification**.** Body robust and cylindrical, tail length moderate. Head distinct from neck. Eye small, with round

Figure 25.45. *Fowlea piscator.* **A. India Avrajjal Ghosh. B. Sakaeret, Thailand Harry Ward-Smith. C. Pha Nam Yod Waterfall, Tha Yang District, Phethaburi Province, Thailand. Photography by Rushen Bilgin.**

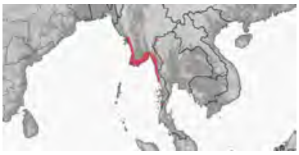


Figure 25.46. The distribution of *Fowlea punctulatus*.

pupil, the diameter of eye equal to, or less than the distance between the eye and the edge of mouth. Loreal present, one preocular, and two or three postoculars. Nine upper labials (rarely 10), 4th and 5th (rarely 5th and 6th) touching eye; 10 (rarely 9 or 11) lower labials. Scales in 17 rows on midbody, smooth or weakly keeled. Ventrals 142-154, cloacal divided, subcaudals 62-83.

Dorsum black with small pale dots, forming incomplete crossbands throughout the dorsum. Upper labials pale cream or white, followed by a narrow "V" pattern on the neck. Pale ventrolateral stripes present, bordered in black. Ventrals light-colored, often with dark margins.

Natural History**.** Mostly aquatic, found in brackish habitats such as tidal palm forest and mangrove swamps. Preys on fish and frogs, presumably predated by larger snakes, monitor lizards, large fish, and wading birds. Oviparous.

Figure 25.47. *Fowlea punctulatus*
Photography by Montri Sumontha.

Tytler's Keelback

Fowlea tytleri (Blyth, 1863)

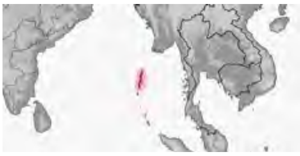


Figure 25.48. The distribution of *Fowlea tytleri*

Distribution and Habitat**.** The Andaman Islands, and possibly Nicobar Islands. Common in forested areas, presumably in or near bodies of water. Type locality: Andaman Island.

Identification**.** Body cylindrical, tail length moderate. Head distinct from neck. Eyes with a round pupil, and the diameter of eye roughly equal to the distance between eye and edge of mouth. Loreal present, one preocular, and three (rarely 4) postoculars. Nine upper labials, 4th and 5th touching eye; 9 (rarely 10) lower labials. Scales in 19 rows on midbody, strongly keeled. Ventrals 131-145, cloacal divided, subcaudals 76-86.

Base color of dorsum pale brown with variable markings; striped, blotched, or both. Juveniles have narrow pink-brown stripes, often broken into a series of spots posteriorly. Some color forms have a wide "V" pattern on the neck. It is cream ventrally.

Natural History**.** Mostly aquatic, diurnal. Preys on frogs and fish. Oviparous.

Burmese White-Barred Keelback

Xenochrophis bellulus (Stoliczka, 1871)

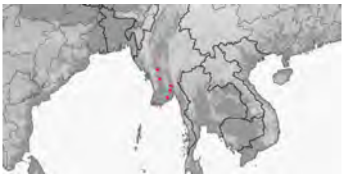


Figure 25.49. The distribution of *Xenochrophis bellulus*

Distribution: As far as currently known, *X. bellulus* is endemic to southcentral Myanmar in the states of Yangon and Bago (Lee *et al*. 2018).

Identification**.** Based on Lee *et al*. 2018 [two males and two females] and an adult male specimen collected by GK, SMF 106048): The head is olive-brown with contrasting cream-colored vertical bars on the upper labials of which one in front of the eye and one just posterior to eye reach to upper margin of eye. Two other such vertical bars are present in the lateral nuchal region. The body is dark grayish olive to black with cream-colored checkering and anterior crossbands arranged on both sides, not reaching dorsal surface. The eyes are large, pupil round, nostril directed dorsolaterally; prefrontal single; internasals two; one loreal; one preocular; three postoculars; temporals 1+1 or 1+2; upper labials usually nine, sometimes ten, with 4th–6th bordering orbit. Lower labials nine or ten, with the 1st–6th contacting the anterior chin shields. Body scales keeled, usually in 19–19–17 rows, sometimes in 19–19–19 rows when transition from 19 to 17 rows happens posterior to midbody (as in GK-7061 that has this transition at ventral scale 70 or 54.2% of SVL); 2–4 preventrals; ventral scales 134–139 in males, 135–143 in females, all unkeeled; cloacal plate divided; subcaudals 71–79 pairs in males, 70–72 in females. SVL 323-429 mm in males, 316-321 mm in females; tail 27.5–28.8% of total length in males, 27.0–27.2% in females.

Natural History Notes: Inhabits seasonally flooded rice fields and grassland with forest patches. Its diet consists of frogs and fish (Lee *et al*. 2018).

Figure 25.50. *Xenochrophis bellulus.*
Photography by Gunther Kohler.

Painted Keelback

Xenochrophis cerasogaster (Cantor, 1839)

Figure.25.51. The distribution of *Xenochrophis cerasogaster*

Distribution and Habitat**.** Pakistan, Nepal, Bangladesh, India. Occurs in or near water bodies, such as ponds and rivers. Type locality: Vicinity of Calcutta, India.

Identification**.** Body slender and cylindrical, with a long tail. Head not distinct from neck. Eye with round pupil. Loreal present, one preocular, and three (rarely 4) postoculars. Nine (rarely 8) upper labials, only the 4th touching eye; 10 (rarely 9 or 11) lower labials. Scales in 19 rows on midbody, strongly keeled except for the outer 2-3 rows. Ventrals 140-158, cloacal divided, subcaudals 68-80 (males).

Dorsum reddish brown, with a thick tan or light brown dorsolateral stripe on each side. The stripe is more prominent posteriorly. In some specimens, this stripe may be rather indistinct. Yellow ventrolateral stripes, and yellowish on the labials. Ventrals and subcaudals marbled red, with dark edges and pale speckling.

Natural History**.** Mostly aquatic, found in still water with thick emergent vegetation. Has been observed resting on lily pads, or grasses at marsh edges. It is expected from late June to November but absent during winter. Diurnal and active, but it is also timid and will flee to the water in the presence of a potential threat. They feed on fish, amphibians, and shrimp. Oviparous, known to lay eggs in early April and hatch during the rainy season (May-July).

Spotted Keelback

Xenochrophis maculatus (Edeling, 1864)

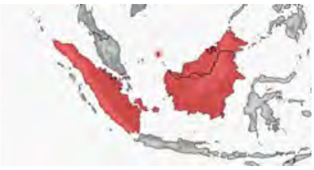


Figure 25.54. The distribution of *Xenochrophis maculatus*

Distribution and Habitat**.** Belitung, Natuna Archipelago, Riau Archipelago, Sumatra, Borneo, Brunei Darussalam, Malaysia, and possibly Singapore. Occurs in lowland forest with small streams and swamps. Type locality: Martapoura, pres de Bandjermasin, Borneo (now Banjarmasin).

Identification**.** Body slender and cylindrical, tail length moderate. Head distinct from neck. Eye exceptionally large with round pupil. Loreal present, one preocular, and three postoculars. Nine upper labials, only 4th to 6th touching eye. Scales in 19 rows on midbody, strongly keeled. Ventrals 140-156, cloacal divided, subcaudals 95-117.

Dorsum olive brown, with four longitudinal rows of small black spots, and two rows of yellow spots. Labials yellow or white, with black sutures. Ventrals and subcaudals yellowish with black edges.

Natural History**.** Mostly aquatic, but more terrestrial than other species of this group. Diurnal, feeds mainly on frogs. Reproductive habits unknown but presumed to be oviparous.

Figure.25.52. X*enochrophis cerasogaster.*
Photography by Avrajjal Ghosh.

Figure 25.53. *Xenochrophis maculatus* **from Marudi, Sarawak, Malaysia (Island of Borneo). Photography by Bernard DuPont.**

Triangle Keelback

Xenochrophis trianguligerus (Boie, 1827)

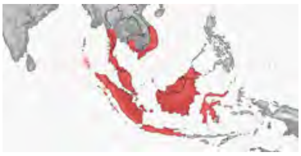


Figure 25.55. The distribution of *Xenochrophis trianguligerus*

Distribution and Habitat. Wetlands (ponds, swamps, rice paddies) close to evergreen forests in Southeast Asia, including the island of Borneo (Brunei Darussalam, Sabah, Sarawak, Kalimantan); Burma (Myanmar), Cambodia, India (Nicobar Islands; Arunachal Pradesh); Indonesia (islands of Nias, Mentawai, Sumatra, Riau Archipelago, Bangka, Billiton, Java, Bali, Sulawesi, Sangihe Archipelago, Ternate); Laos, peninsular Malaysia; Singapore; Thailand, and Vietnam. Type locality: Java.

Identification. The head is olive on the crown, the upper labials are yellow. The body is light brown to olive green with yellow and red highlights. Yel-

Figure 25.56. ***Xenochrophis trianguligerus.***
Photography by Medi Sanyan

low and red coloration towards the neck fading into white towards the tails with black saddle markings running the length of the body. Laterally the body has red triangular markings with the apex near the ventral surface. Each triangle has a pale center. Dorsal scales are keeled and in 19 rows at mid-body. Ventrals are 132-153. Total length up to 1350 mm.

Natural History**.** A nocturnal, semi-aquatic snake. The diet includes fish, tadpoles, frogs, and other small vertebrates. Females are oviparous and lay clutches of 5-15 eggs.

Striped Keelback

Ceratophallus vittatus (Linnaeus, 1758)

Distribution and Habitat**.** Native to Indonesia and West Malaysia. Introduced to Singapore and Puerto Rico. Occurs in lowland areas up to 1000m asl, associated with water bodies such as swamps and rice paddies. Type locality: "America" (in error).

Figure 25.57. The distribution of *Ceratophallus* (*Xenochrophis*) *vittatus.*

Identification**.** Body robust and cylindrical, with a long tail. Head distinct from neck. Eye large with round pupil, diameter of eye greater than distance between eye and edge of lip. Loreal present, one preocular, and three postoculars. Nine upper labials (rarely 8), 4th to 6th (rarely 4th-5th) touching eye. Scales in 19 rows on midbody, strongly keeled. Ventrals 138-155, cloacal divided, subcaudals 66-88. Base color of dorsum light brown, with a black vertebral stripe.

Natural History**.** Mostly aquatic, associated with shallow, still water such as rice paddy fields. It has also been found near streams and rivers, basking on stones during the day. It is a very fast-moving snake and will secrete a musk when captured. Autonomy of the tail has also been recorded. Diurnal, actively hunting frogs and fish. Oviparous. The invasive population in Puerto Rico is eating the critically endangered frog *Eleutherodactylus juanariveroi* and the White-lipped Frog, *Leptodactylus albilabris*.

Note. As this book was going to press Patel et al. (2023) found *Hebius beddomei* (Gunther, 1864) to be the sister to a clade containing *Fowlea* and *Atretium*. Freshly collected specimens and existing museum material allowed us to elucidate the generic status of the species and identify two distinct populations, one of which is described as a new species. A new genus, *Sahyadriophis* was erected to accommodate *Sahyadriophis beddomei*, and a new, second species *Sahyadriophis uttaraghati* . The discovery of the new Oligocene divergent lineage, *Sahyadriophis* adds the the evidence of the Western Ghats being a source of relic lineages.

Figure 25.58. *Ceratophallus* (*Xenochrophis*) *vittatus.*
Photography by Medi Sanyan

On the next page is *Opistjhotropis cheni.* **From Shimentai NR, Yingde City, Guangdong, China Photography by Jian Wang**

26. Asian Stream Snakes & Relatives

26. Asian Stream Snakes & Relatives

This clade contains three genera of poorly known southeast Asian snakes that may range from almost wholly aquatic to mostly terrestrial. The genus *Smithophis* contains four poorly understood fossorial-cryptozoic-semiaquatic snakes. The genus is named in honor of Malcolm A. Smith in recognition of his contributions to the knowledge of Asian snakes and is sometimes called two-colored forest snakes. The degree to which these snakes are aquatic remains to be determined. At least a few of these snakes feed on earthworms and skinks. However, its two sister genera (Giri et al. 2019) are the highly aquatic *Opisthotropis* and the semi-aquatic *Trimerodytes* (formerly *Sinonatrix*). *Opisthotropis* is distributed on mainland Southeast Asia eastwards to the Philippines and the Ryukyu Archipelago of Japan. Most *Opisthotropis* are known only from a few specimens or described based on single specimens, and most inhabit hill streams and nearby terrestrial habitats. They are known to forage at night on juvenile crabs, earthworms, fishes, tadpoles, frogs, and shrimps. *Opisthotropis* is oviparous. *Trimerodytes* likely originated in Hengduan Mountains (eastern Tibetan Plateau) in western China at 23.93 Ma (17.09–31.30) (Gou et al. 2020). While most clade members appear to be oviparous, at least one species of *Trimerodytes* (*T. annularis*) is viviparous.

Arunachal Rain Snake

Smithophis arunachalensis Das et al., 2020

Distribution and Habitat**.** Known from streams at six localities from eastern Arunachal Pradesh, including Roing and Koronu in Lower Dibang Valley District, Dening in Lohit District, and three localities in Namdapha Tiger Reserve in Changlang District of Arunachal Pradesh. The elevation ranges from 310 m in the foothills of Mishmi Hills to 580 m at Namdapha Forest Camp (Das et al. 2020).

Natural History. The holotype was caught while it was moving on the side of a stream in a moist evergreen forest. The type locality was in a degraded forest with extensive bamboo regeneration along both sides of the stream. The stream habitat where the

Figure 26.1. The distribution of *Smithophis arunachalensis*

Figure 26.2. *Smithophis arunachalensis*
Photography by Abhijit Das

snake was collected had large, bryophyte-covered boulders and bedrock near a pool and riffle section. The snake was caught in dim light during heavy rain near dawn at 05:00 hours.

Mizo Rain Snake

Smithophis atemporalis Giri et al., 2019

Distribution and Habitat. Known from secondary forests in Mizoram, India. Type locality: Mizoram University Campus, Aizawl, India, about 833 m elevation. It has an elevational range of 71–1,235 m asl (Remruatpuii et al. 2020).

Figure 26.3. The distribution of *Smithophis atemporalis*

Natural History. It is most frequently encountered during the monsoon season. It has been observed feeding on juvenile skinks and earthworms in nature and on the Bangladeshi Cricket Frog (*Minervarya asmati*) eggs in captivity (Giri et al. 2019). A female (SVL 437 mm) was observed feeding on an earthworm (*Eutyphoeus* sp.; total length 263 mm) in the middle of a road surrounded by a secondary forest used as a plantation. The earthworm had crawled onto the road and was quickly followed by the snake. The snake bit the earthworm and struggled with it for about 5 min while slowly working its way to the posterior end of its prey before swallowing it. The elapsed time from strike to complete ingestion was about 14 minutes (Muansanga and Lalremsanga 2020). It is oviparous, laying a maximum of four eggs per clutch (Remruatpuii et al. 2020).

Figure 26.4. *Smithophis atemporalis*
Photography by H.T. Lalremsanga

Brown Trapezoid Snake,

Smithophis bicolor (Blyth, 1854)

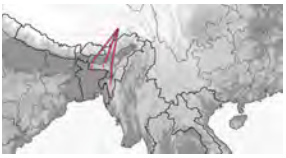


Figure 26.5. The distribution of *Smithophis bicolor.*

Distribution and Habitat. Assam, Meghalaya; Arunachal Pradesh (Deban, Namdapha - Changlang district), Maharashtra, India; northern Myanmar; and western Yunnan, China. Type locality: Assam, India.

Natural History. Feeds on worms and slugs (Smith 1943).

Figure 26.6. *Smithophis bicolor*
Photography by Abhijit Das

Jingpo Mountain Stream Snake,
Smithophis linearis Vogel, et al. 2020

Figure 26.7. The distribution of *Smithophis linearis.*

Distribution and Habitat**.** It has been found along streams in tropical evergreen forests in Yunnan, China. Type locality: Nabang Town, Yingjiang County, Dehong Dai, and Jingpo Autonomous Prefecture, Yunnan Province, People's Republic of China. Elevation ca. 467 m ASL. Known from three localities with a 40 km radius (Vogel et al. 2020).

Natural History. Diet is said to compose mollusks and arachnids.

Gary's Mountain Stream Snake
Opisthotropis alcalai Brown and Leviton, 1961

Figure 26.8. The distribution of *Opisthotropis alcalai.*

Distribution and Habitat**.** Mindanao, Philippines. Type locality: Cugat Creek, on the west side of Dapitan Peak, Mt. Malindang, Zamboanga del Norte Province, Mindanao at 2500 m ASL.

On 17 March 2019, Maglangit et al. (2023) opportunistically encountered a single individual of this species and observed it at 19:30 hrs in heavy rainfall. The snake was feeding on tadpoles (possibly *Leptobrachium lumadorum, Pelobatrachus stejnegeri, Staurois natator* tadpoles), and macro-invertebrates in a temporary pool at 440 meters elevation). The pool was near the fast-moderately flowing water channels of Mambuntan Falls. The habitat was a regenerating secondary-growth forest that transitioned to an agricultural area, approximately 10 meters distance from the locality. The vegetation was characterized by epiphytes, ferns, mosses, shrubs, and dominant flowering plants. The pool microhabitat was shallow (0.7 m) and covered with dead leaves (water pH = 6.7). The location was about 95 km straight-line distance from its type locality.

Figure 26.9. *Opisthotropis alcalai.*
Photography by Sharmaine Bonachita.

Anderson's Mountain Stream Snake

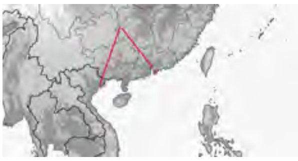


Figure 26.10. The distribution of *Opisthotropis andersonii*

Opisthotropis andersonii (Boulenger, 1888)

Distribution and Habitat. Hill streams and wetlands of Hong Kong and adjacent Shenzhen City it extends north to Guangzhou City, China, and into northern and central Vietnam. It is a low-elevation mountain dweller, commonly found in montane fast or slow-flowing streams, tiniest trickles covered with bare rocks, pools, and ditches, surrounded by moist subtropical evergreen broadleaved forests (Wang et al. 2017).

Figure 26.11. *Opisthotropis andersonii*, **Hong Kong. Photography by Mike Pingleton.**

Natural History. Inhabits small, fast water mountain streams in secondary forest; probably absent from larger streams. During the day it is concealed under rocks or in stream bed gravel, active at night to forage. Speculation on its diet suggests it probably feeds on semi-aquatic earthworms. Reported to do well in captivity on a diet of earthworms. Hatchlings are about 120 mm, most adult specimens 300-400 mm, it may reach a maximum size of 500 mm.

Günther's Mystery Stream Snake

Opisthotropis atra Günther, 1872

Distribution and Habitat**.** Unknown. Type locality: West Africa. This species has never been rediscovered. The genus is not present in Africa. The holotype is in the Natural History Museum in London – otherwise, this species is unknown.

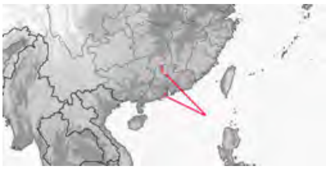


Figure 26.12. The distribution of *Opisthotropis cheni.*

Zhao's Stream Snake

Opisthotropis cheni Zhao, 1999

Distribution and Habitat**.** Hill streams of Guangdong, China. Type locality: Mt. Mang, China. Mangshan Forestry Bureau, Yizhang County, Hunan, China, 480 m elevation fide Zhao (2004).

Cuc's Mountain Stream Snake

Opisthotropis cucae David et al., 2011

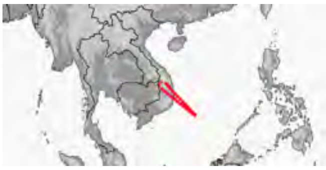


Figure 26.14. The distribution of *Opisthotropis cucae.*

Distribution and Habitat**.** Hill streams of Kon Tum Plateau, Kon Tum Province, Vietnam. Type locality: Chu Mom Ray National Park, Sa Thay District, Kon Tum Province (14° 26.227' N, 107° 43.268' E), 740 m elevation, Vietnam.

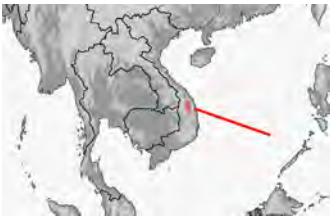


Figure 26.15. The distribution of *Opisthotropis daovantieni.*

Tien's Mountain Stream Snake

Opisthotropis daovantieni Orlov, et al., 1998

Distribution and Habitat**.** Probably restricted to the hill streams of the northern part of Tai Nguyen Plateau in the Annam Mountains, S Vietnam. Type locality: Buoenloy, (14° 20'N, 108° 36'E), 750 m elevation, Ankhe District, Gia Lai Prov., S Vietnam.

Figure 26.16. *Opisthotropis cheni.*
Photography by: A Ho Koon Centre Hong Kong; B-D Jian Wang E. Konrad Mebert.

Durand's Mountain Stream Snake

Opisthotropis durandi Teynié, et al., 2014

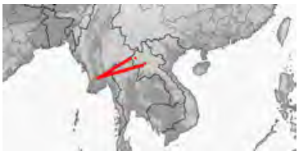


Figure 26.17. The distribution of *Opisthotropis durandi.*

Distribution and Habitat**.** Louangphabang, Laos, may also be present in adjacent Thailand. Type locality: vicinity of Muang Ngoi (20°42'10"N, 102°41'21"E), Ngoi District, Louangphabang Province, Laos, elevation about 370 m.

Figure 26.18. *Opisthotropis durandi*.
Photography by Peter Barkles.

Guangxi Mountain Stream Snake

Opisthotropis guangxiensis Zhao, Jiang and Huang, 1978

Distribution and Habitat. Known from the type locality of Mount Yao (Dayao Shan), Jinxiu, Guangxi Zhuang Automonous Region, China (Zhao and Adler 1993). It has also been recorded from Guangdong (Kadoorie Farm and Botanic Garden, 2004). Zhao (2006) also mentioned Hunan which is not supported with specimens. It is occurs at elevations of 950 to 1,220 m ASL.

Figure 26.19. The distribution of *Opisthotropis guangxiensis.*

Figure 26.20. ***Opisthotropis guangxiensis*** **from Mt. Yunkai, Xinyi City, Guangdong, China. Photography by Jian Wang.**

This species has been recorded living in and near streams in both forests as well as open habitats. It spectulated to feed on semi-aquatic annelids (Zhao 2006). The IUCN considers it near threatened.

Hung-Ta Chang's Mountain Stream Snake

Opisthotropis hungtai Wang, et al., 2020

Figure 26.21. The distribution of *Opisthotropis hungtai.*

Distribution of Habitat. Hill streams of Guangdong, China. Type locality: Heishiding Nature Reserve, Fengkai County, Zhaoqing City, Guangdong Province, 300 m ASL. P.R. China.

Natural History. Currently known from Heishiding Nature Reserve (ca 300 m ASL.) and Dawuling Forestry Station (ca 900 m ASL) in western Guangdong, and Mt. Wuhuang (ca 500 m ASL.) in southeastern Guangxi. The specimen from Mt. Wuhuang was collected in a rocky stream. Besides, specimens from Heishiding Nature Reserve were found in pelitic gutterways along the dirt path, and specimens from Dawuling Forestry Station were collected in a pelitic stream. The collection sites were all surrounded by well-preserved, dense deciduous forest (Wang et al. 2020).

Figure 26.22. *Opisthotropis hungtai* **Mt. Yunkai, Xinyi City, Guangdong, China. Photography by Jian Wang.**

Hai Ha Mountain Stream Snake

Opisthotropis haihaensis Ziegler et al., 2019

Distribution and Habits. Known from the type locality, the forest near Tai Chi Village (ca 950 m ASL), Quang Ninh, northern Vietnam, and Shiwandashan Nature Reserve (ca 500 m ASL), southwestern Guangxi, southern China. The distance between the two localities is approximately 150 kilometers, indicating that the distribution area of this species is the mountain region on the border between China and Vietnam.

Figure 26.23. The distribution of *Opisthotropis haihaensis.*

Figure 26.24. *Opisthotropis haihaensis*
Photography by Jian-Huan Yang.

Chapa Mountain Stream Snake

Opisthotropis jacobi Angel & Bourret, 1933

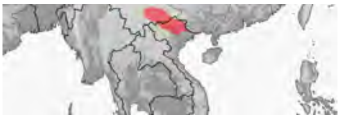


Figure 26.25. The distribution of *Opisthotropis jacobi***.**

Distribution and Habitat**.** Japan (Ryukyu Islands: Kumejima Island). Type locality: Kumejima Island, Okinawa Prefecture, Japan. This species is a highly endangered aquatic or semiaquatic species endemic to Kumejima Island of the Okinawa Group, Ryukyu Archipelago.

Natural History. Field studies suggest the snake is active almost year-round; the snake tends to be diurnal in the warmer and nocturnal in the cooler seasons. And predation on small freshwater crabs, *Candidiopotamon kumejimense*.

Kikuzato's Brook Snake

Opisthotropis kikuzatoi (Okada & Takara, 1958)

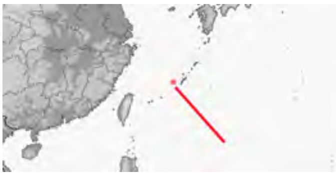


Figure 26.26. The distribution of *Opisthotropis kikuzatoi.*

Distribution and Habitat**.** Hill streams of north Vietnam and Yunnan, China. Type locality: Chapa, Tonkin-Yunnan border (now Sa Pa, Lao Cai Province, northern Vietnam). Recently collected specimens were found at 19:00–22:00 h on rocks along small rocky streams. The surrounding habitat was a secondary evergreen forest of hardwood trees. The air temperature was 19.5–25.1 C and the relative humidity was 75–90% (Ziegler et al. 2018).

Chinese Mountain Stream Snake

Opisthotropis kuatunensis Pope, 1928

Figure 26.27. The distribution of ***Opisthotropis kuatunensis***

Distribution and Habitat**.** The hill streams of Fujian, Zhejiang, Jiangxi, Guangxi, and Hong Kong, China. Type locality: Ch'ungan Hsien, Fukien Province, China.

Figure 26.28. *Opisthotropis kuatunensis.* **Top Hong Kong. Artur Tomaszek; Bottom. Mt.Wutong, Shenzhen, Guangdong, China Jian Wang.**

Natural History. Diet. A female *O. kuatunensis* was observed (Sung and Wag 2011) attempting to swallow an egg of *Paa exilispinosa* (Lesser Spiny Frog) in an artificial pond located in a secondary forest. The pond was connected to a 2 m wide stream. When the egg was ingested halfway, the snake detected our presence, released the egg, and fled. The snake was caught for measurement and a photographic record. Nineteen eggs of *P. exilispinosa* at early tail-bud stage were found in the pond. The clutch of *P. exilispinosa* contains approximately 50–150 eggs, and the entire clutch is typically deposited together in a small pool. The few eggs observed at this site suggest that the snake, or possibly some other predator, had consumed other eggs. Eggs of *P. exilispinosa* are approximately 12–23 mm in diameter, with embryos ranging from 9 to 11 mm, depending upon developmental stage. These are the second largest embryos of any stream-breeding frog in Hong Kong, aside from those of the Giant Spiny Frog (P. spinosa), and their size and oviposition as a group potentially represents a substantial food source for *O. kuatenensis.*

In a second observation at 2040 h on 11 January 2010, at Tai Mo Shan (22.54278°N, 114.28917°E, datum: WGS84; elev. 878 m), New Territories, Hong Kong, a male *O. kuatunensis* (SVL = 32 cm; total length = 38.5 cm) was observed biting the head of a *Leptolalax liui* (Leaf Litter Toad) tadpole (total length ca. 3 cm) in a pool along a natural stream in secondary forest. The tadpole struggled and escaped after being held for 30 seconds, and we were unable to capture it. This sighting confirms that *O. kuatunensis* eats tadpoles in the wild. These two species are commonly sympatric in streams in Hong Kong, and it is likely that *L. liui* tadpoles are regular prey for *O. kuatunensis*. Although the natural diets of stream snakes in southern China are largely unknown, amphibians may be important prey. Lui et al. (2021) sequenced the mitochondrial genome of this snake.

Bicolored Stream Snake

Opisthotropis lateralis Boulenger, 1903

Figure 26.29. The distribution of *Opisthotropis lateralis.*

Distribution and Habitat**.** Streams and stream side habitats in Hoa Binh, North Vietnam and Guangxi, Guizhou, and Hong Kong, China. Type locality: Manson Mountains, Tonkin.

Natural History. A specimen was found in a stream next to the ranger station on Ba Mun Island (16 June) and contained five yellowish eggs with maximum lengths from 19.1 to 21.2 mm.

Figure 26.30. *Opisthotropis lateralis.*
Photography by Kevin Messenger.

Sichuan Mountain Stream Snake

Opisthotropis latouchii (Boulenger, 1899)

Figure 26.31. The distribution of *Opisthotropis latouchii.*

Distribution and Habitat**.** Inhabits the smallest forested streams in southern China - Guangdong, Fujian, Jiangxi, Hunan, Guangxi, Guizhou, Sichuan. Type locality: Kuatun, Fukien Province, China.

Natural History. Diet Pope (1935) describes this species a burrower, that feeds on earthworms. Eggs reported laid under cascading water, partially submerged. This species lives in cold water streams and spends much of its time under submerged rocks.

Figure 26.32. *Opisthotropis latouchii.*
Phototgraphy by Kevin Messenger

Lau's Mountain Stream Snake

Opisthotropis laui Yang, Sung & Chan, 2013

Distribution and Habitat. Known from the type locality at Beifengshan Forest Park in Mt. Gudou, Jiangmen City, Guangdong Province, China. Mt. Gudou is an isolated mountain range situated along the coastline at the western side of the Pearl River Estuary and has been protected as a nature reserve since 2001. The summit, known as Shizitou, is 982 m ASL. Original vegetation of the mountain range has been largely destroyed. Currently it supports secondary forest, as well as shrubland and grassland; the stream valleys generally support more mature natural forest. The Holotype was found swimming in a small stream at night about 2145h, which is shallow, rocky, and about m wide, with young but closed-canopy natural forest. The stream drains pass Taishan City, Guangdong Province, before emptying into the Pearl River Delta.

Figure 26.33. The distribution of *Opisthotropis laui.*

Yellow-spotted Mountain Stream Snake

Opisthotropis maculosa Stuart & Chuaynkern, 2007

Distribution and Habitat**.** Thailand (Nong Khai Province). Type locality: Thailand, Nong Khai Province, Boong Klar District, Phu Wua Wildlife Sanctuary, at marker 027 on footpath to Lad Phleuy Waterfall, 190 m ASL.

Natural History. Known from the Phu Wua Wildlife Sanctuary, Nong Khai Province,

Figure 26.34. *Opisthotropis laui* **from Mt. Gudou, Taishan City, Guangdong, China. Photography by Jian-Huan Yang**

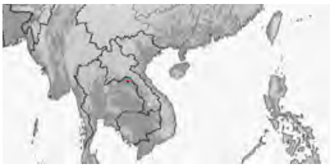


Figure 26.35. The distribution of *Opisthotropis maculosa.*

northeastern Thailand. The Holotype was found swimming at night during a heavy rain. The stream passed through a disturbed bamboo mixed with evergreen forest (Stuart and Chuaynkern 2007).

Figure 26.36. *Opisthotropis maculosa.***and its habitat. Photography by Bryan Stuart.**

Maxwell's Mountain Stream Snake

Opisthotropis maxwelli Boulenger, 1914

Distribution and Habitat**.** Southeast of Guangdong Province, the southwest of Fujian Province and south of Jiangxi Province. It inhabits montane slow-flowing streams with sand and gravel bottom at elevations between 425–1000 m ASL (Wang et al. 2017).

Figure 26.37. The distribution of *Opisthotropis maxwelli.*

Natural History. This species occurs in high-altitude slow moving streams with sand and gravel substrates and often found under stones (Zhao et al. 1998). This is an oviparous species. It inhabits montane slow-flowing streams with sand and gravel

Sumatran Stream Snake

Opisthotropis rugosa (Lidth De Jeude, 1890)

Figure 26.38. The distribution of *Opisthotropis rugosa.*

Distribution and Habitat**.** Sumatra, Indonesia. Type locality: Kajutanam, western Sumatra, Indonesia. Inhabits streams in primary lowland forests. The type locality was previously forested and at an altitude of about 300 m ASL. The second locality is Toru River in Aek Nangali, Batang, within a forested area at about 600 m ASL.

Figure 26.39. *Opisthotropis maxwelli* **from Mt. Muotianshi, Puning City, Guangdong, China. Photography by Jian Wang.**

Shenzhen Stream Snake

Opisthotropis shenzhenensis Wang et al., 2017

Figure 26.40. The distribution of *Opisthotropis shenzhenensis.*

Distribution and Habitat**.** From the low mountain ranges in the eastern Shenzhen and southern Dongguan, Guangdong Province, China, including Mt. Wutong, Sanzhoutian and Mt. Tiantou, and Mt. Yinping. All specimens found at night in slow-flowing streams covered with bare rocks at elevations between 155 and 327 m ASL Type locality: Shenzhen City, Guangdong Province, China.

Smith's Mountain Stream Snake

Opisthotropis spenceri Smith, 1918

Distribution and Habitat**.** Thailand. Type locality: Ngao, Lampang Province, northern Thailand It is also known from Nan Province. It has been collected from streams traversing dry evergreen forest (Chuaynern et al. 2014.)

Natural History. Diet composed of earthworms. Females know to lay clutches of three eggs. In the 100 years following its description this snake was known from only four specimens and little was known about its ecology. In 2015, a location was found where the snakes were abundant, and their feeding behavior could be observed. The snakes were seen to hunt freshly molted crabs (soft shells). They would grab and constrict the crab until its shell burst, then reach inside to swallow the soft inner parts. Then it made a loop in its body that it pulled

Figure 26.41. The distribution of *Opisthotropis spenceri.*

the rest of the crab through until it broke up the hardened shells, and swallowed those parts as well. This was the first time that dismemberment as a feeding strategy had ever been observed among a freshwater snake species.

Figure 26.42. *Opisthotropis spenceri.* **Photography by Montri Sumontha.**

Tam Do Stream Snake

Opisthotropis tamdaoensis Ziegler, David & Vu, 2008

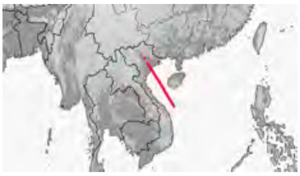


Figure 26.43. The distribution of *Opisthotropis tamdaoensis*

Distribution and Habitat**.** Tam Dao, Vinh Phuc Provinces, north Viet Nam. Type locality: Bac (Silver) stream, Tam Dao, Vinh Phuc Province, northern Vietnam, ca. 750 m elevation.

Figure 26.44. *Opisthotropis tamdaoensis*. **Photography by Tomas Ziegler.**

Borneo Stream Snake

Opisthotropis typicus (Mocquard, 1890)

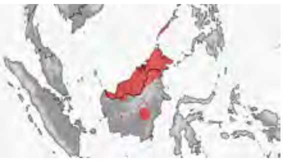


Figure 26.45. The distribution of *Opisthotropis typicus.*

Distribution and Habitat**.** Found in and near streams in primary rainforest. It has been found from sea level to 900m ASL in the Malaysian states of Sabah and Sarawak, and the sultanate of Brunei on the island of Borneo. Type locality: Mt. Kinablau, Sabah, Northern Borneo.

Figure. 26.46. *Opisthotropis typicus.* **Photography by Amaël Borzée.**

Quy's Mountain Stream Snake

Opisthotropis voquyi Ziegler et al., 2018

Figure 26.47. The distribution of *Opisthotropis voquyi*

Distribution and Habitat**.** Small rocky streams in secondary evergreen forest at the Type locality: Type locality: Tay Yen Tu Nature Reserve, Bac Giang Province, 437 m ASL

Natural History. Nocturnal, found in and nest to streams in secondary evergreen forest of medium and small hardwoods mixed with bamboo, shrubs, and vines. The air temperature was 29.2–36.5oC and the relative humidity was 55–73%. Co-occurring species: *Cyclophiops multicinctus, Opisthotropis lateralis, Sinonatrix percarinata, Gekko palmatus, Sphenomorphus cryptotis*, and *Shinisaurus crocodilurus vietnamensis*.

Figure 26.48. *Opisthotropis voquyi*
Photography by Thomas Ziegler.

Zhao's Mountain Stream Snake

Opisthotropis zhaoermii Ren et al., 2017

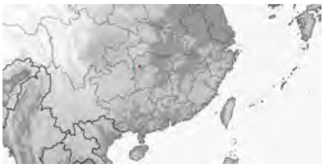


Figure 26.49. The distribution of *Opisthotropis zhaoermii*

Distribution and Habitat**.** Known only from the type locality in western China. Type locality: Zuolong Gorges, Guzhang, Tujia-Miao of western Hunan, China

Natural History. Known only from the type locality where it inhabits small, fast-flowing mountain streams in forested areas, with water temperature and the pH between 19.9–21.2 °C and 7.85–7.93, respectively. Individuals were seen swimming at the edge of the backwater of travertine waterfalls from 2100h to 0100h at night. The holotype was collected during a heavy rainstorm that caused the water to become extreme turbid. When handled, individuals struggled violently and released a musky, pungent, and enduring defensive odor. The scales of the snakes become dehydrated and crimped quickly after leaving the water for about 10 min, but recovered rapidly when returned to water. Similar to other members of the genus in China, this snake may prey on earthworms, tadpoles, freshwater isopods, crabs, and small fish (Pope, 1935; Ren et al. 2017).

Figure 26.50. *Opisthotropis zhaoermii*
Photography by Cen Peng

Annulated Keelback

Trimerodytes aequifasciatus (Barbour, 1908)

Figure 26.51. The distribution of *Trimerodytes aequifasciatus*

Distribution and Habitat**.** Streams in evergreen forests to at least 700 m in China, North Vietnam, and Laos. Type locality: Mt. Wuzhi, Hainan Island, People's Republic of China.

Inhabits streams and waterways in or near forests, including ditches bordering agricultural land (Bain and Truong 2004, Orlov et al. 2000, Stuart 1999). It is oviparous and is active both at day and at night.

Natural History. The diet includes small fish. Pope (1935) considered this species a inhabitant of mountain streams, always finding them in very close proximity to streams and noted they readily drop into the water when disturbed.

Figure 26.52. *Trimerodytes aequifasciatus.* **Photography by (A-B) Artur Tomaszek, (C) Tom Chun Wa Lee**

Red-bellied Annulate Keelback

Trimerodytes annularis (Hallowell, 1856)

Distribution and Habitat**.** Taiwan, Fujian, Jiangxi, Chekiang, Anhwei, Kiangsu provinces China. Type locality: Ningpo, China.

Natural History. Nocturnal, uses rice paddies, swamps, and ponds. Diet includes tadpoles, frogs, and fish. Females give birth to 1-14 neonates.

In 1914, Trimerodytes annularis was reported as a freshwater aquaculture pest in Taiwan (Oshima, 1914). It was widely distributed throughout the low-elevation rice paddies, ditches, and freshwater wetlands of Taiwan before the 1970s' economic and industrial highly development era (Maki, 1931; Horikawa, 1941; Wang and Wang, 1956; Kuntz, 1963). From an ecological aspect, *T. annularis* is a piscivorous rare occasion on frog and high habitat fidelity species with a small home range, reproduction associated with the hydrological dynamic of wetlands, and population size can reach 1,000 snakes in a ca.4-hectare suitable wetland-agriculture mosaic ecosystem, and good population conditions represented on equal sex ratio or skewed female and low body injury or scar ratio

Figure 26.53. The distribution of *Trimerodytes annularis*

(Mao, 2003). Neonates take three years at minimum to reach maturity size, ca. SVL 45 cm in females, lifespan 10-15 years. In 2009, a four-year general survey and habitat assessment focused on the vulnerable Taiwanese watersnake population was conducted, and only two districts retained *T. annularis* populations in north Taiwan (Lai and Mao, 2012). So far, present known populations and habitats of this species are all on private land. One has suffered from a semiconductor science park expansion, habitat pollution, and loss. Another struggle with the multiple factors' twisting of extinction vortex: habitat destruction by landscape hazard prevention engineering, the threat of invasive species, small population paradigm, the unequal sex ratio of male bias, predation, nematode-infected and transmission, high body injury rate from agriculture machine, damaged from pesticide and herbicide, water source shortage causes freshwater ecosystem collapse, extreme climate events, etc. The present status of *T. annularis* in Taiwan is critically endangered.

Figure 26.54. *Trimerodytes annularis.* **Photography by Oscar Yin.**

Hainan Mountain Keelback

Trimerodytes balteatus (Cope, 1895)

Distribution and Habitat. Known from torrents and mountain streams at low to moderate elevations from southern China including Hainan, Guangxi, Guangdong, and Hong Kong), and Vietnam (Hai Phong (Cat Ba Island), and Bac Giang (Tay Yen Tu Nature Reserve).

Figure 26.55. The distribution of *Trimerodytes balteatus*

Figure 26.56. *Trimerodytes balteatus* **Photography by Carol Kwok.**

Natural History. A diurnal species often hides under rocks in the water. Forages in streams or drainage ditches near village; adults were encountered competing for a single loach, where each snake bit on one end of the fish. A strong musk is released when captured. Tail autotomy is also used to escape predators (Pope 1935). This snake was long considered a member of the genus *Opisthotropis*.

Olive Annulate Keelback

Trimerodytes percarinatus (Boulenger, 1899)

Figure 26.57. The distribution of *Trimerodytes percarinatus*

Distribution and Habitat**.** Streams in secondary forests in Vietnam, India, China, Taiwan, Myanmar, Laos, and Thailand. Type locality: Kuatun (now Guadun), Chongan, Fujian Province, China.

Natural History. Nocturnal and arboreal on vegetation hanging above small puddles or pools in streams, under rocks in streams, in secondary forest, in wet hill evergreen forests. Preyed upon by the krait *Bungarus fasciatus*.

Figure 26.58. *Trimerodytes percarinatus*.
Photography by Artur Tomaszek

Jingdong Water Snake

Trimerodytes yapingi Guo, Zhu, and Liu, 2019

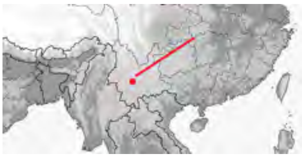


Figure 26.59. The distribution of *Trimerodytes yapingi*

Distribution and Habitat**.** Yunnan, China. Type locality: Jingdong Yunnan Province, China, at an elevation of 1500 m ASL.

Yunnan Annulate Keelback

Trimerodytes yunnanensis Rao and Yang, 1998

Figure 26.60. The distribution of *Trimerodytes yunnanensis*

Distribution and Habitat**.** The distribution of Trimerodytes yunnanensis is disjunct; it has been reported from southern China, Thailand (Chiang Rai Province), Vietnam (Son La Province), and northern Myanmar (Kachin state) and inhabits streams and ponds in montane forests ranging from 400 to 2000 m ASL.

Natural History. Captives ate fish and tadpoles and sometimes held the fish above the water before swallowing them.

Figure 26.61. *Trimerodytes yunnanensis*
Photography by Thai National Parks

Angel's Mountain Keelback

Trimerodytes (*=Paratapinophis*) *praemaxillaris* Angel, 1929

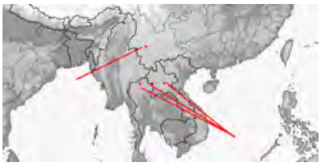


Figure 26.62. The distribution of *Trimerodytes* **(formerly** *Paratapinophis) praemaxillaris*

Distribution and Habitat**.** Rocky streams in northern Laos, Thailand, and China (Yunnan). Type locality: Chieng-Kuang, upper Laos. Natural History. Nocturnal, in fast-moving, rocky streams. On land, this species appears sluggish, whereas it appears much more agile in the water, suggesting that this species is strictly aquatic. It is also found in a flowing rocky stream (c. 2 m broad), running through the forest and fringed by bamboo scrub. Both Nan River females contained digested remains of fish (scales and a mandible) and numerous roundworms (Nematoda), while the three males' stomachs contained only roundworms. The reproductive mode of this snake is unknown, however, *T. praemaxillaris* is known to have an egg tooth, suggesting it is oviparous.

Figure 26.63. *Trimerodytes* (*Paratapinophis) praemaxillaris.*
Photography by Michael Cota

Ren et al. (2019) suggest this snake may belong to the genus *Trimerodytes.* However, they did not assign it to the genus because Murphy et al. (2008) described it as having two pairs of posterior chin shields in an unusual configuration (the second pair of chin shields are separated by another pair of plate-like scales). Therefore, molecular data can resolve the relationships of these snakes.

On the next page. A **Smooth-scaled Blackbelly Snake** *Hydraethiops melanogaster* from Sembe, Congo Photography by Vaclav Gvozdik.

27. African Water Snakes

27. African Water Snakes

Five genera of natricids occur in sub-Sahara Africa (*Afronatrix*, *Helophis, Hydraethiops*, *Limnophis*, *Natriciteres*) and form a clade with the sister being the endemic Seychelle Islands *Lycognathophis seychellensis* (Deepak et al. 2021). The *Lycognathophis seychellensis* lineage likely reached the Seychelles via over water dispersal from Africa, approximately 43–25 Ma. Deepak et al. (2021) suggested that the mainland sub-Saharan African natricids, are relatively poor in species, and are ecologically conservative despite 30 million years of evolution, with all species being predominantly semiaquatic or aquatic (Gibbons and Dorcas, 2004; Vitt and Caldwell, 2009). However, *Lycognathophis seychellensis* appears to be the only sub-Saharan natricid radiation that is predominantly terrestrial. It is encountered on the ground but has also been observed in vegetation at heights of at least five meters as well as on the margins of pools and streams. All mainland sub-Saharan African natricids are oviparous. *Lycognathophis seychellensis* is probably also oviparous but that is not yet supported by direct observation.

Luiselli and Akani, (2002) showed that females of the water snakes *Natriciteres fuliginoides, N. variegata, Afronatrix anoscopus* tended to show body temperatures inversely related to their size (snout–vent length), and that gravid specimens tended to maintain higher body temperatures than non-gravid specimens. However, the high and constant body temperature exhibited at night strongly indicate that these species can maintain high and stable body temperatures with little no thermoregulatory behavior.

As a clade these snakes are understudied and in need of a systematic revision. As might be expected most are poorly known in regard to their natural history.

Brown Water Snake

Afronatrix anoscopus (Cope, 1861)

Figure 27.1. The distribution of *Afronatrix anoscopus.*

Distribution and Habitat**.** Water bodies in rainforests of West Africa from Liberia, Sierra Leone, southern Senegal, Ivory Coast, SW Burkina Faso, Guinea (Conakry), Mali, Nigeria, Cameroon, Ghana, Togo, and Benin. Type locality: Originally reported as Cuba (in error).

Natural History. Field research on these semi-aquatic snakes in southern Nigeria, have provided detailed data on their diets (Akani and Luiselli, 2001; Luiselli et al., 1998, 2003), reproductive biology (Luiselli and Akani, 2002a), thermal ecology (Luiselli and Akani, 2002a), and population biology (Akani and Luiselli, 2001).

Afronatrix anoscopus is among the most abundant snakes in the aquatic habitats of rainforest zones in West Africa (Chippaux, 1999), including southern Nigeria (Butler and Reid, 1990). Nonetheless, until recently, little data were available on their ecology. (e.g., see Butler and Reid, 1986, 1990). The diet is composed of tadpoles and fish, but adult amphibians are also eaten. The tail is prehensile and anchors the snake to submerged debris while it hunts. A total of 332 specimens (59 subadults, 131 males and 142 females) were collected in southern Nigeria to study their diet. The adult male to female sex-ratio (0.92) was not significantly different from equivalence, with female body length being greater than that of males. A total of 60.2 % of the subadults, 39% of the males, and 43.2% of the females had identifiable food items in their stomachs. The diet of all categories (subadults, males and females) consisted of amphibians and fish, with a predominance of anuran tadpoles and the frog *Silurana tropicalis*.

Subadults took significantly more tadpoles than adult frogs.

Figure 27.2. ***Afronatrix anoscopus*** **from Bamenda, Cameroon. Photography by Vaclav Gvozdik**

Marsh Snakes, *Natriciteres*

The Marsh Snakes are found in Sub-Saharan Africa. They are diurnal, oviparous, and they show tail autonomy, but seem unable to re-grow their tail once it is damaged. Their diet is composed mostly of fish and anurans.

Southwestern Forest Marsh Snake

Natriciteres bipostocularis **Broadley, 1962**

Figure 27.3. The distribution of *Natriciteres bipostocularis*

Distribution and Habitat. Zambia, Democratic Republic of the Congo (Zaire: Katanga), central Angola; elevation 1320-1585 m. This is a montane species. Branch (2018) pointed out that there is a large disjunction between the main range of *N. bipostocularis* in Zambia and DRC and the isolated records in western Angola, although the eastern regions of the country remain poorly surveyed.

Collared Marsh Snake

Natriciteres fuliginoides (Günther, 1858)

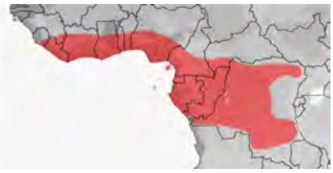


Figure 27.4. The distribution of *Natriciteres fuliginoides*

Distribution and Habitat**.** A semi-aquatic snake that will wander away from water. Guinea, Ghana, Togo, Nigeria, Cameroon, Central African Republic, Democratic Republic of the Congo (Zaire; except in the east), Congo (Brazzaville), Gabon, Sierra Leone, Liberia. Type locality: West Africa.

Natural History. Common in swamp forest and rivers. Haagner (1994) reported it from mangrove forest. They are active in leaf litter during the day or found under logs or debris in marshy areas and riverbeds. One specimen contained the remains of the ranid frog *Dimorphognathus africanus*, while in captivity another ate another the small ranid *Phrynobatrachus auratus*.

Figure 27.5. ***Natriciteres fuliginoides*** **from Motima River, DRC. Photography Vaclav Gvozdik.**

Olive Marsh Snake

Natriciteres olivacea (Peters, 1854)

Distribution and Habitat. Flooded forests and savannas from Sudan south to Mozambique westward to Guinea and Angola. Jackson et al. (2007) found this specxies closely assocaited with flooded forest.

Figure 27.6. The distribution of *Natriciteres olivacea.*

Natural History. A diurnal, savanna and forest species that does not live far from water. It swims well and feeds on frogs and tadpoles, small fish, and some invertebrates while in the water.

Figure 27.7. *Natriciteres olivacea* **(A) an adult, (B) hatchling (C) a melanistic adult (D) from Kanzi, DRC. Photography by (A) Twan Leenders (B) Paul Freed (C-D) Vaclav Gvozdik.**

Pemba Island Marsh Snake

Natriciteres pembana (Loveridge, 1935)

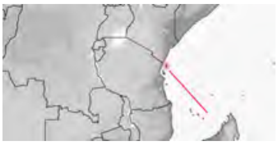


Figure 27.8a. The distribution of *Natriciteres pembana*

Distribution and Habitat. Marshes and swamps (including coastal marshes that are brackish water) of Pemba Island, Tanzania; colonizes agriculture landscapes- wet rice paddies. Type locality: Chake Chake, Pemba Island. Endemic to Pemba Island.

Figure 27.8b. *Natriciteres pembana*
Photography by Frank Glaw.

Forest Marsh Snake

Natriciteres sylvatica Broadley, 1966

Distribution and Habitat. Coastal forest edges from southeast Tanzania south to Kwa Zulu and inland to eastern Zimbabwe border and central Mozambique. coastal forests between elevations of 600-2000 m.

Natural History. The diet includes small fish, frogs, and fish-eating spiders. Females lay five to six eggs in the summer.

Figure 27.10. *Natriciteres sylvatica.*
Photography by Johan Marais

Variable Marsh Snake

Natriciteres variegata (W. Peters, 1861)

Figure 27.11. The distribution of *Natriciteres variegata*

Distribution and Habitat. Southern Democratic Republic of the Congo (Zaire), Gabon, Central African Republic, Equatorial Guinea, Cameroon, Nigeria, Benin, Togo, Ghana, Ivory Coast, Liberia, Sierra Leone, Guinea (Conakry), Burkina Faso. Type locality: Ghana.

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Figure 27.12. *Natriciteres variegata.* **Photography by Vaclav Gvozdik.**

Schouteden's Mud Snake

Helophis schoutedeni (De Witte, 1942)

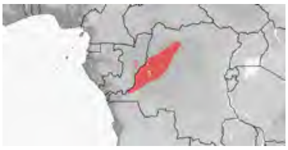

Figure 27.13. The distribution of *Helophis schoutedeni*

Distribution and Habitat. Swamp forests in west and central Democratic Republic of the Congo (Zaire), southeast Brazzaville, Congo. Type locality: "Kwamouth (district du Moyen-Congo) [et ...] Tondu, sur Ie Lac Tumba (district de l'Equateur)" (DRC)

This is a poorly known snake Nagy et al. (2014) noted the majority of distribution records come from the Eastern Congolian swamp forests upriver the Congo River and its tributaries, it raises the question about the origin of the specimens collected in Léopoldville/Kinshasa. The strong current of the Congo River often carries floating vegetation islands, which occasionally introduce fauna and flora from the upriver into the Lower Congo region. This phenomenon might also explain the findings of the Schouteden's Sun Snake outside the swamp forests.

Nagy et al. considered, *Helophis schoutedeni* a semi-aquatic snake because of its dorsally-oriented nostrils, narrow triangular internasals, small eyes with round pupil and stout body.

Observations of captive specimens supported this with a specimen that preferred to stay in water. *Helophis* shows an extreme similarity to the genus *Hydraethiops,* as de Witte (1922) indicated in the original description.

Figure 27.14. *Helophis schoutedeni.*
Photography by Vaclav Gvozdik.

Smooth-scaled Blackbelly Snake

Hydraethiops laevis Boulenger, 1904

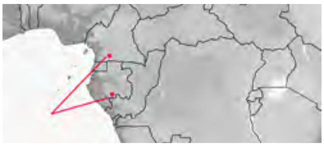

Figure 27.15. The distribution of *Hydraethiops laevis.*

Distribution and Habitat. Small streams in primary rainforest in Cameroon and Gabon. Type locality: Efulen, southern Cameroon. This snake is known from three specimens. The holotype was 510 mm in total length. Deepak et al. (2021) found this species to be the sister of *Heliophis.*

Rough-scaled Blackbelly Snake

Hydraethiops melanogaster Günther, 1872

Distribution and Habitat. Rainforest streams and ponds. Gabon, Democratic Republic of the Congo, Brazzaville, Congo, Central African Republic, and Cameroon. Type locality: Gabon, Africa.

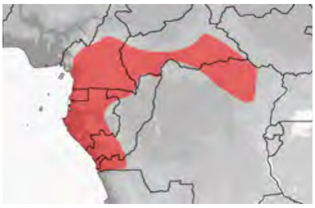

Figure 27.16. The distribution of *Hydraethiops melanogaster*

Natural History. Diet includes fish and tadpoles. A female with 13 eggs in December (Schmidt 1923). Gabon,Africa.

Natural History. A semi-aquatic species found in streams within tropical moist forest, and in gallery forest in savannas. It feeds on amphibians and fish including Mormyridae (elephantfish) (Chippaux 2006, Mamonekene et al. 2006). Diet includes fish and tadpoles. A female with 13 eggs was found in December (Schmidt 1923).

Figure 27.17. *Hydraethiops melanogaster.* **Photographs from Twan Leenders (top), Vaclav Gvozdik (bottom two).**

African Swamp Snakes, The *Limnophis* Clade

The genus ranges from Zambia, west to the Democratic Republic of the Congo (Katanga), E Angola, Botswana, Namibia. Inhabit the freshwater ecoregions: Cuvette Centrale, Kasai, Lower Congo Rapids, Ogooue - Nyanga - Kouilou – Niari, Southern Gulf of Guinea Drainages – Bioko, Northern Gulf of Guinea Drainages. The head is slightly depressed, snout rounded, eyes moderate in size, pupil round; Smooth scales in 19 rows; subcaudals divided. Oviparous

Bangweulu Water Snake

Limnophis bangweolicus (Mertens, 1936)

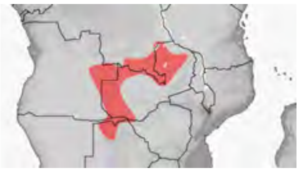

Figure 27.18. The distribution of *Limnophis bangweolicus.*

Distribution and Habitat**.** Moist savannas and floodplains from Zambia, west to the Democratic Republic of the Congo (Zaire: Katanga), east Angola, Botswana, Namibia. Type locality: Nsombo, Northern Rhodesia.

Figure 27.19. *Limnophis bangweolicus.* **Photography by Werner Conradie.**

Bicolored Swamp Snake

Limnophis bicolor Günther, 1865

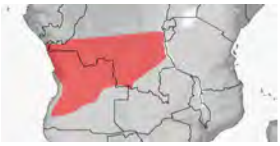

Figure 27.20. The distribution of *Limnophis bicolor.*

Distribution and Habitat. southwest Angola, southern Zambia (Okavango and Zambezi drainage basins), eastern andsouthern Democratic Republic of the Congo (Zaire), elevation 1000 - 1800 m.

Figure 27.21. *Limnophis bicolor.* Photography by Alex Rebelo

Angolan Water Snake

Limnophis branchi Conradie, Deepak, Keates and Gower, 2020

Figure 27.22. The distribution of *Limnophis branchi*

Distribution and Habitat. northeast Angola (Lagoa Carumbo region). Type locality: Luele River area north of Lagoa Carumbo, Lunda Norte Province, Angola.

Figure 27.23. *Limnophis branchi.* Photography by Bill Branch.

28.

The Palearctic Watersnakes

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Konrad Mebert, Daniel Jablonski

Natrix is a Palearctic genus from northern Africa and temperate Eurasia east to Western China and Pakistan with five semi-aquatic snakes (natricines) currently. They attain a total length of usually around 1 meter, with the larger Grass Snakes rarely growing up to 1.5 meters, and exceptionally longer with the record at 2.05 meters of a specimen from Krk Island, Croatia (Schreiber 1912, cit. in Kabisch 1999). The head is well differentiated from the body, and the tail is rather short. They have large eyes with round pupils. Depending on the species, there are 17 to 23 dorsal scales rows, mostly keeled, less along the paraventral rows. Teeth are aglyphic, and sharp. A Duvernoy's gland is present. The diet consists primarily of amphibians and fish. They are oviparous, with females reaching a larger body size than males. Natricines usually swim on the surface but will submerge when disturbed or hunting for fish and amphibians. They occasionally climb into bushes for thermoregulation, and are usually diurnal but switch to nocturnal activity on warm nights. Predator defense is manifold, individually, and locally variable, and can include in all species tight coiling, head hiding under its body, excretion of musk through bilateral anal glands, triangular flattening of the head and also the body, regurgitating undigested food, death feigning, tail vibration or wiggling, hissing. The coloration of juvenile and adult individuals is only slightly different.

Fossil records and current distribution indicate that the genus *Natrix* originated in western Asia (Hecht 1930; Rage and Augé 1993; Ivanov 2001; Guicking et al. 2006). The genus is monophyletic, a complex with five species, including the Viperine Snake *Natrix maura* Linnaeus 1758, the Dice Snake *N. tessellata* Laurenti, 1768 and the Grass Snake group, a complex of three species with the traditional Eastern Grass Snake *N. natrix* Linnaeus 1758, the Ibero-Maghrebian Grass Snake *N. astreptophora*, and the Western Grass Snake *N. helvetica* (Guicking et al. 2006a; Speybroeck et al. 2020). The ancestor of *Natrix* separated in the Miocene and evolved independently into *N. maura* in Northern Africa, and *N. tessellata* in Western Asia. The Grass Snakes (*N. natrix* complex) radiated north into Europe and central Asia, also reaching a few islands by marine transgression (Guicking and Joger 2011).

Natrix tessellata and the Grass Snake group are sister to *N. maura* that occupies a basal position, diverging from the common ancestor about 18–27 MYA. Grass Snakes and *N. tessellata* split about 13–22 MYA. However, newer studies showed more concrete divergence times from a common *Natrix* ancestor to be ca. 21.96 Mya , 18.39 Mya, and 9.58 Mya for *N. maura, N, helvetica*/*natrix*, and *N. tessellata* clades, respectively (Supplementary files in Jablonski et al. 2023).Intraspecific divergence for *N. maura* begun at approximately 5.3 MYA, for the Grass Snakes (*N. natrix* complex) 6.0 MYA, and for *N. tessellata* 6.7 MYA (Guicking et al. 2006a). In the western Mediterranean Basin, the Messinian Salinity Crisis likely led to the split of *Natrix* species (*maura* and *astreptophora*) between the Iberian Peninsula and Northern Africa, whereas latter *Natrix* populations subsequently split into Moroccan and Algerian-Tunisian clades (Guicking et al. 2008; Kindler et al. 2018). Even though these semi-aquatic snakes are good swimmers, the 14 km width of the Strait of Gibraltar (passage from the Atlantic into the Mediterranean Sea) was a significant biogeographic barrier for a population exchange (Guicking et al. 2002).

On the previous page. is a *Natrix maura.* **Photography by Kai Kolodziej.**

Viperine Snake
Natrix maura (Linnaeus, 1758)

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Distribution and Habitat. Type locality: "Algiriae" = Algeria. The Viperine Snake occurs across the African and European countries that form the Western Mediterranean. In Africa, it is present in Morocco, Algeria, Tunisia, and coastal Libya as far east as the springs and irrigation complex around Tawergha (Tauorga), District Misratah (Kramer and Schnurrenberger 1963; Bauer et al. 2017). In Europe, it is present in Spain, Portugal, France, southwestern Switzerland, and northwestern Italy, and has sporadically been observed in Andorra, a small country in the Pyrenean Mountains. On Gibraltar, a British Overseas Territory located at the southern tip of the Iberian Peninsula, the species was found on the isthmus (Cortés 1982), but no new records were reported in the last 40 years. Detailed information on distribution is found in atlases of many of these countries such as Portugal (Santos 2008), Spain (Santos et al. 2002), and France (Santos and Vacher 2010). Overall, the Viperine Snake is predominantly found along bodies of water within open, scrubland and forested habitats. The southern distribution is limited by the aridity of the Sahara Desert (Naulleau and Schätti 1997). However, populations persist in that region along wadis (periodically water-filled valleys) such as Oued Ziz and Oued Drâa (Martínez del Marmol et al. 2019) and other small water bodies (Bons and Geniez 1996; Schleich et al. 1996). The southernmost population is in Assa, Morocco (ca. 28° N) near the Drâa River (de Lepiney and Nemeth 1945-46-47). Cold climate shapes the northern limit and approximately follows the southern sections of the French rivers Seine-et-Marne and Aube into the region of Franche-Compténear, and the Rhone River into Lake Geneva and Canton Valais in Switzerland (Schätti 1999; Santos and Vacher 2010). Italy's distribution in Mediterranean habitats is limited to the northeast by the presence of the closely related Dice Snake *Natrix tessellata*. Both species overlap across ca. 200 km, from the eastern Cuneo Province to the western Parma Province. Although both species partly could compete in sympatry by using similar ecological niches (Schätti 1982), various studies found some niche partitioning, such as smaller, shadier streams preferred by *N. maura* and larger, deeper water bodies in a more open landscape (Mazza et al. 2011; Metzger et al. 2011; Scali 2011); also see the *Natrix tessellata* account herein.

The Viperine Snake inhabits several islands in the western Mediterranean Basin, e.g., Ile du Levant (Toulon-Hyères), Île de Yeu and Île d'Oléron, in the Atlantic close to the mainland in France (Schätti 1999), Mallorca (Spain), Menorca (Spain), Sardinia and some adjacent islets (Italy). Genetic and morphological studies have demonstrated that the distribution in these islands is recent and caused by (historical) human introductions. This is the case of the Balearic Archipelago, where the Romans could have introduced the Viperine Snake (Alcover and Mayol 1981) from the European mainland (Guicking et al. 2006a). In addition, there are a few reports of its presence in marine habitats, e.g., in Italy (Lanza 1983), in southern Spain (Cabo and Olea 1978), and northeastern Spain (Fuentes and Escoriza 2015). Still, it is best known for the thriving populations on the Cies Archipelago, Pontevedra, off the Atlantic coastal city Vigo, northwestern Spain, where they feed exclusively on marine fishes along rocky islets and grow to large body sizes (Galán 2004, 2012).

The habitat of *Natrix maura* is widely influenced by the Mediterranean climate on the Iberian Peninsula, France, and Morocco (Godinho et al. 1999; Santos et al. 1997, 2002; Santos

Figure 28.1: Natural color pattern variation of the Viperine Snake (*Natrix maura*) from: A) High Atlas Mountains, central Morocco; B) northern Morocco; C) southwestern France; D) southern Spain; E) southwestern France; F) western Switzerland; G) Sardinia Island, Italy. Photo credit: A), E), F) Konrad Mebert; B), D) Octavio Jiménez-Robles; C), H) Matthieu Berroneau; G) Laura and Bobby Bok.

2008), where it occupies all natural and artificial water bodies. The Viperine Snake is rare in the driest regions, such as Almeria, southeastern Spain. The species is frequent at elevations between 500–600 m (Pleguezuelos and Villafranca 1997), less common up to 1200 m, with the highest elevations records at 2050 m in the Sierra Nevada Mountains, southern Spain (Pleguezuelos and Feriche 2003), and up to 2600 m elevation at Oukäimeden, Alto Atlas, Morocco (Bons and Geniez 1996). It inhabits all natural water bodies, such as rivers, lakes, streams, wetlands, ponds and lagoons, and river valleys within mountain chains with a cool climate like the Pyrenees. The Viperine Snake also occupies artificial water bodies such as irrigation ponds and channels, fountains, ditches, and pools, showing high flexibility to colonize new water habitats if suitable prey is available. It also occupies brackish water in coastal marshes and rocky seashores where prey is abundant (Cabot and Olea 1978; Del Canto and Busack 2011; Galan 2012). The Viperine Snakes are easily observed swimming and foraging in the water and can be observed basking on land near the water or under rocks. They rarely wander off far from water. Thus, in arid African regions, the Viperine Snake is strictly linked to sites of permanent water bodies, such as oueds and oases (Bons and Geniez 1996; Schleich et al. 1996).

Identification. This medium-sized snake usually does not reach more than 1 m total length, but up to 1.25 m on Cies Archipelago in the Atlantic Sea. Females are the larger sex with males exhibiting a relatively long tail, but on average, about 20% for both sexes. Males have 2-3 more ventral scales and 9-10 more subcaudal scales than females. The head is wider than the neck and body. When threatened by a potential predator, it can be flattened into a viper-like triangular shape, a typical anti-predator posture in natricine snakes. The pupil is round and bordered by a light-colored ring. Usually, there are two preocular and two postocular scales, 6-9 supralabial scales the third and fourth usually contact the eye. Dorsal scales are arranged in 21 rows at mid-body and are heavily keeled except for the rows in contact with the ventral scales.

The most conspicuous characteristic is the dorsal pattern, composed of bilateral alternating dark, round- or rhomboidal blotches along the vertebral line from neck to tail. These dorsal blotches often form a zigzag or slalom-shaped band at some part/s on the body. Lateral spots alternate with the dorsal ones and may form ocelli, a ring-like blotch with a whitish center. Two blotches join on the pileus. Infra- and supralabial scales are light with darker colors in the contact zone between scales. The dorsal background coloration varies from olive, brown and grey tones to reddish. The ventral coloration is grey or yellowish, with black spots in many ventral scales. Albinotic and melanistic individuals have been found in the wild (Schätti 1999).

The visually most intriguing morphological variation is a stripped dorsal pattern. This pattern is composed of two dorsolateral yellow bands formed between the dorsal and lateral blotches (bilineata morph: Schätti 1982). The striped pattern is sometimes overlooked on the zigzag pattern in the same individual. The zigzag pattern is more common (76%, n = 917; Santos et al. 2018) than the bilineata pattern. Often the only morph in many populations is the zig-zag pattern. The bilineata pattern occurs across most of the species' distribution (Schätti 1982). Still, it is linked to open habitats with close populations showing marked differences in the proportion of bilineata individuals (Santos et al. 2018). There is a latitudinal gradient in total body size, with African Viperine Snakes larger than Iberian individuals (Fahd 2001; Saint Girons 1956). However, optimal conditions can result in populations with huge specimens like those on the Cíes Archipelago, northwestern Spain, or the population along Lake Geneva's rocky and fish-rich shore, near Lausanne, Switzerland (Koller and Ursenbacher 1996; K. Mebert unpubl. data). The number of ventral and subcaudal scales is higher in southern populations, with a clinal variation especially marked among African individuals (Schätti 1982, 1999; Fahd 2001).

Phylogeny and phylogeography. Analyses based on cytochrome b sequences by Guicking et al. (2002) showed that the Viperine Snake is structured in three lineages in Tunisia-Sardinia, Morocco, and Iberia-France, with genetic distances between them ranging from 3.9-4.6%. The divergence time was around 3-3.5 Ma, during the Mid or Late Pliocene. The African clades of *N. maura* were older than the European ones, suggesting an African origin of the species. Indeed, the three distinct lineages between Tunisian and Moroccan populations suggest multiple independent migrations between European and African populations as ancient as the Messinian Crisis (Barata et al. 2007; Bauer et al. 2017). A phylogenetic study using mitochondrial markers from the three *Natrix* groups (*maura*, *tessellata*, and *natrix* s.l.) indicated that *N. maura* was basal in the phylogeny and coalescence time among the three species was dated 13-22 Ma ago during the early Miocene or late Oligocene (Guicking et al. 2006b). The genetic structure among European populations is low, with an average genetic distance of 1.3% (Guicking et al. 2008). Haplotype diversity is higher on the Iberian Peninsula than on northernmost populations. The peninsula could act as Pleistocene refugia during glaciations, with rapid recolonization towards its northern range in subsequent interglacial periods. On the Iberian Peninsula, Guicking et al. (2008) also detected higher genetic diversity among river valleys in southern Iberia, compared to northern Iberian populations.

Fossil records of *Natrix* specimens in Iberia were first documented by Sanz and Sanchiz (1980) and Sanchiz (1991). More recently, Blain et al. (2008a) described Viperine Snake fossils at Cueva Victoria (Murcia) dated in the Upper Pleistocene (ca. 1.1 Ma). Blain et al. (2008b, 2010) found fossils at Sima del Elefante and Gran Dolina, Atapuerca (Burgos, Spain) dated 1.2 Ma ago. Other *N. maura* fossils have been recorded in Sète, southern France, and Cueva Gorham, Gibraltar, by Bailón (1991) and Blain et al. (2013), respectively.

Finally, there is morphological evidence for occasional hybridization between *N. astreptophora* and *N. maura* (Gonzalez de la Vega et al. 2021). Furthermore, molecular analysis showed that past hybridization with subsequent genetic introgression happened between *N. maura* and *N. tessellata* (Schöneberg et al. 2023), two species for which no hybrids have been documented to date, neither from the wild nor from captivity (Mebert et al. 2011a).

Population Aspects. The Viperine Snake is one of the most abundant species within its range in Morocco, Spain and southern France (Bons and Geniez 1996; Santos and Vacher 2010; Santos 2014) and can attain dense populations. For example, at the Jalón River, Alicante, eastern Iberian Peninsula, Hailey and Davies (1987a) estimated 4800 adults/ha along a 4 m wide section of the riverbank; The high density was attributed to the lack of predators and the high availability of prey. Similar trends have been noted for the coastal wetlands such as the Ebro Delta and many Mediterranean rivers. However, water contamination, physical habitat degradation, and fish decline have caused the reduction of Viperine Snake populations (Santos and Llorente 2009).

Hailey and Davies (1987d) and Filippakopoulou et al. (2014) have calculated growth trajectory by ectopterygoid annual rings and observed that Viperine Snakes reach an asymptotic plateau as growth ceases after the acquisition of sexual maturity, when snakes start to invest energy into reproduction (Hailey and Davies 1987a). Immature females grow faster than males (3.4 and 2.9 cm/year, respectively, Hailey and Davies 1987d), which explains why they attain larger body size (Filippakopoulou et al. 2014). Also, based on ectopterygoid annual growth lines, the maximum lifespan was estimated to be 22 years (Filippakopoulou et al. 2014), with females living longer than males (Hailey and Davies 1987a).

Activity and Thermal Biology. Emergence from hibernation begins in March (Jaén and

Pérez-Mellado 1989; Santos and Llorente 2001a) or April in colder regions (Galán 1988). However, it might be observed on the surface on sunny winter days in southern Iberia (Santos and Llorente 2001a; Malkmus 1996, 2008). The seasonal activity of the Viperine Snake is accentuated in spring for mating and in autumn for hatching (Galán 1988; Santos and Llorente 2001a, 2001b). During the hot summer, snakes spend copious time in the water (Hailey et al. 1982; Duguy and Saint Girons 1966; Jaén and Pérez-Mellado 1989) or they become more nocturnal (Hailey and Davies 1986b; Pleguezuelos and Feriche 2003; Scali 2011). Experimental studies estimated that the selected temperature of Viperine Snakes ranged from 24.7–29° C (Spellerberg 1977; Hailey and Davies 1986a). At 10° C body temperature, snakes cannot digest prey, whereas digestion was optimal at 35° C (Hailey and Davies 1987c). The body temperature of active snakes covers a wide range between 14–35° C (Jaén and Pérez-Mellado 1988; Santos 2000; Hailey et al. 1982; Hailey and Davies 1987c). Reproductive females attain higher body temperatures than other adults or immature snakes (Santos 2000), and body temperature is higher in summer compared to spring and autumn (Hailey et al. 1982; Hailey and Davies 1986b; Santos 2000). The thermal pattern differs for snakes in and out of the water. Viperine Snakes were active in water at temperatures ranging from 13–34° C (Hailey et al. 1982; Jaén and Pérez-Mellado 1989; Santos 2000). They behaved as thermoconformers with body temperature equaling water temperature. In the Ebro Delta, northeastern Spain, snakes thermoregulated heliothermic, i.e., terrestrially on the surface, in spring, and switched to thigmothermic basking (substrate heating, usually under rocks) during the summer (Santos 2000).

Activity patterns and home range have been estimated using radiotelemetry in the Ebro Delta and by capture-recapture techniques in the Jalón River, Alicante, eastern Spain. Males had larger home ranges in spring (5.8 ha, n=4) compared to summer (0.7 ha, n=7) due to searching for mates (Santos and Llorente 1997). Similarly, snakes covered longer distances in spring compared to summer due to reproductive activity (Santos and Llorente 1997; Duguy and Saint Girons 1966) and the distribution of aquatic prey (Hailey and Davies 1987d). Latter authors detected longer lineal home ranges along the river in females than in males, presumably due to the larger body size of the former sex.

Reproduction. Age and size of sexual maturity varies between the sexes. Females start reproduction at 4–5-year age at 310–350 mm of snout-vent length (SVL), whereas males mature at 2–3-year age and 220–250 mm SVL (references in Santos 2014). Mating starts when snakes emerge from hibernation in the spring (Duguy and Saint Girons 1966; Hailey and Davies 1987b; Santos and Llorente 2001b). A second mating period may occur in autumn (Duguy and Saint Girons 1966). There is one clutch per season in the wild, whereas more than one clutch per year has been observed in captivity (Petch 1991; Schleich et al. 1996). A mating ball has been documented once with eight snakes of which probably only one was a female due to its larger size (Torres-Porras 2008). Females will mate several times (Dumont 1979; Hailey and Davies 1987b) and maintain viable spermatozoa for several years (Quillon and Lamouille 1978).

Spermatogenesis is postnuptial, and males start to produce new spermatozoa after mating which means that testes function were at their maximum in the summer and spermatozoa are stored in the vas deferens until the following spring (Santos and Llorente 2001b). The Viperine Snake is an oviparous species with 70 to 100% of mature females reproducing annually (Feriche and Pleguezuelos 1999; Rugiero et al. 2000; Hailey and Davies 1987b; Duguy and Saint Girons 1966; Santos and Llorente 2001b). Vitellogenesis is prenuptial, as follicles start to grow after hibernation (Duguy and Saint Girons 1966; Feriche and Pleguezuelos 1999; Hailey and Davies 1987b). Females with oviductal eggs were found in June and July. Egg size ranges from 28–37 x 14–19 mm and incubation lasts 40–45 days (Duguy and Saint Girons 1966; Dumont 1979; Feriche and Pleguezuelos 1999; Santos and Llorente 2001b). Thus, neonates appear in mid-August with a total length between 146 and 220 mm (Duguy and Saint Girons 1966). Clutch size ranges from 2–27, with an average of 7.3 and increases with female size (see references in Schätti 1999; Santos 2015). Vitellogenesis is energetically costly for females, which allocate fat bodies stored in the abdomen to grow follicles (Santos and Llorente 2004). However, females can also mobilize other energetic sources during vitellogenesis and gestation, such as feeding and maybe resorption of unfertilized eggs or muscle (Santos et al. 2007).

Foraging and Diet. The Viperine Snake feeds on varied fish and amphibians captured in the water. Prey types, foraging ecology and modes strongly resemble its eastern counterpart, the Dice Snake *Natrix tessellata*, (see chapter herein). Fish species recorded in the diet of *N. maura* vary in body size, swimming speed, position in the water column and schooling aggregation, whereas amphibians varied according to size and water dependency from very terrestrial to almost strictly aquatic species. Fish eaten by the Viperine Snake include the following: Family Anguilidae (*Anguilla anguilla*), Blenniidae (*Salaria fluviatilis*), Centrarchidae (*Lepomis gibbosus*), Ciprinidae (*Barbus bocagei*, *Barbus graellsii*, *Barbus haasi*, *Barbus sclateri*, *Carassius auratus*, *Chondrostoma miegii*, *Chondrostoma polylepis*, *Cyprinus carpio*, *Phoxinus phoxinus*, *Rutilus arcasii*, *Rutilus rutilus*, *Squalius cephalus*), Cobitidae (*Barbatula barbatula*), Gasterosteidae (*Gasterosteus aculeatus*), Gobiidae (*Gobius gobius*), Poecilidae (*Gambusia affinis*, *Gambusia holbrooki*) and Salmonidae (*Oncorhynchus mykiss*, *Salmo trutta*) (references in Santos 2014), although this list is incomplete. Amphibians preyed upon include Caudata: *Salamandra salamandra*, *Pleurodeles waltl*, *Lissotriton boscai*, *Lissotriton helveticus*, *Triturus marmoratus, Chioglossa lusitanica*; anurans: *Alytes muletensis*, *Alytes obstetricans*, *Alytes dickhilleni*, *Bufo spinosus*, *Epidalea calamita*, *Discoglossus galganoi*, *Discoglossus jeanneae*, *Pelobates cultripes*, *Rana iberica*, *Phelophylax perezi*, *Rana temporaria* and *Hyla molleri*, whereas other vertebrates, e.g. small mammals or reptiles, are also preyed on occasionally (references in Schätti 1999; Santos 2014). Ayres (2012) reported snakes scavenging on dead newts (*Lissotriton boscai*) in Galicia, northwestern Spain. Additionally, immature snakes also prey on tadpoles and egg clutches of amphibians, as well as on invertebrate prey such as earthworms, leeches, snails, slugs and insects (references in Schätti 1999; Santos 2014). Predation on reptiles such as the Morish gecko *Tarentola mauritanica* and small mammals has also been reported (Pleguezuelos and Moreno 1989; Vericad and Escarré 1976).

Two main foraging modes were described by Hailey and Davies (1986c): 1) ambush, used by adult snakes which consists of the visual identification of a prey, followed by ambushing at any point in the water column through anchoring the posterior body to the substrate or submerged plant. Upon the prey's approach to within striking distance, the snake launches forward with its anterior body; 2) active foraging, which consists of exploring the water and its substrates using tongue flicking in search for chemical cues, a mode particularly common in shallow waters.

Other studies have described alternative foraging behaviors: Naulleau (1964) described the use of the tongue to lure fish, Martorell (1990) documented snakes ambushing fish from outside the water by anchoring themselves on the bank of a river and partially suspended over the water, waiting for the passage of prey, and Alarcos et al. (2012) documented a snake climbing on cattail leaves to capture *Hyla* frogs. After the seizure of large fish, snakes tend to move their catch to land for swallowing (Meijide and Salas 1989; Pérez de Lanuza 2011), whereas Pleguezuelos and Feriche (2003) observed nocturnal Viperine Snakes maintaining aquatic prey brought on land until the prey dies, before consuming them. Most foraging modes are virtually identical as in the Dice Snake (*Natrix tessellata*), see chapter herein.

The proportion of fish versus amphibians depends on prey availability and local climate. For example, in northern Iberian wetlands, amphibian represents about 50% of prey whereas in southern and Mediterranean-type areas amphibian represents less than 25% of prey (dietary references in Santos 2014). Hence, the Viperine Snake is an opportunistic predator that forages on the most commonly available prey (Hailey and Davies 1986c; Pleguezuelos and Moreno 1989; Rugiero et al. 2000; Santos et al. 2000). However, snakes may also focus on fish species that are easy to catch, such as blenid fish hidden under rocks in the benthic zone of rivers (Santos et al. 2006) or submerged riparian rock formations of Atlantic islands (Galán 2004).

The Viperine Snake shows an ontogenetic shift in their diet. Immature snakes tend to forage on tadpoles, earthworms, and aquatic arthropods (references in Santos 2014), whereas adults can consume prey that represents 80% of the snake's body size (Santos et al. 2006). Hailey and Davies (1986c) found dead snakes that tried to swallow fish that were 60% of the snake's body size. Despite space limitation in the body cavity, gravid females continue foraging (Feriche and Pleguezuelos 1999; Santos and Llorente 1998; Santos et al. 2006).

Predators and Defense. Viperine Snakes have many predators, including birds, such as herons, storks, and raptors, and mammals, such as otters, wild boars, beech martens and other meso-carnivores (references in Schätti 1999; Santos 2014). This high predation pressure varies among localities. For example, coastal wetlands and some Mediterranean rivers with abundant herons and other potential predators, the percentage of Viperine Snakes with broken tails accounted for 18.7% on average. Given that the tail loss indicates predation failure, this high percentage means a high predation pressure on these animals (Santos et al. 2011). Because this is an aquatic snake, parasites found in the digestive tract are abundant and include six trematode, one cestode and six nematode species (Navarro and Lluch 1993; Navarro et al. 1987; García 1987). Parasites have also been found in the trachea (Lluch and Navarro 1986).

Viperine Snakes exhibit several morphological and behavioral defense traits that mimic the sympatric European viper species, a nice example of Batesian mimicry (Aubret and Mangin 2014, Santos et al. 2018). For example, *N. maura* exhibits a viper-like zigzag dorsal pattern and displays head triangulation, a defense coiling body posture, hissing, body inflation, and forward launching of its head/anterior body when threatened. These snakes also excrete feces, a noxious liquid from its cloacal glands, and regurgitate freshly captured prey.

Experimental studies with plasticine models have demonstrated both the aposematic and cryptic value of the viper-like zigzag dorsal pattern. The lack of such a Batesian mimicry function in bilineata Viperine Snakes resulted in a higher attack rate on bilineata plasticine models than zigzag ones (Santos et al. 2018). In addition, field observations showed that both morphs differed in their defensive behaviors: zigzag snakes tended to remain immobile or flee at shorter distances compared to bilineata snakes. As bilineata snakes are more common in open habitats, e.g., marshes, Santos et al. (2018) concluded that snakes with the lined pattern benefit from reduced detection or catchability by a visual predator in grass and reed-dominated habitats.

Conservation. The Viperine Snake is listed in Appendix III of the Bern Convention. It is protected by national legislation in Switzerland and Spain. The global IUCN category is Least Concern (Mateo et al. 2009) and the same in regional IUCN Red Lists (Santos et al. 2002; Vacher and Geniez 2010). Despite this apparent protection, aquatic contamination, freshwater habitat degradation, and prey decline in streams, rivers, and wetlands, threaten some populations (Mateo et al. 2009) with observed declines in many localities (Naulleau and Schätti 1997; Santos et al. 2002). Natural and artificial ponds have small snake populations that may face local extirpation when these habitats dry up or become contaminated. Pesticides from agriculture and chemicals from industrial processing are taken up by aquatic organisms and move along the trophic webs. Consequently, high amounts of organochlorine compounds such as polychlorinated biphenyl (PCB), hexachlorobenzene (HCB), hexachlorocyclohexanes (HCH) and dichlorodiphenyltrichloroethane (DDT) accumulate in Viperine Snakes (Santos et al. 1999). Although DDT was banned from the 1970s on, its presence in snake tissues 20 years later demonstrates that these pesticides persist in the wild for long periods. Pesticide effects in Viperine Snakes have not been demonstrated but their negative effects on other organisms are well known. They are presumed to be one of the leading causes of Viperine Snake decline at the Ebro Delta, northeastern Spain (Santos and Llorente 2009). In addition to habitat degradation, traffic mortality also affects Viperine Snakes (Llorente et al. 2005; Meek 2009). In an extensive study, Llorente et al (2005) found that 18% of snakes found dead on Catalan roads (northeastern Iberia) were Viperine Snakes. Despite being a docile and harmless snake, people frequently kill it in areas with dense populations (Hailey and Davies 1987d; Santos, pers. obs.).

Restored freshwater habitats and newly constructed artificial ponds stocked with alien fish species are rapidly colonized by Viperine Snakes, that opportunistically feed on the rich diet source (Rugiero et al. 2000; Pleguezuelos and Feriche 2003). The consumption of some alien fish with hard and long dorsal spines can end fatally during ingestion, as was concluded from snakes found death with recently consumed *Lepomis gibbosus* and *Micropterus salmoides* in the stomach (Santos and García-Cardenete 2006; Alarcos et al. 2009). Large introduced fish species behind dams and in big rivers can also consume Viperine Snakes as, for example, the Pikeperch, *Sander lucioperca* (Pérez-Bote and Roso 2009).

Ecological competition with *Natrix tessellata* in areas of sympatry has also been responsible for Viperine Snake decline in Italy (Naulleau and Schätti 1997) and Switzerland (Metzger et al. 2009, 2011). In the latter country, *N. tessellata* introduction at Geneva Lake appeared to be a cause of *N. maura* decline (Mazza et al. 2011), whereas the existence of hybrids has long been known only from captive specimens, historic hybridization between these species has been indicated by molecular analysis (Mebert et al. 2011a; Schöneberg et al. 2023; chapter on *N. tessellata* herein).

Grass Snakes

Eastern Grass Snake

Natrix natrix (Linnaeus, 1758)

Daniel Jablonski and Konrad Mebert

Western Grass Snake

Natrix helvetica (Lacépède, 1789)

Konrad Mebert and Daniel Jablonski

Ibero-Maghrebian Grass Snake

Natrix astreptophora (López-Seoane, 1884)

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Grass Snakes are among the most common and best-known snakes in Europe and temperate Asia. They are widespread, polytypic and experienced a complex taxonomic history with four (Thorpe 1979) up to 13 subspecies (Kabisch 1999). Fritz and Schmidtler (2020) present a cleaned and updated revision of Grass Snakes taxonomy. Finally, molecular-based studies by Pokrant et al. (2016) and Kindler et al. (2017) on phylogeny and biogeography revealed genetic barriers between three parapatric groups, partly confirming Thorpe's multivariate analysis of quantitative traits of "then" *Natrix natrix* in the 1970s (Thorpe 1973, 1975a, b, 1979), and leading to the recognition of three Grass Snake species: the Eastern Grass Snake *Natrix natrix* (Linnaeus, 1758), the Western Grass Snake *Natrix helvetica* (Lacépède, 1789), and the Ibero-Maghrebian Grass Snake *Natrix astreptophora* (López-Seoane, 1884); described initially as *Coluber, Natrix* Linnaeus, 1758, *Coluber helveticus* Lacépède, 1789 and *Tropidonotus natrix* var. *astreptophorus* López-Seoane, 1884, respectively.

However, two comprehensive works were composed of detailed information on the Grass Snakes before their recent split into three species: Kabisch (1999) with 67 pages and Blanke et al. (2008) with 312 pages. Therefore, chapters in the following account begin with summary information on the Grass Snakes species as one group, where they exhibit similar traits, but add separated information in subsequent paragraphs where the three species differ from each other, primarily on distribution, morphology, and regional ecology, or present examples of local studies. The order of species treatment roughly follows the chronology of their description and body of information: *natrix, helvetica, astreptophora*.

Distribution and Habitat. The Grass Snake group includes three continents (Hecht 1930; Kabisch 1978, 1999). They occur across most of Europe, north to the limit of the Arctic Circle, and east to central Asia as far as western Mongolia/China. In the south, Grass Snakes occur in northwestern Africa and again in the Levant (eastern Mediterranean) from Lebanon, Israel (historically), and northeast across Turkey to the southern shores of the Caspian Sea.

Grass Snakes inhabit a great variety of wetlands, from small streams to large rivers, swamps, marshes, and ponds to lakes, where they find their main prey, anurans. But it is also found along coastal habitats and can regionally venture away from water to feed on toads in the humid countryside. Grass Snakes occupy cooler, often shadier, aquatic habitats than the largely sympatric Dice Snake *N. tessellata*, which prefers more open and rockier areas and is primarily a fish predator. The distribution of the single Grass Snake species is as follows:

The Eastern Grass Snake *N. natrix* (type locality: Fada mill pond, Berga-Tuna Estate, Nyköping, Sweden) ranges from northern Europe between Norway, and Finland, with the most northern record from near Gällivare in northern Sweden (Holm 1934 cit. in Kabisch 1999), south to Estonia, Latvia, Lithuania, Poland, Denmark, central (longitude) and eastern Germany, northeastern Switzerland, central eastern Austria, northeastern Italy, Belarus, Ukraine, Czech Republic, Slovakia, Hungary, Romania, Moldova, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Kosovo, Macedonia, Greece, Albania, Türkiye (Turkey), Russia, Georgia, Armenia, Azerbaijan, Syria, northeastern Iraq, northwestern Iran, southern Kazakhstan, eastern Turkmenistan, northern Uzbekistan, northern Kyrgyzstan, northeast to Aral and Baikal Lakes, northern Mongolia and northwestern China. In the Republic of Georgia, the Eastern Grass Snake is expected in the humid west, where they are observed in ratios of a couple of dozen *N. natrix* to one Dice Snake *N. tessellata*, latter becoming more abundant in drier landscapes (Frotzler et al. 2011). This species also inhabits some eastern Mediterranean islands and archipelagos, including Cyclades and Cyprus but not Crete. In central Europe, there is a contact zone with some hybridization between *N. natrix* and *N. helvetica* that runs approximatively along and east of the Rhine River in Germany and northeastern Switzerland but deviates farther east and passes through the eastern Alps shared by southeastern Germany, western Austria, and northeastern Italy (Sindaco et al. 2013; Kindler et al. 2017; Schultze et al. 2020; Asztalos et al. 2021a; di Nicola et al. 2021; Milko et al. 2021). Cline analyses with genetic markers and color pattern characters revealed concordant steep clines across those hybrid zones (Fritz et al. 2023). The presence of the species in Lebanon and Israel might be still possible, but remains currently unconfirmed and probably very rare due to anthropogenic habitat changes during 20th Century (see Martens 1996; Grillitsch and Werner 2009). The Eastern Grass Snake is known for elevation as high as 2000 m in the Lesser Caucasus Mountains (Tuniyev et al. 2019) with a new elevational record of 2350 m on the Meskheti Range (authors unpubl. data).

The range of the Western Grass Snake *N. helvetica* (type locality: Jorat, western Switzerland) continues adjacent west to that of the Eastern Grass Snake and stretches from extreme western Germany across France, Netherlands, Belgium, Luxembourg, United Kingdom, and reaching Scotland in the north (Cathrine 2014). In the south it ranges across most of Switzerland, Liechtenstein, western Austria, Italy, and the Mediterranean islands of Corsica (France), Sardinia, and Sicily (both Italy). The highest elevation for the Western Grass Snake is 2300 m in the Italian Alps (Camerano 1891) and 2160 m in Ticino, southern Switzerland (authors, unpubl. data). Niche modelling of *N. h. cetti* from Sardinia Island found its habitat to be positively correlated with higher elevation, precipitation, and accordingly cooler temperatures (Di Nicola et al. 2023). In the eastern Alps (Austria and Germany), the Western Grass Snake inhabits the mountainous areas. In contrast, the Eastern Grass Snake occupies the lowlands, with some hybridization between them where these two different topographic areas meet (Asztalos et al. 2021a). In far southern France, *N. helvetica* contacts but rarely hybridizes with the Ibero-Maghrebian Grass Snake *N. astreptophora* just north of the Pyrenean Mountains (Pokrant et al. 2016). This hybridization is more frequent in the northeast than in the northwest of the Pyrenean Mountains (Asztalos et al. 2020).

The Ibero-Maghrebian Grass Snake *N. astreptophora* (type locality: La Coruña, Galicia, Spain) occurs southwest of the Western Grass Snake, from the northern coast of Spain, eastward along the southern slopes of the Pyrenean Mountains to its eastern end where they crossed north into a few departments of southern France. It occupies the following habitats (IUCN Habitats Classification Scheme v. 3.1): temperate forests, temperate grasslands, permanent rivers/streams, bog/marshes/swamps, permanent lakes, seasonal lakes, permanent pools, seasonal pools, springs, alpine wetlands, and sandy shoreline (Pleguezuelos et al. 2010). *Natrix astreptophora* ranges across the entire Iberian Peninsula (Portugal and Spain), at 0–3,200 m ASL and becomes more montane in central and southern Iberia (González-Miras et al. 2008). It is homogenously distributed and abundant in the north, inhabiting the border of beech and mixed forests, dense scrubs, and river valleys, including those with a high hydrologic seasonality (Santos et al. 2002; Escoriza 2018). To the south, river-associated habitats become more important, but it also dwells in other artificial biotopes, such as humid meadows, ponds, and ditches (Santos et al. 2002; Segura et al. 2007). It is absent from most of the dry Guadalquivir Valley and the arid southeast, where rainfall is below 600 mm (Santos et al. 2002, 2008) and the Balearic Islands (Kindler et al. 2018b). In northwestern Africa, scarce records from northern Morocco, Algeria and Tunisia are mainly restricted to wetlands and humid mountainous forest between 0–2000 m. Secondarily, it occupies rivers and lagoons close to the Mediterranean coast, where amphibians are numerous, but was occasionally observed also far from water (Schleich et al. 1996; Sindaco et al. 2013; Kalboussi and Achour 2018; Martínez del Mármol et al. 2019). In areas of frequent forest fires in on the western Iberian Peninsula, *N. astreptophora* was only recorded in unburnt plots (Muñoz et al. 2021). On an aridity gradient in the western Mediterranean, the species mainly occupies the more pristine aquatic habitats (Escoriza and Pascual 2021). Mean annual temperature and precipitation values for northwestern Africa are 16.9ºC and 838 mm, respectively (Escoriza and Ben Hassine 2017). Within southwestern France, it marginally occurs in the departments of Eastern Pyrenees, Aude and Ariege (Geniez 2015; Pokrant et al. 2016; Kindler et al. 2018a; Asztalos et al. 2020; Fritz and Schmidtler 2020).

Identification. The morphological variation of the Grass Snake group led in the past to the description of many subspecies and regional morphs, with the most prominent ones detailed in Kabisch (1978, 1999), that often do not correspond with recently presented molecular phylogenies. It resulted in many misidentifications and unclear distribution patterns. The following accounts summarize morphological characteristics for all three species together, but adds specifics in subsequent paragraphs where each species differs.

Commonly, the Grass Snakes are slender to robust snakes with a total length up to 150 cm, rarely more, with both *Natrix natrix* and *N. helvetica* have been reported of exceptional maximum length > 180 cm (Kabisch 1999), whereas *N. astreptophora* remains smaller with 112.5 cm SVL for a female from the Iberian Peninsula (García-Antón et al. 2017). Females attain larger size with a relatively longer tail in males, e.g., 22.7% of total length for males versus 20.2% for females in southeastern Spain (Feriche et al. 1993). Their dorsal color usually consists of shades of grey, but brown and even reddish tones can also occur (Jablonski et al. 2022). Four rows of dorsal spots or blotches vary in size depending on geographic variation, species, and age. Another traditional name for this group is Ringed Snake, which refers to their white to yellow collar spanning across the neck or being separated into bilateral lunar spots. The collar is orangish in subspecies *N. natrix scutata* of Transcaucasian countries and Russia. On the body and adjacent to the light collar are large, bilateral blotches, often curved and pointed posteriorly. The light collar may disappear in fully grown individuals, whereas the post-collar blotches remain, most frequently in adult *N. astreptophora*. Melanism is widespread and occurs occasionally in single individuals or represents a sizeable proportion in some populations. The iNaturalist dataset showed that the frequency of dark body coloration increases from south to north and west to east (Fritz and Ihlow 2022). The ventral pattern is checkered with black blotches on white ground, with the blotches often exhibiting a concave outer edge (Gonzalez de la Vega 2021). The black proportion of the ventral body increases in size posteriorly to become almost entirely black. Main scale characters (Boulenger 1913; Kreiner 2007; Scali et al. 2011) are dorsal scales keeled and usually arranged in 19 rows midbody, less prominent keeled to smooth in the lowest (paraventral) two rows; the keeling is also reduced or disappears at the end of the tail. Ventral scales vary geographically but are within 159–189 in males and 155–181 in females, and similarly for subcaudal scales vary within 56–90 in males and 47–74 in females. All three Grass Snake species share the following characteristics: Anal scale is usually divided. Preocular scales: 1, rarely divided. Postocular scales: usually 3, rarely 2 or 4. Upper Labial scales: 7 (rarely 6 or 8); 3rd and 4th touch the eye. Temporal scales: 1 (rarely 2) anterior and 2 (rarely 3) posterior. R.S. Thorpe has analyzed more detail on geographic variation in multiple studies (see his references from 1973–1989).

In the Eastern Grass Snake *Natrix natrix* northern populations are usually greyish, individually in different tones, and with four rows of small dorsal spots. In southern populations of *N. natrix*, the dorsal pattern contrasts with four rows of larger dorsal blotches, and the lateral ones extended to vertical bars. Individuals with two light dorsal lines along the body (persa morph) occur in southeastern populations from the Balkans to Turkey, Caspian Sea, and Lebanon (subspecies *vulgaris*, *moreotica*, *scutata,* and possibly *syriaca*). Some distinct color pattern expression on insular populations led to descriptions of different subspecies and morphs (e.g., *N. n. fusca* from Kea Island in Greece, *N. n. gotlandica* from Gotland, Sweden, *N. n. cypriaca* from Cyprus, or *N. n. schweizeri* from the southern Cyclades, e.g., Milos Island, Greece), that are invalid from the evolutionary point of view (Kindler and Fritz 2018). Interestingly, *N. n. cypriaca* and *N. n. schweizeri* have similar body coloration variation: first, the more contrastingly heavily blotched morph on light gray, without or only partly visible light collar band, a second wholly or partly melanistic individual. And third a stippled morph with more minor black and olive-grey flecks, the so-called *picturata* variation (Baier et al. 2009; Zotos et al. 2021). However, current genetic data (Kindler et al. 2013; Asztalos et al. 2021b) support the existence of only four subspecies of *N. natrix* without any insular endemics, even though the southern subspecies, including the polymorphic Aegean populations of *N. n. moreotica*, show generally a higher variability than northern ones (Jablonski et al. 2023a; and see below). Thus, these insular phenotypes apparently represent adaptation to local environments in the Mediterranean area. Their scalation characteristics are those of the entire Grass Snake group, however, with a restricted range in the number of ventral and subcaudal scales, 163–188 and 53–89, respectively. The number of ventral scales of males is slightly higher on average than in females, whereas the number of subcaudal scales is significantly higher in males. The Eastern Grass Snake is slimmer and smaller than western species, with patches behind the head usually richer in yellow to orange, especially in the easternmost populations, ssp. *scutata*, that is generally missing the lateral vertical bars. *Natrix natrix* females are more robust and reach longer sizes than males. Specimens > 120 cm in total length are uncommon to rare, with the largest specimen found killed on Krk Island, Croatia, and subsequently measured as 205 cm (Schreiber 1912; Kabisch 1999). The weight of the Eastern Grass Snake from central Europe ranges in males from 100–140 g, in females 300–350 g (Günther and Völkl 1996; Kabisch 1978, 1999).

The Western Grass Snake *Natrix helvetica* dorsal pattern usually consists of two rows of dorsal spots/blotches and vertically elongated lateral bars. The black nuchal blotches are often only little indicated (Kabisch 1999). Specimens of the Italian Grass Snake *N. helvetica*

Figure 28.2: Natural color pattern variation of Eastern Grass Snakes (*Natrix natrix*) from: A) Poland; B) Slovakia; C) northeastern Turkey; D) southwestern Turkey; E) and F) Milos Island, Greece. Photo credit: A), C), D) Konrad Mebert; B) Daniel Jablonski; E) Andre Schmid; F) Laura and Bobby Bok.

sicula from far southern Italy, e.g., Sicily Island and southern Calabria, are characterized for their orange snout tip and chin. Melanistic specimens are known. The subspecies *N. helvetica cetti* from the islands of Sardinia and Corsica (Vanni and Cimmaruta 2011; di Nicola et al. 2021; Schultze et al. 2020) show a more distinctive morphology: Ventral scales: 158–178 (males 160–178, females 158–173). Subcaudal scales: 47–64 pairs (males 56–64, females 47–53). Preocular scales 1, but often 2 at least on one side of the head. Adult individuals of the Western Grass Snake sometimes lack the typical light collar band.

An external character of *Natrix astreptophora* relates to its epithet "*astreptophora*" (López-Seoane 1884: p. 15) that denotes the absence of the white to the yellowish collar in adults, which is still present in juveniles (Braña 1998; Fritz and Schmidtler 2020). Besides the black blotches posterior to the light collar standard in most Grass Snakes, some juvenile *N. astreptophora* also show an additional distinctive black parietal band anterior to the light collar band (Pleguezuelos 2018). Most specimens show a reddish iris, the most visible external diagnostic character to distinguish against the parapatric *N. helvetica* (Pokrant et al. 2016), but also exhibit a black patch crossing diagonal over the lower anterior portion of the iris that also occurs in some southern *N. natrix* and *N. helvetica* (Gonzalez de la Vega 2021). Newborn body color is brown to olive or ocher after the first ecdysis, whereas adults are grey with the occasional reddish-brown morph (Gonzalez de la Vega 2021). On the dorsum, 3–6 longitudinal rows of 41–56 black spots often disappear in adults (pattern less), and rarely fuse across the back, as in other Grass Snakes (Geniez 2015). Up to 5.4% of individuals in Cantabrian Mountain populations are melanistic (Meijide and Pérez-Melero 1994; Albadalejo 2008). The Ibero-Maghrebian Grass Snake has a wide head and stout muscular body, showing differences in skull bones from the other Grass Snakes (Pokrant et al. 2016).

Phylogeny and phylogeography. The extant diversity within Grass Snakes (Deepak et al. 2022) suggests that the group originated in Asia, afterward dispersing to the western Paleartic, where they diversified into the current species of the genus (Schöneberg et al. 2023). First comprehensive morphological studies on Grass Snakes by Thorpe (e.g., 1973, 1975a, b, 1984, 1979) were followed by molecular studies (Guicking et al. 2006; Fritz et al. 2012; Kindler et al. 2013). They evaluated phylogeographic structure and time of divergences with subsequent studies of hybrid zones, morphology, and osteology (Pokrant et al. 2016; Kindler and Fritz 2018; Kindler et al. 2017, 2018a,b; Schultze et al. 2020; Asztalos et al. 2020, 2021a, b), finally resulting in significant changes in the taxonomy and phylogeny of the traditional Grass Snake *Natrix natrix*, by recognizing three well-separated parapatric species. The Ibero-Maghrebian Grass Snake *N. astreptophora* was the first to diverge from other Grass Snakes in Europe at 9.6–10.6 MYA, resulting from the uplift of the Pyrenean Mountains (Pokrant et al. 2016). This was reanalyzed and adjusted to a slightly younger split by Schöneberg et al. 2023, see below. Subsequently, the Grass Snakes in Europe split into the Eastern Grass Snake *N. natrix* and the Western Grass Snake *N. helvetica* approximately 8.2 to 7.3 MYA (Fritz et al. 2012; Kindler and Fritz 2018; Kindler et al. 2017). The Big-head Grass Snake *N. megalocephala* (Orlov and Tuniyev, 1987) from the Caucasian region and northeastern part of the Black Sea coast was often listed as a separate species. However, the molecular-phylogenetic analysis showed that this taxon is only a phenotypic variation, possibly an ecomorph or ecophenotype of *N. natrix*, occurs more widespread as far as Switzerland (Göçmen et al. 2011a) and was ultimately synonymized with this species (Kindler et al. 2013; Asztalos et al. 2021a).

The Eastern Grass Snake *N. natrix* continued diversification around 6 MYA (Kindler et al. 2017) with the following, currently recognized subspecies (Kindler and Fritz 2018; Fritz and Schmidtler 2020; Asztalos et al. 2021a, b): *N. n. natrix* (Linnaeus, 1758); *N. n. vulgaris* (Laurenti, 1768); *N. n. moreotica* (Bedriaga, 1882), *N. n. scutata* (Pallas, 1771), with one potential subspecies, *N. n. syriaca* (Hecht, 1930), that requires more attention. According to new data based on mitochondrial and nuclear DNA, *N. n. natrix* occurs in Sweden, Norway, Finnland, Denmark, and most of Germany, except the western part. It forms possible broad contact zones with the subspecies *N. n. vulgaris* in Poland, the Czech Republic, and Slovakia. This subspecies is probably widespread in Poland, southern Central Europe, northeastern Italy at least as far south as Argenta and Ravenna, and large parts of central Balkan countries. It is replaced in western and southern Balkan and Western Turkey by *N. n. moreotica.* The areas farther east, from the Baltic republics through Ukraine, the Middle East and Iran to Mongolia is inhabited by the subspecies *N. n. scutata* (Asztalos et al. 2021a, b; Jablonski et al. 2023b)

Diversification in the Western Grass Snake *N. helvetica* began after establishing the oldest lineage for in the most southern (Italian) populations with an estimated mean age of 6.8 MYA. Currently, three or four subspecies are recognized: first, *N. h. helvetica* of western Europe, and second *N. h. sicula* (Cuvier, 1829) of Italy that includes now also *N. h. lanzai* (Kramer, 1970). The Tyrrhenian Grass Snakes from the Italian island of Sardinia, *N. h. cetti* (Gené, 1839), and the neighboring French island of Corsica, *N. h. corsa* (Hecht, 1930), represent the third and fourth subspecies, or they become synonymized with each other, pending further investigation (Fritz et al. 2012; Kindler and Fritz 2018; Fritz and Schmidtler 2020; Schultze et al. 2020). The nominotypic *Natrix h. helvetica* also occurs across most of Switzerland and France, and to northern Netherland including Belgium and Luxembourg (van Riemsdijk et al. 2020; Ahnelt et al. 2021) and Great Britain, barely reaching into Scotland (Cathrine 2014);southwards it reaches the Spanish Valle de Arán in the northern slope of the Pyrenean Mountains. It introgresses in northwestern Italy into *N. helvetica sicula*, the Italian Grass Snake, that primarily inhabits mainland Italy and Sicily Island, but also southern Switzerland and across the Alps of Western Austria into far southern Bavaria, Germany (Schultze et al. 2020; Asztalos et al. 2021a, b).

The Ibero-Maghrebian Grass Snake *N. astreptophora* is the sister taxon to *N. helvetica*. These two Grass Snakes species from western Europe and northweastern Africa form the sister clade to the older group of Eastern Grass Snake *N. natrix* (Schöneberg et al. 2023). *Natrix astreptophora* split from the Western Grass Snake *N. helvetica* in the upper Miocene (7.3 Mya, confidence interval 5.86–10.59 Mya; Schöneberg et al. 2023). There is also morphological and molecular evidence for some hybridization between *N. astreptophora* and *N. maura* (Gonzalez de la Vega 2021; Schöneberg et al. 2023). *Natrix astreptophora* is genetically structured into three clades. First, the European (Portugal and Spain) and northwest African *N. astreptophora* diverged 5.44 MYA from each other (Kindler et al. 2018a). Second, the North African Grass Snakes split again into two groups on both sides of the Mouluya Valley, forming the Moroccan and Tunisian/Algerian clades. Both previous splits likely occured as a result of the Zanclean flooding event of the dried Mediterranean Basin at the end of the Messinian Salinity Crisis (Kindler et al. 2018a). Latter group was subsequently re-established as *N. astreptophora algerica* (Hecht, 1930) by Fritz and Schmidtler (2020). On the northern side of the Pyrenean Mountains in southeastern France, *N. astreptophora* and *N. helvetica* are parapatric, with a steep genetic transition from one taxon to the other, and rare hybridization (Pokrant et al. 2016; Asztalos et al. 2020). This contact zone had established after the mid-Holocene range expansion from glacial refuges on the Iberian Peninsula (*N. astreptophora*) and southwestern France (*N. helvetica*).

Population Aspects. Newborns of all three *Natrix* species exhibit a total length of 14–22 cm (usually 18–19 cm) and weigh around 2–4 gr (Kabisch 1999). Before their first hibernation, they reach a total length of 25–30 cm, to 50–60 cm at five years, to 70 cm at 7–8 years, and to > 100 cm at 15 years of age; usually only females' growth larger than 80 cm of total length, some of them reaching 17–18 years of age (Madsen 1983; Braña 1998). Females grow faster than males but require more time to mature and generally attain greater length and weight. In *N. natrix*, males reach sexual maturity at about 50 cm total length and 50 g weight at the age of three years, whereas males of *N. astreptophora* in southeastern Spain, mature at 30 cm snout-vent length (SVL; approximately 40 cm total length). Females of all Grass Snake species reach sexual maturity in the fourth or fifth year of life, at approximately 60 cm SVL and 80 g in weight (Jusczyk 1974; Madsen 1983; Rehák 1992; Feriche 1998). In northern Morocco a male at 38.7 cm snout-vent length and a female at 67.8 cm snout-vent length were adults (Fahd 2001). After the age of 8–9 years, growth slows down and may become negligible (Madsen 1983). However, locally reduced food availability can result in females growing slower and to a smaller size; for example, an insular population in Sweden that feeds exclusively on generally smaller newts (the only available amphibians) than females from the mainland that were feeding on larger anurans (Madsen and Shine 1993). The sex ratio of *N. natrix* for males:females from northern populations ranges from 1:1.36 to 1:1.5, respectively (Rehák 1992, refs. in Kabisch 1999), whereas those from Iran were 1:1 (Ahmadzadeh et al. 2011), for *N. astreptophora* 1:1.9 in northern Spain (Braña 1998) and 1:1.4 in southeastern Spain (Feriche 1998).

Grass Snakes can be very common in suitable habitats with about 1–7 individuals/ha and reach high densities of close to one individual per square meter during aggregation for mating and feeding when mates and prey temporarily occur at high densities (Tuner 1977; Mertens 1995; Kabisch 1999 and refs.; Sidorovich et al. 2008). The mean total home range for individuals in Sweden and Germany were 21.2 ha and 16.4 ha, respectively, and the adjusted home range that excludes large areas never used by the snakes showed a mean of 11.8 ha and 15.1 ha, respectively (Madsen 1984; Mertens 2008), and increased to 39,7 ha in agricultural impacted area, where seasonally required sites were more distant to each other (Wisler et al. 2008). Indeed, seasonally varying locations have been found for different annual activities, including hibernation, mating, oviposition, and foraging in *N. natrix* in Germany and *N. helvetica* in the Netherlands, with migratory distances of up to 7 km between seasonal sites (Janssen and Völkl 2008) Maximum age by mark-recapture methods was given as 28 years from a Swedish population (Edelstam 1989).

Activity and Thermal Biology. In Central Europe, the Eastern Grass Snake starts emerging from hibernation (rodent burrows, rock crevices, cellars, composts, piles of leaves, subterranean tree roots) in late March or early April and remains active until late September to early October. In southern France, they emerge from hibernation usually on day 95 (Julian calendar; Prodon et al. 2020). Exceptionally, this species can also be found in November or in February, for example, during short spells of warmer temperatures, or probably is more active throughout the year in warmer regions of southwestern Asia, e.g., Azerbaijan (Rehák 1992, D. Jablonski, unpubl. data). In spring and autumn, activity peaks in the warmest hours of the day, usually mid-day into the afternoon, whereas the summer activity has two peaks, in the morning, beginning between 0630 h and 0800 h, and late afternoon/evening, respectively (Mertens 2008). During hot days, activity can occasionally be switched to nights. In contrast, nocturnal activity can be added in the cooler spring, April and May, when high amphibian breeding activity (e.g., Albania, Northern Macedonia, Switzerland, Germany, Mertens 1994, 2008, authors pers. obs.). Referenced accounts in Kabisch (1978, 1999) show that *N. natrix* (and likewise *N. helvetica*) experience a wide range of environmental temperatures during daytime activity, as low as 6° C and > 30° C, but usually somewhat between 18–25° C (Gregor 1980; Kühnel 1993), with preferred body (cloaca) temperatures ranging from 29–33° C (Mertens 1994, 2008). Severe cold weather during the winter months is survived in hibernacula, sometimes with other reptiles such as the Northern Viper (*Vipera berus*), Smooth Snake (*Cor-*

onella austriaca), or Slow Worm (*Anguis fragilis*). Mertens (2008) radiotelemetry hibernating Grass Snakes in complex rodent burrows and found their subterranean position constantly at 5–15 cm depth, and only during a freezing period with temperatures below –10° C snakes move into lower layers, between 25–50 cm depth.

Often, the visibly highest activity relates to the mating period in the spring months when males search for females. For example, in a mosaic landscape of woods, pastures, agricultural fields and ponds in Sweden, Madsen (1984) observed an average movement of 54.8 m per day by Grass Snakes, whereas later in the summer, they remained more sedentary (average movement per day 13 m). However, neither a higher movement of male Grass Snakes nor a reduced summer activity was found in a similar study and habitat in central Germany (Mertens 2008). Instead, larger individuals followed large toads that had left the ponds/pools into more lightly forested sections, whereas smaller individuals remained in the ponds to forage on water frogs. Yet only 4.8% of telemetered individuals were detected in water (Mertens 2008).

The Western Grass Snake *N. helvetica* yields a comparable variation of activities and thermal biology as its eastern sister species (see accounts in Kabisch 1999). For example, in western Switzerland, female *N. helvetica* used monocultures managed by a cropping system, e.g., wheat, potato, and corn (Wisler et al. 2008). The monocultures provided suitable basking sites, favorable foraging grounds, and low pressure from avian predators. Adjacent edge habitat (dam, canal bank, forest edge) was preferred for the period of shedding and oviposition. After oviposition, the females returned to the monocultures to hunt amphibians primarily. The mean home range size was 34 ha (Wisler et al. 2008). While the latter study found no nocturnal behavior, night foraging was observed in populations of the Western Grass Snake occupying warmer regions, exemplified by the predominantly nocturnal in the Sardinian subspecies *N. helvetica cetti* (Capula et al. 1994).

The activity season of the Ibero-Maghrebian Grass Snake *N. astreptophora* ranges between March and October in southeastern Spain (Feriche 1998) and between the end of February and early November in the western part of the Iberian Peninsula (Galán and Fernández-Arias 1993; Malkmus 1997), with most records from April to September (Galán 1988). In northern Morocco, active individuals have been found between May and October (Fahd 2001), whereas in Tunisia, *N. astreptophora algerica* is also active during mild winter days (Kalboussi and Achour 2018). Communal hibernation dens with up to three individuals have been detected in Galicia (Galán and Fernández-Arias, 1993). In southeastern Spain, the mean annual body temperature of active individuals was 26.6° C (range 22–32° C), higher during summer with 27.8° C (24.3–32.0° C), less with 26.8° C (19.0–30.0° C) during spring and autumn (Hailey and Davies 1986a; Hailey et al. 1982).

Reproduction. All three species of Grass Snakes appear to have a similar reproductive base strategy, which likely has been adapted to local environmental conditions rather than species constraints. In general, the mating period for *N. natrix* begins soon after emergence from hibernation, in March/April, and can last into May/June, followed by oviposition between June and August (Feriche 1998; Kabisch 1999; authors pers. obs.). Males begin courtship primarily after first shedding, raise their head next to a receptive female, twitching their bodies, frequently tongue flicking, and pressing their bodies against the female, wrapping their tail around her tail. Then, with the opening of the female´s cloaca, one of the hemipenes, rarely both, penetrates. Copulation takes several minutes, sometimes hours (Rehák 1992). There are mating aggregations with up to 50 snakes (Berec et al. 2015), while some engage in a mating ball consisting of one receptive female with up to 20 males entangling her (Kabisch 1999). Larger males are more successful in this case, even though no direct fights for females have been observed (Luiselli 1996).

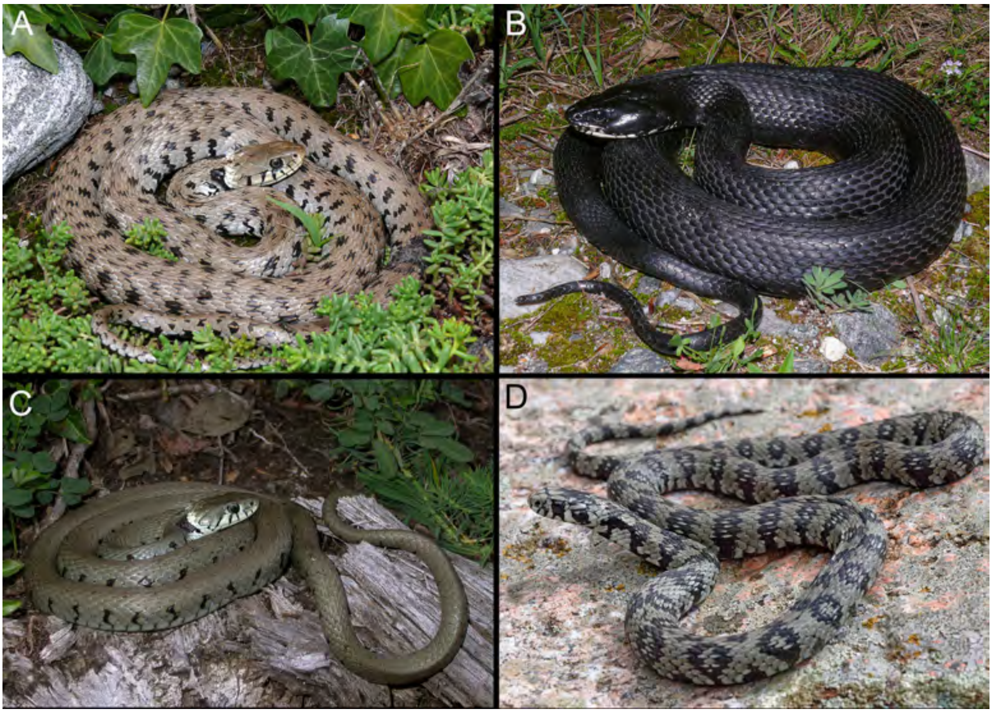


Figure 28.3: Natural color pattern variation of Western or Barred Grass Snakes (*Natrix helvetica*) from: A) and B) Ticino, southern Switzerland; C) western Switzerland; D) Sardinia Island, Italy. Photo credit: A), B), C) Konrad Mebert; D) Matteo Riccardo di Nicola.

Mating in autumn (September/October) occasionally occurs in Germany, with egg clutches discovered in November/December (Kabisch 1999 and refs. therein). Spermatogenesis in males persists until the end of the mating season. After mating, sperm remains in the female's body, and fertilization is delayed until the onset of ovulation next spring (Berec et al. 2015). In northern Iran (*N. natrix*) and Spain (*N. astreptophora*), females start vitellogenesis in May/early June, with the growth of ovaries continuing at least until mid-July to August (Galán and Fernández-Arias 1993; Feriche 1998; Ahmadzadeh et al. 2011; Shiravi et al. 2012). In cool and rainy Asturias, northern Spain, there are female *N. astreptophora* with oviductal eggs during July and embryogenesis in the early stages at oviposition (Braña 1998). Males from Iran (*N. natrix*) and Spain (*N. astreptophora*) showed signs of a postnuptial spermatogenesis with slow and constant growth in late spring, reaching its height in August and September, ending in November, with sperms stored over the winter for the next spring mating (Faghiri et al. 2011; Arragayago and Bea 1988). Sperm storage may last long, exemplified by a solitary kept Grass Snake that produced fertilized eggs after > 2 years (Hediger 1971; cit. in Eckstein 1993).

Oviposition ranges from June to August, with clutch size from 8–32 eggs per female (Kabisch 1999). Clutch size can geographically range, for example, for *N. astreptophora*: 9-26 eggs in Asturias, northern Spain (Braña 1998), 12-29 eggs in southeastern Spain (Feriche 1998), 6-50 eggs in Galicia (Galán and Fernández-Arias 1993), 10-50 eggs in all of Morocco (Bons 1967), and 11–28 eggs only in northern Morocco (Fahd 2001). Clutch size is also positively correlated with female body size and age for all Grass Snake species (Madsen 1983; Rehák 1992; Feriche 1998). For example, petite females from a food-depauperated habitat on Gotland Island, Sweden, laid only 2–3 eggs (Edelstam 1989), whereas huge females exceptionally deposited around 70–100 eggs (Kabisch 1999 and refs. therein). The size of the egg ranges from 21–40 x 11–24 mm, and the eggs increase in weight by ca. 30% during the incubation (Kabisch 1999). Clutches are deposited in manure piles, sawdust, and rotting vegetables under rocks and rodent burrows. Several females might lay clutches in one suitable place, sometimes with other species, e.g., *Natrix maura* or Aesculapian Snake *Zamenis longissimus*. Communal nests have been recorded in different countries, e.g., 400 hatchling Grass Snakes emerged from one nest in Galicia, Spain (Galán and Fernández-Arias 1993), 558 eggs in the Czech Republic (Berec et al. 2015), and even between 3000–4000 eggs in a pile of sawdust in eastern Germany (Kabisch 1999). Depending on their geographical location, the young hatch from July to September after an incubation period of approximately two months.

Foraging and Diet. Grass Snakes are diurnal, terrestrial, and visually guided active hunters (Hailey et al. 1982; Hailey and Davies 1986a, b), that hold on to their slippery prey until the ingestion process begins (Galán and Fernández-Arias 1993). However, they switch to crepuscular and nocturnal foraging during summer or in generally warmer regions in the south (e.g., Hailey and Davies 1986a; Schleich et al. 1996, pers. obs.). For example, Ibero-Maghrebian Grass Snakes, *N. astreptophora* from Galicia, Spain, avoided activity during the hot midday hours in captivity but under natural light and temperature conditions (Galán 1988). There are also a few reports of marine observation, some for foraging, e.g., a Grass Snake that became entangled in a fishing net at 8–9 m depth in Norway, whereas others might be drifted away by sea currents, one up to 47 km (Kabisch 1999 and refs.). Small prey can be swallowed underwater, while larger prey is carried and then swallowed on land (Schleich et al. 1996). One prey, the Natterjack Toad *Epidalea calamita*, avoids shelter containing the scent of *N. astreptophora* (Gonzalo et al. 2008).

Studies have revealed a broad diet for Grass Snakes, yet always with a focus on common amphibians, primarily frogs of the genus *Rana* and *Pelophylax*, and toads of the genus *Bufo*, rarely the genus *Pelobates* (Kabisch 1999). In contrast, other prey types are less frequently consumed, e.g., poisonous amphibians such as the Fire-bellied toads *Bombina* spp., salamanders and newts, lizards, invertebrates, birds, eggs, and mammals (Rehák 1992; Luiselli et al. 1997; Scali et al. 2011; di Nicola and Bruni 2020). Grass snakes consume a lot of available food at once and can fast for a long time, reportedly until about one year (Dobreff 1939). During the metamorphosis of *B. bufo* tadpoles, *N. natrix* can eat many juvenile toads (Berec et al. 2015). For more information on the diet across all three grass snake species, see also: Luiselli and Rugiero (1991); Gled-Owen (1994); Filippi et al. (1996); Reading and Davies (1996); Luiselli et al. (2005); Faraone et al. (2010); and a particularly extensive account given in Kabisch (1999).

Some specific diet studies on the Eastern Grass Snake *N. natrix* show the proportion of fish consumed: 4.1% of the catch in Bulgaria (Beshkov and Dushkov 1981), 40.8% in Croatia with the remainder being amphibians (Janev Hutinec and Mebert 2011), whereas a Swedish populations fed mainly on fish from the seashores (Andrén and Nilson 1981). In an alpine population of *N. natrix* in northeastern Friuli Venezia Giulia, Italy, anurans were the most frequent diet (*Bufo bufo* 46%, *Rana temporaria* 40%), followed by urodeles (*Salamandra atra* 6%, *Ichthyosaura alpestris* 5%), but also a few lizards (*Zootoca vivipara*) and mice (*Apodemus sylvaticus*) were consumed (Luiselli et al. 1997).

In southeastern England, the diet of small and medium-sized of the Western Grass Snake *N. helvetica* is mainly based on aquatic prey with a predominance of anurans (63%, primarily introduced *Pelophylax* spp.), fish (25%) and rarely a bird (1%). Grass snake usually swallowed prey headfirst (65%), however, this depended on the prey type (Gregory and Isaac 2004). The principal prey of *N. helvetica* on the Italian mainland consisted primarily of the toad species *Bufo bufo* and the frog genus *Rana*, and rarely included rodents, fish, saurians, invertebrates and passerine (Scali et al. 2011; Di Nicola & Bruni, 2020). The main prey of Sardinia´s *N. helvetica cetti* were the frogs *Discoglossus sardus* and *Hyla sarda*, and rarely lizards such as *Podarcis tiliguerta* (Scali et al. 2011). Amphibian larvae, including those of newts, are food mainly for juveniles.

Data from Galicia, Asturias, and Levante for the Ibero-Maghrebian Grass Snake *N. astreptophora*, show the major prey are amphibians. Species include *Discoglossus galganoi, Bufo spinosus, Alytes obstetricans*, and the urodele *Salamandra salamandra* and less often oligochaetes, insects and microtines (Braña 1998; Pleguezuelos 2018). Furthermore, prey species recorded for *N. astreptophora* are anurans (*Epidalea calamita, Pelophylax perezi, Rana temporaria, R. parvipalmata, R. iberica*), urodeles (*Lissotriton boscai, L. helveticus, Triturus marmoratus, T. alpestris*) and amphibian larvae, fishes (*Leuciscus* sp., *Phoximus* sp.), other vertebrates (*Riparia riparia*), and insects (Garzón 1974; Valverde 1974; Vericad and Escarré 1976; Galán 1988; Meijide 1989; Galán and Fernández-Arias 1993; Braña 1998; Díaz 2004; Galán and Ferreiro 2010; Ayres 2012; S. Busack per. com.). Frequency of amphibian prey is between 80–98%, but certainly will vary by season and location. In Morocco, the anurans *Discoglossus scovazzi, Pelophylax saharicus,* and the lizard *Chalcides* sp. have been recorded as prey (Bons 1967). In Tunisia, *N. astreptophora* is a potential predator of *Bufo spinosus* (Ben Hassine and Escoriza 2014).

Predators and Defense. The Eastern Grass Snake *N. natrix* faces a broad spectrum of vertebrate predators, from fish to reptiles, and carnivorous mammals including domestic cats (Galán 2013), but primarily from dozens of different bird species (Kabisch 1999). Young Grass Snakes are frequently preyed on even by invertebrates such as the Golden Ground Beetle (*Carabus auratus*), but also by anurans, passerines, chickens, hedgehogs, moles, and mice (Kabisch 1999). For all Grass Snakes, the Short-toed Snake Eagle (*Circaetus gallicus*) has a particular reputation as a formidable snake hunter (Pleguezuelos 2018; Pleguezuelos and Ontiveros 2010). According to Zebe (1936, cit. in Kabisch 1999), an adult pair of Short-toed Snake Eagle and their single young may consume up to 1000 snakes per season, although when preying on larger colubrids compared to smaller vipers, the figure of 450 snakes per eagle family and season, is more credible (unpub. data of the authors). In the Minsk region of Belarus, Short-toed Snake Eagles almost exclusively preyed on *N. natrix* (Glutz von Blotzheim et al. 1971)

Likewise for the Western Grass Snake *N. helvetica* from Loir-et-Cher, France, where the Short-toed Snake Eagle only fed on that species and the Asp Viper *Vipera aspis* (Perthuis 2008), which locally represented the most frequent and sizable snake species (Maumary et al. 2012). However, in the Montados of southern Portugal, this snake rarely appears in the diet of the Short-toed Snake Eagle (Onofre and Sampaio 2020). Furthermore, all Grass Snakes are preyed by herons and egrets, storks, owls, kites, falcons, Egyptian Vulture, otters, felines, martens, and also by other snakes, in particular by the Western Montpellier Snake *Malpolon monspessulanus* preying on *N. helvetica* and *N. astreptophora*, whereas the Eastern Montpellier Snake *M. insignitus* preys on *N. natrix* (Díaz-Paniagua 1976; Schleich et al. 1996; Kabisch 1999; Vacher and Geniez 2010; Pleguezuelos 2018).

The Eastern Grass Snake *N. natrix* is infected by many parasites. From Iran, Yossefi et al. (2014) reported *Rhabdias fuscovenosa* (Nematoda), *Telorchis assula* (Digenea), and *Ophiotaenia europaea* (Cestoda). In Turkey *N. natrix* was infected by five species of Digenea: *Astiotrema monticelli*, *Encyclometra colubrimurorum*, *Macrodera longicollis*, *Paralepoderma cloacicola*, and *Telorchis assula*; two species of Cestoda: *Ophiotaenia europaea* and *Spirometra erinaceieuropae*; and two species of Nematoda: *Rhabdias fuscovenosa* and larvae of *Eustrongylides excisus* (Yildirimhan et al. 2007, and refs. therein for other countries). Lewin (1992) reported 21 types of parasites from Poland, including six adult trematodes, five meso- and metacercariae, one cestode larva, five adult nematodes, two nematode larvae, one acanthocephalan and one tick. A more recent review from Poland revealed > 25 species of parasites for *N. natrix* (Kuśmierek et al. 2020; Belcik et al. 2022). There is no comparable information on the Western Grass Snake *N. helvetica* whereas the Digenian trematode *Leptophallus nigrovenosus* has been found in the Ibero-Maghrebian Grass Snake *N. astreptophora* (Navarro et al. 1987).

Adult Grass Snakes typically flee by the approach of a potential predator, with the fleeing distance being rather short (Schleich et al. 1996). When cornered without a reasonable escape option, a Grass Snake may coil the body and hide the head in the center or under a body coil, or flattens the entire trunk, and transforms the head into a triangular shape by displacing the quadrate bones. It may hiss loudly and strike with a closed mouth in an example of Batesian mimicry of coexisting *Vipera* species (de Solan et al. 2020), but they rarely bite (Kabisch 1999; di Nicola et al. 2023). Some individuals even raise their forebody and may also spread their necks horizontally like cobras (Schweizer 1911 cit. in Kabisch 1999; Pokrant et al. 2017; photos in turkherptil.org). The throat can also be inflated vertically, and even open mouth striking or biting has been observed but is extremely rare (Kabisch 1999; authors unpubl. data). If these behaviors do not deter the potential predator, a Grass Snake begins to simulate death by adopting a state of thanatosis (faking death) by becoming limp, open its mouth and let their tongue hang out, sometimes enhancing the deterrence effect by mouth bleeding; often also turning on their back to display the contrasting black and white belly (Eckstein 1993; Kabisch 1999; Malkmus and Sauer 2013; unpubl. data by authors). When handling Grass Snakes, they often regurgitate their stomach content, emit an obnoxious fluid from their anal glands, and sometimes defecate.

The white-orange collar band may function as an anti-predator mechanism by mimicking aposematically colored unpalatable insects (Madsen 1997). In northwestern Spain large toads *Bufo spinosus* avoid juveniles of *N. astreptophora* that display the striking collar pattern (Galán and Fernández-Arias 1993). Finally, defensive behaviors occur at lower body temperatures, while aggressive behaviors are more common at higher body temperatures (Eckstein 1993).

Conservation. Grass Snakes have suffered a decline across their entire range, but most severely in densely populated regions of central and western Europe and in landscapes heavily used for agriculture in Europe and west Asia (Blanke et al. 2008). These human-made modifications resulted in habitat fragmentation and the decline of local amphibian populations that added to the threats of Grass Snakes and justified its listing as threatened in many central European countries.

Other human activities also have very negative consequences. It is well known that many fishermen kill these snakes due to their fear of these semi-aquatic snakes competing for fish. High mortality caused by traffic, especially when roads cross traditional migration corridors near water, is also an important source of snake decline (e.g., Ioannidis and Mebert 2011; Gezova and Jablonski 2018). Gruschwitz et al. (1993) included seven studies, and Blanke et al. (2008) produced a complete summary with 24 articles on primarily conservation aspects of *N. natrix* and *N. helvetica* from Germany, Netherlands, Switzerland, and Cyprus. They proposed a 4-step-concept species action plan: 1. basic investigations on historical and present distribution/habitat; 2. protection and management of existing populations, including maintaining and improving foraging, oviposition, and hibernation sites; 3. re-establish former distribution (where possible) by constructing corridors between isolated populations, and potentially support weak populations by head-starting with captive-reared snakes; 4. conduct ongoing monitoring. For the Western Grass Snake *N. helvetica* a study by Meister et al. (2012) suggested that conservation actions in landscapes altered by humans should focus

Figure 28.4: Natural color pattern variation of Ibero-Maghrebian **Grass Snakes (***Natrix astreptophora***) from: A), B) and G) southern France; C) northwestern Spain; D) northern Morocco; E) Portugal; F) northern Spain. Photo credit: A), B), G) Konrad Mebert; C) and F) Octavio Jiménez-Robles; D) Abdellah Bouazza; E) Benny Trapp.**

on maintaining a habitat mosaic with anuran breeding ponds and adequate oviposition sites. Luckily, in most regions where it is still present, the Grass Snakes are considered a common snake species and accordingly listed with the IUCN category Least Concern. However, the status of the Eastern Grass Snake (*N. natrix*) populations along its southeastern borders in some Asian countries is very poorly known (Iraq, Lebanon, Mongolia, or Turkmenistan; Afrasiab et al. 2011; Asztalos et al. 2020). Also, the Critically Endangered Cyprus Grass Snake is at risk of extinction, despite some recent new findings (Blosat 2008; Zotos et al. 2021).

Alien Grass Snakes may negatively impact the conservation of native populations like the Eastern Grass Snake *N. natrix* that were introduced into indigenous populations of *N. helveti-*

ca in the Netherlands, where they likely hybridize (van Riemsdijk et al. 2020). Other related examples of alien Eastern Grass Snake species introduced or accidentally translocated into local native Western Grass Snake populations in England, France, Italy, and Germany can be found in Asztalos et al. (2021c). In addition, there are two locations in Switzerland where alien *N. natrix* were introduced into native populations of *N. helvetica* and have persisted there through decades. In the first location in western Switzerland the alien *N. natrix* hybridized with the native *N. helvetica* (Dubey et al. 2017). In contrast, no such introgression was found between these Grass Snake species in the second location, in central Switzerland (Kieffer Merki et al. 2018).

Natrix astreptophora is not listed in the global IUCN red list but is categorized as Least Concern in Spain and Portugal (Santos et al. 2002; Cabral et al. 2005), and as Near Threatened in Morocco (Pleguezuelos et al. 2010). Within the Iberian Peninsula, threats differ by region; in the northern belt, the species is rather abundant and not threatened (Galán and Fernández-Arias 1993; Santos 2008). However, in northeastern Spain, its presence is negatively influenced by the presence of alien fishes (Escoriza 2018). In central and southern Iberia, the populations are much smaller and survive in ever fewer water bodies that are often heavily degraded (Santos 2002). Consequently, the number of records of the Ibero-Maghrebian Grass Snake in the last 40 years decreased by half in Spain and by even two thirds relative to the number of non-snake reptiles in Languedoc-Roussillon, southern France, suggesting upgrading its current IUCN threat category under the A2 criterium of the red listing process (Santos et al. 2022). In northern Morocco, most of the populations are restricted and isolated to mountainous areas and experience high vulnerability to climate change (Martínez-Freiría et al. 2013; Escoriza and Ben Hassine 2017). In Algeria, the populations are also threatened by drastic degradation and loss of their aquatic habitats (Beddek 2017). The fungal pathogen *Ophidiomyces ophidiicola*, that causes snake fungal disease, has been documented in this species (0.6% of pathogen prevalence; Blanvillain et al. 2022). Finally, populations of *N. astreptophora* are genetically more diverse than those of the more northern species Grass Snakes (Kindler et al. 2018a, b), something well known for Western Palearctic species whose range was affected by the Quaternary glaciations; this represents an added value for the conservation of *N. astreptophora*.

Dice Snake

Natrix tessellata (Laurenti, 1768)

Konrad Mebert

Two large and biologically comprehensive accounts have been composed on much of what is known about the Dice Snake *Natrix tessellata* today: Gruschwitz et al. 1999 (65 pp.) and Mebert 2011a (456 pp.). This information is summarized and complemented with subsequent publication since then.

Distribution and Habitat. Type locality "Japidia, vulgo Cars" = Istrian Peninsula, Croatia. The Dice Snake is one of the few snake species occurring naturally on three continents: Europe, Asia, and Africa. In the latter case, it ranges at least for a few hundred kilometers into Egypt (Baha El Din 2011), but possibly being in the process of expanding farther south along the Nile River towards Sudan. Countries of well known occurrence in approximative west to east and north to south order are: Germany, southern Switzerland (native) and western to central-northern Switzerland (introduced), eastern and southern Austria, Italy, Czech Republic, Slovakia, Hungary, Slovenia, Croatia (including some Adriatic islands, e.g., Krk, Cres), Serbia, Kosovo, Bosnia and Hercegovina, Montenegro, North Macedonia, Albania, Moldova, Romania, Bulgaria, Greece (incl. several islands such as Crete, Lesbos, Samos, Corfu, Kithira, Serifos, Euböa, Tinos), Russia, Ukraine, Georgia, Azerbaijan, Armenia, Turkey, Cyprus, Syria, Jordan, Lebanon, northeastern Egypt, Israel, Iraq, Iran, Kazakhstan, Kyrgyzstan, Uzbekistan, Turkmenistan, Tajikistan, Afghanistan, Pakistan, and in Xinjiang Province north-western China (Mebert 2011a; Jablonski et al. 2023c, d). The single record from southern Poland (Vlček et al. 2010) was recently confirmed with more material by Zając et al. (2019, 2022). Its limits are primarily set by unsuitable habitats, such as a) the water-poor arid areas in north-western China, southern Iran, and Arabian countries as far as western Egypt, and b) cold regions north of the 53° latitude and those of high elevations from the Chinese Tibetan plateau south to the Karakoram-Himalaya massif in eastern Pakistan and India (Mebert and Masroor 2013; Jablonski et al. 2023c, d). The second most relevant limiting factor appears to be the same or similar ecological niche occupation by a different natricine species. For example, the Viperine Snake (*Natrix maura*) inhabits habitats in south-western Europe and north-western Africa that is otherwise typically occupied by Dice Snakes. Similarly, the Asiatic Watersnake (*Fowlea piscator*) appears to replace the Dice Snake in extreme south-eastern Afghanistan (Kabul River) into southern and central Pakistan and farther east (Mebert et al. 2013). *Natrix tessellata* was erroneously reported from Yemen by a single juvenile specimen (Scortecci 1932), stored today at that Museo Civico di Storia Naturale, Milano, Italy, and was subsequently doubted by Leviton (1977). The author herein has personally inspected and compared that specimen in his wider graduate research of > 500 *N. tessellata* (Mebert 1993, 2011b). Indeed, color pattern and scale characters did not differ from Italian Dice Snakes, suggesting the Yemeni specimen to represent a possible mis-labeled or mis-placed Italian *N. tessellata* instead.That juvenile Dice Snake was initially deposited at a non-secured military hospital in Florence, Italy (Escuola di Sanita Militare di Firenze; Scortecci 1932), where local Dice Snakes may easily have brought in and addeed to an enthusiastically composed reptile collection. On the other hand, Scortecci has been known to have mislabeled preserved specimens before (W. Böhme, K. Mebert, unpubl. information). Another source of erroneous reports of Dice Snakes in Yemen relates to the potential confusion with some phenotypically very similar and piscivorous specimens of the Wadi Racer *Platyceps rhodorachis* occurring in Yemen; see dark-blotched on grey and fish-devouring Wadi Racer on p. 48 in Egan 2007). Other records from France, Belgium and other countries originate from introduced or escaped captive specimens, without the establishment of a population, and will not be further discussed. There is a potential that specimens from the introduced population at the northern shore of Lake Geneva, Switzerland, could cross the lake to reach the southern French coast (see also general accounts and references in Gruschwitz et al. 1999; Mebert 2011a).

Inventories. Based on a renewed monitoring to assess the conservation status of Dice Snakes in Ticino, southern Switzerland, Mebert et al. (2011b) calculated a detection probability of 61% and a site occupancy of 78% of historically known locations. On a national level, Smole–Wiener (2011) and Kammel and Mebert (2011) summarized basic data of *Natrix tessellata* from southern Austria, with latter also reporting on the recolonization of river segments by the Dice Snake after a larger river rehabilitation program and looking at the effects of hydroelectric power plants. Other studies in Mebert (2011a) provided first or updated national accounts on variably combined aspects including distribution, conservation status, habitat and other ecological aspects of *N. tessellata*, e.g., for Slovenia (Žagar et al. 2011), Croatia (Jelić and Lelo 2011), Romania (Strugariu et al. 2011), Bulgaria, including also morphology (Naumov et al. 2011), Ukraine (Kotenko et al. 2011), Georgia (Frotzler et al. 2011), Egypt (Baha el Din

2011), Syria (Shehab et al. 2011), Jordan (Amr et al. 2011), Iran, including morphological variation (Rajabizadeh et al. 2011), and China (Liu et al. 2011), whereas separate restricted surveys were conducted for Kazakhstan (Dubrovsky 1967), Kyrgyzstan (Yakovleva 1964), Tajikistan (Said-Aliev 1979), Uzbekistan (Bogdanov 1960; Tashmuradov 1975; Vashetko 1981), Afghanistan and Pakistan (Mebert and Masroor 2013; Mebert et al. 2013; Wagner et al. 2016; Jablonski et al. 2023c). Regionally within a country, Dínçaslan et al. (2011) showed variation of blood serum proteins and morphology in lake populations from southwestern Türkiye, and Ahmadzadeh et al. (2011) recorded basic morphology and reproductive development in Dice Snake populations from the south-eastern coastal region of the Caspian Sea in Iran. Tuniyev et al. (2011) updated distribution data, accounts on color pattern variation, activity, and conservation of Dice Snakes along the Caucasus isthmus, except for most of Georgia.

Several new peripheral populations and surprising rediscoveries of Dice Snakes have been reported relatively recently, such as the 500 km range extension across the Tarim desert in China (Liu et al. 2011), first populations from the Baltic Sea Drainage Basin (Vlček et al. 2011), rediscoveries on the island of Cyprus (Göçmen and Mebert 2011), recolonization of the capital of Romania, Bucharest, (Strugariu et al. 2011), and the Czech Republic, Prague (Velenský et al. 2011), rediscovered or first confirmation on Croatian islands in the Adriatic Sea, Krk (Vlček et al. 2015) and Cres (Burić and Baskiera 2014). The recent discoveries of Dice Snakes in a valley of the Karakoram-Himalaya mountain range in Pakistan were assessed in terms of glacial refugial expansion routes from Uzbekistan and Afghanistan and the required transgression over a high pass at 3,700 m elevation during the warming period in the Holocene Climatic Optimum (Mebert et al. 2013), recently supported based on genetic and environmental data (Jablonski et al. 2023d).

Dice Snakes generally inhabit a large array of wetlands, including modest saline seas and estuaries, freshwater lakes, ponds, rivers, streams and mountain brooks. Their aquatic habitats are usually rich with fish, the principal prey, but they can switch to frogs where necessary. Originating from wide steppes in Central Asia, they occupy relatively open and even arid areas as long as wetlands provide food and rocky shores or dense reed mats for shelter. These habitat characteristics are distinct from its largely sympatric Grass Snake *N. natrix* and *N. helvetica*, which tends to occupy shadier, thus cooler and more humid, aquatic habitats and is primarily an amphibian predator.

Identification. Summarized from Gruschwitz et al. (1999), a medium-sized snake with a total length up to around 120 cm, claimed up to 130 cm for one insular population (Black Sea); a narrow, pointed head; heavily keeled dorsal scales, usually 4 to 5 alternately arranged rows of dorsal spots/blotches, some blotches of the two middle rows maybe medially fused, usually distinct from sympatric/parapatric Grass Snakes (including *N. helvetica, N. natrix*) and Viperine Snake (*N. maura*) by a combination of 2 to 3 preocular scales, 3 to 4 postocular scales, 8 supralabial scales, of which the fourth or the fourth and fifth supralabial scale touch the lower margin of the eye; further distinct from the other *Natrix* species by 19 scale rows around mid-body, higher ventral scale counts, strongly keeled scales on the upper side of the tail, and the lack of semi-lunar anterior bright/posterior black blotches on the neck as well as the lack of lateral ocelli (ring-shaped blotches).

There is an extensive scale variation across the Dice Snake´s vast distribution, which is underlined by a constant sexual dimorphism (Mebert 2011b, c; Werner and Shapira 2011) with females being considerably larger, exhibiting region-specific lower number of ventral scales (on average 5 less) and subcaudal scales (on average 10 less) than males, but females also exhibit a more posterior reduction of dorsal scale-rows on the trunk, a less posterior position on the tail, a greater relative tail length, body width and posterior head length, and a narrower head, whereas head shape and size also differ between separate Greek island populations in accordance to their principal prey type, anuran vs. fish (Brecko et al. 2011). Principal scale characters (number of ventral and subcaudal scales) vary clinally, mostly with increasing values from west (Italy) to east (Turkey) and from south (Egypt to Iraq) towards north, with the highest scale number in the lowland region of Ukraine and Russia between the northern shore of the Black Sea and the north-western coast of the Caspian Sea. In this region, *Natrix tessellata* exhibits 18 ventrals more than conspecifics in Western Europe. On a microgeographic scale, more than 50 morphological characters were sufficiently powerful to detect significant geographic variation across relatively short distances of 40 to 100 km and helped to identify the origin of introduced Dice Snakes without genetic data (Mebert 2011d), albeit such was later confirmed by molecular studies (Gautschi et al. 2002).

The ground color of *Natrix tessellata* varies from olive to beige, grey, and brown, with 4–5 rows of dorsal blotches common across its large distribution. Small spotted specimens are common in populations from the southeastern Mediterranean between Lebanon and Egypt. Melanistic and spotless (concolor) morphs can be locally absent to be abundant, in particular in a region between the southern Balkan and the Caspian Sea, but occur locally over most of its huge range, including recently discovered ones in the Czech Republic and Italy (Mebert 2011b), Slovakia (Jablonski and Kautman 2017), Montenegro (Gvozdenović and Schweiger 2014) and Slovenia (Cafuta 2011). In addition, a rare striped morph or at least one with longitudinally stretched blotches is known from the Caspian Sea (Tuniyev et al. 2011), Syria, Lebanon, and southern Iran (Mertens 1969, E. Kramer, unpubl. data). It has occurred constantly at Lake Iliki, Greece (Mebert 2011b).

Furthermore, Mebert (2011d) and Gautschi et al. (2002) elaborated on the high frequency of scale abnormalities in introduced Dice Snakes in Switzerland and related deformed ventral scales to fused vertebrae. This and the occurrence of exceptionally short Dice Snakes with up to 20% fewer body segments viewed in the context of inbreeding in introduced populations, following a severe bottleneck of the founding population of ca. 20 adult snakes. Brecko et al. (2011) found a prey-dependent head shape in Dice Snakes, with those consuming frogs exhibiting significantly narrower and more streamlined frontal heads than in populations that consumed fish, suggesting a phenotypically plastic response to the local abundance of prey types. Herrel et al. (2008) found that among the semi-aquatic snakes, frontal striker species, such as *N. tessellata*, have generally smaller heads but also reduced frontal and projected frontal surface areas compared to lateral strikers like *Nerodia fasciata*.

Histological investigations about the Duvernoy's' gland in the Dice Snake, a secretion apparatus in Natricines homolog to the venom glands of viperid and elapid snakes, were conducted by Gygax (1968, 1971), Ovadia (1984), Akat et al. (2011) the skin sensory organs by Walztöhny and Ziswiler (1979), embryonic development by Korneva (1969), and karyology in Manuilova and Pisatets (2008). Other studies on skull morphology are analysed in Andjelković et al. (2016) and referenced in Gruschwitz et al. (1999), with the latter also containing small chapters with references on the postcranial skeleton, hemipenis, and blood cells.

Phylogeny and phylogeography. Analyses by mitochondrial cytochrome *b* sequences and nuclear ISSR-PCR genomic fingerprinting identified nine mitochondrial DNA haplotype clades associated with animals from Europe except for southern Greece, Jordan/Egypt, Turkey, Caucasus, Kazakhstan, Uzbekistan, Crete, and Iran, respectively (Guicking et al. 2009; Guicking and Joger 2011, Kyriazi et al. 2013). Genetic data indicate that *N. tessellata* originated in southwest Asia during the Miocene (first split off by the Iran clade at 9.6 Mya), followed by basal radiation around the Miocene-Pliocene boundary with further differentiation of the European lineages during the Pleistocene (Jablonski et al. 2023d). Excluding rather distinct *N. tessellata* from southwestern Balkan (Greece, Albania), geographic mitochondrial differentiation among European populations is low, reflecting a severe population bottleneck during the late Pleistocene followed by a rapid expansion (Guicking and Joger 2011, Gautschi et al. 2002). In Asia, the Anatolian and Central Asia clades of Dice Snakes show deep divergence from European populations. The two Asian clades began divergence at 3.7 MYA in the Pliocene, with their three, respectively four, mitochondrial lineages radiating ca. 1 M years later (Jablonski et al. 2023d). Their distributions are affiliated with specific river systems and are further restricted by high mountains and extreme deserts.

The oldest fossil records of *N. tessellata* originate from the middle Pliocene and suggest a continuous presence across the East European Plains since that period, with range contraction and expansion following the frequent climatic and topographic fluctuations (Ratnikov and Mebert 2011). During cooler periods and after range contraction, some populations survived isolated in thermally warmer pockets, as for example the four remaining populations in Germany, but also similar accounts for isolated northern populations in the Ukraine and Russia (Kotenko et al. 2011; Litvinov et al. 2011).

Population Aspects. In ideal habitats, such as open rocky shores along fish rich water bodies, either natural or man-made by riparian reconstruction, Dice Snakes are known to reach high densities and large populations, even when introduced (Mebert 2011a, d; Velensky et al. 2011; Metzger et al. 2011; Sterijovski et al. 2011; Tuniyev et al. 2011). Large scale research by international teams found huge numbers of Dice Snakes at such ideal habitats. For example, a Swiss team marked/recaptured Dice Snakes at an introduced site in Central Switzerland and estimated a population size of > 2000 individuals along a 3 km shoreline habitat, corresponding to about 1 snake/m (Bendel 1997). In Romania, Carlsson et al. (2011), did a mark/recapture study along the shore of a brackish water lake next to excavated Hellenistic-Roman ruins at Histria. They individually marked > 2300 Dice Snakes along a 200 m stretch in the first year and > 1500 snakes in the two subsequent years, estimating a population size of > 10’000 individuals. As the ruins are the only rocky microstructure for hibernation for the greater surrounding, likely, in the months close to hibernation, individuals from nearby water bodies within a few kilometers were also present. Sterijovski et al. (2014) marked > 6000 Dice Snakes on Golem Grad, North Macedonia, a small island of 18 ha, estimated to be inhabited by at least 10’000 *N. tessellata*, respectively > 500 snakes per ha. Pauwels et al. (2020) reported a total of nearly 2000 Dice Snakes that were counted basking and foraging for fish along both sides of a one-kilometer-long rocky pier penetrating the Caspian Sea, amounting to a density of 1 Dice Snake/m. Mebert, in Burton (2021), suggested that Dice Snakes were the ideal and likely candidate for Hannibal’s “Bithynian snake bombs”, by catapulting clay pots full of the “viper-like” Dices Snakes thrown a the enemies’ ship during a naval battle at 184 BCE.

Natrix tessellata is also well known for entering saline water. For example, Dice Snakes have been seen in seawater off the coasts of Crete Island (Van der Meijden 2006), the Italian sector of the northern Adriatic Sea (between Trieste and Venice) and observed by fishermen a few km offshore (Mebert 2011e), and all along segments of rocky shores around the Black Sea and offshore islands (e.g., Serpilor Island at 30 km distance from the mainland). In the Azerbaijan sector of the Caspian Sea, *Natrix tessellata* has been observed on abandoned wooden oil drilling platforms up to 8–9 km from the mainland (Tuniyev et al. 2011). In addition, Dice Snakes have colonized recently built artificial islands in the Kazakh sector of the Caspian Sea (Pauwels et al. 2020). The minimal distance between the mainland and these new islands where Dice Snakes were observed is about 50 km. Whether these snakes were accidentally imported with barges importing limestone boulders and soil from the mainland to construct the artificial islands or they were swimming/drifting the large distance remains unclear. Numerous photographic and anecdotal evidence exist from around the Caspian Sea with Dice Snake seen several kilometers offshore, approaching boats, and also climbing into boats and travel like that one Dice Snake that was riding 10 days on an environmental survey ship from the mainland until reaching one of the artificial islands, where it left the ship voluntarily (Pauwels et al. 2020). A study on *N. tessellata* from a marine coastal (Black Sea) environment showed that these snakes could display hypernatremia (e.g., increased plasma sodium) without any apparent ill effect on physiological and behavioral traits and thus are relatively tolerant to salinity. This strongly suggests specific physiological adaptations to withstand hyperosmolality (Brischoux and Kornilev 2014; Brischoux et al. 2017). However, their salt tolerance appears to be particularly suitable to sustain large populations in the Black Sea and Caspian Sea, which are 2–3 times less saline than the Mediterranean.

Activity and Thermal Biology. A radiotelemetric study at three different sites in Ticino, southern Switzerland, revealed an annual linear "home range" of approx. 500 m of terrestrial habitat parallel to the shoreline, consisting primarily of man-made rock walls along a river or lake shore (Conelli et al. 2009, 2011). Within this home range, the radio-tracked Dice Snakes were found only in the immediate surroundings of the open water surface, with 97% of the locations occurring less than 20 m from the water. However, movements showed site-dependent variations. At two sites, Dice Snakes foraged, mated, thermoregulated, and hibernated in the same area. In contrast, at the third site, the snakes revealed substantial seasonal movements for different summer and winter habitats). In spring, they migrated to their summer habitat, a backwater system next to a lake, for all activities (Conelli et al. 2009, 2011). In the fall, the snake returned to the hibernation site, a dam-like rock construction to support an elevated road next to a floodplain. All animals studied remained within the riparian zone during hibernation (maximum distance from water ≤ 10 m), and selected shelters of at least 1.5–4 m above the mean water level, thus, reducing the risk of drowning during late winter high water while still in hibernation. Microclimatic conditions of hibernacula allowed animals to maintain a body temperature between approx. 4–10° C, even when external temperatures decreased below 0 °C in January and February.

A radiotelemetric study was conducted at Prague Zoo, Czech Republic, where wild Dice Snakes colonized a relatively new, rocky embankment, completed in 1989, between Vltava River and the zoo (Velenský et al. 2011). This embankment yielded a higher slope, more crevices, and less shade than the previous embankment. The first Dice Snakes showed up in the mid-1990s. The population increased over the years to reach a density of approximately 180 individuals per hectare, resulting in a population size between 700–800 individuals in 2008. During the study, Dice Snakes hibernated up to 238 days to mid-April. In early spring, the snakes migrated several hundred meters through the zoo's territory in a few days to reach a summer habitat along the river embankment. There, the snakes mated, foraged, thermoregulated, and oviposited, with some individuals regularly entering the zoo to use its gullies and fishponds to hunt. In the fall, some Dice Snakes crawled back through the zoo to return to their hibernacula on a slope at the other side of the zoo. In contrast, some remaining individuals hibernated directly in the river's embankment. Oviposition happened within the first two weeks of July, after which female snakes were left with as little as 40 days to acquire enough food and energy for the following hibernation. Basking was frequently observed on days with a thin cloud cover but sufficient solar radiation to warm the upper surface. On hot summer days, Dice Snakes usually moved under rocks and practiced thigmothermy, i.e. gaining sufficient body temperature by acquiring heat from the warm surface.

At the most northern population of *N. tessellata* near Samara along the Volga River, Russia, Litvinov et al. (2011) investigated thermal behavior of that all-melanistic population. They survive around southern exposed rocky riparian bluffs. Snakes were active at surface air temperatures ≥ 14.0° C and substrate temperature ≥ 13.2° C. Females selected more open areas than males. When internal body temperature reached 28° C, Dice Snakes moved to cooler sites.

Reproduction. Males are generally the first gender to emerge from hibernation, supposedly to activate spermatogenesis (e.g., Kärvemo et al. 2011). Test activity in males lasted the entire season, whereas vitellogenesis in females is seasonal. Mating usually follows a few weeks after hibernation, primarily in April–June, less frequent in March or July (Gruschwitz et al. 1999). Mass mating and mating ball formations are common in dense populations (Mebert and Ott 2011), whereas late summer/fall mating rarely occurs (Gruschwitz et al. 1999; Ajtić et al. 2013). Females begin with their yolk deposition early in May, with large follicles reaching a maximum level in summer, late June–early July, and oviposition during July and early August, e.g., in Switzerland (Bendel 1997, 2001), northern Iran (Ahmadzadeh et al. 2011), and North Macedonia Ajtić et al. (2013). Latter authors also found that 54% (336 of 621 individuals) of adult females examined were gravid. The mean clutch size was nine (range 1–20) among 699 females, where the follicles could be counted by palpation. In central Italy, the mean clutch size was approximately 15 (Luiselli and Rugiero 2005), whereas a maximum number of 37 eggs in captivity was given by Dimitropoulos (1989).

Foraging and Diet. *Natrix tessellata* primarily consumes fish in its European range but often feeds on frogs in western Asia and occasionally adds a newt or salamander, and even rarer a young rodent, duck, lizard, or invertebrate (Gruschwitz et al. 1999; Weiperth et al. 2014, and references therein). Non-fish species in the diet were especially pronounced in deserts, high mountains, and dry Asian and Mediterranean areas. Generally, any fish is preyed that an individual Dice Snake can overcome. They forage during day, but also during warm nights (at ca. 20°C or more), in fresh or saline water, e.g., with large populations in the Black Sea and Caspian Sea, but have also been observed in the Adriatic and Mediterranean Seas. Open water fish are ambushed by anchoring tail on rock or submerged water plants, whereas ground fish are actively searched in crevices of subterranean rocks at least as deep as 10 m. In populations where *N. tessellata* show a white tip on an otherwise black tongue, the snakes have been observed to slowly tongue-flick when a fish has approached near striking distance (Mebert 2007).

Radiotelemetric studies revealed that *N. tessellata,* inhabiting a rocky wall and bank along a river in Germany, descended only every 4–5 days from their terrestrial shelter to forage in the water up to 15 m away and 100 m along the shore. Still, they else remained on land to rest and thermoregulate (Neumann and Mebert 2011). They were mainly active at air temperatures between 20–26 °C on a partially cloudy sky. Extensive accounts were summarized for a lake population in North Macedonia by Ajtić et al. (2013): all Dice Snakes observed fishing were in ambush position near the shore (< 5 m offshore), sometimes in high density; snakes were rarely observed swimming more than 100 m from the shore (n < 5); the proportion of fed snakes varied across seasons; these snakes rarely foraged early in the active season in spring (late April to early May); only 15.4% of the snakes were observed with prey in their stomach with this proportion increased markedly (44.1%) in summer (June–August), and the snakes ceased to fish in autumn (September–October).

A study on the stomach content of Turkish Dice Snakes showed the usual dominance of fish (72.4% of items), followed by amphibians (14.5%), but also a few unusual stomach items, such as insects (7.9%), gastropods (2.6%), one reptile, and one mammal (Göçmen et al. 2011b). While the invertebrates may have been ingested indirectly through primary prey, the reptile, a large Balkan Green Lizard (*Lacerta trilineata*, approx. TL 200 mm), and an adult Forest Dormouse (*Dryomys nitedula*, approx. TL 320 mm), were found in large female *N. tessellata*. The gastropod *Lymnaea stagnatilis* and even a juvenile Northern Viper (*Vipera berus*) were found in the stomach of Dice Snakes from the Volga Basin, Russia (Bakiev et al. 2011).

Long-term studies in central Italy investigated the biological aspects of *N. tessellata* at three sites (Capula et al. 2011). Among others, they found an ontogenetic shift in the lower size limit of prey in all three study areas. The larger snakes were selected against smaller prey sizes, as the minimum prey size increased with snake size (Luiselli et al. 2007). This is true especially for females, likely due to the high energy demands of females for reproduction. Likewise, a remarkable and significant inter-sexual variation in the composition of the diet is correlated with the considerable body size differences between the two sexes (females being more significant than males). For subsequent digestion, gravid females selected significantly higher substrate temperatures than non-gravid ones.

Mebert and Pölzer (2011) presented two fatal accidents of Dice Snakes by which the hunted groundfish snapped back and locked onto the snakes' upper jaw with subsequent drowning of both prey and predator. Velikov (2011) illustratively presented material of Dice Snakes feeding on introduced spiny fish, whereas Mebert (2011f) revealed the unusual stomach contents of three Dice Snakes that consumed rocks or peach stones.

Predators and Defense. Various predators feed regularly on Dice Snakes: Smaller mammals such as the Brown Rat (*Rattus norvegicus*), introduced Muskrat (*Ondatra zibethicus*), Short-tailed Weasel (*Mustela erminea*) Least Weasel (*Mustela nivalis*), reptiles such as the Large Whip Snake (*Dolichophis jugularis*) in Israel, and numerous bird species (especially *Ardeidae* herons, Black-headed Gull (*Chroicocephalus ridibundus*), Kingfishers (e.g., *Halcyon smyrnensis*) are listed and referenced in Gruschwitz et al. (1999).

Predators on Dice Snake on Golem Grad Island, North Macedonia, included European Otter (*Lutra lutra*), with > 50 feces usually containing large amounts of snake scales and vertebrae, and different birds that preyed heavily on the snakes (e.g., *Bubo bubo, Ardea cinerea, Accipiter* sp., *Buteo* sp., *Larus* sp.). Nose-horned Viper (*Vipera ammodytes*) also commonly preyed on Dice Snakes (Ajtić et al. 2013). The Balkan Whip Snake (*Hierophis gemonensis*) and the Gull (*Larus cachinnans*) have been documented as predators in Croatia (Jelic and Laus 2011a, b), and the Raccoon Dog (*Nyctereutes procyonoides*) in Musilová and Zavadil (2011). Finally, ecto- and endoparasites have been frequently analysed and summarized in Gruschwitz et al. (1999), Mihalca (2011) and Bakiev et al. (2011), but also in newer studies, for example Kirillov and Kirillova (2019).

Active defensive behavior is manyfold and individually variable. It can include vomiting of freshly captured food, excretion of faeces with an intense fish odor, secretion of a yellow liquid from glandular fields next to the cloacal opening that smells of butyric acid, balling – primarily associated with hiding the head in or under the coils of the body, violent tail wagging, and body undulating when lifted, but also a viper-style defense, such as flattening of the entire body, audible hissing, and fake bites. Such supposedly Batesian mimicry with head flattening and fake striking in Dice Snakes has been found in populations in proximity or sympatry with local vipers instead of viper-free localities (Bijelica et al. 2023). However, in 20+ years of experience handling 1000s of Dice Snakes, the author has never observed a true bite (K. Mebert, unpubl. Data). A death reflex, like that of the Grass Snake (*Natrix natrix* group) or Hognose Snake (*Heterodon platirhinos*) is also part of individual defense repertoire and a combination with reflex bleeding in the mouth area, albeit rarely.

Sympatric *Natrix* species. Grass Snake spp., *N. natrix* sensu lato, prefer small, temporary, and permanent water bodies, such as ponds in forested situations, wet meadows, and marshes, with large breeding concentrations of their preferred prey, frogs, and toads. In contrast, *N. tessellata* is more aquatic, frequent comparatively more open water courses in rockier and drier areas and prefers more fish. The habitat partitioning was also confirmed in sympatry in southern Croatia (Janev Hutinec and Mebert 2011) where the diet of *Natrix natrix* consisted mainly of amphibians with the occasional open water fish, whereas *N. tessellata* fed exclusively on fish, and dove deeper to hunt for benthic fish. An increased underwater vision ability of *N. tessellata* compared to *N. natrix* has been technically investigated and confirmed by Schaeffel and Mathis (1991). Both can be common and coexist in large reed grass habitats in the lowland of Eastern Europe and semi-arid landscapes, yet *N. tessellata* is generally viewed to be more aquatic (Gruschwitz et al. 1999).

Few studies compared *N. tessellata* with the ecologically similar Viperine Snake *N. maura*. They are largely parapatric and occupy the same habitat, *N. tessellata* in southeastern Europe and *N. maura* in southwestern Europe. Scali (2011) compared temperature and other ecological variables between these two species at one of their few sites of natural sympatry in northern Italy. Dice snakes were observed in comparatively deeper streams, being more piscivorous and less nocturnal, possibly benefitting from such habitats along the Po River, the principal large river system across northern Italy. These two species were also compared at a site in Lake Geneva, Switzerland, where *N. maura* is native, and *N. tessellata* was introduced many decades ago. Compared with the Viperine Snake, the Dice Snake occupied shore zones that were relatively more open and inhabited more often steep slopes (Mazza et al. 2011). Metzger et al. (2011) found a large overlap in the trophic niche between both species at the same site, regarding seasonal preferences and prey types. A higher fecundity and a larger body size render the alien *N. tessellata* probably a more competitive capacity and possibly a key role in the population decline of the native *N. maura* over the last decades. Finally, much like in other natricines, interspecific hybrids between *N. natrix* and *N. tessellata* have been produced in captivity up to the F2 generation and are rarely observed in nature, whereas a hybrid between *N. tessellata* and *N. maura* has been reported only once between captive specimens (Mebert 2010; Mebert et al. 2011a), but was recently shown by molecular analysis (Schöneberg et al. 2023).

Conservation. Major threats through habitat degradation, including water contamination, are ubiquitous for agricultural, housing, industrial, and traffic purposes. For example, a high number of road-killed *N. tessellata* was recorded during the summer along a stretch of 2.1 km on the north shore of Prokopos Lagoon near Strofylia in southern Greece (Ioannidis and Mebert 2011). Extrapolated to the entire season, they estimated that> 1000 Dice Snakes are killed on that road segment yearly. Another threat resulted in high mortality of Dice Snakes through illegal fishing around Golem Grad Island, a protected national park in North Macedonia. A total of 44 Dice Snakes drowned in a single small fishing net, set for 3–4 hours in the water after they became entangled themselves chasing fish embedded in the mesh. Thousands are killed yearly in protected water around the island (Sterijovski et al. 2011, 2014).

In Central Europe, Lenz and Schmidt (2011) summarized the results of extensive measurements to support the three remaining populations of Dice Snakes in western Germany. On the river Mosel, the core habitat was improved by reconstructing the lentic water courses with protective boulders and rock walls, providing piles of decomposing plants, branches, and organic waste material for oviposition. They also tested different guidance and deflection systems to avoid road-kills. Open gravel areas were recreated on the river Lahn, and two new founder-populations were started with captive-bred juveniles Dice Snakes (Trobisch and Gläßer-Trobisch 2011). A fourth isolated population at the river Elbe in northeastern Ger

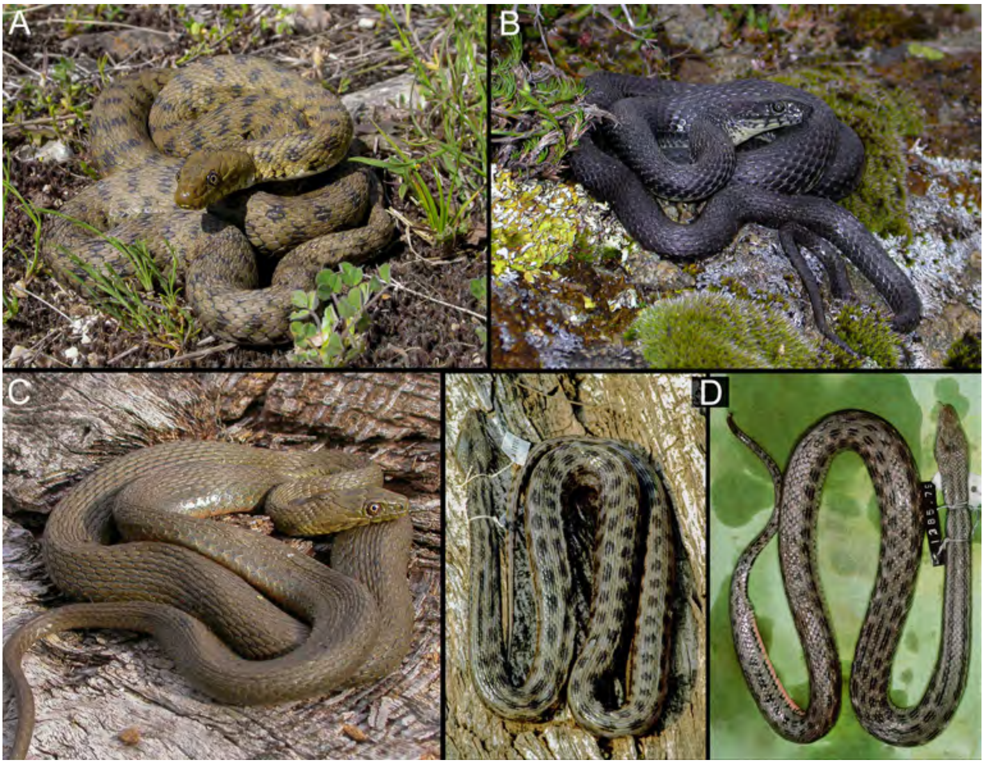


Figure 28.5: Natural color pattern variation of Dice Snakes (*Natrix tessellata*) from: A), B), C) trinational Lake Prespa, North Macedonia, Albania, and Greece. Such co-occurring variations are common in some dense populations, including Lake Prespa, Lake Beysehir in Turkey, or Caspian Sea; D) partially striped specimens, here deposited at the Museum of Natural History Geneva, Switzerland, were known from Lake Yliki, Greece, and occasionally other sites from its more southeastern distribution. Photo credit: A)-D) Konrad Mebert.

many has become extinct but was successfully repopulated with specimens from the nearest populations (same river system) from the Czech Republic (Obst and Strasser 2011, Strasser and Peters 2014, Strasser 2020). In fact, bank and shoreline reinforcements made of big stone blocks (rip-rap) with an abundance of interstices and herbaceous vegetation or little shrub cover appear to be particularly attractive to Dice Snakes. New rip-raps along the river between a retention basin in the forest and the watercourse farther down the village have been colonized within less than three years after their construction (Conelli et al. 2009, 2011). Dry stone and rip-rap walls offer many places for safe shelters and thermoregulation and are potential sites for oviposition.

On the next page.The Eastern Ribbon Snake, T*hamnophis saurita* from central Florida. Photography JCM

29. Thamnophiine Clade

29. The Thamnophiine Clade

The New World natricids snakes are monophyletic, descended from an ancestor that immigrated from the Old World. They form the clade Thamnophiine, with some of the planet's most studied serpents. Zaher et al. (2019) found the genus *Storeria,* the sister to all the other New World natricids clade members. *Storeria* comprises five ground-dwelling cryptozoic snakes that feed primarily on worms and mollusks. While they tend to live on damp soils, often near bodies of water, they are not semi-aquatic. All species are viviparous.

The most basal Thamnophiine clade recovered by Zaher et al. (2019) included the *Liodytes, Clonophis, Haldea,* and *Virginia* gener*a.* These are a mixture of fossorial, terrestrial, and semi-aquatic species. *Clonophis* exploits an unusual aquatic habitat – crayfish burrows; both *Haldea* and *Virginia* are small fossorial species. *Liodytes* contain some of the most aquatic North American snakes.

The ancestor of North American natricids immigrated from Eurasia sometime before the early Miocene (~19–18 Ma). We know this because the earliest known Western Hemisphere natricid fossils date to the early Miocene, and we know they shared an ancestor because of shared anatomy and DNA.

Alfaro and Arnold compared three genes from many North American natricid snakes. They found that they shared a distant ancestor and formed three distinct clades: a water snake clade, a garter snake clade, and a novel semi-fossorial clade. Living around the suburban quarry were members of each of the three clades. Alfaro and Arnold's work suggested that the most basal Western Hemisphere natricids is the fossorial Kirtland's Snake (*Clonophis kirtlandi*). While Kirtland's Snake is unknown from the area around the quarry, there is a population within 10 miles. Both the Kirtland's Snake [Figure 11–6b] and its sister, Dekay's Snake, occur in wet prairie or grassland habitats. Kirtland's Snake is fascinating because it is primarily fossorial and appears to use the chimney building crayfish burrows as a hibernation site (suggesting it hibernates underwater or at least in the water). *Clonophis* has a fractured distribution with isolated populations widely scattered over Illinois, Indiana, Ohio, and bordering states.

North American natricids are perhaps the best-known serpents. Garter snakes, water snakes, and brown snakes are often abundant in urban areas with remnant habitats. Natricids have continually adapted to aquatic habitats and reverted to a life on land, only to return to the water. At least a few garter snakes are entirely terrestrial, but many forage along streams or ponds, while others are aquatic.

Jean-Claude Rage proposed that natricids invaded North America from Europe via a land bridge. Since the oldest natricid fossils are from the early Miocene, the land-bridge migration and colonization must have occurred before this date. An early Eocene land bridge connecting Europe-Greenland-North America with a subtropical climate may explain the expansion of these snakes into the Western Hemisphere. But how probable is it that snakes used a high latitude land-bridge to disperse from Europe through Greenland and into continental North America in a mild or cold climate?

A snake den in an abandoned railroad yard in Portage County, Wisconsin, provided a valuable clue. A friend had discovered the snake den near his summer house and took several of us for a tour. The circular cement foundation was mostly covered with rusted metal; it had been used as a giant turntable to switch railroad cars from one track to another. The cement cistern was about 2.4 m deep and partially filled with water. Shade from the metal covering had insulated the layer of ice and kept it from melting, but the ice cover was completely solid and transparent. Eastern Garter Snakes (*Thamnophis sirtalis*) and Western Fox

Snakes (*Pantherophis vulpinus*) were submerged beneath the ice with their posterior bodies wrapped around debris. The snakes had been in the water since the previous fall; this was early May. With a solid ice cover in place since January or earlier, the snakes had not filled their lungs with air for at least five months.

Field observations and experiments by Costanzo (1986, 1989a, 1989b, 1989c) compared submerged and non-submerged garter snakes from this Wisconsin den and found submerged snakes in water at 5° C. reduced their oxygen consumption by 54% and their heart rate by 77% over experimental snakes hibernating in the air under the same conditions. Snakes hibernating underwater lived in acidic (5.5–6.5 pH), hypoxic (dissolved oxygen was 2.9 ppm) groundwater. And yet, the snakes were carrying out aerobic respiration, using oxygen that diffused through their skin from the water for five months, a remarkable ability, but one that could have been anticipated. Carpenter (1952) studied garter snakes in Michigan in the early 1950s and observed five Eastern Garter Snakes hibernating in the burrow of a crayfish. He wrote,

> "…many snakes hibernate completely submerged in water in underground tunnels. It seems that this should be possible, provided the water is very cold."

Costanzo's experiments and the significance of snakes being able to spend months submerged in cold water have been long overlooked. The ability of natricids to survive submerged under the ice for months is valuable for surviving long Midwestern winters and could explain how snakes dispersed from Eurasia to North America by colonizing high-latitude land bridges. Even if the land bridges had a seasonally cold climate, these snakes could have made the intercontinental trip.

Ulrich (1989) noted that freshwater snakes usually hibernate on land. Still, they appear capable of aquatic hibernation, and many do not do so because of the risk of death from anoxia. Some terrestrial snakes are known to hibernate underwater and can do so in the laboratory for months. This behavior is considered opportunistic in the field, as there is no evidence to suggest that snakes can tolerate extended anoxia.

More than 100 species of natricids use aquatic environments to varying degrees; most feed on aquatic animals. Bilcke et al. (2007) compared feeding behavior in natricids believed to be dietary generalists and specialists. The generalists were thought to forage for food by open-mouth searching, holding their mouth open, and sweeping it through the water until they made contact with prey. These species strike slowly to the side, perpendicular to the body's long axis, and do not seem to depend upon vision. Specialists were thought to hunt from ambush, be visually alerted by the presence of prey, and strike forward parallel to the long axis of their body. However, Bilcke and colleagues also looked for a correlation between prey density and strike behavior. Two European natricids (*Natrix tesselata* and *Natrix maura*) were compared to the North American *Nerodia fasciata*. They found that prey-capture strategies in natricid snakes were not correlated with diet but with prey density. For example, snakes feeding on fish in a school or concentrated in shallow water use the open mouth technique, while snakes feeding on fish at a low-density strike from ambush.

Striped Crayfish Snake
Liodytes alleni (Garman, 1874)

Distribution and Habitat. Wetlands include marshes, slow-moving streams, and swamps in Florida and southeastern Georgia. The type locality is in the vicinity of Jackson-

Figure 29.1. Distribution of *Liodytes alleni.*

ville, Florida.

Identification. The total length is 330–500 mm. The stripes are indistinct and located laterally on the dorsum. The ventral surface is yellow with dark spots. Average adults have total lengths of 500-600 mm, and the maximum reported total length is 70.5 cm (Demuth 1997). Neonates are 153-291 mm in TL. The head is not much wider than the body. The nares are directed dorsolateral, and compared to congeners, the eye is large with a small pupil. The scales are smooth except on the dorsal area of the tail, where they are always keeled. Females have 110-133 ventrals (males average 2-3 fewer) and 53-61 subcaudals (males have 59-69). Dorsal scale counts are 19- 19- 19 (or 19-19-17 in some males). A single internasal, coupled with smooth dorsal scales, distinguishes *L. alleni* from other members of the genus. Other scale characteristics include two prefrontals, a single preocular, two nasals (partially divided by the nostril), three or four postoculars, loreal present, 1 + 2 temporals, eight (sometimes seven or nine) upper labials, 11 (sometimes nine or ten) lower labials, and a divided cloacal scute. Females are the larger sex. It can be distinguished from the Glossy Crayfish Snake (*Liodytes rigida*) by the single row of ventral spots (*L. rigida* has two rows) (Dorcas et al. 2003).

Natural History. The diet is composed of hard-shelled crayfish. However, this nocturnal, highly aquatic species will also feed on aquatic salamanders, small frogs, tadpoles, glass shrimp, and the larvae of dragonflies and damselflies. Predators include crayfish, large fishes, sirens, alligators, other snakes (*Coluber constrictor*, *Lampropeltis getula*, *Agkistrodon piscivorus*), river otters, raccoons, Red-shouldered Hawks, Great Blue Herons, Great Egrets, and Sandhill Cranes.

Mating probably occurs in the spring, and the young are born in the late summer or early fall. Litter size is 4-12, with larger females producing more young.

Black Swamp Snake

Liodytes pygaea (Cope, 1871)

Distribution and Habitat. Black swamp snakes are highly aquatic and extremely secretive. Individuals hide under debris or vegetation at the water's edge, particularly on sunny spring days. Open aquatic habitats include Carolina bays, roadside ditches, sphagnum bogs, sawgrass prairies, and the margins of heavily vegetated ponds and lakes. Large populations occur in wetlands with dense vegetation that dry periodically and lack fish but have abundant amphibians. They inhabit the Gulf Coastal Plain from North Carolina southward to Florida and west to southeast Alabama. Type locality: Volusia Co., Florida.

A polytypic species with three subspecies recognized. [*S. p. cyclas*: Florida; Type locality: Indian Prairie, 2-8 miles NE of Lakeport, Glades County, Florida; *S. p. paludis*: North Carolina, South Carolina, Georgia; Type locality: Camp Davis, Near

Identification Head distinct from the body; eyes medium, about the same size as the distance between the anterior margin of the eye to the nostril. Black dorsum with faint pale lines running through the center of three to five lateral scale rows. Ventrals metallic red with the dorsal color extending on the anterior edges for about one-third of the width; labials grayish olive. A small snake, maximum length, about 425 mm. Body moderately slender with a short tail (0.15-0.25 of total length. Rounded rostral, two internasals, two prefrontals, a frontal, two supraoculars, and two parietals. Nasal single, nostril near upper margin with a suture extending to the labial border. Eight upper labials and nine lower labials. Two pairs of chin

Figure 29.2. L*iodytes alleni* from Florida.
Photography by Jance Carter.

shields, subequal in length. Dorsal scales are smooth, rounded, and without apical pits. Lower scale rows are widest, decreasing width dorsally; dorsal scale rows 17 at midbody reduced to 15 posteriorly. Ventrals 112-134; cloacal plate divided; subcaudals paired, 35-45 in females; 46-56 in males (Dowling 1950).

Natural History. Black Swamp Snakes are active day and night and forage in submerged vegetation. Diet includes small fish, tadpoles, and small frogs. This species has been found

Figure 29.3. Distribution of *Liodytes pygaea.*

to prey on aquatic salamanders, particularly larval and paedomorphic mole salamanders, and leeches in South Carolina. Elsewhere they feed on aquatic salamanders in the family Plethodontidae. They can survive long (multiple years) droughts by aestivating within dried wetlands and survive better than other water snakes. They recover rapidly from droughts by feeding during pregnancy and investing ingested energy directly into offspring (income breeding). Swamp snake populations seem to thrive post-drought years when amphibian prey is abundant. Females give birth to up to 23 live young in late summer (Winne et al. 2005).

Figure 29.4. *Liodytes pygaea* **from North Carolina.**
Photography by JCM

Glossy Crayfish Snake

Liodytes rigida (Say, 1825)

Distribution and Habitat. Eastern Texas, southeast Oklahoma, southern Arkansas, Louisiana, Mississippi, southern Alabama, southern Georgia, northern Florida, South Carolina, eastern North Carolina, and Virginia. Type locality: the southern states. A polytypic species with three recognized subspecies. *Liodytes r. sinicola*: Texas, Louisiana, Florida, Alabama; Type locality: Beaumont, Jefferson County, Texas. *Liodytes r. deltae* Louisiana; Type locality: Paradis, St. Charles Parish, Louisiana.

Identification A small- to medium snake with glossy skin, maximum size 797 mm. The head, body, and tail dorsum are uniformly chocolate brown, with two narrow, black stripes on either side of the midline that are difficult to detect. The ventral surface is cream with two rows of black spots, often half-moon shaped on either side of the midline. Cream pigmentation on the venter invades the first dorsal scale row and fades into brown. The pale centers on the first scale row form a lateral stripe; labial scales are white. Ventrals 120-136; subcaudals 51-63; dorsal scales keeled, in scale rows 19 at midbody; upper labials seven; lower labials 10; loreal scale absent; one preocular; two postoculars; one primary temporal scale, secondary temporal may be one to three.

Figure 29.5. Distribution of *Liodytes rigida.*

Natural History. The diet is primarily on crayfish, and its prey-handling strategy includes attacking, then coiling to immobilize the chelipeds of the crayfish. Followed by orienting the abdomen so the snake's upper jaw can bite the ventral abdomen's soft tissues, resulting in immobilization or death of the prey, followed by consumption from the caudal end (Tumlison and Roberts 2018). The crayfish *Creaserinus danielae* is eaten by this snake, which uses the burrows made by this crayfish (Loughman et al. 2020). Durso et al. (2013) found this species to be a strict dietary specialist that relies only on crayfishes. This species was notably absent from wetlands without fishes, partly because their probability of site occupancy in this area is strongly related to its proximity to flood plain habitats than to the abundance of their preferred prey. Females give birth to litters of 6-14 young in late summer or fall.

Kirtland's Snake

Clonophis kirtlandii (Kennicott, 1856)

Figure 29.6. Distribution of *Clonophis kirtlandii.*

Distribution and Habitat. The species ranges from northeastern Missouri and southeastern Wisconsin through Illinois, southern Michigan, most of Indiana, and Ohio to western Pennsylvania and north-central Kentucky (Conant, 1943). Tucker et al. (1977) reported localities in Illinois, Indiana, Kentucky, and Ohio. Wet meadows and adjacent woodland; several populations are known from urban areas. Conant (1943) stated that *Clonophis* is a typical snake of the Prairie Peninsula, where it had survived as a relict population of the postglacial period when prairie conditions were widespread. Type locality West Northfield, Illinois.

Identification. A small (maximum total length: 622 mm), moderately stout natricid snake. Upper labials are 4-7 (usually six) and 6-9 (usually seven). Ventrals number 121-137; subcaudals 44-69.

Dorsal scales overlap, are strongly keeled, and slightly notched posteriorly with two faint apical pits (absent in many individuals, according to Conant (1961). The typical scale row formula is 19-17 with an occasional further reduction to as low as 14. Tail length constitutes 19-24% of the total length in adult females and 23-28% in adult males. The dorsal pattern consists of four alternating longitudinal rows of 43-65 rounded black or dark brown blotches on a brown to gray-brown (often with a red tint) ground color. Blotches tend to be indistinct posteriorly. Some specimens may also have dark spots adjacent to the venter that alternate with the lower row of large blotches. The venter is pink to brick red medially, becoming yellow anteriorly, often with dark stippling. Laterally the ventrals are gray with large black spots

Figure 29.7. *Liodytes rigida,* **northern Florida.**
Photography by Jake Scott

that form two conspicuous rows. The top and sides of the head are black, dark brown, or olive, plain or inconspicuously mottled. The labials, chin, and throat are yellow or cream except for a dark area extending down from the side of the head onto the last upper labial. Juveniles are often so dark that the dorsal pattern is obscured; the venter is bright and like adults.

Natural History: Diet includes earthworms, leeches, and slugs. A highly secretive, nocturnally active species that shelters beneath logs and surface debris, and in crayfish burrows, by day. When threatened, it flattens its body and becomes rigid. Mates in May and gives birth to 4-15 young in August or September. Neonates are 100-170 mm in total length.

Predators include other snakes and birds. This fossorial snake uses an unusual aquatic microhabitat, crayfish burrows. Brust et al. (2020) found a Kirtland's Snake outside its hibernaculum on 26 December in Fulton Co., Illinois, with dried mud adhered to its skin at 15°C.

Conant (1943) noted that *C. kirtlandii* is far less aquatic than members of the genus *Nerodia*. He said that it swims readily and usually occurs in wet meadows rather than in the water. Its habits are much more like those of *Thamnophis butleri*, *Thamnophis s. sirtalis*, and *Storeria dekayi* than they are to *Nerodia*. The species avoids large bodies of water and frequently occurs in small ponds, streams, bogs, and woodland pools that are temporary or seasonal. In the more open habitats, its presence is usually associated with precipitation, abundant during and after rainy periods and absent during droughts.

Graham's Water Snake

Regina grahamii Baird and Girard, 1853

Distribution and Habitat. The margins of mud-bottom and rocky-edged marshes, oxbow lakes, rivers, and streams in areas with abundant crayfish are frequently inhabited. Marshes and other wetlands in Texas, western Mississippi, Louisiana, Oklahoma, southeast Kansas, southeast Nebraska, Iowa, Missouri, Arkansas, Illinois, and western Alabama. Type locality: Rio Salado, Texas.

Identification. A brown dorsum with a yellow venter and three light stripes running the length of the body, a yellow, light olive, or tan lateral stripe encompasses the lower three scale

Figure 29.8. *Clonophis kirtlandii*
Photography by Stephen Barten

rows. It is bordered below by an irregular, narrow black line on the outer margins of the ventrals and occasionally bordered above by a fainter dark line between the third and fourth scale rows. In addition, a dark median stripe 2–3 rows in width may be present. The pattern and a single cloacal plate will distinguish this species from other striped and semiaquatic natricids. Most specimens are 460–710 mm; the maximum known length is 1.194 m. Dorsal scale rows are keeled in 17–20 rows at midbody; males 162–175 ventrals; females 155–178 ventrals; male subcaudals 51–67; female subcaudals 60–67. Head scales are one loreal, two preoculars; two or three postoculars, upper labials seven or eight; lower labials nine to eleven (Anton 2019).

Figure 29.9. Distribution of *Regina grahamii*

Natural History. Of 104 digestive tracts examined by Hall (1969), 32 (30%) contained food. Of the 38 food records, 33 were crayfish remains, and five could not be unidentified. Crayfish remains were easily identified by the presence of the digestion-resistant gastroliths. Several stomachs contained unidentified nematodes. All the crayfish in the digestive tract had soft exoskeletons, indicating that they may have been in the process of molting at the time of death. Crayfish had been swallowed headfirst and abdomen- first with approximately equal frequency.

Reproduction. Females usually are capable of reproduction before their third spring. One 422-mm female carrying eggs may have been a year older than most individuals her size but stunted in growth. Thirteen of 21 potentially reproductive females were gravid. (All nongravid females were in the 50- to 60-cm size range.) Litter sizes range from 10 to 27, and oviductal eggs are 9-39 (Hall 1969).

Queen Snake

Regina septemvittata (Say, 1825)

Figure 29.10. Distribution of *Regina septemvittata.*

Distribution and Habitat. Branson and Baker (1974) described the optimal habitat for Queen Snakes as small to medium, shallow streams with moderate currents and rocky banks and bottoms. Forested streams, ponds, and quarries from Southeast Ontario, Canada, southward into the eastern USA, including the states of Arkansas, southeast Wisconsin, northeast Illinois, Michigan, Indiana, Ohio, western New York, Pennsylvania, Maryland, Delaware, West Virginia, Virginia, Kentucky, Tennessee, North Carolina, South Carolina, northwest Georgia, Alabama, Mississippi, southwest Missouri, northwest Florida. Type locality: Pennsylvania.

Identification. The dorsal color is brownish to olive, with a yellow stripe on each side, flanking three narrow dark dorsal stripes. Four brown stripes mark a yellow venter. The labials, chin, and throat are cream to yellow. Dorsal scales are weakly keeled, with two apical pits, and occur in 19 rows at midbody, reduced

Figure 29.11. *Regina septemvittata***. Will County, Illinois. Photography by JCM**

to 17 rows posteriorly. The venter has 118-159 ventrals, 47-89 subcaudals, and a divided cloaca1 plate.

Natural History. Queen snakes are dietary specialist feeding on recently molted crayfish, and they are highly aquatic and less secretive than other crayfish snakes. They are often observed along streams and rivers basking on rocks or streamside vegetation, often alongside Northern Watersnakes (*Nerodia sipedon*). Queen snakes will take refuge under rocks along stream edges. However, unlike glossy and striped crayfish snakes, queen snakes generally avoid hard-shelled crayfish, restricting their diet to soft, newly molted crayfish. Queen snakes are primarily active during the day and occasionally active near aquatic habitats at dusk. Mating occurs in the spring, and females give birth to 5–23 live offspring in the late summer. Densities of 6 to 63 *R. septemvittata* per kilometer of the stream were estimated in central Kentucky by Leuenberger et al. (2019).

Figure 29.12. *Regina grahamii* **(A) DuPage Co., IL, (B) Sedgewick Co. Kansas.**
Photography by Nathan Kutok

Four geographically distinct mitochondrial lineages within *R. septemvittata* were found, and multilocus species delimitation analyses showed support for recognizing these lineages as different species by Flilpen (2016). Species divergence time estimates indicated all lineage divergences for *R. septemvittata* occurred relatively recently during the Pleistocene. Historical demographic analyses indicated the Northern lineage, which occupies formerly glaciated areas, had the highest recent increase in population size, likely due to post-glacial range expansion. Ecological niche modeling analyses indicated lineages occupy unique niches, but niche conservatism has been the more prominent pattern of niche evolution.

Conservation Status: Queen snakes are common in the Piedmont and mountains. They are not protected in most of their range but are protected throughout the state of Georgia. Observations suggest that this species may have declined in many areas of the Piedmont, presumably due to the siltation and channelization of small streams. Maintenance of clean, rocky streams and rivers so that an abundance of crayfish remains critical for this species.

Green Water Snake

Nerodia cyclopion (Duméril, Bibron & Duméril, 1854)

Distribution and Habitat. Uses wetlands, lakes, and streams that may be open or wooded from eastern Texas, Louisiana, Arkansas, southeast Missouri, s Illinois, extreme western Tennessee, southern and western Mississippi, southern Alabama, southeastern Georgia, extreme northwest Florida, southern South Carolina, extreme western Kentucky. Type locality: New Orleans. Type locality: Indianola, Calhoun Co., Texas. It will also use salt marshes and has been reported to be as common in salt marshes as in freshwater (Brown 1950; Guidry 1953).

Identification A heavy-bodied snake reaching 1295 mm. Neonates are 187-305 mm in total length. Dorsal coloration is olive or brown, and subocular scales keep the labials from entering the orbit. Dorsal scales are in 25 or 27 rows at midbody and are keeled to two apical pits. Ventrals 133-148, subcaudals 57-78. *Nerodia cyclopion* and its sister *N. floridana* can be distinguished from other North American *Nerodia* by the presence of one or more subocular scales and an indistinct pattern of about 50 mid-dorsal bars alternating with a lateral series of bars.

Natural History. A highly aquatic species that leaves the water during heavy rains and moves as much as 100 m from the water (Kofron 1978). It basks during the day and adjusts its behavior by season. The diet of this species seems to be opportunistic. Gibbons and Dorcas (2004) consider this species an opportunistic aquatic feeding species that will take salamanders, fish, and crayfish. However, Camp et al. (2020) proposed it is likely a fish specialist suggested by its small eyes. Mushinsky and Hebrand (1977) found almost all fish in the diet of a Louisiana population.

Reproduction. Copulation occurs in the water and on land (Krofron, 1977; Mead, 1934) in the spring (April-May), and parturition has been reported in July and August. The smallest reproductive female had an SVL of 637 mm. Litter sizes range from 8-37.

Florida Green Water Snake

Nerodia floridana (Goff, 1936)

Distribution and Habitat. It uses wetlands choked with vegetation and rarely occurs in rivers or streams. *N. floridana*. It also uses lakes, ponds, ditches, and occasionally in brackish waters from Southern South Carolina into northeast Georgia. The species is absent from most of Georgia, and the gap forms two disjunct populations. The southern population is in southeast Georgia, extends into Florida, and extends west to Alabama. The type locality is near Leesburg, Florida, at the Alsa-Brook Prairie between Lake Griffin and Lake Yale.

Figure 29.13. Distribution of *Nerodia cyclopion*.

Identification A heavy-bodied watersnake and the longest species of *Nerodia,* reaching 1880 mm. The dorsum is olive, brown, or reddish. Dorsal scales are keeled, with two apical pits, and organized in 25-27 midbody rows. Ventrals 129-142, subcaudals 63-84. Suboculars prevent labials from bordering the orbit.

Natural History. The diet is composed of aquatic vertebrates (frogs and fishes). The diet has been summarized by Gibbons and Dorcas (2004). In southern Florida, *N. floridana* is

Figure 29.14. *Nerodia cyclopion*. **(A) Brazos Bend State Park, Needville, TX. Photography by J. Batch. (B) Photography by Mike Pingleton.**

active year-round, but on the northern edge of the range, it hibernates/brumation during the winter. The snake can be seen basking on sunny days. In southern Florida, it often travels overland on rainy days.

This species does not respond well to droughts. Seigel et al. (1995) studied a watersnake community during a drought and noted that this species was not seen for five years after the drought ended. Willson et al. (2002) did a similar study and found this species to be extirpated.

Reproduction. Mating has been reported as early as February, and parturition occurs in captives between June and August. Litter sizes as small as seven and as large as 132 have been reported (Gibbons and Dorcas 2002).

Figure 29.15. Distribution of *Nerodia floridana.*

Salt Marsh Snake

Nerodia clarkii (Baird and Girard, 1853)

Distribution and Habitat. Coastal salt meadows, swamps, and marshes rarely enter freshwater systems from Florida, Louisiana, Mississippi, Alabama, southeast Texas, and northern Cuba. (Fossil remains known from Abaco in the Bahamas in the late Pleistocene). The type locality is Indianola, Calhoun Co., Texas.

Identification Dorsal coloration is highly variable, gray, olive, black, yellow, or brick red.

Figure 29.16. *Nerodia floridana.* **Central Florida. Photography by Jake Scott.**

The pattern may be uniform, striped, or banded. Dorsal scales are keeled with two apical pits and organized in 21-23 rows at the midbody. Subocular scales present. Ventrals 123-138, subcaudals 57-88. Size of adults 380-760 mm; to the maximum size 933 mm; neonate size 197-266 mm;

A polytypic species with three subspecies:

Nerodia clarkii clarki (Baird and Girard, 1853). The type locality is coastal Texas and Alabama. Adult dorsum ranges from dark gray to red-brown with four yellow longitudinal stripes (two on each side). The venter is dark gray to red-brown with one to three rows of pale spots.

Nerodia clarkii compressicauda Kennicott 1860. The type locality is south of Tampa Bay, Florida. Adults can be gray, gray-olive, brown, tan, or rusty orange, with patterns of dark longitudinal stripes or transverse bands on the dorsum. However, some individuals may be uniform; some individuals may be almost entirely black (melanistic).

Nerodia clarkii taeniata Cope 1860. The type locality is Volusia, National Gardens, Volusia County, Florida. Adults have a dorsal pattern of dark brown and pale stripes anteriorly with dark blotches on a pale olive ground color over much of the body. Ventral surface dark with a central row of cream or yellow spots.

Figure 29.17. Distribution of *Nerodia clarkii*

Natural History. The diet includes fish and crabs, with the snakes frequently sustaining an injury from the crabs. (Miller and Mushinsky 1990; Mullin 1994). *Nerodia clarkii compressicauda* forages in and among the prop roots of mangroves. It has also been reported to feed with the tidal cycle and is active day and night.

Lingual luring has been described in this species (Hansknecht 2008). It involves the tongue curling upon itself distally to form a conspicuous loop. The typical chemosensory tongue flicking is absent, although the terminal loop does exhibit some vertical and horizontal movement. The duration of luring tongue flicks is significantly greater than chemosensory tongue flicks.

Reproduction. Trauth (1991) collected gravid females and males undergoing spermatogenesis were found in July. Therefore, parturition presumably takes place in August or early

Figure 29.18. *Nerodia clarkii* **Salt Marsh Snakes**
Photography by JCM

September.

Population and Biomass. Ackley and Meylan (2010) studied variation in population size and biomass of *Nerodia clarkii compressicauda* population in two artificial ponds in St. Petersburg, Florida, USA. The population's substantial biomass (25.4 kg/ha, one of the highest observed in snakes) was maintained for at least six months until the herbicide Aquamaster™ (glyphosate) was applied to the study area. Two months after application, the dead emergent vegetation collapsed into the pond. The population declined because of emigration after the change in habitat structure.

Conservation. Salt marsh snake populations appear to be fractured into isolated neighborhoods on the order of 50–80 km, according to a study done by Jansen et al. (2007). Despite its apparent local abundance, they suggest *N. c. compressicauda* needs conservation protection. The combination of extremely low dispersal, narrow habitat requirements, and, most importantly, extensive habitat alteration resulting from coastal real estate development may mean that *N. c. compressicauda* is highly susceptible to population extirpation and extinction.

Plain-Bellied Water Snake

Nerodia erythrogaster (Forster, 1771)

Distribution and Habitat. Permanent wetlands, rivers, and lakes from Iowa and Texas eastward to Delaware and northern Florida, southward into the Mexican states of Durango, Zacatecas, Coahuila, and Nuevo León. This is often considered a polytypic species, even though little genetic evidence supports the subspecies (Makowsky et al. 2010).

Plain-bellied Water Snake, *Nerodia erythrogaster alta* (Conant, 1963) inhabits Mexico (Zacatecas). The type locality is in the Rio Trujillo (also known as the Rio Florido), at the village of Rio Florido, approximately 15 miles NW of Fresnillo, Zacatecas.

Bogert's Water Snake, *Nerodia erythrogaster bogerti* (Conant, 1953). The type locality is in the Rio Nazas, near La Goma, approximately 15 miles southwest of Lerdo, Durango.

Redbelly Water Snake, *Nerodia erythrogaster erythrogaster* (Forster, 1771). The neotype locality is near Parker's Ferry, Edisto River Swamp, Charleston County, South Carolina.

Yellowbelly Water Snake, *Nerodia erythrogaster flavigaster* (Conant, 1949). The type locality is Frenier Beach, St. John the Baptist Parish, Louisiana.

Copperbelly Water Snake, *Nerodia erythrogaster neglecta* (Conant, 1949). The type locality is approximately 3 miles east of Mount Victory, Hardin County, Ohio.

Blotched Water Snake, *Nerodia erythrogaster transversa* (Hallowell, 1852). The type locality is Arkansas, Boundary of Creek Nation, Arkansas River.

Identification. A large watersnake, reaching 1636 mm in total length. Olive gray dorsum with faint crossbars. The ventral surface may be red, yellow, or orange. Dorsal scales keeled with paired apical pits; dorsals in 23-25 rows at midbody. Ventrals 132-116, subcaudals 46-90. No suboculars.

Natural History. They will wander far from the water and spend considerable time out of the water. They are active day and night in the warmest months of the year. They can be seen basking on logs or shorelines in the spring and fall. They hibernate during the coldest months of the winter. Prey includes fish and amphibians.

Figure 29.19. Distribution of *Nerodia erythrogaster*

Nerodia erythrogaster neglecta is well studied because, in 1997, it was designated a threatened species in Ohio, Michigan, and northern Indiana under the Federal Endangered Species Act. It migrates seasonally from its summer bottomland forests and shrub swamp habitat to more upland habitats through vegetated corridors to wetland areas. However, some populations stay in their lowland habitat and hibernate in rotten stumps and burrows made by other animals. Sometimes these burrows are flooded and are in saturated soils. Copperbelly Water Snakes emerge from their upland hibernation sites in early spring and migrate through wooded habitats to wetlands. When the woodland swamps begin to dry in late spring or in early June, the snakes again disperse and move through wooded or vegetated corridors to their summer habitat areas. Summer activities usually center around forests and forest edges (Conant 1951, Kingsbury and Coppola 2000).

Figure 29.20. *Nerodia erythrogaster.* **(A) Photography by Mike Pingleton (B)** *N. e. transversa* **from Kansas. Photography by JCM.**

For this reason, an upland habitat is essential for the snake's summer foraging activities. In late fall, Copperbelly Water Snakes seek out hibernation sites. It was believed that Copperbelly Water Snakes use hibernation sites at elevations higher than the flood line in pond areas (Sellers 1991). However, in radio-telemetry studies, Kingsbury and Coppola (2000) found they use bottomland hibernation sites. Bottomland hibernation sites have been identified as cavities in felled tree-root networks (Lodato 1985), crayfish burrows (Kingsbury and Coppola 2000), dense brush piles, rockpiles, and perhaps beaver and muskrat lodges (Sellers 1991). A mid-winter flood and freezing temperatures could be lethal and decimate the local population if floodplain and riverbank areas are the only hibernation sites available.

This species is known to form small groups in the spring and fall. Groups of snakes have been observed swimming, feeding, courting, and resting together (Conant 1934; Sellers 1991).

Copperbelly Water Snakes have a more extended gestation period than other water snakes sharing their range, and their average litter size (18) is also smaller (Schmidt and Davis 1941). Young snakes are born in the fall near, or in, the hibernaculum and may not become active until the following spring.

The diet comprises fish, crayfish, salamanders, and frogs. It uses both active foraging and sit-and-wait strategies to find food. Prey is seized and swallowed without constriction. Like some other *Nerodia,* this species has been observed swimming underwater with its mouth open. Platt et al. (2020) reported this species stealing food (kleptoparsitism) from a *Nerodia rhombifera*. McAllister (2021) wrote a female from McCurtain Co., Oklahoma, that contained remains of arthropods; a caterpillar, a grasshopper, beetle wings, and a harvestman. Perkins and Eason (2017) reported them feeding on the Bowfin, *Amia calva*, and the Pirate Perch, *Aphredoderus sayanus*.

Mating occurs April-June in the southeast USA, and parturition occurs in August-September. Litters of 55 have been reported. Most, however, contain 18 young. Parthenogenesis has been documented in this species.

Predators are terrestrial and aquatic and range from other snakes and large fish to wading birds and carnivorous mammals. Unlike the typical water snake, the plain-bellied water snake will leave the water and try to escape over land if threatened (Gibbons and Dorcas 2004).

The Plain-bellied Water Snake is considered a conservation risk because it tends to travel over land on roads and highways. Destruction or damage to wetlands also threatens the species' habitat. It is not a protected species in the southeastern states. Everitt and Philips (2019) reported death feigning in this species.

Banded Water Snake

Nerodia fasciata (Linnaeus, 1785)

Distribution and Habitat. Lakes, marshes, ponds, and streams from Texas eastward to Florida as far north as southern Illinois and North Carolina. In 1992, *Nerodia fasciata* and *N. sipedon* were found at three sites in California by the US Fish and Wildlife Service. In 2009, more than 300 banded water snakes were caught in the suburbs of Los Angeles by the *Nerodia* Working Group of USFWS. Then in May 2016, the species was found in the Colorado River basin near Yuma, Arizona, where a well-established population can be seen today.

This is a polytypic species with three subspecies.

Nerodia fasciata confluens (Blanchard, 1923) has its type locality in Butler County, Missouri. They were distinguished by 11 to 17 dorsal transverse bands (Clay 1938).

Nerodia fasciata fasciata (Linnaeus, 1766) has a type locality of Carolina. It is identified by the shape of the ventral markings that are quadrangular near the anterior margins of the ventrals (elongated in *pictiventris*) and by the presence of more than 128 ventrals (fewer in *pictiventris*) (Clay 1938).

Nerodia fasciata confluens has 11-17 dorsal blotches and *N. f. fasciata* has 19 to 30 (Clay 1938). *Nerodia fasciata pictiventris* (Cope, 1895) has a type locality in Gainesville, Florida. It can be distinguished by 26-35 red-brown to black cross bands; mature individuals have lateral interspaces that sometimes become darker than the lateral portions of the cross-bands and thus produce an appearance of alternating dorsal and lateral spots (Clay 1938).

Identification. A large watersnake, to 1588 mm. Dorsum can be gray, tan, brown, or red-brown with dark brown transverse bands (older individuals may be a uniform black). Ventral surface yellow or cream marked with dark spots or transverse bars. Dorsal scales are strongly keeled with a pair of apical pits; at midbody, the scales are in 17 rows. The ventrals are 120-143, and the subcaudals are 50-89.

Figure 29.21. Distribution of *Nerodia fasciata.*

Natural History. The diet includes fish and frogs with an ontogenetic shift from fish to frogs with maturity (Mushinsky et al. 1982). Many fish species are eaten, as well as frogs, salamanders, small turtles, snakes, birds, crayfish, and earthworms (see Ernst and Ernst 2003 for a complete list). A Florida specimen was found to have eaten an introduced Asian clariid catfish (Donini 2018). Lamb and Ljustina (2018) reported a specimen coiled under water below a film of Green Frog eggs and was feeding on the spawn. Fuchs et al, (2020) found an individual with its jaws stuck in the shell

Figure 29.22. *Nerodia fasciata.* **A. From central Florida. Photography by JCM. B. Photography by Mike Pingleton**

of the snail *Pomacea maculata* in an apparent attempt to prey on the snail.

Females reach sexual maturity at body lengths of 450 mm and males at 520 mm. Females provide nutrients and calories via a placenta to their embryos. Gestation is 48-109 days, depending on temperatures. Litter size varies from 9 to 50. Newborns are 200–310 mm long (Ernst and Ernst 2003).

Hybridization with *Nerodia sipedon*. Mebert (2005/2008) found widespread hybridization in the contact zone between *Nerodia sipedon* and *Nerodia fasciata* in the Carolinas with most specimens exhibiting a backcrossed hybrid status. However, the distributions of diagnostic genetic markers between species are asymmetric, and the frequencies of snakes resembling a F1 interspecific hybrid (50/50% *fasciata/sipedon*) are very low. This and the pronounced morphological characteristics of *N. fasciata* in most of the studied hybrid zone is in accordance with the habitat relating more with that species.

Tail autotomy has been reported in this species and some other species of thamnophiini (*N. erythrogaster, N. sipedon, Thamnophis sirtalis, T. sauritus*) (Donini 2019). In addition, Everitt and Philips (2019) reported death feigning in this species.

Brazos Water Snake

Nerodia harteri (Trapido, 1941)

Distribution and Habitat. Rock-strewn shorelines along the Brazos River system in Central Texas and stream impoundments. Restricted to the upper Brazos River drainage, along 303 km of the stream, it is in two reservoirs; this snake has one of the smallest ranges of any North American snake species (Scott et al. 1989). The species is not restricted to rocky riffles in flowing rivers but also inhabits pools and lakes. Several sections of the Brazos do not support this species because the rocky riffles needed by juveniles are absent or are separated by greater distances on the uninhabited stretches of the river. Adults are not restricted to the riffles. Scott et al. (1989) observed them swimming or on land within 3 m of the shoreline of a river or lake, and the great majority were within one meter of the water. They may follow intermittent streams a short distance during high water. The type locality is north of Palo Pinto, Palo Pinto County, Texas.

Figure 29.23. Distribution of *Nerodia harteri*

Figure 29.24. ***Nerodia harteri*.**
Photography by Mark Pyle.

Identification. A small, slender water snake that reaches 900 mm (most are less than 600 mm). The dorsum is brown, gray, or orange, with a lateral pattern of spots that may fuse on the midline to form saddles. Dorsal scales keeled with two apical pits in 17 rows at midbody. Subocular scales absent. Ventrals 143-151, subcaudals 67-88.

Natural History. Active in spring and summer, they winter underground. Fish are likely the most important prey; the species may also eat tadpoles and frogs. Males reach sexual maturity in one or two years at a body length of 42-52 cm. Females mature in two or three years. Litters of 4-24 are born in late July – September. Litter size correlated with female body size.

Concho Water Snake

Nerodia paucimaculata (Tinkle and Conant, 1961)

Distribution and Habitat. The Concho River system in Coke, Runnels, San Saba, and Tom Green Counties. The type locality is the Colorado River south of Robert Lee, Coke County, Texas city limits. It inhabits shallow, fast-flowing water with a rocky or gravel substrate.

Identification. Closely related to *N. harteri* but smaller, it reaches 652 mm. Dorsum red-brown or olive-brown with dark brown spots. Dorsal scales are keeled with a pair of apical pits and organized into 21 rows at mid-body. Ventrals 139-151, subcaudals 64-83. Subocular scales absent.

Natural History. This species is a fish specialist, Green et al. (1994) found it feeds primarily on cyprinid fishes but will also eat the hylid frog *Acris crepitans*. Feeding occurs from mid-April to early November, and gravid females feed until early June and resume after parturition. Specimens from lacustrine environments can be observed on the bottom or in shallow water.

Hibernation begins in late October to late November, depending upon weather and temperatures. Most adults probably hibernate in burrows of other animals, particularly crayfish, and juveniles use crevices under rocks on gravel bars (Werler and Dixon 2000). The snakes emerge in mid-March to mid-April.

Reproduction. Males reached sexual maturity at SVLs of 380 mm and females at 460 mm. Mating occurs in April and May; gestation is about three months, and parturition occurs from late July to mid-August. About 85% of the females in the population are gravid each year. Litter size ranges from four to 29 and averages 11—neonates average 175 mm in total length (Greene et al. 1992).

Conservation. Its limited range resulted in a threatened species status. It was placed on the state endangered list by the State of Texas in 1977. Flury and Maxwell (1981), in a detailed report on *Nerodia paucimaculata*, estimated its total population at only 332-613 individuals. In 1986 it was considered threatened. The Concho water snake was removed from the U.S. Endangered Species list in 2011. When delisting, Janecka et al. (2021) recently monitored the snake by conducting extensive surveys and a population genetic structure assessment. They found no Concho Water Snakes along the Concho River, part of the previously known range, and fewer snakes on the Colorado River than in previous studies. Several population genetic analyses showed concordant patterns of population substructure along the Colorado River, and genetic bottlenecks were detected. Habitat modification and low water flow during periods of drought may have contributed to existing patterns. The genetic-based results demonstrate that the Concho Water Snake exists as small subpopulations along the Colorado River.

Figure 29.25. Distribution of *Nerodia paucimaculata.*

Diamondback Water Snake
Nerodia rhombifer (Hallowell, 1852)

Distribution and Habitat. Slow-moving rivers, lakes, marshes, swamps, and anthropogenic bodies of water from eastern Kansas, extreme southeastern Iowa, southern Illinois, and southwestern Indiana southward through western Kentucky and Tennessee, central Alabama, Mississippi, Missouri, Arkansas, Oklahoma, and eastern two-thirds of Texas southward into Mexico to Tabasco and southwestern Campeche.

This polytypic species has three subspecies: *Nerodia rhombifera blanchardi* (Clay, 1938). The type-locality is Mexico, within a radius of 85 miles of Tampico in the triangle formed by the Rio Tamesi and Rio Panuco.

Nerodia rhombifera rhombifera (Hallowell 1852) has a type-locality in the Arkansas River and its tributaries near the northern boundary of the Creek Nation. Revised to Arkansas River between Keystone and Tulsa, Tulsa County, Oklahoma by Conant (1969).

Nerodia rhombifera werleri (Conant, 1953). The type locality is the Alvarado-San Andres Tuxtla road (Mexico No. 180), approximately 18 miles southeast of Alvarado, Veracruz, Mexico.

Identification. This is a large water snake reaching 1753 mm. The dorsum is brown or gray with connected dark brown squares or diamonds. The venter is cream to yellow with dark half-moon blotches. The dorsal scales are keeled with paired apical pits; at midbody, they are in 21 rows. Ventrals 132-152, subcaudals are 56-88. Subocular scales absent.

Figure 29.26. *Nerodia paucimaculata.* **Photography by (A) Romey Swanson (B) Scott Wahlberg (C) Paul Freed.**

Natural History. The literature on this snake is extensive and not completely covered here. A laboratory investigation of the feeding behavior of juvenile *Nerodia rhombifera* (Savitzky and Burghardt 2000) found neonates were negatively buoyant, foraged only in the water, and were successful in catching fish. The open-mouth foraging behavior seen in adults was rudimentary in neonates. There was an ontogenetic shift for more underwater foraging, less foraging on the surface, and increased open-water use. The results were congruent with field observations.

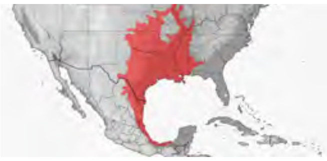


Figure 29.27. Distribution of *Nerodia rhombifer.*

Diet. The prey base for this species is highly diverse. In a literature survey combined with stomach content analysis, Kalki et al. (2018) found 55 species of fish, nine species of amphibians, eight species of insects (some of these may represent secondarily ingested items), five crustaceans, and one species each of the following taxa: snake, turtle, bird, and a bat. Perkins and Eason (2017b) reported this snake feeding on the Pirate Perch, *Aphredoderus sayanus*.

Figure 29.28. *Nerodia rhombifer*. **Photography by (A) Mike Pingleton (b) Paul Freed (c) JCM.**

Reproduction. Both sexes mature in 2.5 to three years; the smallest reproductive male was 475 mm (but most do not mature until they reach 680-800 mm, and females mature at 650 mm to 680 mm. Mating occurs after emergence from hibernation in April and May. Parturition usually occurs from late July to early November. However, one female from Texas had full-term embryos in February, suggesting that reproductive timing in this snake is variable.

Litter size ranges from eight to 62; the mean is 26.8. Neonate size is 200-332 mm in total length. There is a direct correlation between litter size and female body size.

Northern Water Snake

Nerodia sipedon (Linnaeus, 1758)

Distribution and Habitat. Natural and anthropogenic bodies of water from rivers and lakes, stream impoundments, canals, roadside ditches, wetlands, marshes, and swamps from Maine, southern Quebec, and southern Ontario westward to southeastern Minnesota, then southwestward through Nebraska to northeastern Colorado. The range extends to the southeast from Colorado throughout most of Kansas, eastern Oklahoma, and Arkansas, and eastward through Missouri to the Mississippi River. East of the Mississippi River, it occurs from Canada to the Gulf Coast in Louisiana; from there, it ranges eastward to the Florida Panhandle and throughout the remainder of the eastern states except below the Fall Line in Georgia and the Carolinas. *Nerodia sipedon* and *Nerodia fasciata* are sympatric at numerous points and hybridize in some areas (Gibbons and Dorcas 2004). The type-locality, North America, was reported by Linnaeus (1758). *Nerodia sipedon* is primarily freshwater, but some coastal populations inhabit brackish water.

This is a polytypic species.

Nerodia sipedon insularum (Conant and Clay 1937) Type-locality, Pelee Island, Lake Erie. This pale subspecies is confined to islands in Lake Erie's Ohio and Ontario portions. The dorsal pattern is reduced or completely lacking, and the dorsal ground color is usually green or brown with an occasional pinkish or orange tinge. The dorsal pattern, when visible, is like that of the nominate subspecies. Ventrals range from 141–153 (average 146.3) in males, and 137–152 (average 145.9) in females, with subcaudals ranging from 70–81 (average 75.6) in males and 58–68 (average 63.3) in females (based upon Walley et al. 2012).

Figure 29.29. Distribution of *Nerodia sipedon.*

Nerodia sipedon pleuralis (Cope) has an unknown type-locality. Cochran (1961) gave it as Summerville, Dorchester, South Carolina. A neotype designated by Clay (1938) is at USNM. The dorsal pattern is like that of *N. s. sipedon*, but the dark dorsal markings usually number 30 or fewer and are separated by paler interspaces that are wider than the bands (Gibbons and Dorcas 2004). The crescentic ventral blotches often break up and disappear with age and are not nearly as bright as those of *N. s. sipedon*.

Nerodia sipedon williamengelsi (Conant and Lazell). Island Creek on Ocracoke Island, Hyde Co., North Carolina, is the type-locality. This coastal subspecies closely resembles *N. s. sipedon* in scale count data differs in having the adult dorsum essentially black with the interspaces between the crossbands and blotches so dark that pattern details may be obscured. The taxon is restricted to brackish marshes along the margins of Pamlico and Croatan sounds. This taxon occurred in salt marshes and tidal creeks and was common in such habitats on the barrier islands. Gaul (1996) noted clinal variation in several morphological characters within its known range. These clines correspond with clines in salinity in the coastal waters of North Carolina (Gaul and Mitchell 2007).

Identification. A medium to large water snake that reaches 1500 mm in total length. The dorsum is tan to gray with wide red-brown, alternating, quadrangular blotches along the midline of the back. The venter is cream to yellow with a half-moon marking present. Older snakes tend to become uniform black. Dorsal scales are keeled with two apical pits and are organized into 23 rows at mid-body. Ventral scales are 123-155, subcaudal scales are 42-84.

Natural History. The Northern Water Snake is one of the best-studied aquatic snakes. The extensive distribution from Maine and southern Canada southward to the Gulf Coast of Alabama results in northern populations spending September to April-May in hibernation. The southern populations may not hibernate; if they do, they spend only a few days to weeks escaping cold temperatures. Hibernation sites include rock crevices, stream banks, cavities formed by the roots of large trees, and animal burrows. These may be close to water or a significant distance from water (hundreds of meters) and may be in upland situations or lowland areas. They occasionally use beaver, muskrat lodges, or terrestrial rodent burrows for hibernacula. They are known to hibernate alone as well as in communal groups.

Body Temperatures. *Nerodia sipedon* spends significant time basking along shorelines on the substrate, vegetation, or emergent debris. Therefore, body temperatures in the field generally range from 20.8 to 34.7 °C with a mean of 28.0 °C.

Figure 29.30. *Nerodia sipedon williamengelsi.* is a salt marsh dwelling population of this species. Photography by JCM.

Diet. Northern Water Snakes are fish specialists. Ernst and Ernst (2004) list prey records from free-living specimens containing 71 species of fish, 11 species of salamanders, 15 species of anurans, one species of snake, and two species of mammals. They also report invertebrates: crayfish, other arthropods, snails, earthworms, and leeches.

Reproduction. The population's latitude influences the timing of maturity and the development of gametes. Males mature at 370 to 450 mm SVL at 21-24 months. Females mature at SVLs of 500-650 mm and 24-36 months of age (Feaver 1976, King 1986, 1994). Females grow their ovarian follicles in a four-to-six-week period in the spring. They increase the yolk before ovulation. Females carry fertilized eggs in June, and gestation is 9 to 12 weeks. *Nerodia sipe-*

Figure 29.31. *Nerodia sipedon* **from northeastern Illinois. JCM**

don embryos do have a placental connection to the female. However, there is some evidence that the placenta transfers water and minerals but not nourishment to their embryos (see Weatherhead et al. 1999). Males produce spermatozoa after the breeding season, use some in the fall, and store some until the following spring. Mating starts immediately after emergence from hibernation. Males actively search for females, following pheromone trails formed by the female. Females mate with multiple males, and litters have numerous fathers. Senter and Senter (2020) have described courtship and mating.

Defense and Predators. When confronted by a predator, *Nerodia sipedon* will always try to escape, often diving into the water. If it cannot escape, it will flatten its head and body, strike, and bite if it can. If the snake is seized, it will not hesitate to release foul-smelling cloacal musk. In addition to smelling bad, it may be toxic and irritating to mucus membranes. The range of predators is diverse – predatory fishes, bullfrogs, alligators, snapping turtles, other snakes, wading birds, raptors, gulls, carnivorous mammals, and of course, humans.

Brown Water Snake

Nerodia taxispilota (Holbrook, 1838)

Distribution and Habitat. Flowing, permanent waters such as rivers, canals, blackwater cypress creeks, and stream impoundments on the Coastal Plain and Piedmont regions of the southeast USA from southern Virginia southward through all of Florida and westward to eastern Alabama. Brown Water Snakes are found throughout Georgia and South Carolina but are absent from the mountainous regions of extreme northwestern South Carolina and northern Georgia. Their preferred habitat has overhanging vegetation, emergent snags, or rocky riverbanks where snakes may bask. The type-locality was given as the South Carolina seaboard and the Altamaha River neighborhood in Georgia.

Identification. A large water snake that reaches 1766 mm in total length. It has a thick body with a brown dorsum and three rows of dark brown blotches. The ventral surface is cream to tan with half-moon markings. The dorsal scales are keeled with two apical pits and are organized into 29-31 rows at the midbody. The ventrals are 128-152; the subcaudals are 59-87.

Natural History. Brown water snakes were studied by Mills (2002) on the Savanna River. He found they were not randomly distributed but were significantly associated with the steep-banked outer bends of the river and the availability of potential perch sites. Sections of the river with the highest number of captures were clustered within 200 m of backwater areas. Seventy percent of 164 recaptured snakes were less than 250 m from their previous capture site; however, three moved more than a kilometer. Only eight large individuals (800 mm snout-vent length) crossed the river (approximately 100 m).

Brown Water Snakes are active in all months of the year but are most infrequently seen from November through February in the Savanna River. However, they are likely active year-round in Florida and much of its range. Radiotelemetry studies suggest *N. taxispilota* will emerge and sometimes move short distances on warm winter days regardless of water level. However, they do not actively forage, mate, or move long distances. They are diurnal but may shift to nocturnal behavior at the warmest time of the year.

Diet. Brown Water Snakes are fish specialists, and the largest portion of their diet comprises ictalurid catfishes (Camp et al., 1980). Mills (2002) supports this with his data from the Savannah River. Of the identifiable food items, all were fish, and 62% were catfishes in the genera *Ictalurus* and *Noturus*. Snakes over 60.0 cm SVL consume almost exclusively catfish. Although a variety of other non-fish prey has been reported in the diet, including frogs, crayfish, a turtle, small snakes, and lizards, these observations are few. They may represent secondarily ingested prey (Neill and Allen, 1956).

Reproduction. The seasonal reproductive cycle of *Nerodia taxispilota* in southeastern Virginia was found to resemble other temperate zone colubrids by White et al. (1982). Testes are small during April-June and largest in August, decreasing in size during September-November. Spermatozoa produced in late summer are stored in the vas deferens through winter and used the following spring. The female cycle is annual. Vitellogenesis occurs from April to June, ovulation is in late June, and parturition is in early to mid-September. Fecundity increases with increasing female body size. The average total clutch size is 33.9, and the mean size of full-term embryos is 28.0. Sequential stages of embryonic development are described. Males average significantly smaller than females. The percentage of tail breaks is about equal in both sexes, but adults have higher proportions of tail breakage than juveniles. Sex ratios do not differ significantly from 1:1; however, males predominate in autumn. Males mature at about 503 mm SVL (about two or three years of age), and females mature at about 725 mm (about four or five years of age) (White et al. 1982, Ernst and Ernst 2003).

The Genus *Thamnophis* - Garter Snakes

Figure 29.32. Distribution of *Nerodia taxispilota.*

The garter snakes, genus *Thamnophis,* include some of the western hemisphere's most abundant and well-studied snakes. A few species spend considerable time in the water; a few are terrestrial or terrestrial-arboreal. Molecular studies in the past two decades have suggested the two species of *Adelophis* belong to *Thamnophis*, but no one has formally moved them to the garter snake genus. There are 37 species, including the two species *Adelophis*.

The distribution of *Thamnophis* extends further north than any other squamate in the western hemisphere, there are populations of *Thamnophis ordinoides* in southeast Alaska and Canada's Northwest Territories, and the genus is represented as far south as Panama. Garter snakes are primarily diurnal; they use ambush and actively foraging to capture prey, and they use venom for subduing prey. They have chorioallantoic and yolk-sac placentation. At least a few species can hibernate underwater. And a few species have been documented to have facultative parthenogenesis.

Most recently, Hallas et al. (2022) found support for two clades of *Thamnophis*, a northern North American clade and a southern North American clade. Divergence time estimates and biogeographic analyses suggest *Thamnophis* originated in the mid-Miocene of Mexico. Their studies of morphological traits associated with feeding ecology showed differences in particular cranial morphologies between aquatic specialists and garter snakes that are terrestrial-aquatic generalists, independent of evolutionary history. Hallas et al. (2022) consider

Figure 29.33.. *Nerodia taxispilota* **from northern Florida. JCM.**

Thamnophis atratus, T. couchii, T. gigas, T. hammondii, T. melanogaster, T. nigronuchalis, T. rufipunctatus, and *T. validus* aquatic specialists, and grouped all the remaining species as terrestrial or aquatic generalists. Considering all other *Thamnophis* as terrestrial-aquatic generalists may be misleading. Many taxa could be partitioned into different categories based on diet, terrestrial habits, and feeding ecology.

Aquatic-specialists occur in both clades. For example, species that hunt aquatic prey have long, narrow muzzles to reduce hydrodynamic drag. In contrast, those with broader or mostly terrestrial diets have wider muzzles and deeper heads to accommodate an array of potentially large prey (Hallas et al. 2022).

Aquatic Garter Snake

Thamnophis atratus Kennicott, 1860

Distribution and Habitat. Fast-flowing streams with rocky substrates, sluggish streams with soft bottoms, ponds, small lakes, and adjacent terrestrial habitats in woodlands, transitional woodland-grass ecotones, or chaparral. It is closely tied to water, but individuals sometimes move overland. The Aquatic Garter Snake ranges from Coos and Douglas counties in southwest Oregon southward to Santa Barbra County, California (Nussbaum et al. 1983, Rossman et al. 1996, Ernst and Ernst 2003, Stebbins 2003).

This is a polytypic species with three subspecies. *Thamnophis a. atratus* is restricted to the outer coastal area of San Francisco Bay, California. The type locality was given as California but limited by Fitch (1940) and Cochran (1961) to San Francisco, California.

Thamnophis a. hydrophilus Fitch, 1936 occurs north of San Francisco Bay northward to southwest Oregon. Type Locality is Trail Creek six miles from its mouth in Jackson County, Oregon.

Thamnophis a. zaxanthus Boundy, 1999 occurs from the Inner Coast Range from Napa and Solano to Santa Barbara counties and the Santa Lucia Range. The type locality is two miles south of Gilroy Hot Springs, Santa Clara County, California.

Identification. The species reaches a maximum of 1060 mm. Dorsal scales are organized in a maximum of 19 or 21 rows. Dorsum gray, brown, dark brown, or black may have two rows of black spots between the stripes; the vertebral strip may be distinct, indistinct, or absent. Lateral stripes are confined to rows two and three.

Natural History. Adults have been observed anchoring their tails around submerged rocks in deep water and striking at fish swimming by (Boundy, 1999), and neonate snakes fed on smaller prey that inhabited shallow stream margins (Lind and Welsh 1994). Lind and Welsh (1994) found adults took a wider variety of prey, but they focused on the Pacific Giant Salamander, *Dicamptodon tenebrosis*, larvae, and neotenes, in the mid-stream substrates. Juvenile and Consumption of large prey by adults and smaller prey by juveniles indicate a shift in foraging strategy from frequent feeding on small prey to infrequent feeding on large prey.

Neonates have an unusual feed behavior described by Welsh and Lind (2000), while adults are active foragers feeding on the aquatic Pacific Giant Salamanders on streambed substrates. Although juvenile snakes use primarily ambush tactics to capture larval anurans and juvenile salmonids along stream margins, their behavior includes lingual luring. Luring snakes are in an ambush position and extend and hold their tongues out and rigid, with the tongue-tips quivering on the water's surface; apparently, this mimics insects and attracts young fish within striking range.

Preston and Johnson (2012) investigated the diet of *T. atratus* in the San Francisco Bay Area. At one-hundred and eighty-five ponds, they captured 139 *T. atratus,* and 60 contained

Fiogure 29.34. The distribution of *Thamnophis atratus*..

identifiable stomach contents. Native amphibians were found in 93% of the snakes containing food. Pacific Chorus Frogs (*Pseudacris regilla*) were the most important amphibian prey, followed by Western Toads (*Anaxyrus boreas*), California Newts (Taricha torosa), and California Red-legged Frogs (*Rana draytonii*). *T. atratus* at a pond was positively associated with all native amphibian species but negatively associated with introduced American Bullfrogs *Lit*hobates *catesbeianus*. The mean species richness of native amphibians at ponds where they detected *T. atratus* was also higher than that in ponds without the garters snakes (2.45 vs. 1.74), and the odds of finding *T. atratus* at ponds with native amphibians was 12 times greater than at ponds without native amphibians.

Figure 29.34. *Thamnophis atratus*. Photograph from Mike Pingleton

Bogert's Garter Snake

Thamnophis bogerti Rossman and Burbrink, 2005

Figure 29.35. Distribution of *Thamnophis bogerti.*

Distribution and Habitat. Oak woodland, pine-oak forest, and pine-oak- madroño forest in the Mesa del Sur of Oaxaca, exclusive of the Sierra de Juarez. The type locality is Mexico, Oaxaca, El Tejocote, at 2377 m ASL. They are probably restricted to elevations of 2195-2743 m (Rossman and Burbrink, 2005).

Identification. The male holotype was 298 mm. The dorsum is brown, with two rows of black spots between the stripes. Dorsal scales are in 17 rows at the midbody. The top of the head is unpatterned. Ventrals average 145 in males, 140 in females. Subcaudals average 70 in males and 62 in females.

The dorsum is brown, with small, irregular black spots barely visible. The light vertebral stripe is confined to the vertebral row and is difficult to discern on the lower edge of dorsal scale row three. The nuchal blotches are predominantly black and fused mid-dorsally (the vertebral stripe is separated from the interparietal notch by 4-1 /2 scales). Prominent black barring along the posterior margins of upper labials 2-5 extends ventrally 50-75% of the height of each suture; along the posterior sutures of SL 6 and SL 7 (which includes anterior upper labial eight), the bars reach the lip. A black stripe extends along the anterior temporal's lower margin, connecting the two posterior most SL bars. The lower labials are unmarked except for a black bar along the lower labials nine and ten suture. (Rossman and Burbrink, 2005).

Natural History. Unknown.

Figure 29.36. ***Thamnophis bogerti*** **(A) from San Vicente Nuñú, Oaxaca, MX. Photograph from José Luis Mendoza Betanzos (B) from San Agustín Loxicha, Oaxaca, Mexico. Photograph from hfranz.**

Conant's Garter Snake

Thamnophis conanti Rossman and Burbrink, 2005

Figure 29.37. Distribution of *Thamnophis conanti.*

Distribution and Habitat. Oak woodland is confined to the southern interface of the Mesa Central and the Sierra Madre Oriental near the Puebla-Veracruz state line. Recorded elevations likely to be valid range from 2134-2256 m ASL. Type locality: Mexico, Puebla-Veracruz state line at Mexico Highway 125 [number in error, it is Highway 150 that extends north from Tehuacana, Puebla, to the state line at Puerto del Aire (Rossman and Burbrink, 2005).

Identification. Males reach 520 mm. Dorsal scales are in 17 rows at the midbody. Top of head unpatterned. The area between the stripes is brown,

with two rows of relatively small black spots between the light vertebral and lateral stripes. Ventrals average 150 in males and 144 in females. Subcaudals average 72 in males and 64 in females.

Figure 29.38. *Thamnophis conanti*
Photograph from Mike Pingleton.

Liner's Garter Snake

Thamnophis lineri Rossman and Burbrink, 2005

Figure 29.39. Distribution of *Thamnophis lineri.*

Distribution and Habitat. Confined to pine-oak forest and pine-oak- madroño forest in the Sierra de Juarez portion of the Mesa de! Sur in Oaxaca. Elevations range from 2700-2786 m. The type locality is Mexico, Oaxaca, Llano de las Flores, 2786 km elevation.

Figure 29.40. *Thamnophis lineri* **(A) From Llano de las Flores, Oaxaca, MX. Photograph from Iván Ahumada/Herp.mx . (B) is from San Juan Bautista Atatlahuca, Oaxaca, MX. Photograph from Eli Garcia-Padilla.**

Identification. The adult male holotype was 307 mm. The dorsum is brown, with two rows of spots between the stripes. Dorsal scales are in 17 rows at the midbody. Maxillary teeth 18-20. The top of the head is unpatterned. Ventrals average 140 in males and 136 in females. Subcaudals average 62 in males and 55 in females.

Short-headed Garter Snake

Thamnophis brachystoma (Cope, 1892)

Distribution and Habitat. It occurs in old field habitats near marshes and is frequently under rocks. They are known from southern Michigan, northwest Pennsylvania, and western New York. The type locality is the Allegheny River near Franklin, Venango County, Pennsylvania.

Figure 29.41. Distribution of *Thamnophis brachystoma.*

Identification. Maximum total length 556 mm. Dorsum is brown or gray-brown, the stripes are yellow-tan, and the area between the stripes is unspotted. Dorsal scales in 17 rows, occasionally 19 rows. Upper labials six, lower labials seven. The lateral stripe is confined to rows two and three.

Natural History. This is a very terrestrial species of garter snake. The diet is composed of almost entirely earthworms. Males mature at about 28.0 cm in total length; females mature at 330 mm. Males produce sperm as they emerge from hibernation, and the testes reach maximum size by late July or early August. Sperm over winter in the vas deferens and epididymitis. Mating occurs in the spring; parturition occurs in August-September. Neonates are 118-145 mm in total length. Lethaby and Gray (2015) estimated the population size to be 93 snakes and was estimated at 26 snakes/ha. The estimated biomass was 1.42 kg. At a second site, the population was estimated to be 161 snakes. The density of snakes was estimated at 34 snakes/ha with a total biomass of 1.72 kg.

Figure 29.42. *Thamnophis brachystoma* **Photograph from (a) Brandon Hunsberger and (b) Jeff Tome.**

Butler's Garter Snake
Thamnophis butleri (Cope, 1889)

Figure 29.43. Distribution of *Thamnophis butleri.*

Distribution and Habitat. Mesic prairies, marsh shorelines, grassy shorelines of streams and canals, and old fields in Northeastern Indiana, Ohio, Michigan, and southeast Wisconsin, USA, and in southern Ontario, Canada. The type locality is Richmond, Indiana.

Identification. The species reaches a maximum length of 737 mm. The dorsum is olive-brown or tan to black. Pale individuals tend to have spots in two rows. The stripes are yellow and involve rows 2 and 3. The ventral surface has two rows of spots on the outer edges of the ventrals. Ventrals 129-151, subcaudals are 49-72.

Figure 29.44. *Thamnophis butleri* **from Ontario, Canada. Photograph from Joshua Vandermeulen.**

Natural History. This species is an annelid worm specialist. Experimental evidence suggests that they recognize the odor of worms within days of birth. They will eat fish and amphibians but have a strong preference for worms. They search the ground for worms and will burrow into the soil to find them below ground.

Lethaby and Gray (2016) marked individuals at two sites in Pennsylvania and found maximum distance traveled by two males at one location was 10 m over seven days. The maximum distance traveled by a male at the second site was 70 m over 62 days. A female traveled 37 m in 14 days, and at another location, a female traveled a maximum distance of 66 m in 21 days.

Reproduction. The smallest mature gravid female was 34.5 cm SVL, and a 32,1 cm SVL male was observed courting a female. *Thamnophis butleri* of these sizes would be in their second spring. Mature males have tubercles on their mental scale and chin shields. Mating occurs upon emergence from hibernation, and males scramble to mate with females. Multiple males will follow a female's pheromone trail and try to mate, forming a "ball of snakes" (mating aggregation). Parturition July-September (Vogt 1981). Clutch size about 4-20, increasing with female size. Sexually mature in 2nd or 3rd year (Fitch 1970). Litters of 4-20 have been reported, but most litters have 8-10 young that are 125-185 mm in total length (Ernst and Ernst 2003).

Golden-headed Garter Snake

Thamnophis chrysocephalus (Cope, 1885)

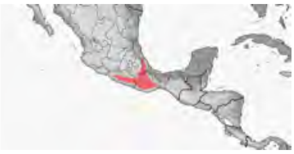


Figure 29.45. Distribution of *Thamnophis chrysocephalus.*

Distribution and Habitat. Streams, ponds, and adjacent terrestrial habitats in pine-oak forests of the southern Sierra Madre Oriental in Guerrero, Oaxaca, Puebla, and Veracruz, Mexico. The type locality Orizaba, Veracruz.

Note: Taylor (1940) described *Thamnophis eburatus* from the type locality of Cerro San Felipe, Oaxaca, Mexico. This snake is a melanistic *Thamnophis chrysocephalus.*

Figure 29.46. *Thamnophis chrysocephalus.* **Photograph from Mike Pingleton.**

The maximum length is 692 mm. The dorsum is a uniform black or brown. The vertebral stripe is only on the anterior body; the lateral stripe is confined to scale row 2. Dorsal scale rows at midbody are in 17 rows. Ventrals 135-155, subcaudals 69-87.

Natural History. A poorly known species. Reportedly active day and night. Observed swimming in streams at night and several meters from a stream in the afternoon; observed foraging at the bottom of a shallow pool (Rossman et al. 1996).

Sierra Garter Snake

Thamnophis couchii (Kennicott, 1859)

Figure 29.47. Distribution of *Thamnophis couchii.*

Distribution and Habitat. Streams, ponds, and reservoirs (permanent and seasonal) in oak woodlands, montane coniferous forests, grassy valleys, and chaparral in California and western central Nevada at 91-1438 m ASL. The type locality is the Pitt River, California.

The maximum length is 957 mm. The dorsum is olive-brown to dark brown or black. Two alternating rows of spots occur between the stripes. The lateral stripe is confined to rows two and three. The vertebral stripe is yel-

Figure 29.48. *Thamnophis couchii* **Photograph from Mike Pingleton.**

low and may be visible on the anterior body but fades posteriorly. The lateral stripe may be bright yellow or absent. Some populations are melanistic. Dorsal scale rows are 21 at mid-body and resuced to 17 posteriorly, some individuals have 19 at midbody. Ventrals 161-187, subcaudals are 68-99.

Natural History. A diurnal snake with seasonal activity that varies with elevation. Lowland populations may be active from March to December, while higher-elevation populations are active for three or four months (Rossman et al. 1996). Morning basking in tall grass is followed by foraging. Diet changes with the habitat of this highly aquatic snake. In seasonal aquatic habitats, it feeds on amphibians (anurans and salamanders), and in permanent streams, it feeds on fish. Juveniles tend to ambush fish and tadpoles in shallow water or from the edge of the shoreline, while adults crawl along the bottom and tongue flick, actively foraging for prey (Drummond 1983, Lind 1990). If the prey is large, it may be dragged into shallow water before the snake starts to swallow it. Litter size varies from five to 38. Gravid females may form aggregation. Parturition occurs from late July to September (Rossman et al. 1996; Ernst and Ernst 2003). Predators include a variety of birds and carnivorous mammals; defense behavior involves escape, biting, and the release of musk.

Black-necked Garter Snake

Thamnophis cyrtopsis (Kennicott, 1860)

Figure 29.49. Distribution of *Thamnophis cyrtopsis.*

Distribution and Habitat. Southwestern USA from southern Colorado, Utah, Arizona, Texas, and New Mexico; in Mexico, it ranges from Aguascalientes, Chiapas, Tamaulipas, San Luis Potosí, Quéretaro, Oaxaca, Jalisco, Sinaloa, Hidalgo, Guanajuato, Puebla, Guerrero, Nayarit, Morelos, and southward into Guatemala. Type locality: Rinconada, Coahuila, Mexico.

This is a polytypic species with three subspecies.

Thamnophis cryptopis collaris (Jan 1863) occurs from southern Sonora, Durango, and Chihuahua, through western and southern Mexico to west central Guatemala.

Thamnophis crytopsis cyrtopsis (Kennicott 1860) ranges from southwestern Texas and New Mexico; southward into Mexico (Coahuila, Nuevo León, Chihuahua).

Thamnophis crytopsis ocellatus (Cope 1880) ranges from southcentral Texas and the Edwards Plateau west to the Big Bend. Type locality: Texas, near Helotes.

Identification. Dorsal scales in 19 rows at midbody. Upper labials eight. The black nu-

Figure 29.50. *Thamnophis cyrtopsis.* **Photograph from (A) Mike Pingleton, (B) Paul Freed, (C) JCM.**

chal collar is not divided into two nuchal blotches. The dorsum of head is gray or brown. The brown to black dorsolateral areas show some evidence of a checkerboard pattern (most prominent anteriorly). The narrow vertebral stripe is distinct. The first three scale rows are white, devoid of markings or having irregular small black markings; A prominent row of black marks along the margin of the first scale row and ventral scales. Black marks are usually lacking on lower labial sutures (except the most posterior) (Webb 1980).

Natural History. The diet comprises anurans, with some evidence that salamanders, lizards, and small birds may be eaten, and some invertebrates (earthworms and *Triops*). Neonates feed on small fish and worms. Foraging along the bank of a stream and ambushing prey while they float or conceal themselves in stream bed rocks or algal mats have been reported.

Reproduction. The gametic cycle of both sexes of this species was examined by Goldberg (1998). In spermiogenesis, metamorphosing spermatids and mature sperm were present. Sperm were present in the vasa deferentia during all months (March-November) indicating *T. cyrtopsis* has the potential of breeding throughout the year. Mating occurs the following spring utilizing sperm stored overwinter in the vasa deferentia. Some mating likely occurs during autumn. Mating coincides with hypertrophy of the kidney's sexual segment.

The smallest reproductive female measured by Goldberg (1998) was 412 mm SVL. Mean clutch sizes for 25 females averaged 8.4 (3-24 range). A significant positive correlation existed between female body size and enlarged follicles (six mm, or embryos). Litter sizes from Arizona and Texas ranged from 6-22 and were born in July and August (Goldberg 1998).

In prenuptial secondary vitellogenesis, the female's reproductive cycle is like that of other *Thamnophis* species. Females enter hibernation with small, previtellogenic follicles. Yolk deposition occurs in spring. Females with enlarged follicles six mm in diameter or developing embryos were found March-June. The presence of some reproductively inactive females in March-June suggests that not all mature females produce litters each year. About 61% of females from March-June produced a litter. It is unknown if the March and June females undergoing yolk deposition would have been produced. Data on reproductive frequency for other species of *Thamnophis* suggests most females reproduce each year, although some females may not breed yearly (Rossman et al. 1996). This appears to be the case for *T. cyrtopsis* females. Neonates were found from June to August. The date of birth, size of neonates at birth, and growth rates likely show geographic and yearly variation (Goldberg 1998). Neonates are 145-281 mm in total length.

Western Terrestrial Garter Snake

Thamnophis elegans (Baird and Girard, 1853)

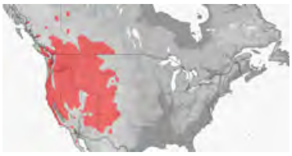


Figure 29.51. Distribution of *Thamnophis elegans.*

Distribution and Habitat. Many habitats, including coastal marine habitats, are used but usually close to water. The species ranges from southwest Canada into Washington state, southward to Oregon, eastward to Montana, Colorado, and Nebraska, and southward to Baja California Norte, Mexico. A polytypic species with at least three subspecies.

Other subspecies have been described, but Hallas et al. (2021) and previous authors found morphological and genetic evidence that cast doubt on the validity of those taxa. Hallas et al. (2021) used molecular data and found *Thamnophis elegans* is composed of distinct evolutionary lineages, each with its geographic range and history of diversification. In addition, *Thamnophis e. elegans* and *T. e. terrestris* show unique patterns of diversification as populations dispersed from east to west.

Thamnophis elegans elegans (Baird and Girard. 1853) ranges from central California and southwest Oregon. The type locality is El Dorado County, California.

Thamnophis elegans terrestris (Fox 1951) ranges from extreme southwest Oregon to Santa Barbara County, California, west of the Central Valley. The type locality is Strawberry Canyon, Berkeley, Alameda County, California.

Thamnophis elegans vagrans (Baird and Girard. 1853) is widespread in the western USA (Washington, Oregon, Nevada, NW New Mexico), W Canada (British Columbia, Saskatchewan, Alberta). Type locality "California" in error. Likely Santa Fe, Santa Fe County, New Mexico [see Maslin 1958 and Maslin et al. 1959].

Identification. Maximum size 1090 mm. A highly variable species. A vertebral stripe is usually present and can be white, red, orange, or tan but is absent in some subspecies. On scale rows two and there is a dorsal lateral stripe that can be off-white or red. Dorsal scale keeled (except the first row) in 17-21 mid body, and posterior rows are reduced to 15-17. Ventral scales in males 148-185, subcaudals in males 71-101; in females ventrals are 137-177; subcaudals are 61-91. Head scales. Upper labials eight, 4-5 border the orbit; one preocular

Figure 29.52. *Thamnophis elegans* **(A)** *T. e. elegans*, **Plumas County, CA (B)** *T. e. terrestris*, **San Mateo County, CA, (c)** *T. e. terrestris*, **San Mateo County, CA, Brian Hubbs; (D)** *T. e. vagrans* **from Taos County, NM. James N. Stuart; (E) from Coconino County, AZ Robert Dobbs (F) A juvenile** *T. e. vagrans* **from Boulder County, CO, photo by aiknight13.**

sometimes two; usually three postoculars; posterior chin shields little may be longer than anterior pair.

Natural History. The diet is exceptionally diverse and includes gastropods (slugs), annelids (worms and leeches), mollusks (snails), fishes, anurans (tadpoles, frogs), small birds, and mammals. It also will scavenge on carrion. Foraging is usually diurnal and may occur in water and on land. Fitch (1940) examined 69 *T. e. vagrans* that contained prey: 37 specimens had aquatic prey, while 32 had terrestrial prey. Amphibians are preyed upon in the high Sierra Nevada, California (Jennings et al. 1992), and it is also known to feed on ictalurid fish (Gimbel and Zahratka 2021) and rodents (voles) Blais et al. 2021. Prey taken by this snake is subdued with venom that has proteolytic and myonecrotic effects (Jansen 1987, Finley et al. 1994).

Reproduction is similar to other temperate *Thamnophis*. However, the timing of the gametic cycles and emergence from hibernation, mating, and parturition are influenced by the latitude and altitudes of the population (Fox 1952, 1982). Males mature at 370-420 mm total length; females mature at 420-460 mm. Neonates are 167-276 mm and average 21.5 cm (Ernst and Ernst 2003). Harmer (2019) observed the sea anemone *Anthopleura sola* consuming a small *T. e. terrestris* in a tidal pool. Bowley et al. (2020) reported *T. e. vagrans* using thermal hot springs in Yellowstone National Park; the water had a pH of 2.73 and a temperature of 36.8°C. Bowley et al. discuss the neutral nature of keratin and explain how it may give the snake resistance to acid.

Mexican Garter Snake

Thamnophis eques (Reuss, 1834)

Distribution and Habitat. Permanent water with emergent vegetation in southern Arizona and southwest New Mexico in the USA; in Mexico, it ranges from the vicinity of the Pico de Orizaba northwestward to and south to Aguascalientes, Sonora, and Chihuahua, Quéretaro. Rossman et al. (1996) showed disjunct colonies in Oaxaca and Nuevo León, Hidalgo, San Luis Potosí, Guanajuato, Puebla, Guerrero, Nayarit, and Morelos, Mexico. It has been associated with stock tanks, cienegas, and streams flowing from them; they also occur along large rivers, shallow wetlands, and wet meadows. This polytypic species has ten subspecies; these have not yet been evaluated using molecular data. The maximum size for this snake is 1240 mm in total length (Suarez-Varon et al. 2016).

Thamnophis eques carmenensis Conant 2003 is distributed from Tlaxcala, La Lagunilla del Carmen, Mexico. The type locality is near El Carmen, Tlaxcala, Mexico.

Thamnophis eques cuitzeoensis Conant 2003 occurs in Michoacán, Mexico. The type locality is 100 m east of the southern end of the south–north causeway across the Lago de Cuitzeo, Michoacán, Mexico.

Thamnophis eques diluvialis Conant 2003 is known from Jalisco, Cajititlán, and several isolated localities. The type locality is near Villa Corona at the north end of the Laguna de Atotonilco, Jalisco, Mexico.

Thamnophis eques eques (Reuss, 1834) ranges along the southern edge of the altiplano and in the Sierra Madre del Sur in the states of Nayarit, Jalisco, Michoacan, Mexico Distrito Federal, Puebla, Veracruz, and Oaxaca.

Thamnophis eques insperatus Conant 2003 is known from Michoacán, Mexico. The type locality is on a highway 6 km southeast of Zacapu, Michoacán, Mexico.

Thamnophis eques megalops (Kennicott 1860) is known from Arizona and New Mexico in the USA and ranges southward into Mexico along the Sierra Madre Occidental in the Chihuahuan Desert and north of the Mexican altiplano in the Mexican states of Sonora, Chihuahua, Durango, Guanajuato, Hidalgo, and SanLuis Potosi.

Thamnophis eques obscurus Conant 2003 is known from Jalisco, Mexico. The type locality is in the town of Chapala, Jalisco, Mexico.

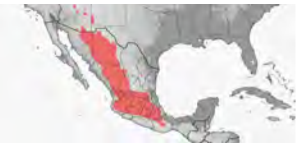


Figure 29.52. Distribution of *Thamnophis eques.*

Thamnophis eques patzcuaroensis Conant 2003 is known from Michoacán, Mexico. The type locality is the lakeshore north of Pátzcuaro, Michoacán, Mexico.

Thamnophis eques scotti Conant 2003 occurs in Jalisco, Mexico. The type locality is near Magdalena, Lago de Magdalena, Jalisco, Mexico.

Thamnophis eques virgatenuis Conant 1963 occurs in the

Figure 29.53. *Thamnophis eques* **(A) Zacapu Garter Snake (*Thamnophis eques insperatus*), Photograph from Ricardo Arredondo T. (B) Northern Mexican Garter Snake, *T. e. megalops* from Yavapai County. Photograph from Scott Sprague. (D) Lake Chapala Garter Snakes, *T. e. obscura* Photograph from J. Carlos Cuevas. (E) Magdalena Garter Snake, *T. e. scotti from* Teuchitlán, Jalisco, MX, Photograph from Julio Alejandro Alvarez Ruiz. (F) Blue-Striped Mexican Garter Snake, T*hamnophis eques* virgatenius from Pueblo Nuevo, Durango, MX. Photograph from Heriberto Avila G. (G) *Thamnophis eques patzcuaroensis* from Pátzcuaro, Michoacán, Mexico. Photograph from R. Enrique Llanos-Romero.**

highlands of Durango and Chihuahua, Mexico.

Natural History. The diet comprises fish and amphibians, with juveniles taking worms. Adults occasionally consume birds and mammals (Rossman et al. 1996). While some studies have suggested this threatened taxon requires small, soft-rayed native fishes, Emmons et al. (2016) found that it will prey upon larger, invasive prey such as Bullfrogs, Largemouth Bass, and Bullheads. In Arizona, Rosen and Schwalbe (1988) found females do not show follicle enlargement until the spring, which is unusual for *Thamnophis,* which often indicates follicular growth in the fall. They reported an average litter size of 13.6, noted that neonates are 13.7-19.4 cm in SVL, and that the introduced Bullfrogs prey on this species. Bourne et al. (2021) reported predation by the invasive crayfish *Oronectes virilis*.

Conservation. Wood et al. (2018) used genome-wide nuclear markers to study the population structure and genetic diversity of *Thamnophis eques megalops*. They found that populations along the lower Colorado River Basin are highly differentiated from sister species and populations located further south in Mexico. Colorado River populations exhibit reduced genetic diversity relative to populations along the Sierra Madre Occidental. Within the lower Colorado River Basin, genetic analyses revealed highly structured genetic groups that point to shared contemporary and historical drivers of differentiation. They found most sites in the lower Colorado River Basin have low genetic diversity and effective population sizes below the threshold required to retain adaptive potential.

Mexican Wandering Garter Snake

Thamnophis errans Smith, 1942

Figure 29.54. Distribution of *Thamnophis errans*

Distribution and Habitat. Pine-oak forests in Chihuahua, Durango, Jalisco, Nayarit, Mexico. The type locality is Colonia Garcia, Chihuahua, Mexico.

Dorsal scale rows 19 at midbody. Ventrals 155 to 166; subcaudals 72 to 91; upper labials seven or eight; sixth labial large and not narrowed above; vertebral and dorsolateral stripes poorly defined, vertebral stripe covering one scale row where visible; spots between stripes small, those of the outer row usually very poorly defined or absent; top of head dark; upper labial region pale, except for black posterior edges on most of the labials (modified from Smith 1942). Additionally, it has a black tongue (Fitch 1980), while other members of the *elegans-ordinoides* group have red tongues.

Natural History. Poorly known. Fitch (1985) reported the average liter was 7.8, ranging from 6 to 10.

Figure 29.56. Mexican Wandering Garter Snake, *Thamnophis errans* from Mezquital, Durango, Mexico. Photograph by Chris Grünwald.

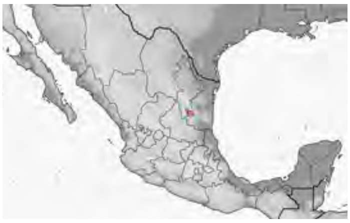


Figure 29.55. Distribution of *Thamnophis exsul*

Exiled Garter Snake

Thamnophis exsul Rossman, 1969

Distribution and Habitat. Dry pine forest at higher elevations in Tamaulipas, Nuevo León, Coahuila, Mexico. The type locality is a relatively dry pine forest, 11 mi. E, 3.5 mi S San Antonio de las Alazanas, Coahuila, at about 9,100 feet elevation.

The smallest known species in the genus, having a maximum recorded length of 460 mm. Dorsum almost uniform gray-brown with three indistinct pale stripes or having three or four alternating rows of spots or blotches with the light stripes partially or entirely suppressed. Specimens from Nuevo Leon show a marked ontogenetic pattern variation. Juveniles have three or four rows of prominent spots. The vertebral stripe is absent or faint and sometimes interrupted at intervals by dorsal spotting. Dorsal scales in 17 rows with no posterior reduction; upper labials seven, lower labials eight; ventrals 142-150 ventrals; subcaudals 52-56. The subadult spotted condition is not as prominent as in juveniles and is barely evident in larger adults (modified from Liner 1992). Natural History. This garter snake may be entirely terrestrial. Unknown.

Figure 29.56. *Thamnophis exsul* **from the Sierra de Pena Nevada, Nuevo Leon, Mexico. Photograph from Alan de Queiroz.**

Mesoamerican Highlands Garter Snake

Thamnophis fulvus (Bocourt, 1893)

Figure 29.58. Distribution of *Thamnophis fulvus.*

Distribution and Habitat. Endemic to the highlands of central Chiapas, Mexico, southern Guatemala, southwest Honduras, and adjacent El Salvador, at 1,400 to 3,700 m. It is known from the montane forest: including broadleaf forests (rain and cloud forest) and mixed and coniferous forests (pine-oak and pine forest), and páramo grassland with opine pine woodland within 150 m (Johnson et al. 2010; Acevedo et al. 2010; Eisermann et al. 2016). The type locality is Alta Verapaz, Guatemala.

Adults reach at least 62.5 cm. Dorsum olive-brown dorsum and two alternating rows of black spots that may increase in size on the forebody and intrude on the vertebral stripe. The vertebral stripe is tan, and the lateral stripe is pale yellow. The ventrals may have two rows of small spots laterally, have an indistinct mid-ventral stripe, or be unmarked. Some specimens have black blotches or vermiculations on the frontal and parietal scales. The tongue is black. Dorsal scale rows are 19 or 21 at midbody. Ventrals 132-154; subcaudals 56-80 (based on Rossman et al. 1996).

Natural History. Frequently found near water. Dietary records were two hylid frogs and tadpoles. Reproduction is poorly known; females are known to be gravid in May and October. One female gave birth to a single dead neonate 39 months after it had access to a male (Rossman et al. 1996).

Figure 29.58. *Thamnophis fulvus* **from Francisco Morazan, Distrito Central, Honduras. Photograph from (a) Josue Ramos (b) Juan Rabasa (C) San Cristóbal de las Casas, Chiapas, MX Photograph from Eric Eberman.**

Giant Garter Snake

Thamnophis gigas Fitch, 1940

Figure 29.59. Distribution of *Thamnophis gigas.*

Distribution and Habitat. Freshwater marshes, streams, and wetlands with soft bottoms and emergent vegetation; and their adjacent associated upland habitats throughout the length of the Sacramento and San Joaquin valleys in Central California. Only about five percent of its historical wetland/upland habitat acreage remains today. The type locality is Gadwall, Merced County, California. Elevational distribution ranges from sea level to 122 m.

Dorsum brown to olive with a cream, yellow, or orange vertebral stripe and two pale lateral stripes. Some individuals may have a checkered pattern of black spots between the dorsal and lateral stripes. Background coloration, prominence of the checkered pattern, and the three yellow stripes are individually and geographically variable (Hansen 1980). Individuals in the northern Sacramento Valley tend to be darker, with more pronounced vertebral and lateral stripes. The ventral coloration can be cream, orange, olive brown, or pale blue with or without ventral markings. Upper labial scales are dull brown and usually lack distinct wedge markings.

Figure 29.60. *Thamnophis gigas* **from Glen County, California US. Photograph from Brian Hubbs.**

Dorsal scales are in 23 or 21 rows; females have 23 rows more frequently than males.; the scale rows are reduced posteriorly to 17. Ventrals 162-168 in males and 156-164 in females; subcaudals range from 73-81 in males and 65-73 in females. On the head, one preocular, three postoculars; upper labials eight, lower labials 10 or 11.

Size. The Giant Garter Snake reaches a total length of 162.6 cm. Neonates 15.2-23.2 cm in SVL

Natural History. Diet. Anuran prey is taken more often than fish. Native treefrogs and the introduced Bullfrog are eaten most often, and the fish captured are usually cyprinids, including Common Carp, Fathead Minnows, Red Shiner, and Golden Shiner. Giant Gartersnakes selected native frogs over any other prey type and selected all frogs, native and introduced, more than introduced fishes. Even though invasive prey is dominant in their environment, given a choice, Giant Gartersnakes prefer to eat the less abundant native tree frogs. Thus, the management of native prey communities that also limits the abundance and distribution of invasive prey will preserve historical trophic dynamics and will likely benefit Giant Gartersnakes and other native predators of the Central Valley (Ersan et al. 2020). This snake has been reported to eat the rodent *Microtus californicus* (Fulton and Munoz 2018).

Reproduction. Litter sizes range from 10 to 46, with a mean of 23.1 (Hansen and Hansen 1990). Rose et al. (2018) found average litter size from X-rays was 15.9, and captive-born litters averaged 15.5; but captive-born litters had high stillbirth rates; of 202 neonates born, 154 survived. Fecundity is positively related to maternal snout-vent length, and there is some evidence that larger litters contained smaller neonates. The proportion of gravid X-rayed females was 0.50 in 2014, 0.47 in 2015, and 0.64 in 2016. Central California experienced an exceptional drought from 2012–2015, which may have affected the reproductive output.

The Giant Garter Snake was listed as endangered on December 27, 1991. However, the Fish & Wildlife Service reevaluated the status of the snake before adopting the final listing rule, and it was listed as a threatened species on October 20, 1993.

The loss and subsequent habitat fragmentation are the primary threat to the Giant Gartersnake throughout the Central Valley of California. Habitat loss has occurred from urban expansion, agricultural conversion, and flood control. Habitat fragmentation has ultimately resulted in the snake being extirpated from the southern one-third of its range in the San Joaquin Valley. The Giant Garter Snake also faces other threats: traffic, climate change, and predation by non-native species. Climate change has been linked to the intensity of weather events (heat waves, droughts, and storms) that may cause mass mortality by affecting habitat or ecosystem characteristics.

Godman's Garter Snake

Thamnophis godmani (Gunther, 1894)

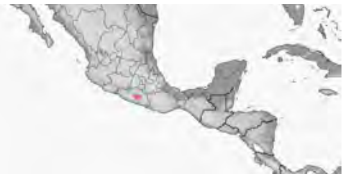


Figure 29.61 Distribution of *Thamnophis godmani.*

Distribution and Habitat. Pine-oak Forest and cloud forest in the Sierra Madre del Sur of Guerrero. Recorded from elevations of 1768-2438 m. A record from Acahuizotla at 853 m is suspect because a habitat suitable for this species would unlikely occur at such a low elevation. The type locality is Mexico, Guerrero, Omilteme, and Amula (Rossman and Burbrink, 2005).

Dorsal scale rows 17 at midbody. Top of the head un-patterned. Two rows of small black spots between light vertebral and lateral stripes. Ventrals average 144 in males and 138 in females; subcaudals average 79 in males, and 71 in females (Rossman and Burbrink, 2005).

This species was initially composed of four distinct populations; Rossman and Burbrink (2005) described each population as a different species (*T. bogerti*, *T. conanti*, *T. lineri*) based on morphology. Little is known about their natural histories. Rossman et al. (1995) report observations by Caldwell and Rossman, who observed them under logs, tar paper, oak-pine forests, and swimming in streams. One specimen disgorged a mouse when captured.

Figure 29.62. *Thamnophis godmani* **is from Chilpancingo de los Bravo, Guerrero, MX. Photograph from Edgar Salmeron Barrera.**

Two-Striped Garter Snake

Thamnophis hammondii (Kennicott, 1860)

Distribution and Habitat. Streams, creeks, and pools in oak woodlands and mixed oak chaparral and sparse pines, cedars, and scrub oak from Monterey County, California, southward into Baja California, Mexico. It has a population on Catalina Island and an isolated population in Baja California Sur. Its elevational distribution is from sea level to 2130 m.

Figure 29.63. Distribution of *Thamnophis hammondii.*

Figure 29.64. *Thamnophis hammondii.* **(A) Photograph from Mike Pingleton. (B) From Los Angles Co., CA. Photograph from Kaiyuan Chen. (C) From Santa Monica Mountains National Recreation Area, Los Angeles County, CA. Photograph from Brad Alexander.**

Natural History. Because this species was long confused with *Thamnophis elegans* and *T. couchii,* its natural history is poorly known. The diet is composed of fish and amphibians in all their life stages. They may also feed on annelid worms. Foraging occurs day and night, in the water and on land. Sexual maturity of males occurs at 37.3 cm SVL, and females mature at 38.8 cm SVL (Wright and Wright, 1957). Mating occurs in the spring (April-May), and parturition occurs from July to October. Litter sizes of 3-36 (average 15-16) have been reported, and neonates are 20.0-22.0 cm in total length (Cunningham 1959, Rossi and Rossi 1995).

Checkered Garter Snake

Thamnophis marcianus (Baird and Girard, 1853)

Figure 29.64. Distribution of *Thamnophis marcianus.*

Distribution and Habitat. Deserts and dry grasslands to premontane forests (Abarca and Solórzano 2020) in Costa Rica. It ranges from southern Kansas to California and southward into Mexico, Belize, Guatemala, possibly El Salvador, Honduras, Nicaragua, and Costa Rica. Elevational ranges extend from near sea level to 2200 m. This is a polytypic species with three or four subspecies. The type locality is Indian Territory between Camp 5 and Red River (Tillman County near Hollister, Oklahoma, fide H. A. Dundee, cited in Cochran 1961: 182. Taylor (1949) restricted the type locality to Red River, Arkansas. Originally the type locality included New Braunfels, Sand Pedro, and Indianola, Texas. *Thamnophis marcianus* is a polytypic species.

Thamnophis marcianus bovalli Dunn 1940 occurs in Nicaragua, northern Costa Rica. The type locality is Granada, Nicaragua. Dunn diagnosed it as a *Thamnophis* without stripes; but with equidistant black lateral bars alternating with black dorsal spots anteriorly. The ventrals are black-bordered anteriorly; one preocular; 140-144 ventrals; tail about 25% of total length.

Thamnophis marcianus marcianus (Baird & Girard, 1853) ranges southward from Texas, New Mexico, and Oklahoma to Chihuahua, Mexico. Type locality: Indian Territory between Camp 5 and Red River (Tillman County near Hollister, Oklahoma). Note that Taylor 1949 restricted the type locality to Red River, Arkansas. It originally included New Braunfels, Sand Pedro, and Indianola, Texas.

Thamnophis marcianus praeocularis ranges

Figure 29.65. *Thamnophis marcianus* **(Baird & Girard, 1853). Photograph from (A) Mike Pingleton (B-C) JCM.**

southward from Mexico Yucatan, Quintana Roo, Mexico to Belize. Type locality Belize. A broad vertebral stripe with two rows of small spots on each ventral has the fewest ventrals and the greatest number of maxillary teeth of any *marcianus* population (Rossman 1971).

Thamnophis marcianus ruthveni Hartweg and Oliver 1938. From Oaxaca, Mexico. The type locality is three miles northeast of Tehuantepec, Oaxaca, Mexico. The tan vertebral stripe is restricted to the vertebral row. The ground color is brown.

Natural History. The species can be diurnal, crepuscular, and nocturnal activity may change with the temperature. Seasonal activity extends from February to December in Texas, northern Mexico. Central American populations are likely to be active year-round. Diet mainly comprises amphibians, but fish, mammals, birds, and various invertebrates. Gatica-Colima and Hernandez-Alvarez (2019) found a Chihuahua specimen that had eaten a *Fundalus zebrinus*, an invasive species in Mexico.

Blackbelly Garter Snake

Thamnophis melanogaster (Peters, 1864)

Distribution and Habitat. Streams, lakes, and marshes in Mexico (Distrito Federal, Durango, Guanajuato, Jalisco, Michoacán, Nayarit, Querétaro, Zacatecas, San Luis Potosí, Aguascalientes, Sonora, Hidalgo). Rossman et al. (1996) consider this a polytypic species with four indefinable subspecies. *Thamnophis melanogaster canescens* Smith 1942 Mexico (Durango, Jalisco), the type locality is Chapala, Lake Chapala, Jalisco. For a detailed analysis of this snake's color pattern, see Gregory et al. (1983). The coloration and pattern are polymorphic.

Figure 29.66. Distribution of *Thamnophis melanogaster.*

Figure 29.67. *Thamnophis melanogaster.* **(A)** *Thamnophis melanogaster canescens* **from Jocotepec, Jalisco, MX. Photograph from Emmanuel Guevara Lazcano. (C)** *Thamnophis melanogaster chihuahuaensis* **from Madera, Chihuahua, MX. Photograph from Javier Cruz Nieto (D) From Jalisco, MX. Photograph from Iván Ahumada/Herp.mx .**

Thamnophis melanogaster chihuahuaensis Tanner 1959. Mexico (Chihuahua, Durango). This subspecies lacks the black ventral surface of the other subspecies.

Thamnophis melanogaster linearis Smith, Nixon and Smith 1950. The type locality is Lerma, México.

Thamnophis melanogaster melanogaster (Peters 1864). Type locality Mexico.

Natural History. A diurnal snake, much of the year. It transitions to nocturnal behavior in midsummer. Conant (1963) observed basking behavior in the late morning during the winter. Diet. Prey reported as fish (57%), leeches (20%), tadpoles (16%), and lesser numbers of earthworms, crabs, and adult frogs (Drummond 1983). *Thamnophis melanogaster* mainly forages at temperatures above 20C (Manjarrez and Drummond 1996). Foraging behavior includes swimming on the surface and diving to catch prey. Underwater searching involves slowly swimming with the mouth closed; chemosensory cues do not seem as essential as visual cues in this species (Drummond 1983, 1985). Reproduction is initiated by females releasing pheromones to attract males. Females from Lake Cuitzeo, Michoacán, gave birth in June and July, the average clutch size was 12.9, and the number of neonates was related to female size (Ford and Ball 1977).

Adelophis are most closely related to *Thamnophis melanogaster* and are discussed here. The phylogenetic placement of *Adelophis* within New World natricines has always been problematic. The generic name means "uncertain snake," a reference to its unclear phylogenetic affinities. *Adelophis* superficially resemble other semi-fossorial natricines, such as *Storeria* and *Tropidoclonion*, and have historically been placed in these genera. They possess unique scale counts and specialized osteological traits (Hallas et al. 2022). I am following Hallas et al. (2022) and recognizing them as members of *Thamnophis*.

Cope's Mountain Meadow Snake

Thamnophis copei (Dugès in Cope, 1879)

Distribution and Habitat**.** Guanajuato, Jalisco, and Morelos Mexico. Type locality: Guanajuato, Guadalajara, Mexico.

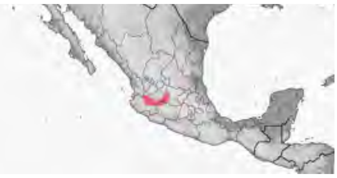


Figure 29.69. Distribution of *Thamnophis copei.*

Figure 29.70. *Thamnophis copei* **Dugès, 1879 from Tecolotlán, Jalisco, MX. Photograph from Iván Ahumada/ Herp.mx .**

A small garter snake reaches 39.2 cm. Dorsal scales in 15 rows; the absence of a loreal; ventrals 132-138; subcaudals; background ground color. Modified from Rossman and Wallach (1987).

Figure 29.71. Distribution of *Thamnophis foxi.*

Fox's Mountain Meadow Snake

Thamnophis foxi (Rossman and Blaney, 1968)

Distribution and Habitat**.** Known only from the type locality in southwestern Durango, Mexico, it occurs in a damp mountain meadow surrounded by pine forest.

Dorsal scales in 17 rows with no reduction; a loreal present; 132-139 ventrals; subcaudals 48-57; dorsal pattern with one pale stripe and four dark stripes on a gray-brown or olive-brown ground color; 20-21 maxillary teeth. Modified from Rossman and Wallach (1987).

Tamaulipan Montane Garter Snake

Thamnophis mendax Walker, 1955

Figure 29.72. Distribution of *Thamnophis mendax.*

Distribution and Habitat. Oak-pine forests in Tamaulipas, Mexico. Type locality near La Joya de Salas, Tamaulipas, at about 6,000 ft ASL. Known specimens were taken along the mountain trail (1050-2110 m ASL) between Gomez Farias and La Joya de Salas, at various points between Rancho del Cielo and La Joya, and Valle de la Gruta, about 1.5 miles northwest of "Rancho del Cielo.

The largest of seven specimens was 71.0 cm in total length. A narrow mid-dorsal stripe bordered by a single row of black-edged blotches on each side, the lower margins of blotches usually involving the lowermost body scale row or the outer edges of the ventrals; no lateral stripes; dorsal scales in 17 at midbody,

Figure 29.73. *Thamnophis mendax* **from Fagáceas del Noreste de México, Gómez Farías, MX. photo by Mario Álberto Álvarez Lara courtesy of Elí García Padilla**

reduced to 15 rows posteriorly; a low number of ventrals, males have 145-149 females have 141-145; subcaudals in males 68-69 and in females 57-61 (based on Walker 1955).

Natural History. The stomachs of two specimens contained remains of salamanders of the genus *Pseudoeurycea*. This is likely to be a primarily terrestrial garter snake.

Southern Durango Spotted Garter Snake

Thamnophis nigronuchalis Thompson, 1957

Distribution and Habitat. Southwest Durango and Nayarit, Mexico. The type locality is San Luis, about 2743 m elevation Durango, Mexico. The Nayarit record is based on a single specimen (CAS 169660) collected from "along Arroyo Santa Rosa, west of Santa Teresa, Mesa del Nayar, Municipio de El Nayar" by D. B. Breedlove on 5 October 1979 at an elevation of 2,095 m. The habitat is described as a "rocky ridge with *Pinus*, *Quercus* & *Arbutus* dissected by a grassy spring-filled valley." (Woolrich-Piña et al. 2016).

Figure 29.74. Distribution of *Thamnophis nigronuchalis.*

A single-stripe garter snake, medium-sized (to 57.4 cm), with a stocky build, closely related to *T. rufipunctatus and T. unilabials* (Wood et al. 2011). Dorsal scales in 21-19-17 scale rows; 149-165 ventrals; 63-70 subcaudals; an ovate head; two upper labials entering the orbit; two preoculars; a distinct and undivided black nuchal blotch; a dorsal color pattern consisting of 5-10 rows of red-brown spots outlined with black; no dorsal or lateral stripes; heavily pigmented ventrals, the pigment tending to form an irregular black longitudinal stripe.

Natural History. Tanner (1986) suggested this snake is confined to high-elevation basins where it uses deep pools. Rossman observed it swimming on the surface and lying on the bottom of a mountain stream and observed them basking near the stream on cool days and concealed under logs on the bank.

Figure 29.75. *Thamnophis nigronuchalis* **(A) Durango, MX. Photograph from Alan de Queiroz; (B) a juvenile from Durango, MX. Photograph from Eric Centenero-Alcala**

Northwestern Garter Snake

Thamnophis ordinoides (Baird and Girard, 1852)

Figure 29.76. Distribution of *Thamnophis ordinoides*

Distribution and Habitat. Most terrestrial snakes use edge habitats (Dixon-MacCallum et al. 2017) from southwest British Columbia in Canada, western Washington, western Oregon, and northwestern California. Alaska has an isolated population (Neuman-Lee et al. 2011). The type locality is Puget Sound. Its elevational distribution extends to 5000 feet (1500 meters) (Stewart, 1965). The northern part of the range in British Columbia has not been well defined. The range extends east of the Cascade Mountains in southern Washington (Slater, 1963).

Figure 29.78. *Thamnophis ordinoides* (A) Lake County, Oregon. Photograph from Claire Goodfellow (B) Washington County, Oregon. Photograph from Sabine Baer.

It is a polytypic species with three subspecies:

Thamnophis o. leptocephali (Baird and Girard 1853) Washington, USA, and a type locality on Puget Sound.

Thamnophis o. ordinoides (Baird and Girard 1853), the type locality is Puget Sound.

Thamnophis o. rubristriata Meek In Meek & Elliot 1899. The type locality was restricted to Port Angeles, Clallam County, Washington, by Marx (1958), with a type locality in the Olympic Mountains.

A medium-sized species reaching a total length 96.5 cm. Dorsal scale rows are usually 17 at midbody but occasionally 19. There typically are seven upper labials and eight lower labials. Ventrals 134-162, subcaudals 49-82. Color and color patterns vary substantially. Dorsal color is usually some shade of brown, olive, gray, or black. A yellow, orange, red, or blue middorsal stripe usually is present, and a yellowish or white lateral stripe sometimes is present. Dark spots and light fecks may occur between the stripes. The ventral surface is usually paler than the dorsal color but maybe suffused with dark pigment or red.

Natural History. On the Sausalito Peninsula of California, this species inhabits eroded canyons with scrub oaks and groves of laurels, manzanita, and willows. Frogs were uncommon, while salamanders were abundant, but Thompson (1951) found they feed almost exclusively on slugs of the genus *Ariolimax*. Gregory (1978) reported the principal food of this species on Vancouver Island to be slugs and earthworms. In Puget Sound, snakes emerge from hibernation in late March to April, mating occurs, ovulation occurs from June 7th to June 15, and gestation lasts about nine weeks from June 15 to August 20. Embryos number 3-15 and average 8.8. Fall mating occurs from September to October. Females mature at about 33.0 cm (Hebard 1951). In Saanich, British Colombia, Dixon-MacCallum and Bell (2016) captured 54 female snakes in August and found 32 (59%) were gravid females. The average litter size was 8.3, and the range was 2-17. Dixon-MacCallum et al. (2017) found that overall, litter depth, canopy cover, a lack of bare ground, and woody vegetation were the essential habitat variables for determining where snakes were located. They suggest that the edge habitat is necessary.

Tepalcatepec Valley Gartersnake

Thamnophis postremus Smith, 1942

Figure 29.77 Distribution of *Thamnophis postremus*

Distribution and Habitat. It inhabits dry tropical scrub forests that reach 1067 m in elevation and is restricted to the Tepalcatepec Valley of Michoacan. The type locality, EI Sabino, Michoacan.

Total length 101.5 cm. The vertebral stripe is indistinct—pale brown dorsum with small, dark alternating blotches extending the length of the body. The first three scale rows are pale, mostly unicolor, but often have scattered small black flecks. Black upper labial markings are well developed, with a characteristic large comma or thorn-shaped mark on the next to last suture. Seven upper labials, sometimes eight (37%). There is often more than one black mark on the infralabial sutures. Small, paired black spots usually occur laterally on ventrals. Ventral scales (136-151) (based upon Webb 1980); subcaudals 71 to 72; lateral light stripes not apparent; middorsal stripe but very little lighter than ground color, scarcely or not evident; dark spots very much reduced, alternating with each other in two series on either side; mid-dorsum not traversed by spots; the outer row of dark spots on first and second scale rows greatly reduced, generally scarcely visible; no distinct dark spots on venter (Smith 1942).

Natural History is poorly known. However, the species appears abundant near temporary pools where frogs are breeding. A 57.6 cm SVL female gave birth to 25 neonates on 20 June. The neonates were about 13.5 cm SVL and 17.6 cm in total length (Duellman 1961).

Western Ribbon Snake

Thamnophis proximus (Say, 1823)

Figure 29.79 Distribution of *Thamnophis proximus.*

Distribution and Habitat. They use upland habitats near wetlands, thick growths of grass in swamps, the margins of pools, swamps, marshes, lakes, rivers, creeks, peat bogs, desert springs, and roadside ditches. In addition, they will use mangroves (salty water) and savannas in the tropics. From southern Wisconsin, Indiana, and the Mississippi Valley westward through the Great Plains to southeastern Colorado and eastern New Mexico, southward through eastern Mexico to central Costa Rica. It occurs on Mexico's Pacific coast from the vicinity of

Figure 29.80. *Thamnophis proximus* **(Say, 1823). Photograph from (A) Mike Pingleton (B) from Union Co., IL USA. Photograph from JCM.**

Acapulco, Guerrero, to the Isthmus of Tehuantepec in Oaxaca (Liner and Dundee 1969; Rossman 1970). The type locality is a stone quarry on the west side of Missouri, three miles above the mouth of Boyer's River.

This polytypic species is based mainly on Rossman (1963):

Thamnophis proximus diabolicus Rossman 1963 from Western Texas and New Mexico, USA. A subspecies of Thamnophis proximus characterized by an olive-gray' to olive-brown dorsum, an orange vertebral stripe, a narrow dark ventrolateral stripe, and frequent reduction in the width of the lateral stripe on the posterior portion of the body in the southern part of the range.

Thamnophis proximus orarius Rossman 1963 from southeastern Texas and Louisiana; an olive-brown dorsum, a broad gold vertebral stripe, and a lack of a dark ventrolateral stripe characterize it.

Thamnophis proximus proximus Say 1823 from northeastern Texas, Oklahoma, Arkansas, and Louisiana USA; characterized by a black dorsum, a narrow orange vertebral stripe, and a lack of a dark ventrolateral stripe.

Thamnophis proximus rubrilineatus Rossman 1963 from Central Texas, USA; characterized by an olive-brown to olive-gray dorsum, a bright red vertebral stripe, and a narrow dark ventrolateral stripe or none.

Thamnophis proximus rutiloris Rossman 1963 from Guerrero and Oaxaca, Mexico, southward to Costa Rica; characterized by an olive-brown dorsum, a broad grayish-tan vertebral stripe, yellow-orange labials, a narrow lateral stripe, and a moderately narrow ventrolateral stripe.

Adults can reach 127.0 cm. A three-striped garter snake with a long tail; dorsal scale rows 19 at midbody reduced to 17 posteriorly. Ventrals 141 to 181, subcaudals 82 to 131. The lateral stripe on dorsal scale rows three and four on the anterior body; labials and ventrals without black markings; dark ventrolateral stripe absent or narrow in most populations; parietal spots fused, brightly colored, and usually large.

Natural History. A diurnal species with activity extending from March to October in northern populations and more southern populations are likely active year-round. During the hottest part of the year, it may become nocturnal. The diet comprises amphibians, and will take fish and lizards occasionally. It will actively forage frogs by probing leaf litter debris or grasses with its anterior body until a frog is flushed from hiding (Wendelken 1978). Prey taken by a Brazos County, Texas population was mostly the frogs *Gastrophryne olivacea*, *Pseudacris clarki*, *Incilius valliceps*, and *Lithobates* sp. (Clark 1974). Adams and Childress (2018) found a dead specimen that had attempted to feed on the toad *Incilius nebulifera*. It is unknown if the snake died from asphyxiation or the toxins from the toads. Ignoring age differences, Clark (1974) found average movements for individuals in the Texas population were 2.5 m/day for males and 1.1 m per day for females. Mating occurs in the spring (April-May), and parturition occurs in June-July. Litter size ranges from 6-18, and neonates are 13.0-17.4 cm SVL. Beutelspacher-García (2015) described arboreal aggregation behavior that may be associated with mating.

Yellow-throated Gartersnake

Thamnophis pulchrilatus **(Cope, 1885)**

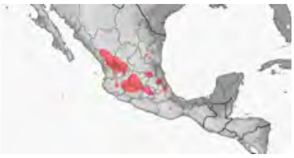


Figure 29.81. Distribution of *Thamnophis pulchrilatus*

Distribution and Habitat. Boreal pine-oak forests from Durango to Tamaulipas and Nuevo Leon to Oaxaca. Elevational distribution ranges from 2240 to 3000 m.

A three-striped garter snake with pale stripes. The dorsolateral areas are either dark brown with an indistinct checkerboard pattern of black blotches or are black and confluent with the black nuchal collar. Pale keels on most dorsolateral scales often form thin longitudinal lines. The ventrolateral stripe is black (paler in young) or brown-black, including a regularly spaced series of black spots or two black dots (one above the other). There are seven upper labials. The characteristic is a prominent black, bar-like mark between the last two upper labials. None of the infralabial sutures (except posterior most) is black (based on Webb 1980). On the head, one preocular, three postoculars, seven upper labials, and ten lower labials. Dorsal scale rows are in 19 rows at midbody reduced to 17 posteriorly. Ventral scales 152-173; subcaudals 68-94.

Natural History. Díaz and Aguirre-Ramírez (2014) found a female under a rock on 28 August 2013, at 2012 h. It was 43.4 cm SVL; tail length = 10.9 cm; 11 g) at Mesa del Huarache, Municipality of Calvillo, Aguascalientes, México. The habitat was grassland with patches of oak forest and tropical scrub forest ecotone. When they flipped the stone, the snake tried to escape and finally formed concentric rings, hiding the head and raising its tail in sinuous movements while secreting musk. Following capture, the snake was palpated and regurgitated a partially digested *Dryophytes eximius*. Similarly, on 15 August 2013, at the same locality, another female (SVL = 510 mm; tail length = 13.2 cm; 20 g, elevation 2380 m) was discovered basking in the grass and displaying the same defensive behavior. On 12 June 2010, at Ciénega de Quijas, Sierra el Laurel, Aguascalientes, another specimen was found beneath a rock. It flattened the anterior half of its body, including the head, showing the bright blue in the interspaces between the scales for at least 30 sec, then tried to escape. A 49.4 cm total length female gave birth to a litter of seven on 21 May from Mexico's Distrito Federal 19.1-20.7 mm total length and weighed 2.1-2.6 grams (Garcia-Vazquez et al. 2012). Mcvay et al. 2015 recovered this snake as the sister to *Thamnophis cyrtopsis*.

Figure 29.82. ***Thamnophis pulchrilatus*** **from Jalisco, MX. Photograph from Iván Ahumada/Herp.mx.**

Plains Garter Snake

Thamnophis radix (Baird and Girard, 1853)

Distribution and Habitat. Wet prairies, meadows, marshes, often near streams, vacant lots, and open woodlands from Southern Manitoba, Alberta, and Saskatchewan, Canada, southward into the USA - Montana, North Dakota, South Dakota, Nebraska, Kansas, E Wyoming, E Colorado, NE New Mexico, Oklahoma, N Texas, Minnesota, Iowa, Wisconsin, Missouri, Illinois, Indiana, and Arkansas. Disjunct, relictual colonies in north-central Ohio and on the Illinois-Missouri border. In Saskatchewan, T. radix is restricted to grasslands and aspen parklands in the southern portion of the province (Secoy 1976). The type locality is Racine, Wisconsin, limited to the "vicinity of Chicago, Cook County, Illinois" by Smith and Brown (1946).

Figure 29.83. Distribution of *Thamnophis radix.*

The maximum total length of 1095 mm. A three-striped garter snake with a black, gray, or olive-brown dorsum. The middorsal stripe is yellow, orange, or orange-yellow, and the lateral stripes vary from yellowish gray to blue-cream and involve scale rows 3-4. Two rows of dark spots usually occur above the lateral stripes and another row of dark spots below them. The top of the head is usually dark, with two tiny pale spots on the parietal scales. The upper labials are yellow or cream in coloration, with prominent dark lines along the scale edges. The ventral surface is yellow to green, often with black spots at the outer edges of the ventral scales. Dorsal scales are in 19 or 21 at midbody and reduced to 17 posteriorly. Ventrals 135-175, subcaudals 54-88. Upper labials 7-8, and lower labials 9-10.

Eutainia haydenii Kennicott (1860) and *Eutainia radix twiningii* Couse and Yarrow 1878 have been considered subspecies of *T. radix*. However, given the comments of Walley et al. (2004) I do not recognize them here.

Natural History. A well-studied, mostly terrestrial garter snake, the species is active throughout its distribution from April to October. It is diurnal; during the hottest months, it may shift its location to crayfish burrows. Its diet is catholic, but it does consume many earth-

Figure 29.84. *Thamnophis radix.*
Photograph from (A) Tom Anton, (B) JCM

worms and leeches. Ballinger et al. (1979) observed these snakes feeding on larval amphibians; they wrote, "On one occasion, 30-40 adults were actively diving and capturing salamander larvae. Once a salamander was caught, it was carried to shore and eaten.

Mating in this species involves scramble competition and produces small mating balls of snakes (this is probably true for all *Thamnophis*). Litter sizes range from 3-36, with an average clutch size of 11.6 from Boulder, Colorado, to 17 in the Chicagoland area. Neonates have body sizes of 13.1 to 13.7 cm. Tuttle and Gregory (2014) captured gravid females from 10 May to 3 September at Miquelon Lake in central Alberta, close to the northern edge of the range. The average size of gravid females was 62.15 cm SVL. The litter size averaged 22.7 and ranged from 7 to 41. There was a positive correlation between the size of females and litter size. They presented data consistent with the hypothesis that Miquelon Lake *T. radix* exhibits a relatively 'fast' life history. These snakes grow quickly and reach reproductive maturity early, like more southerly populations (Tuttle and Gregory, 2012), but they produce more significant numbers of slightly larger young than lower-latitude snakes. Additionally, the proportion of adult females that are reproductive increases with SVL. Finally, despite a lower food intake during pregnancy (Tuttle and Gregory, 2009), their results demonstrate that annual reproduction occurs in this northern population, although the frequency remains uncertain.

Rossman's Garter Snake

Thamnophis rossmani Conant, 2000

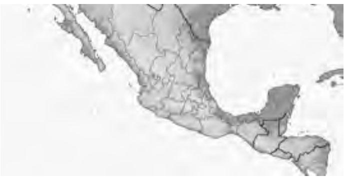


Figure 29.85. Distribution of *Thamnophis rossmani*

Distribution and Habitat. Springs, seepages, and ditches near the San Cayetano River flow northward to and beyond Tepic (Conant 2000). Nayarit, Mexico. The type locality is an open roadside ditch 1.4 km northwest of the small settlement of San Cayetano, Nayarit, Mexico.

The maximum size is 74.5 cm (Conant 2000). The three longitudinal stripes are pale yellow-green. Central stripe occupying a middorsal row of scales and adjacent

Figure 29.86. *Thamnophis rossmani*
Photograph from Ivan Ahumada /Herp.mx

halves of paravertebral rows. Lateral stripes occupying scale rows 3-4 anteriorly and rows 2 and 3 near the tail. The color between the stripes is medium brown. A black blotch above the rictus. Venter is pale gray-green, darkening slightly toward the rear of the body. Chin and throat a uniform pale yellow. Underside of the tail and anal scute yellow, also uniform. The anterior edge of each ventral is marked with a narrow dark gray stripe—dorsal scale rows 19 at midbody and reduced to 17 posteriorly.

Natural History. The spring rills were inhabited by small fishes, unidentified but probably cyprinids measuring roughly 25 mm to 50 mm in length. When the rills were not in flood, there were occasional riffles along them over which the fishes had to flip their way. On two occasions, Conant (2000) watched individuals of *Thamnophis rossmani* lying in wait and catching fish as they crossed the riffles.

Narrowheaded Garter Snake
Thamnophis rufipunctatus (Cope, 1875)

Distribution and Habitat. Perennial streams and intermittent streams with pools and riffles, and a substrate of cobbles or boulders in east central Arizona and west central New Mexico in the USA, and southward into Chihuahua, Coahuila, Sonora, and Durango, Mexico. The type locality is S Arizona.

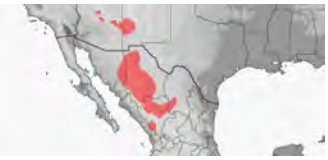


Figure 29.87. Distribution of *Thamnophis rufipunctatus.*

A moderate to large-sized garter snake (to 70.0 cm total length). No stripes are present. Dorsal color is dark brown to olive brown, usually with six rows of dark brown or rust-colored middorsal spots involving 3-5 scales extending from the nape onto the tail. The ventral pattern is irregular dark spots or a series of dark brown cross bars, often on the anterior edge of the ventral scales. The head is narrow, elongated, and laterally compressed, with one loreal, two preoculars, 3-4 postoculars (the lower may or may not contact the 4th upper labial), upper labials 8-9 (usually 8), lower labials 9-10 (usually l0). Dorsal scales in 21 rows at midbody reduced to 17 rows posteriorly. Ventrals range from 151-179; subcaudals 62-88.

Figure 29.88. ***Thamnophis rufipunctatus*** **Photograph from (A) JCM (B) Scott Sprague.**

Natural History. At San Francisco Hot Springs in New Mexico Hibbits et al. (2002) studied *Thamnophis rufipunctatus*. The diet was exclusively fish, of which a large proportion was the introduced *Gambusia affinis*. They feed on native fish, including suckers, dace, and trout. In 1996, the San Francisco Hot Springs population was about 7.2 adult snakes/ha; however, they did not find snakes in subsequent visits. *Thamnophis rufipunctatus* use streams with a steep riverbed slope and large rocks of uniform size. The San Francisco Hot Springs population of *T. rufipunctatus* was one of the most robust in the United States, and it completely disappeared in a decade. Christman et al. (2021) reported a Speckled Dace (*Rhinichthys osculus*) regurgitated by a captured specimen, and the same specimen had a larval *Anaxyrus microscaphus*.

Hibernation for telemetered snakes in Oak Creek Canyon, Arizona, began in late October to late November, and snakes emerged in early to late March (Nowak 2006). Telemetered snakes were not active outside of the hibernacula during the winter. Hibernation sites are above the 100-year floodplain and include rock outcrops, rocky slopes, and rock piles, often within 30-200 m from the water.

The mating occurs in the spring and early summer, and litters of 8-18 neonates are born in July - August (Rossman et al. 1996). Males reach sexual maturity around 2.5 years, females mature about year two, and they may reproduce every year (Rosen and Schwalbe 1988, Degenhardt et al. 1996). Although courtship has not been described for this species, evidence suggests mating occurs from late July into August (Degenhardt et al. 1996). Snout-vent length for neonates ranges from 16.0 – 20.5 cm (6.3 – 8.0 in).

Narrowheaded Gartersnakes have experienced recent extirpations. At a stream in Arizona, reliable snake records were known from 1992; recent surveys (before 2018) in the vicinity have had mixed but mostly negative results. The colonization of the invasive Northern Crayfish (*Orconectes virilis*) may be a factor in the decline. The crustacean has been observed in the tens of thousands in habitats that previously supported this species. The population decrease was likely the result of crayfish predation on the neonate snakes and the native fish prey base.

Eastern Ribbon Snake

Thamnophis saurita (Linnaeus, 1766)

Distribution and Habitat. Creek-beds, streams, lakes, wet woodlands, swamps, and marsh areas are found east of the Mississippi from southern Ontario, Canada, and southern Maine southward to the Florida Keys and the northern side of Lake Pontchartrain in Louisiana. An isolated colony occurs in central Nova Scotia, and perhaps another in northeastern Wisconsin. The species is uncommon or rare in much of the interior of the eastern United States. Waifs have been reported near the Atlantis Resort on Paradise Island in the Bahamas (John-

Figure 29.89 Distribution of *Thamnophis saurita*.

Figure 29.90. *Thamnophis saurita* . (A) *T. s. nitae* from central Florida. Photograph from JCM. (B) Photograph from Mike Pingleton (C) *T. s. saurita* from se Michigan. Photograph from JCM.

son and Sancois 2018). Type-locality was given as Carolina. The holotype is likely lost. A neotype designated by Schmidt and Conant, 1956-57 was collected 15 miles NNE Charleston, Berkeley County, South Carolina. This polytypic species has four subspecies. The Eastern Ribbon Snake, *T. s. saurita,* has a brown dorsum with three distinctive stripes, a yellow vertebral stripe, and yellow lateral stripes that alternate with the brown dorsum. It ranges from New York to Florida, west to the Mississippi River. Northern Ribbon Snake, *T. s. septentrionalis* Rossman, 1963 has a dark brown to black dorsum with a yellow vertebral stripe and lateral stripes. It ranges from Maine through Ontario and Indiana. Southern Ribbon Snake, *T. s. sackenii* (Kennicott, 1859) has a tan or brown dorsum without a vertebral stripe but with yellow lateral stripes on scale rows 3-4; it ranges from South Carolina south through Florida. The Bluestripe Ribbon Snake, *T. s. nitae* Rossman, 1963 has dark dorsum with no vertebral stripe but with light blue lateral stripes; on the Gulf Coast of north-central Florida. Hallas et al. (2022) found it, and *T. proximus* and *T. sirtalis* clade strongly supported as the sister to the remaining northern clade species, a pattern also recovered in some other analyses.

Maximum length 101.8 cm. A two or three-striped garter snake with no black markings on the labials or ventrals; a dark ventrolateral stripe always present and broad, dorsal scale rows 3-4 (row 2 is occasionally involved); parietal spots frequently lacking; when present, they are small and rarely in contact or brightly colored. A short-body (or long-tailed) *Thamnophis* is characterized by 19 scale rows at midbody, reduced to 17 rows posteriorly; upper labials seven or eight; ventral scales 143-177, subcaudals 94-136.

Natural History. Diet. Nocturnal foraging and feeding are common, especially in the southern part of the range and during the warm months. The diet consists of fish and adult and larval amphibians. Older literature on this snake suggests it is insectivorous. But the evidence was lacking and was likely based on secondarily ingested items.

Reproduction. Carpenter (1952) found that female ribbon snakes in southern Michigan attain sexual maturity between two and eight years when they attain a minimum body length of 42.1 cm; he did not present corresponding data for males. McCauley (1945) reported a gravid female from Maryland 84.1 cm in SVL. Mating occurs in April in the northern portion of the range, where emergence from hibernation occurs in late March. Mating probably occurs earlier in the extreme southern part of the range, where no true winter hibernation occurs. The young are usually born in August in the north, and July in the south, with considerable overlap. Dates range from 2 July through 4 October. The smallest gravid female Rossman (1963) measured had a body length of 35.0 cm.

Mexican Alpine Blotched Garter Snake

Thamnophis scalaris Cope, 1861

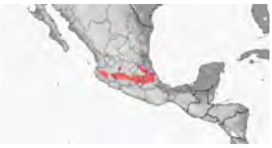


Figure 29.91. Distribution of *Thamnophis scalaris.*

Distribution and Habitat. A terrestrial, montane garter snake that uses alpine coniferous forests and grasslands in Mexico in the Distrito Federal, Guanajuato, Jalisco, Mexico. Michoacán, Oaxaca, Querétaro, Tamaulipas, San Luis Potosí, Veracruz, Morelos, Hidalgo, and Puebla at elevations of 2103-4273 m. The type locality is Jalapa, Veracruz, Mexico.

A small, maximum length 60.1 cm, three-striped garter snake with the anterior stripes connected by large black-edged, brown blotches, usually in one row on each side, but occasionally in two alternating rows. The blotches may or may not reduce to narrow black bars posteriorly. The prominent nuchal blotches also are brown with black borders, and they may or may

Figure 29.92. *Thamnophis scalaris*
Photograph from Ivan Ahumada /Herp.mx

not be continuous with the brown coloration of the parietals. The vertebral stripe involves at least the adjacent margins of the paravertebral rows. All upper labials have the same ground color, and there often are short, narrow, black wedge-shaped marks on the upper part of some anterior upper labial sutures. Dorsal scale rows are in 19-19-17 rows. The ventral scales have irregular dusting or peppering. Ventrals are 130-147; subcaudals are 50-85.

Natural History. The only prey known for this species are lizards of the genus *Sceloporus* and *Barisia.* Two litters born in the second half of May had eight and fifteen neonates 16.8 to 18.1 cm long.

Mesa Central Blotched Garter Snake

Thamnophis scaliger (Jan, 1863)

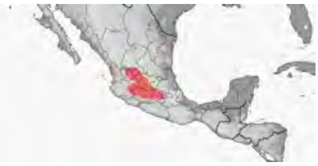


Figure 29.93 Distribution of *Thamnophis scaliger*

Distribution and Habitat. Semiarid desert scrub valleys, oak and coniferous forests, and pastures at high elevations (2500-2720 m ASL) in the Mexican states of Jalisco, Aguascalientes, Michoacan, San Luis Potosí, Puebla, and Guanajuato. The type locality is unknown (Smith and Taylor 1945, Mociño-Deloya et al. 2009b).

Adult females can reach 43.9 cm; adult males reach 36.9 cm. Dorsal scales in 19 rows at midbody. A brown dorsum and a series of black-edged dark brown blotches two scales long. The ventral surface is pale gray with black vermiculations on the anterior edge of many ventral scales. Nuchal blotches are transected by the vertebral stripe. A pale Y-shaped marking is present on the interparietal and frontal-parietal sutures. Upper labials are cream or white with black sutures. The vertebral stripe is pale yellow. The lateral stripes are also yellow (distinct or indistinct) and are on scale row two or two-three: seven upper labials, nine lower labials, one preocular, and three postoculars.

Natural History. The diet consists primarily of earthworms. However, they will take larger prey Mociño-Deloya et al. (2009a) reported one specimen consumed a *Thamnophis scalaris* and summarized the literature noting that they have been reported to feed on amphibians, lizards, and rodents, and one consumed a neonate *Crotalus triseratus*.

Of 27 pregnant females examined by Feriche et al. (2016), 44% recently had fed. However, females feeding during pregnancy did not produce heavier litters or larger neonates.

Feriche et al. (2016) examined the female reproductive strategy. Gravid females were

Figure 29.94. ***Thamnophis scaliger*** **from Toluca, Mexico, MX. Photograph from Juan Carlos Garcia Morales.**

collected in the field and maintained in captivity until birth. The low percentage of gravid females each year suggested they did not reproduce annually. This result probably was driven by the seasonal constrained availability and low-energy content of earthworms, which preclude females from acquiring sufficient energy to fuel more frequent reproduction. However, females produced relatively large litter sizes, suggesting significant investment in reproduction. In addition, Feriche et al. (2016) also found that females who reproduced later benefited most from foraging opportunities during the short rainy and high prey-availability period and remained in better body condition.

Most females delayed reproduction until achieving a body size approximately 2.7 times that of neonates. Also, most females matured at a body size of about 73% of the maximum body size recorded (SVL = 439 mm), although some mature at 61% of this body size. Suggesting some females delay the first reproductive event to increase body size to ensure high reproductive output. Therefore, the range in body sizes for mature females is relatively small (approximately 14.2 cm), which may obscure correlations between female SVL and reproductive output, a typical snake pattern (Feriche et al. 2016). Parturitions occurred between 26 June and 15 August.

Common Garter Snake

Thamnophis sirtalis (Linnaeus, 1758)

Figure 29.95 Distribution of *Thamnophis sirtalis*

Distribution and Habitat. It ranges from central Canada in the Northwest Territories, Manitoba, Alberta, Saskatchewan, New Brunswick, Ontario, and Prince Edward Island southward into the USA. It extends from the Atlantic and Gulf Coasts and west to Washington, Oregon, and California's Pacific Coasts and southward into Mexico – there is an isolated population in Chihuahua. It is also present in the Bahamas (Buckner and Franz 1998). And it maintains populations in Wood Buffalo National Park (59°49'N, 112°W), Northwest Territories, Canada). Wright and Wright (1957) found 154 habitats used by this species – the 20 most used were: woods, near water, lakes, fields, meadows, swamps, borders of rivers, marshes, along streams, gardens, roadsides, parks, clearings, margins of a ditch, margins of creeks, moist situations, swimming in the water, in water, and low ground. To this list, I (JCM) would add some personal observations. This snake has/had populations in urban environments where they can spend the winter in spaces around building foundations, crevices under sidewalks, and roadways.

Recently, Jones et al. (2023) used the Common Gartersnake, to understand the influence of major river basins and the transition from forest to grassland within the Interior Plains on genetic structure, they employ phylogenetic analysis, population structure analysis with spatial considerations, and demographic analyses using single nucleotide polymorphism data. Additionally, they investigate the species' historical range expansion with ecological niche modeling and data on geographic locations and historical climate conditions.

They (Jones et al. 2023) identified four distinct phylogeographic lineages, each showing varying degrees of connectivity. Interestingly, they observe differences in population structure patterns between genetic markers associated with sex chromosomes and those from autosomal loci, particularly concerning the central North American lineage compared to coastal lineages. They also found evidence supporting the existence of Pleistocene refugia in the southeastern region, where recent secondary contact occurred during the Last Glacial

Maximum. Furthermore, they detected signs of both northern and southern refugia in western North America.

Jones et al. found compelling evidence indicating a Pliocene origin for *Thamnophis sirtalis* in the central-southeastern part of North America. This origin predates the species' rapid expansion across the continent, which occurred before the middle Pleistocene and was influenced by climatic factors leading to lineage formation. They propose that major river networks within the Mississippi watershed played a significant role in repeated westward expansion events across the Interior Plains. It's worth noting that the study supports previous conclusions that phenotypic differences among subspecies do not reflect shared evolutionary history.

This is a polytypic species, and the following subspecies continue to be recognized.

Thamnophis sirtalis annectens Brown 1950 ranges from east-central Texas and adjacent Oklahoma and the Texas panhandle; SW Kansas has a disjunct population. The type locality is a small branch of Boggy Creek, one mile east of Austin, Travis County, Texas.

Thamnophis sirtalis concinnus (Hallowell 1852) occurs in Washington and Oregon. The type locality is in Oregon, probably in the lower Willamette Valley near Oregon City (Fitch, 1941).

Thamnophis sirtalis dorsalis (Baird and Girard 1853) ranges from the Rio Grande Valley and north-central New Mexico southward to El Paso, west Texas, with disjunct populations in northeast New Mexico, USA. In Mexico, there are disjunct populations in Chihuahua. The type locality is Fort Conrad, New Mexico.

Thamnophis sirtalis fitchi Fox 1951 occurs in California, Oregon, Idaho, and Utah in the USA. The type locality is Gray-lodge Refuge, 9 mi W of Gridley, Butte Co., California.

Thamnophis sirtalis infernalis (Blainville 1835) occurs in California. The type locality is California.

Thamnophis sirtalis lowei Tanner 1988 occurs in Chihuahua, México; The type locality is Yepómera, Chihuahua, Mexico.

Thamnophis sirtalis pallidulus Allen 1899 occurs from southern Quebec and the eastern shore of James Bay to the Gulf of St. Lawrence and Nova Scotia in Canada; in the USA, it ranges from New England to extreme northeastern Massachusetts.

Thamnophis sirtalis parietalis (Say 1823) occurs in Canada from southern Alberta and Manitoba. It extends southward into eastern Nevada, southern Idaho, and Utah, south to New Mexico, north Texas, and east to Iowa, Minnesota, Wisconsin, Oklahoma, and Missouri. And it extends southward into Mexico to Chihuahua, Coahuila, and Tamaulipas. The type locality is a stone quarry on the west side of the Missouri River, 3 miles above the mouth of the Boyers River.

Thamnophis sirtalis pickeringii (Baird and Girard 1853) occurs in Washington, USA. The type locality is Puget Sound, Washington.

Thamnophis sirtalis semifasciatus (Cope 1892) occurs in northeastern Illinois and adjacent portions of Indiana and Wisconsin. The type locality is Aux Plaines [=Des Plaines], Illinois.

Thamnophis sirtalis similis Rossman 1965 ranges from western Florida's Wakulla Co. to the Withlacoochee River of Florida.

Thamnophis sirtalis sirtalis (Linnaeus 1758) occurs in southern Canada (Ontario, Quebec), through the eastern USA to the Gulf of Mexico, and west to Minnesota and SE Texas; Type locality: Canada; the neotype is from Quebec County, Quebec.

Thamnophis sirtalis tetrataenia (Cope in Yarrow 1875) California, USA. The type locality is the Pitt [Pit] River, California.

Figure 29.96. *Thamnophis sirtalis*
Photograph from (A-C) Mike Pingleton. (D) Nathan Kutok, (E-F) JCM. (G) Joe Peck.

Natural History. As Rossman et al. (1996) pointed out, the extensive distribution and plasticity of its ecological traits and life history make generalizing these aspects of its biology nearly impossible. Its activity varies with latitude and local climates. It has an exceptional cold tolerance. It can be active in northern Canada for five months of the year. I (JCM) once found a young one frozen in the ice covering a pond following a few warm March days. I chipped it out of the ice, brought it home, and released it at the capture site a month later. At some southern locations, the species may be active year-round. While it is diurnal, it may become active at night during warm rain. Larsen and Gregory (1989) found a snake just out of the northern Alberta, Canada den, with a cloacal temperature of 0.5°C. Telemetered snakes had body temperatures of 1.8 to 6.5°C (Macartney et al. 1989). Some Canadian snakes were found to have activity ranges that were 142,000 m^2 while other studies report this snake's recapture points were within 160 m of their original capture site (Fitch 1965, Freedman and Catling 1979).

Diet. A wide variety of aquatic and terrestrial invertebrates and vertebrates are preyed upon. The species is positively buoyant and hunts while swimming at the surface. And it will hunt earthworms using chemoreception to locate burrows, pushing its way into the soil to capture them (Rossman et al. 1996). This snake will also scavenge corpses, Vanek et al. (2021) reported a specimen from Lake Co., Illinois, feeding on a dead American Bever.

Reproduction. Mating occurs in the spring when the snakes emerge from hibernation and in the fall when the snake aggregates at den sites. Parturition occurs from mid-summer to early fall, but the young may be born as early as May at more southern locations. Litter sizes range from an average of 7.6 in Manitoba to 32.5 in Maryland. Females may not reproduce yearly; they may extend reproduction to once every three years or more at higher latitudes. Neonates range from 15.4 to 20.1 cm in total length.

Note: Key et al. (2019) investigated the taxonomic status of the Texas garter snake, *Thamnophis sirtalis annectens*, a taxon needing conservation. They test the hypothesis that an integrative approach to species conservation has greater utility than using only a single data type (e.g., molecular, morphological, behavioral, or ecological). They demonstrated how ecological niche modeling and molecular genetics could synergistically resolve taxonomic classifications. Using a phylogenetic analysis based on molecular data, they found that some putative *T. s. annectens* specimens represent a co-occurring subspecies (the Redsided Garter Snake, *Thamnophis sirtalis parietalis*), which is not of conservation concern. However, both *T. s. annectens* and *T. s. parietalis* are genetically distinctive from *Thamnophis sirtalis sirtalis*. Furthermore, the ecological distinctness of *T. s. annectens* from *T. s. parietalis* suggests that *T. s. annectens* is, in fact, a distinct evolutionary subunit. Only when genetic and ecological information was included was the distinctiveness of *T. s. annectens* apparent.

Sumichrast's Garter Snake

Thamnophis sumichrasti (Cope, 1866)

Figure 29.97. The distribution of *Thamnophis sumichrasti*.

Distribution and Habitat. Humid montane forest with small streams in the Mexican states of Oaxaca, Chiapas, Queretaro, San Luis Potosí, Tabasco, Puebla, Veracruz, and Hidalgo. The type locality is Orizava, México.

A one-stripe or no-stripe garter snake with spotted and blotched morphs can occur in the same litter. The spotted morph has black-edged, lateral brown spots 0.5 to 2 scale rows long on dorsal scale rows 3-5 or 3-8 with vertebral bars. Sometimes present are alternating rows or rows of spots on the first dorsal scale rows. Spots are best developed in young animals and may disappear with age. The blotched morph has 34-49 black-edged blotches that extend from the vertebral line to the first dorsal scale row. The blotches are 3-3.5 scale rows long - stripes are always absent in this morph. Comma-shaped nuchal blotches with the tails ending on the parietal scales.

Eight upper labials, ten lower labials. Dorsal scales in 19 rows and lack apical pits. Ventral scales are 147-161, subcaudals 57-80.

Natural History. This snake has been reported to feed on the toad *Incilius cristatus* (Cerón-de la Luz et al. 2020) and a *Pseudoeurycea* salamander (García-Bañuelos et al. 2020).

Figure 29.98. *Thamnophis sumichrasti* **from Agua Zarca, Tenango de Doria, Hidalgo, México. Photography by Fernandez Ballido.**

Madrean Narrowheaded Garter Snake

Thamnophis unilabialis (Tanner, 1985)

Figure 29.99. Distribution of *Thamnophis unilabialis*

Distribution and Habitat. A highly aquatic *Thamnophis* Rock-strewn stream in the Mexican states of eastern Sonora, Chihuahua, and Durango. The type locality is 0.5 mi SW of Bocoyna, Chihuahua, Mexico.

Adults can reach 93.5 cm. Overall this snake is brown with little pattern, which contrasts with the coloration of adults from western Chihuahua that are dark brown with five or more rows of reddish to black spots or black-bordered red spots on the dorsum (Lemos-Espinal and Smith 2007). Neonates in Sonora show the more typical spotted pattern. Ventral scales are 151-169, subcaudals are 65-82. In addition, it has two enlarged nape spots, six rows of dark brown or rust-colored spots on the body, and ventral scales usually have anterior margins heavily pigmented to form a light-and-dark, crossed-barred pattern.

Natural History. Most were found under rocks near streams; one was captured in a minnow trap. An unvouchered specimen from Arroyo La Presita had a *Gila minacae* in its stomach (Rorabaugh et al. 2019).

Figure 29.100. *Thamnophis unilabialis.* (A) From Temósachic, Chihuahua, MX. Photograph from Jorge H. Valdez. (B) From Guadalupe y Calvo, Chihuahua, MX. Photograph from Eric Centenero Acala (C) From Casa Blanca, Durango, MX. Photograph from Ivan Ahumada / Herp.mx

Mexican Westcoast Garter Snake

Thamnophis validus (Kennicott, 1860)

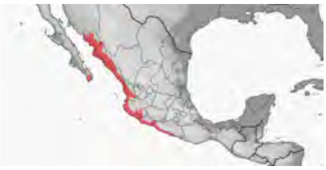


Figure 29.101. Distribution of *Thamnophis validus*

Distribution and Habitat. Marshes, meadows, canyon pools, streams, and irrigation canals in Baja California Sur, Chihuahua, Jalisco, Sonora, Guerrero, Sinaloa, and Nayarit. The type locality is Durango, Mexico (in error). Conant (1969) corrected it to Río Presidio on the coastal plain of southern Mexico. A polytypic species with three subspecies.

Thamnophis validus celaeno (Cope, 1861) has a type locality in Cape St. Lucas, Lower California, revised to San Jose River, Cape San Lucas, Baja California, Mexico (Cochran, 1961) and distinguished by lateral pale stripes involving dorsal rows 1-3. Dorsal coloration is variable but with dark and pale morphs. The dark morph is dark brown or black with little or no pattern except for the lateral stripes. The venter is virtually uniform black or very dark brown. The dorsum is pale gray or brown in the pale morph with 75-97 dark spots in four rows like mainland *N. v. validus*. The venter is white or yellow and may be immaculate or with a pale wash or stippled with slightly darker pigment. There is a single preocular and usually three postoculars. Ventrals are 135-146 in males and 134-145 in females; subcaudals are 74-82 in males and 67-75 in females (modified from McCranie and McAllister 1988).

Thamnophis validus isabellae (Conant, 1953) is on the west coast of Guerrero, Mexico. The type locality is Pie de la Cuesta, Laguna Coyuca, Guerrero. They are distinguished by a brown or chocolate brown dorsum, a pale stripe on the first two or three rows of dorsal scales on each side, a low number of ventral scutes, and a slightly higher mean number subcaudals. The venter gradually changes from a dull yellow on the anterior portion to a pale pinkish posteriorly. There are usually four rows of dark spots on the dorsum, each spot occupying only the anterior edge of anyone scale. The preocular is single, and there are three postoculars. Ventral scales in males are 131-137, 130-138 in females, 76-81 subcaudals in males, and 68-76 in females (modified from McCranie and McAllister 1988).

Thamnophis validus thamnophisoides (Conant, 1961) Nayarit, Mexico. The type locality is along the Rio San Cayetano also known as the Rio de Tepic on some maps and locally called the Rio Mololoa), approximately 3.5 miles southeast of Tepic, Nayarit, Mexico. They are distinguished by a distinct pale middorsal stripe and pale scales on the first three dorsal scale rows that form a lateral stripe on each side of the body. Dorsum coloration varies from brown to olive brown, and the venter is a pale yellow with no dark pigment. There are a single preocular and three postoculars. Ventrals in males are 130-140, in females 127-139; subcaudals in males 69-80, in females 65-73 (modified from McCranie and McAllister 1988).

A three-striped or two-striped garter snake that is semi-aquatic. There are 127-150 ventrals, eight upper labials (occasionally 7 or 9), and usually ten lower labials (sometimes 9 or 11) (modified from McCranie and McAllister 1988).

Size. Neonates are 16.5 cm, and adult females reach 1100 cm.

Adult males average significantly smaller than adult females. The largest measured by Conant (1946) was a 92.5 cm female from Mazatlan, Sinaloa. The largest male was 60.5 cm.

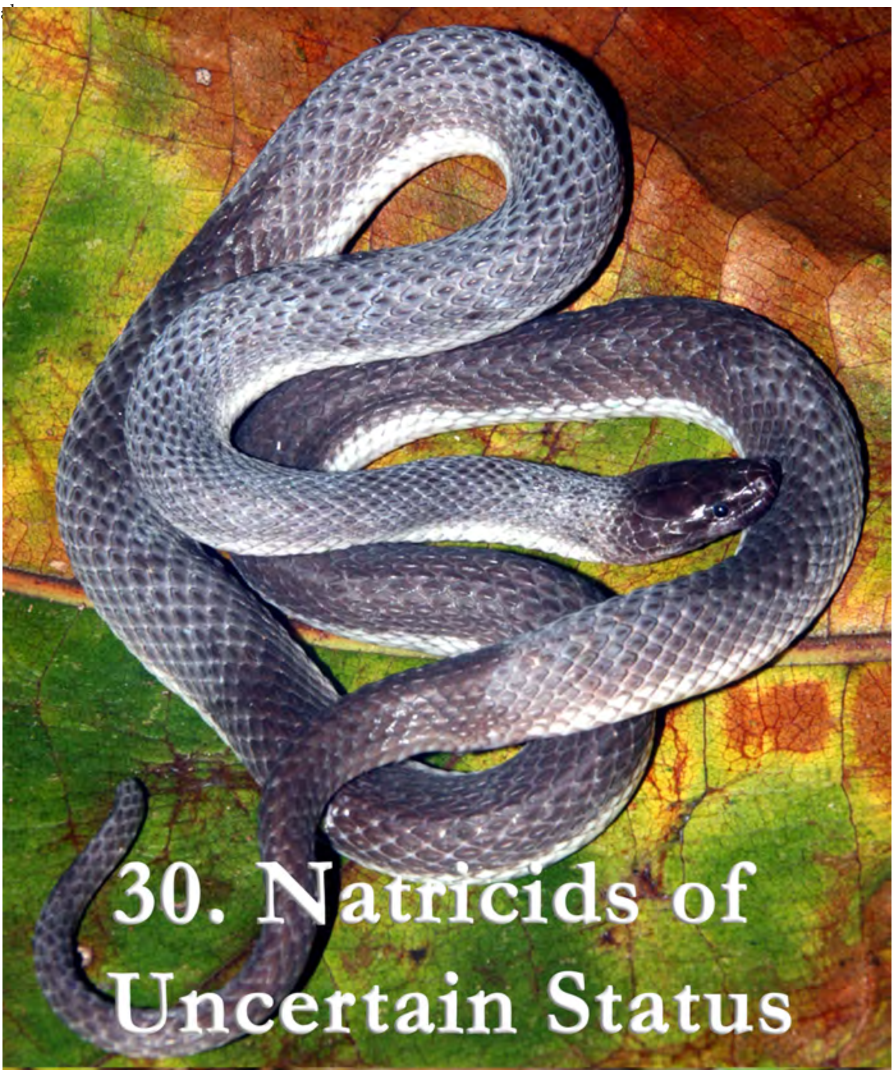
Natural History. The species is diurnal and active year-round, but activity is reduced from November to February (Grismer 2002). Adult Red Spotted Toads and their tadpoles, Pacific Treefrogs, Couch's Spadefoots, and mosquito fish are listed as prey by Conant (1969) and Grismer (2002). Although reproduction is poorly known, Grismer observed neonates from

Figure 29.102. *Thamnophis validus*. **Top Mexican West Coast Garter Snake (T***hamnophis validus validus)*. **Near Huatabampo, southern Sonora, Mexico. Photograph from Mike Pingleton.Top left. Cape Garter Snake (***Thamnophis validus celaeno*). **Baja Sur; bottom Cape Garter Snake (T***hamnophis validus celaeno*) **from Boca del Sierra. Photograph from Mike Pingleton.**

early August to October and had a captive female that gave birth to 10 neonates in August.

At Laguna Coyuca this species inhabits mangrove forests, but the water is almost fresh. Dunson (1980) placed adults in 100% seawater and found they lost only 0.76% of their body weight daily. He also tested neonates and found they were not as tolerant to salinity as the adults.

On the next page. The Borneo endemic ***Hydrablabes periop*****s. Photography by (A) Paul Freed.(B) Chien C. Lee . When I examined musuem specimens of these snakes it was clear that there are multiple species hiding under the names** ***Hydrablabes periops*** **and** ***H. praefrontalis.*** **(JCM).**



30. Natricids of Uncertain Status

30. Natricids of Uncertain Status

These are species that have not been exsamined using molecular evidence to determine how that are related to other groups.

Sumatran Keelback

Anoplohydrus aemulans Werner, 1909

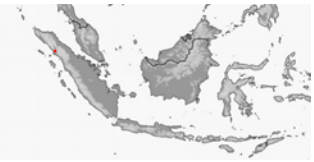


Figure 30.1 The distribution of *Anoplohydrus aemulans*

Distribution and Habitat. Sumatra, Indonesia. Type locality: Pudang, Distrikt Babongan, Sumatra. This may be Ujungpadang, Bakongan district, Aceh Provence. Known only from the holotype.

The position of the nostrils and eyes suggests this species is aquatic. The generic name also suggests Werner believed this snake was aquatic in its habits (Nguyen et al. 2010). David and Vogel (1996) considered it a semi-aquatic natricid inhabiting wet forests. Murphy (2007) suggested it may be a homalopsid.

Boonsong's Stream Snake

Isanophis boonsongi (Taylor and Elbel, 1958)

Figure 30.2 The distribution of *Isanophis boosongi.*

Distribution and Habitat**.** Northeast Thailand. Type locality: Phu Lang, Ban Khok, Na Phung, Dan Sai, Loei, Thailand.

Based on David et al. (2015), the posterior maxillary teeth are much enlarged but not grooved. The nostrils are dorsolateral and directed obliquely upwards; and the eye diameter is slightly greater than the eye-nostril distance and distinctly greater than the distance between its lower margin and the margin of the lip. The pupil is round; dorsal scales are strongly keeled with a thick median keel throughout the body. The body is stout; the head is distinct from the neck, and the prefrontal scale is single.

Figure 30.3 *Isanophis boonsongi* **from Lowei Province, Thailand. Photographer credit Merle J. Cox.**

Borneo Small-eyed Snakes

Boulenger (1891) described this genus as having; “Maxillary teeth small, equal, about 18; mandibular teeth small, equal. Head small, not distinct from neck; eye small, with a round pupil; nostril valvular, an oblique slit between two nasals; three pairs of chin-shields. Body cylindrical, elongate; scales smooth, without apical pits, in fifteen or seventeen rows. Tail moderate subcaudals in two rows.” This genus may be confused with *Opisthotropis* in the literature. Seven specimens I (JCM) have examined had either 17 dorsal rows or 15 rows at mid-body. A few had 21 or 19 rows just behind the head. They can have two or three pairs of chin shields.

Bernstein and Ruane (2022) extract and sequence the DNA of homalopsid snakes from several natural history collections and two specimens of *H. periops* from the Field Museum of Natural History (FMNH). They use a high-throughput target capture approach to sequence ultraconserved elements anchored hybrid enrichment loci and nuclear protein-coding genes (NPCGs) commonly used in squamates.

They found the placement of *H. periops* supported the familial taxonomic status of *Hydrablabes* as a natricid, rejecting the hypothesis that this species is a homalopsid (Murphy and Voris, 2014). They also obtained divergence dates of natricids slightly younger than those of Burbrink et al. (2020). Given its distribution, the close relation of *H. periops* to other Asian natricids is not unexpected. Containing *H. periops* (about 20.9 mya) may indicate population dispersal into Borneo from the mainland, with subsequent extinction events outside Borneo. Alternatively, the lineage ancestral to this clade may have dispersed into Borneo, followed by an in situ speciation event. The divergence dates of *H. periops* and *Trimerodytes* occur at the rise of the Hengduan Mountains of the eastern Tibetan Plateau (Western China) are considered a diversification driver of *Trimerodytes* about23.9 mya (Guo et al., 2020).

Olive Small-eyed Snake

Hydrablabes periops (Günther,1872)

Figure 30.4 The distribution of *Hydrablabes periops.*

Distribution and Habitat. Forest streams of East Malaysia, Borneo/Sabah, Sarawak), and Indonesia (Kalimantan), and Brunei Darussalam. The type locality is Matang, Borneo. Elevational distribution from sea level to 710 m ASL. See the cover photos for this chapter on page 601.

Mocquard’s Small-eyed Snake

Hydrablabes praefrontalis (Mocquard, 1890)

Distribution and Habitat. Forest streams East Malaysia (Borneo: Sabah), Indonesia (Kalimantan), and Brunei. The type locality is Mount Kinabalu, Sabah, Malaysia, Island of Borneo.

31. African Rain Forest Water Snakes

31. African Rain Forest Water Snakes

The genus *Grayia* is widespread in the lowland forests of central Africa and present in the countries of Angola, Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo, the Democratic Republic of the Congo (Zaire), Equatorial Guinea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Kenya, Liberia, Niger, Nigeria, Rwanda, S Chad, S Mali, Senegal, Sierra Leone, Sudan, Tanzania, Togo, Uganda, Zambia.

The genus was long considered part of the family Colubridae but has more recently been placed in its own family, Grayiidae. and even more recently suggested to be the sister of the Colubrinae (Ruane and Austin 2017; Zaher et al. 2019) and considered a subfamily of the Colubridae (Chaney et al. 2021). The genus is endemic to tropical Africa and is the only genus in the Grayiidae.(or Grayiinae)

Local people hunt these snakes for “bushmeat” and various medicinal uses. Unfortunately, conservative morphology makes identification difficult, and several “*Grayia*” samples on GenBank included misidentified specimens in other genera. Chaney et al. (2021) used molecular and morphological data to reconcile the current taxonomy of *Grayia*. They describe them as locally abundant, notoriously tricky to catch, and note that they occur in areas where fieldwork is challenging. Habitat includes seasonal rainforest swamps, streams, and permanent water bodies. The diet is composed of fish and frogs. Females deposit eggs in the leaf litter accumulated between the buttress roots of trees during the dry season. These snakes are unusual in depositing their clutch in small batches of three or four eggs at different times and more than one nest site rather than laying all the eggs simultaneously. The genus contains four species.

Long-tailed African Water Snake

Grayia caesar Günther, 1863

Figure 31.1 Distribution of *Grayia caesar.*

Distribution and Habitat. A central African forest species in seasonal rainforest swamps, streams, and permanent water bodies from Equatorial Guinea, C/E/S Cameroon, Democratic Republic of the Congo (Zaire), Brazzaville, Congo, Gabon, Central African Republic, and Angola. Type locality: Fernando Po.

A single female specimen of this species was described by Schmidt (1923) and was collected at Niapu. The specimen agrees with Boulenger’s description except for having only two posterior temporals. The color is grayish-brown above, with thirty light, narrowly black-edged crossbars, occasionally interrupted on the vertebral line. Tail faintly crossbarred. Ventral surface is entirely uniform gray-yellow. Lower labials are immaculate, except the last. Upper labials are pale, with dark markings mostly on the sutures. The top of the head is black, with a faint light spot on each parietal and still fainter ones on the frontal. A pale postocular stripe is followed by a sharply defined one from the mouth’s rictus to the parietals’ rear corner.

Natural History**.** The diet seems to be composed chiefly of fish, particularly catfish. It hunts in the water. It may also hunt from arboreal perches but see the following account.

On the previous page is Smyth’s African Water Snake, *Grayia smythii.* **Photography by Kate Jackson.**

Ornate African Water Snake

Grayia ornata (Bocage, 1866)

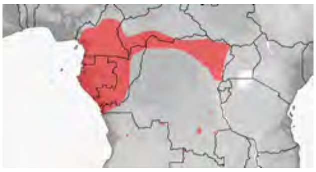


Figure 31.3 Distribution of *Grayia ornata*

Distribution and Habitat. A central African forest species present in seasonal rainforest swamps, streams, and permanent water bodies in Angola; the Democratic Republic of the Congo (Zaire; except in the west); Brazzaville; Congo; Gabon; Equatorial Guinea; Cameroon; Zambia; Central African Republic. Type locality: Duque de Bragança, Bayão, Angola.

Grayia ornata has two distinct color patterns: the typical transverse bar color phase and the rare longitudinally striped phase. Spawls and Branch (1995) noted the extreme similarity between the cross-barred color phase of *G. ornata* and the sympatric aquatic cobra *Naja annulata*.

The following is based on Schmidt (1923). The largest male measures 1240 mm., and the largest female 1385 mm. The tail length varies from 0.25-0.32 in males, mean 0.28, and from 0.24- 0.26 in females, mean 0.25. The ventrals range from 148 to 155, mean 153, in males, and from 153-160, mean 156, in females; subcaudals 69-87, mean 82, in males, 69-78, mean 74, in females—one preocular, two postoculars, and temporals 2-3 in every specimen. The lower anterior temporal is frequently separated from the postoculars. Five specimens have both loreals fused with the prefrontals; three have the loreal of one side fused. The upper labials number 8-10, and the lower 10 or 11. Three specimens from Medje and Niangara represent the longitudinally striped form. The light ventral color extends on the sides to the middle of the third scale row. Two interrupted black lines are distinct on this ground color, one on the ends of the ventrals and the first scale row and a second between the first and second scale rows. These lines consist of streaks six or seven scales in length, with interspaces of two or three scales. The upper half of the third scale row, the fourth, and the lower half of the fifth are occupied by a black band extending from the last upper labial. In adaption to its habitat, the tail is markedly compressed.

Natural History. Diet is composed mainly of fish. They will bask in branches overhanging the water and dive in when disturbed. Chippaux's (1999:83) report that *G. ornata* can hunt from branches overhanging streams was refuted by people interviewed by Pauwels et al. (2002) on the Massif du Chailiu, Gabon. The species is considered an excellent climber and likes to bask on branches overhanging the water, sometimes two to three meters high. When alerted, they fall into the water and quickly disappear into holes in the banks. They are said to be solitary and to hunt underwater at night, during which they actively explore every nook and crevice for prey items. It is believed in the Lunda area of north-eastern Angola that *G. ornata* live in pairs (Laurent, 1964: 102), but Pauwels et al. (2002) did not support this.

The stomach contents were usually fish (especially silurids), but frogs, shrimp, and small rodents sometimes were in stomachs. At Boussimbi, Diangui and Iboundji Pauwels et al. (2002) were told that the smell of G. ornata strongly attracts fish. Fisherwomen search the places where this snake lives as they think there will be many fishes there. Perhaps in support of this belief, one of the authors observed cyprinid fishes (genus *Barbus*) feeding on excrement defecated by *G. ornata* in the Loeme River, Kouilou Region, Republic of Congo. Itsiba inhabitants reported that otters often destroy hoop nets to eat the entrapped fish and dibomina (= *G. ornata*). Several fishermen of Diangui told Pauewels et al. (2002) sometimes find dibomina in the stomachs of the crocodilians *Crocodylus cataphractus* and *Osteolaemus tetraspis*.

Figure 31.4. ***Grayia ornata*** **(A) Kate Jackson with a *G. ornata* in a fishing net, and (B) a *G. ornata* from Ganganya Brousse, Republic of Congo. (C-D) A juvenile ornate from Umangi, DRC, (E) Photography by (A-B) Kate Jackson, (C-E) Vaclav Gvozdik**

Villagers in Itsiba and Moudouma use *G. ornata* as the essential remedy for delivery problems during childbirth. It is also used as a preventive measure a few days after a baby is born; some people take the viscera of *G. ornata* (first dried in the smokehouse) and use it as a bangle around the ankle of the baby. This bangle is believed to suck out sickness: "Like the dibomina can go out of the water, the sicknesses can go out of the body." The authors were also informed in Diangui that the fat of dibomina (as well as that of other snake species, mainly *Python sebae*), collected while cooking, can be used to treat sprains by direct application on the skin. This latter use is also current by the Pounou at least in Mouila. In the southern Republic of Congo, the fat of this species is applied on the skin to facilitate removing a thorn or a splinter. At Boussimbi, Diangui and Iboundji, *G. ornata* is used by fishermen for two magical purposes, to obtain excellent swimming ability and to be a successful fisherman (Pauwels et al. 2002).

Shadow African Water Snake

Grayia obscura Chaney, Greenbaum and Pauwels 2023

Distribution and Habitat. DRC and northeastern Angola, this cryptic species ranges from the Middle to Upper Congo River and its tributaries. In the Middle Congo River, it is probably sympatric with *G. ornata* sensu stricto. In the Middle Congo River, It is moleculary and mporphologically *G. ornata*. The holotype is from Mungombe in the South Kivu Province of the Democratic Republic of Congo.

Natural History. A single individual ontained the clariid catfish, *Clariallabes platyceps*. Although the authors speculate that a *Grayia ornata* was discussed by Broadley in1983, was most likely a *Grayia obscura* from Zambia. The prey was identified as the frog *Rana angolensis* (now *Amietia delalandii* or *A. chapini*) . The type locality and the locations of the paratypes are located in a transitional forest between the lowland rainforest of the Congo Basin and the foothills of the western Itombwe Plateau.

Figure 31.5. The Shadow African Water Snake, *Grayia obscura*.
Photography Konrads Mebert.

Smith's African Water Snake

Grayia smithii (Leach, 1818)

Distribution and Habitat. A western and central African forest species in seasonal rainforest swamps, streams, and permanent water bodies in southern Sudan; Uganda; Kenya; Tanzania; Rwanda; Burundi; Angola; Democratic Republic of the Congo (Zaire); Brazzaville, Congo; Equatorial Guinea; Cameroon; Nigeria; Benin; Togo; Ghana; Ivory Coast; Liberia; Guinea (Conakry); Guinea-Bissau; Senegal; Burkina Faso; Sierra Leone; Gambia; Central African Republic; probably southern Mali; Niger. Type locality Boma, Zaire.

Leach (1818) spelled the name *smythii* in the original description. He named the species after the Norwegian botanist Christen Smith (1785-1816). Some subsequent authors changed the spelling to *smithii* because the spelling "*smythii*" was considered inappropriate. Wallach et al. (2014) followed the original spelling, as do I.

The following is based on Schmidt (1923). This species is considerably larger than *G. ornata*. The largest male measures 1535 mm., and the largest female 1350 mm (tail incomplete). The tail length in three males varies from 0.29-0.33 of the total; the single female with a complete tail is 0.29. Ventral scales range from 149-160 in males, 157-162 in females; subcaudals 90-96 in males, 92 in one female. Dorsal scales 17-17-15, 19 on the neck on one specimen. One preocular, two postoculars, and temporals 2-3 in all specimens. Three or four slightly enlarged occipitals. Upper labials 7, the last very large, lower 10 or 11. There are twenty-three narrow light crossbands, with indications on the sides of eleven more. Adults have black crossbars, always with a row of light spots on the black scales, more or less in the middle of the bar. In two specimens, more than thirty such bars are visible; the posterior ones are merely indicated dorsally. In other specimens, the color becomes uniform on the posterior two-thirds of the body, with ten or twelve crossbars anteriorly. The tail scales are outlined with black, giving it a longitudinally lined effect and a similar line edges the venter. The throat is white, the lower labials black-edged. The parietal shields are gray, with black borders.

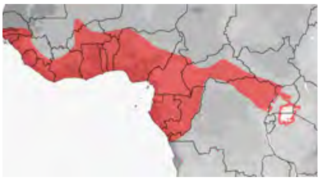


Figure 31.6 Distribution of *Grayia smithii*

Natural History. The ecology of the water snake, *Grayia smythii* was examined by Akani and Luiselli (2001) using a population in a seasonal rainforest swamp of the Niger Delta (southern Nigeria). The two sexes were similar in body sizes (SVL) and head sizes, but males had tails significantly longer than females. The diet consisted of frogs and fish. The major prey was the frog *Xenopus tropicalis*, followed by the fishes *Tilapia* sp. and *Clarias* sp. The adult sex-ratio was 1:1. Sloughing of skin and oviposition occurs during the dry season in the humid enclosure of buttress roots amongst leaf litter.

Clutch size ranged from 8 to 14 eggs per female, with a mean of 10. The smallest gravid female was 78.2 cm SVL. In at least two to three different sites, eggs were laid in batches of three to four eggs at a site. The eggs averaged 3.1 cm in length, 2.1 cm in width and had a fresh weight ranging from 18,2 to 22.1 g. Maternal size significantly influenced the number of eggs produced by females, but not their average size. A statistically significant negative correlation existed between the number of eggs and mean egg size. Predators of this snake in the study area were herons and fishermen.

Figure 31.7. Smith's African Water Snake, *Grayia smithii.* (A) is a juvenile (B) is an adult. Photography by (A) Vaclav Gvozdik (B) Kate Jackson.

Tholloni's African Water Snake

Grayia tholloni Mocquard, 1897

Distribution and Habitat. A savanna species in seasonal wetlands, streams, and permanent water bodies in southern Sudan, Uganda, Kenya, Tanzania, N/E/S Democratic Republic of the Congo (Zaire), Congo, Angola, Central African Republic, Ethiopia, Gambia, Senegal, Nigeria, Guinea (Conakry), maybe Cameroon, Zambia, and southern Chad. Type locality Brazzaville, Congo.

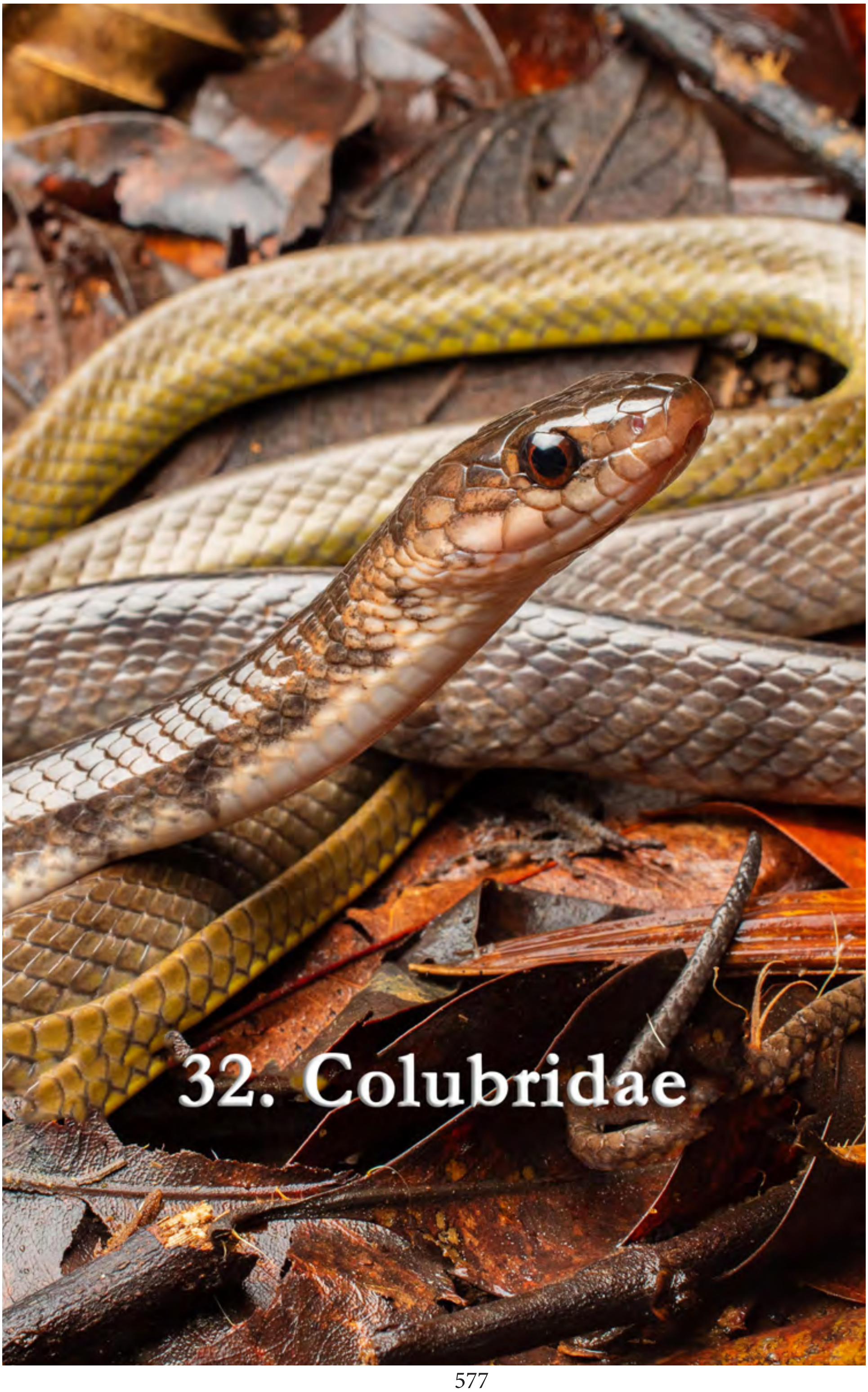
Schmidt (1923) examined two specimens; both specimens had incomplete tails. The

Figure 31.8 Distribution of *Grayia tholloni.*

head pattern distinguishes *G. tholloni* from *G. caesar*. Also the fifth labial, instead of broadly entering the orbit it is separated from it by a lower postocular or enters the orbit. *Grayia caessar* and *G. tholloni* agree in having much narrower postoculars than *G. smythii* and *G. ornata*, as well as in the larger eye. Color gray-brown above, with very indistinct light crossbars. The venter and underside of the tail are immaculate light yellow, outlined with black at the juncture with the dorsal color. Upper and lower labials were black-edged, and the black between the last two upper labials continued upward as a bar across the temporal scales.

Figure 31.9. ***Grayia tholloni.*** **Photography by Konrad Mebert.**

On the next page is a ***Xenelaphis hexagonotus*** **from Singapore. Photography by Kenneth Chin.**



32. Colubridae

32. Colubridae

Aquatic colubrids (or Colubrinae) are scattered in several clades, two in Africa and one in Asia. The members of the genus *Crotaphopeltis* were examined for genetic structure (Engelbrecht et al. 2017, 2019). The widespread, terrestrial *Crotaphopeltis hotamboeia* did not show cryptic diversity at the species level, although there was a clear phylogeographic structure (Engelbrecht et al. 2017, 2019). *Crotaphopeltis hotamboeia* diverged from its more aquatic Central and East African sister taxa, *C. degeni* and *C. tornieri*, in the mid-Miocene, a period characterized by a global cooling event. This caused the fragmentation of a west-to-east African forest belt and the emergence of savanna in Africa. The habitat changes likely induced allopatric speciation of forest and open habitat specialist species within this genus. Diversification took place at the forest-savanna ecotone in East Africa. Intraspecific diversification for *C. hotamboeia* commenced during the Miocene-Pliocene transition period, ca. 6 Ma (Engelbrecht, 2017). The Early-Pliocene forest expansion, which extended into coastal Kenya, Tanzania, and Ethiopia (Pickford, Senut, & Mourer-Chauvire, 2004; Sepulchre et al., 2006) probably excluded *C. hotamboeia* from East Africa.

Barotse Water Snake

Crotaphopeltis barotseensis Broadley, 1968

Figure 32.1. The distribution of *Crotaphopeltis barotseensis.*

Distribution and Habitat. It inhabits the papyrus swamps of Zambia, northern Botswana (Okavango Swamp, along Chobe River to upper Zambezi River), and Angola. It is also present in Ethiopia. Type locality: Kalabo, Barotseland, Zambia.

Natural History. A nocturnal frog-eating snake. Anurans were 97% of the food taken in one study. The taxonomic diversity of the prey items was large, with six families represented among the 51 anurans identified to family; however, bufonids (39%), ranids (29%), and microhylids (25%) comprised the bulk of the diet. These snakes feed all year except for midwinter. The smallest sexually mature female was 295 mm SVL. The smallest sexually mature male was 240 mm SVL. Clutch sizes ranged from four to 12 eggs. Females appear to yolk their ovarian follicles rapidly, starting in September. Egg deposition commences in October and continues through January. The only significant decrease in testicular activity was in mid-winter (July). Thus, spermatogenesis coincides with female follicular development and ovulation (Keogh et al. 2000).

Figure 32.2. The distribution of *Crotaphopeltis degeni.*

Degen’s Herald Snake

Crotaphopeltis degeni (Boulenger, 1906)

Distribution and Habitat. Moist savannas, swamps, and floodplains. Southern Sudan, Uganda, Kenya, Ethiopia, Tanzania (relict population), eastern Central African Republic, Cameroon, and Chad. Type locality: Entebbe, Uganda.

Fig.32.3. *Crotaphopeltis barotseensis* **Photography by Piet-Hein Stutterheim.**

Figure 32.4. *Crotaphopeltis degeni.* **Defence posturesPhotography by Konrad Mebert.**

The Genus *Platyceps*

A widespread genus of about 30 speicies tend to be habitat and dietary .generalists. The degree to which either of the two species discussed here use aquatic envirnments is uncertain.

Sarso Island Racer

Platyceps insulanus (Mertens, 1965)

Figure . 32.5 The distribution of *Platyceps insulanus.*

Distribution and Habitat. Coastal environments of Sarso Island, Farasan Archipelago in the Red Sea, Saudi Arabia. The type locality is Insel Sarso, Farsan-Archipel, Rotes Meer, SW-Arabien. The holotype of *Platyceps insulanus* was collected by W. Kost on 26 November 1964, during the Senckenberg-Museum's Meteor Expedition in the Indian Ocean. The type specimen was found swimming in shallow waters just off-shore of the island (Mertens, 1965). The species was characterized by a uniform dull lead grey coloration of the upper parts (Mertens, 1965). The holotype is preserved at the Senkenberg Museum Frankfurt (SMF). The species is represented only

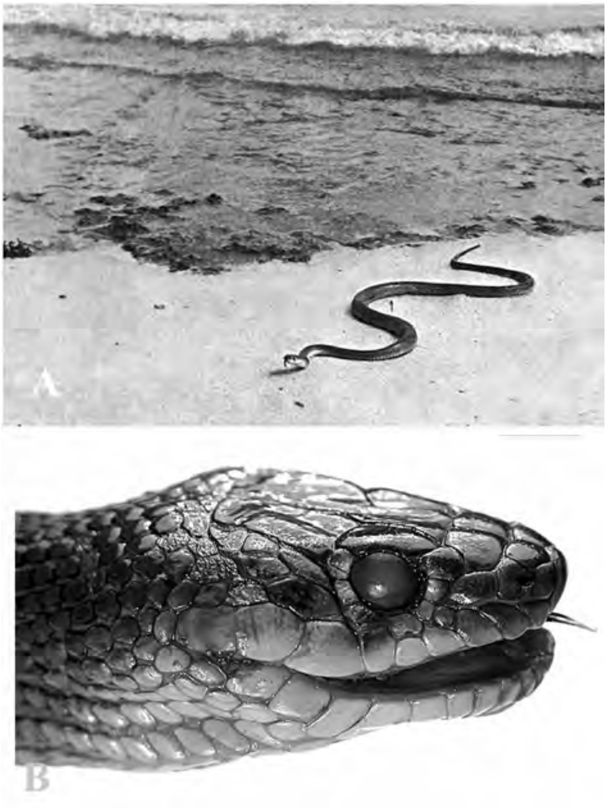


Figure 32.6. *Platyceps insulanus*. (A) The specimen collected by W. Kost on the 26th November 1964, in the course of the "Meteor" - Expedition launched by the Senckenberg-Museum in the Indian Ocean. Its type specimen was found while swimming in shallow waters just off-shore of the island (from Mertens, 1965). (B) The holotype of *Platyceps insulanus* is preserved at the Senkenberg Museum Frankfurt, SMF 60027 (Michael Franzen, Senkenberg Museum Frankfurt). Note both photos from Masseti (2014).

by this specimen, possibly subadult (Mertens, 1965) and its shed skin. The total length of the only known specimen is 760 mm (Mertens, 1965; Gasperetti, 1988). Mertens (1965) originally believed that Sarso was an island of the Dahlak archipelago, of the coast of Eritrea. Following Kost's report and the subsequent description by Mertens (1965), the snake was never found again, either on Sarso or on other nearby islands. Masseti (2014) suggests that this species is extinct.

Jan's Cliff Racer

Platyceps rhodorachis (Jan, 1863)

Distribution and Habitat**.** A widespread species that uses many different habitats. Known from Turkey, Algeria, Egypt, possibly Sudan, Eritrea, Ethiopia, Somalia, Chad, Syria, Jordan, Saudi Arabia (incl. Farasan Islands), United Arab Emirates, Oman, Iraq, Iran, Yemen, Afghanistan, W Pakistan, NW India, southern Turkmenistan, southern Uzbekistan, northwest Tajikistan, western Kyrgyzstan, southern Kazakhstan, and China (Tibet). The type locality is Persia; restricted to the Arabian Peninsula; Shiraz, Iran.

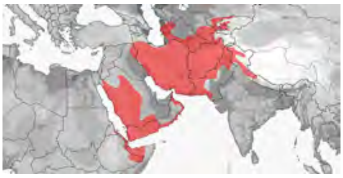


Figure 32.7 The distribution of *Platyceps rhodorachis.*

Figure 32.8 *Platyceps rhodorachis* **from Natanz, Isfahan Province, Iran. Photography by Hossein Nabizadeh.**

Inhabits arid regions with stone, and gravel substrates. Often desert habitats with associated hills and cliffs. It also penetrates desert along the Tejen and Murgab river valleys and is found in rocky situations bordering floodplains, including dry irrigation canals (Ananjeva *et al.* 2006). It can also be found in mountain steppes and juniper scrub (Ananjeva *et al.* 2006). It may be found close to cultivated land and villages, and swimming in wadis. Oviparous, lays 3-4 eggs per clutch; 4-9 per clutch have been reported in Kazakhstan (Els et al. 2001).

The Genus *Philothamnus*

Angola Green Snake

Philothamnus angolensis Bocage, 1882

Distribution and Habitat. Reed beds, stream banks, Namibia, northern Botswana, Zimbabwe, southern Mozambique, Okavango Swamp, Caprivi Strip, Angola, Democratic Republic of the Congo (Zaire; except in the north), Congo (Brazzaville), Cameroon, Central African Republic, Sudan, South Sudan, Tanzania, Zambia. Type locality: Capangombe, Angola. Known from sea level to 2,000 m. Natural History. The diet is composed mainly of frogs and lizards. Females lay 5-16 eggs that hatch in December-February (Broadley 1983).

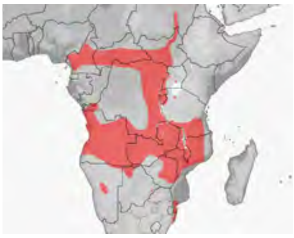


Figure 32.9. The distribution of *Philothamnus angolensis*

Southeastern Green Snake

Philothamnus hoplogaster (Günther, 1863)

Distribution and Habitat. Marshes, ponds, and rivers in Zimbabwe, S Mozambique, Zimbabwe, Tanzania, Kenya, Malawi, E/S Democratic Republic of the Congo (Zaire), Rwanda, Burundi, Zambia, Republic of South Africa (Transvaal, Natal, Cape, Swaziland), Botswana, Namibia, Angola. Type locality: Port Natal (= Durban, South Africa.)

Natural History. Young individuals will eat coleopterans, orthopterans, and other insects. However, fish, frogs, and lizards are the most frequent prey of adults. Females lay clutches of 3-8 eggs in early summer (Broadley 1983).

Figure 32.11. The distribution of *Philothamnus hoplogaster*

Figure 32.10. *Philothamnus angolensis.* **Photography by Vaclav Gvozdik.**

Figure 32.12. *Philothamnus hoplogaster.* **Photography by Paul Freed.**

Three Asian colubrids that show aquatic habits

Frog-eating Rat Snake

Oocatochus rufodorsatus (Cantor, 1842)

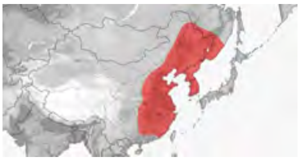


Figure. 32.13. The distribution of *Oocatochus rufodorsatus.*

Distribution and Habitat. Primorskiy Territory, Amur Oblast in Russia, Korea, Taiwan, northeast China. The type locality is Zhejiang, Chusan island, China (Cantor, 1842).

Natural History. Diet includes frogs (Pelophylax nigromaculatus) including the invasive American Bullfrog (Heo et al. 2014). Radiotracking 21 snakes over two seasons on agricultural land during two active seasons. Lee et al. (2011) demonstrated both sexes stayed close to aquatic habitats such as paddy fields and agricultural ponds during breeding and non-breeding periods, except when they moved to dry areas to hibernate in late fall. The use of structural features in the habitat (ground, tree, underground, and water) depended on the temperatures, the female's reproductive conditions, and the time of day. Both sexes moved about 17 m daily and postpartum females moved farther than antepartum females. The home ranges of males and females were 0.45 ha and 0.47 ha, respectively, and the year-round home range of this species was approximately 1.54 ha. Therefore, conserving a population of *rufodorsatus* would require aquatic and terrestrial habitats within a radius of 150 m from a pond habitat. require aquatic and terrestrial habitats within a radius of 150 m from a pond habitat.

Figure 32.14. *Oocatochus rufodorsatus.*

Photography by Amaël Borzée

Ornate Brown Snake

Xenelaphis ellipsifer Boulenger, 1900

Distribution and Habitat. Primary inhabits and old secondary forests from lowlands to 1100 m in elevation. Known from six specimens from Sumatra, Indonesia, and the island of Borneo. At least one specimen was taken from a fish trap. Other specimens were taken from streams and stream edges. Malaysia (Malaya and East Malaysia; Sarawak). The type locality is the Sarawak River.

Natural History. Adults probably feed on fish and rodents, while juveniles prefer fish, frogs, and lizards (Malkmus et al. 2002). Collectors found this snake foraging in and along a moderately flowing stream and were quick to escape when approached. The same snake was observed along the same stream multiple times, which might suggest a small home range.

Malayan Brown Snake

Xenelaphis hexagonotus (Cantor, 1847)

Distribution and Habitat. Inhabits peat swamps, scrublands, agricultural fields and freshwater swamps to elevations of 500 m. Indonesia (islands of Bangka, Belitung, Java, Kalimantan, Riau Archipelago, Sumatra, Borneo); peninsular Malaysia; Singapore; Thailand; Vietnam. Its presence in Myanmar is questionable.

Fig. 32.15. Distribution of *Xenelaphis hexagonotus*

Type locality: Great Hill of Pinang (Pulau Pinang, West Malaysia) .

Natural History. A diurnal semi-aquatic snake that preys upon fish, amphibians, and mammals.It reaches a length of 200 cm.

Figure. 32.18. *Xenelaphis hexagonotus*
Photography by Teo Eng Wah (Vincent).

33. Conservation

Above is a Lake Chapala Garter Snake, *Thamnophis eques obscurus*, from Jocotepec, Jaloisco, MX. Photography by Ethan Hazel. This snake and at least one other were entangled in a gill net on the shore of Lake Chapala. This snake is considered Vulnerable under Mexican law.

33. Conservation

Michael J. Jowers

According to the International Union for the Conservation of Nature (IUCN) globally, 9% of seasnakes are threatened, 6% are near threatened, and 34% are data deficient (Elfes et al. 2013).

Elfes et al. (2013) reported on only two seasnakes (*Aipysurus apraefrontalis* and *A. foliosquama*) threatened as Critically Endangered (CR), both reef inhabitants found at Ashmore and Hibernia reefs, respectively, in northwestern Australia and have undergone dramatic population declines. Nevertheless, their assessment in IUCN assessment from 2018 reports them as Data Deficient (DD) today. One species is endangered (EN); the reef species *Aipysurus fuscus* has similarly undergone population reductions (~70%). Seven species are Vulnerable or Near Threatened primarily due to small geographic ranges and habitat degradation. Two Vulnerable species are known from a single lake system each. *Hydrophis semperi* is a freshwater species only found in Lake Tall in the Philippines. Still, its population status is unknown, and *Laticauda crockeri* is endemic to Lake Te-Nggano on Rennell Island in the Solomon Islands. The third Vulnerable species, *Laticauda schistorhyncha*, is endemic to the island of Niue, while the Near Threatened species with restricted ranges include *Laticauda frontalis* (endemic to Vanuatu) and *Laticauda guineai* (endemic to Papua New Guinea). Five of the eight species in the genus Laticauda are classified as Vulnerable or Near Threatened.

Many of the seasnakes considered in this book are listed by the IUCN as Dada Deficient, yet many of these species require conservation status. An example is *Enhydris jagorii*, endemic to the Chao Phraya-Ta Chin basin in Thailand and threatened by habitat change and destruction, with large areas where it is found transforming into urban and agricultural areas and threatened by uncontrolled fishing. Despite the species-restricted distribution, it is under the category of Data Deficient, while the evidence may suggest a Critically Endangered status (Pongcharoen et al., 2016). Widely distributed species have been extensively studied from a conservation perspective (Roe et al., 2003, 2006, Mebert 2011), but species restricted to isolated locations or endemic in remote areas remain mostly Dada Deficient. Overall, for many of the species listed in this book, despite them being listed as Least Concern, limited information, or no information at all is available on threats. Their population trends are mostly unspecified, as well as most populations being listed as not severely fragmented, which might result from lack of accurate data rather than actual knowledge.

Studies on conservation of freshwater aquatic or semi-aquatic snakes are lacking and overall are challenging to summarize. Their worldwide distribution and taxonomic differences as well as their natural history and freshwater biota habitat, adds implicit complexity to assess their conservation in a review. From the data available from the IUCN there are apparent differences in the species group assessments, which reflect their taxonomy, where they are found, as well as their economic importance. For example, the data on the risks and threats of giant snakes (boids, pythons, anacondas) is ample, as is their conservation action. This is in strong contrasts to those of general such *Pseudoxenodon, Thermophis, Farancia, Coniophanes, Helicops, Hydraethiops, Limnophis, Thamnophis, Hydrablabes*, among others, that remain almost blank in their IUCN assessments.

Needless to say is that such a vast group of reptiles inhabiting the world's aquatic or semi-aquatic freshwater and marine biotas are under diverse and multiple threats. Here we list some of the most reported or better known threats to such taxa.

Habitat degradation

Sea kraits (genus Laticauda) have unique habitat requirements, being dependent on intact shallow coral reefs, supralittoral nesting sites, and appropriate intertidal and inland resting sites (Lillywhite et al. 2008; Bonnet et al. 2009), and minimal disturbances to these habitats will have important consequences to seasnake populations inhabiting them. Areas where species were common seem to have undergone dramatic population declines. For example, ten species were common in Ashmore Reef (Minton and Heatwole 1975; Guinea and Whiting 2005) while several surveys have only found one species in the reef (Elfes et al., 2013). Declines have also been noticed on sea kraits with broader geographic distributions, suggesting some kind of habitat deterioration. In fact, coral reefs are threatened by pollution, climate change, and diseases (Hughes et al. 2003; Pandolfi et al. 2003; Wilkinson 2008). Such factors might have important ecological consequences in the trophic system, having negative impacts on seasnake prey abundance in their hunting grounds. Seasnakes are dependent on undisturbed small islands and are more often than not encountered less than a few meters from the water edge on beach rock which is used as necessary terrestrial refugia (Bonnet et al. 2009). Therefore, minimal disturbances to such delicate ecosystems have resulted in population declines (Brischoux et al. 2009.)

Many aquatic or semi-aquatic snakes require both, aquatic and terrestrial habitats and remain a dependent on aquatic habitats, and many wetland reptiles require movement through, or extended refuge within terrestrial habitats for nesting, hibernation, migration, dispersal, foraging, etc. Wetlands constitute vastly large and important habitats for reptiles, but in some countries such as the USA, they are being lost quickly (Dahl, 1990), and so are the species inhabiting them (Gibbons et al., 2000). Habitat alterations that change the spatial distribution of wetlands, such as the loss of small isolated wetlands, are believed to have increased mortality rates for *Nerodia e. neglecta*. Conservation strategies for vagile wetland animals inhabiting variable aquatic resources over large spatial scales should take advantage on protecting and restoring large areas with numerous, heterogeneous wetlands (Roe et al., 2004). Simulations of small wetland loss shows that highly vagile species such as *N. e. neglecta* would move longer distances to find suitable habitat, suggesting that protection and restoration of wetland landscapes are critical for the long-term persistence of many wetland-associated species (Roe et al., 2003). Similarly, studies on radiotracking of population movement of *Oocatochus rufodorsatus* suggest that this aquatic species also uses terrestrial habitats within 150 of the core pond habitats, which need to be preserved (Lee et al. 2011.)

Many wetland reptiles migrate or disperse at a temporal and spatial scale, and such associated movements put them at risk especially in areas heavily modified by humans. Consequently, in addition to threats imposed by wetland loss, many wetland reptiles may have a high vulnerability to dispersal through roads. Despite the high mortality of reptiles on roads, conservation hardly addresses the threats that roads impose to wetland species. Roe et al. (2006) used models integrating road maps, traffic volume and snake movements to assess the mortality of species with their vagility in three regions of the USA. Their findings revealed that the vagile species *Nerodia e. neglecta* mortality accounted for between 14-21% of its populations, while the more sedentary species *Nerodia sipedon* mortality was much lower (3-5%). They concluded that conservation measures should consider not only the quality of wetlands and nearby terrestrial habitats, but also terrestrial corridors between wetlands and safe passage for wildlife.

Climate change is a global problem affecting all species worldwide, however, its effects will likely be seen sooner rather than later in marine and freshwater ecosystems and their associated wildlife. In freshwater ecosystems, drought will impose strong pressures on species survival. Vogrinc et al. (2018) assessed the effect of drought on semi-aquatic snake population occupancy in South Carolina before (year 2006) and after the drought (year 2013). They found that site occupancy decreased dramatically following drought for *Nerodia fasciata* (0.95 to 0.69) and *Nerodia floridana* (0.32 to 0.05), but was relatively unchanged for *Seminatrix pygaea*, *Farancia abacura* and *Regina rigida*. This study concluded that species lacking adaptations to adapt to drought may become locally extinct if climate change projections are correct or if landscapes are degraded or fragmented in ways that prevent drought.

Santos and Llorente (2009) conducted a demographic study to evaluate the relative densities of snakes in natural lagoons in 1995 in the Ebro Delta (Spain). In 2008, they repeated the same study in the same area and season. The field work consisted of 29 censuses and their potential prey. In 1995, they recorded 27 *Natrix maura* (0.93 animals/ha), occupying 48% of the sites but in 2008 no snakes were encountered. However, prospected rice fields nearby detected a great number of snakes, with 25% occupancy overall. They attributed such findings to habitat transformation and degradation, natural predator increment, decrease in prey populations, pollutants in rice fields, death on roads, and thorough human persecution. They argue that the recovery of the *N. maura* population in the rice fields in the region depends on agricultural management changes, reducing of pollutants, the recovery of snake prey, and the maintenance of favorable habitats to prevent predation.

Pollution

Seasnakes can be used as bioindicators for the health of the marine environment because of the uptake of trace elements via the ingestion of prey, and the snake's accumulation of trace elements over time. Marine snakes in fishing areas could indicate regions where fish consumption may have important health implications.

Pollutants are carcinogenic and accumulate in different parts of the snakes´ body, such as the liver, kidneys, blood, and fatty tissues. Gillet et al. (2017) found that several species in southern Queensland (Australia) suffered from pancreatic, liver and kidney neoplasia, thought to be derived from toxigenic or viral etiology. In a recent study, Goran et al. (2017) surveys revealed that in the seasnake *Emydocephalus annulatus*, melanism is more frequent in urban-industrial sites than in less polluted locations. High trace-element concentrations in sloughs of sea kraits from close to a river-mouth suggest that melanism may benefit seasnakes in many areas. Importantly, concentrations of trace elements were higher in darker than in lighter bands within the same slough.

Growing evidence in recent years suggests increased seasnake mortality caused primarily by marine debris and plastics on a global scale, but what the actual effects on species and populations remain largely unknown. The bioaccumulation of marine contaminants and pollutants and the threshold required for the accountable detrimental effects on snake populations and the regions of the highest impact are key points for population management.

Pollutants are not only found in the marine environment, and can are traceable in freshwater species too. In a recent review of pollutants detected in snake tissues**,** Quoc Hoang et al. (2021) found that concentrations of polychlorinated biphenyls (organic chlorine compounds) were found in numerous snake tissues. Within the USA, some reported species were Diamondback Watersnake (*Nerodia rhombifer*), Blotched Watersnake (*Nerodia erythrogaster*), Northern Watersnake (*Nerodia sipedon*), Cottonmouth (*Agkistrodon piscivorus*). In Canada; the Lake Eire Water snake (*Nerodia sipedon insularum* and *N. s. sipedon*), and in China, the

Chinese Mudsnake (*Myrrophis chinensis*). Traces of flame retardants have also been found in Chinese Mudsnake. Other known pollutants are pesticides, as seen in Lake Erie Watersnake (*Nerodia sipedon insularum*).

The mining industry has affected the distribution pattern of the Copperbelly Watersnake, *Nerodia erythrogaster*. Populations have been isolated, making them more vulnerable to threats. The major causes for population fragmentation is coal mining, drainage and damming of wetlands, channelization, diversion of streams and rivers, and development of upland habitat. Although the impact of the mining industry on freshwater snakes remains unreported and unknown, it is likely that mining has profound implications for both the health and the fragmentation of populations. Large mining operations likely cause whole snake populations to relocate to other areas, affecting niche resource partitioning and creating competitive displacement between species. The frequent use of water in mining (eg., gold mining) has devastating effects on natural river drainages, increasing water turbidity, pollution by heavy metals, and changing water systems for snakes to breed. In addition, the effects of mining acoustic pollution remain unreported, but is likely to cause habitat shift of snakes and their prey for much larger areas than the mining regions. Interestingly, Lacki et al. (2005) found that Copperbelly snake populations abundance was higher after mines had been closed and the land reclaimed. The use of human made ponds and drainage systems suggested that populations could fully recover. However, future studies should address how the presence of pollutants in the reclaimed lands might pose a health hazard to the population.

Plastics have not received much attention regarding snakes, but França et al. (2018) removed a plastic balloon from the esophagus and stomach of a *Helicops angulatus* and it was notable that no other prey items were in the digestive tract.

Fishing bycatch

Seasnakes are vulnerable to trawler fishing techniques and they are an unfortunate bycatch of these fishing practices. Seasnakes have been commercially exploited since 1934 (Dunson, 1975) in the Philippines, where protection laws have been necessary to avoid their overexploitation. However, seasnakes have been harvested in several countries (Australia, Japan, Taiwan China, Thailand, and Vietnam) directly or as a by-catch product of fishing. Despite some countries (eg. Australia) reporting snake by-catch and having introduced species licensing requirement to collect seasnakes, many other countries continue to avoid such documentation and the overall impact remains worryingly unknown. Rasmussen et al. (2011) suggest that the main threat to seasnakes are indifferences to conservation issues in local communities. Education can solve this problem. In addition, they argue that the limited knowledge of marine snake natural history and biology in Asia continues to be a problem. Thus the main threat to seasnakes is the cultural indifference to conservation issues and, the subsequent commercial exploitation. Gathering more information on species biology is pivotal, especially in poorly studied regions such as Asia. Data on breeding cycles, growth rates, sexual maturity, population estimates, and accurate taxonomy and systematic knowledge are needed to fully protect species.

The effects of by-catch on the seasnakes are almost unknown – the exceptions are the Philippines and Australia (Milton 2001; Tonks et al., 2008; Courtney et al., 2010, Wassenberg et al., 1994). In Australia, between Koolan Island and Cape York (northern Australia) circa 80,000 snakes were reported to have been captured by trawlers in 1990 (Ward 1996), while Wassenberg et al. (1994) estimated 70,000-165,000 were by-catch from commercial prawn trawlers in the Gulf of Carpentaria in 1991, with a 60% survival. Later work by Wassenberg et al. (2001) estimated that the overall mortality of trawl-caught snakes was 48.5%, mostly from injuries while trawling. Analysis of the species of conservation interest of seasnake data indicated that for 2003, Queensland trawlers incidental catch an annual maximum of 4,840 (year 2003) an annual minimum of 1,640 (in 2006). Between 2003 and 2008, a total of 17,640 snakes were reported, with 5% mortality and 2% injury (Courtney et al. 2010). Currently, the impact of prawn fishing on seasnake populations in northern Australia has declined substantially with the reduction in the size of the fleet and the fishing effort since 2004 (Milton et al. 2008).

Courtney et al. (2010) attempted to estimate a by-catch of the Queensland East Coast Trawl Fishery based on sixty-seven trawl fishers in a voluntary study. Their data collected 3,910 snakes belonging to 12 species (*Lapemis* and *Aipysurus* mostly) from 8,289 trawls between 2003-2007. Using this data they extrapolated the estimated mean catch at 105,000 per year. About 8.5% of snakes were reported dead, and about 17.4% dying shortly after, giving a combined incidental mortality rate of 25.9%. Reef-associated fishing for Redspot King Prawns accounted for most of the seasnake by-catch, with mortality at 58.9% with 84.5 %.

A study of Queensland's trawl fishery evaluated the effects of three different bycatch reduction devices (BRDs) on the catch rate of seasnakes, as well as prawns in 2006. The fisheye and square mesh codend BRDs significantly reduced the catch rate of seasnakes without incurring any significant reduction in targeted (≥ 20 mm carapace length) prawn catch rates. Seasnake by-catch was approximately 60% lower than control nets. Additionally, the distances of the BRDs installed from the codent drawstring significantly affect effectiveness of avoiding bycatch, 50 meshes is recommended. Reports of by-catch reductions of 87% have been recorded when the device was installed 70 meshes from the drawstring (Raudzens, 2007). Similarly, other studies have concluded that the Yarrow fisheye BRD reduced the weight of small fish bycatch and seasnakes by a mean of 22% and 43.3%, respectively, with no loss of tiger prawn catch (Heales et al. 2008). Similar results were observed by Milton et al., (2009), where using a control versus treatment nets in 1,365 trawls, 43% of seasnake catches were reduced with Fisheye BRD positioned less than 70 meshes for the codent. They also concluded that using 'popeye' Fishbox BRD reduced seasnake catch by 85%. They argue that a BRD positioned within 70 meshes of the codend could reduce the seasnake catch and mortality.

Fishing by-catch of snakes is not only present in marine snakes. Thousands of freshwater snakes are killed yearly (e.g. *Natrix tessellata*) in the nets set by poachers, notably gravid females, raising population viability concerns and causing population declines (Sterijovski et al., 2014).

Trade

Commercial trade is a major driver of the over-exploitation of marine and freshwater snakes. Nguyen et al. (2014) inspected several squid fishing vessels in the Gulf of Thailand from 2008-2013. Fishermen trades indicated that *Lapemis curtus* and *Hydrophis cyanocinctus* constituted more than 85% of the total seasnake biomass harvested, and other six species made up the remaining portion of the catch: *Acalyptophis peronii*, *Aipysurus eydouxii*, *Hydrophis atriceps, H. belcheri, H. lamberti*, and *H. ornatus*. In Vietnam, seasnakes are not protected, and their harvest is legal as the catching of seasnakes is regulated by the United Nations Convention on the Law of the Sea, Section II, Conservation and Management of the Living Resources of the High Seas, that is dependent on domestic laws. Domestically, seasnakes are not protected, and their harvest is completely within the legal framework of Vietnam. Market demand has increased in recent years, while in the past seasnake bycatch in the province of Quang Ngai was discarded due to fear of bites and a lack of market. In 2011 their price was US$10–35/kg. Overall, Nguyen et al. (2014) estimated average biomass of seasnakes removed from the Gulf of Thailand via Song Doc and Khanh Hoi at circa 82 tones, about 225,500 specimens per year. On the South China Sea coast, the total biomass of seasnakes harvested through southern Vietnam was no less than 100 tons (more than 275,000 specimens) per year.

Seasnake meat is used in products such as soup blood mixed with alcohol to improve health, various organs are used in elixirs, and dried skins from whole seasnakes are added to the wine (Nguyen et al., 2014). Seasnakes are also reported to be a source of rheumatism, used to treat various joint, bone, and mental health conditions (Nguyen et al., 2014). The causes of declining seasnakes in the Gulf of Thailand since 2009 are not clear but include overharvesting and anthropogenic disturbances such as trawling and pollution (Nguyen et al., 2014). Auliya (2011) reported a tannery in West Malaysia harvesting 6,000 individuals per month.

The United Nations Environment World Conservation Monitoring Centre (UNEP-WCMC) (2018) categorized three species under consideration for examination for EU trade imports (Appendix D) under CITES convention for the period 2007-2016. In this report *Subsessor bocourti* was used for skin trade and human consumption and as crocodile food in Cambodia. Captive breeding farms producing aquatic snake species, including *S. bocourti* were reported in the Mekong Delta, with 174 government registered farms and circa 80,000 individual snakes held in farms in Vietnam as of 2014 (Aust, 2015). In addition, this species is also found in reptile shops in Vietnam.

Homalopsis buccata was listed in Annex D of the EU Wildlife Trade Regulations on 01/06/1997 with the annotation that the listing “applies only to live specimens; whole or substantially whole, dead specimens; and whole or substantially whole skins, raw or tanned.” Direct imports of *Homalopsis buccata* comprised circa 3.5 million skins. Skins were predominantly imported from Thailand (49 per cent), Indonesia (38 per cent) and Singapore (12 per cent). Import of skins to the EU-28 increased in 2007-2015. Indirect trade to the EU-28 predominantly comprised 725,405 skins, of which 93 per cent were reported without a purpose or source code and the remainder were wild-sourced for commercial purposes. Most skins indirectly imported by the EU-28 originated in Indonesia and were predominantly re-exported via Singapore.

Brooks et al. (2010) commented that, the pattern of demand and how it responds to changes in supply is poorly known. In his region, mostly *Enhydris enhydris, Enhydris longicauda, Homalopsis buccata, Erpeton tentaculatum*, *Fowlea piscator, Cylindrophis ruffus, Subsessor bocourti* are heavily fished (Brooks et al. 2008). In Cambodia, the largest driver of snake exploitation is the domestic trade in snakes as crocodile food. Brooks et al. (2010) estimate that farmed crocodiles consume between 2.7 and 12.2 million snakes yearly. This over-exploitation of snakes is the result of a progressive decline in the market price of crocodile skin since 2003, and preference for snakes helps maintain the farms functioning, and snake food is highly dependent of other substitute available resources such as fish.

Other Asian countries, such as China sell snakes such as *Sinonatrix annularis*, some *Enhydris* spp. and *Homalopsis* in large numbers at the markets and restaurants (Zhou & Jiang, 2005). In western central Africa, *Grayia ornata* plays an important role in local culture food, as well as in magic and traditional medicine (Pauwels et al., 2002). Similarly, in Brazil, among other snakes, *Eunectes murinus* commercialized in outdoor markets, and they are used for medicinal and for magic–religious purposes (Alves and Filho, 2007).

Steps forward towards conservation

The status of most snake populations (mainly marine species) remains data deficient.

Lack of knowledge in most areas, especially in Southeast Asia, suggests that there is no comparative means to address the status of populations and if species and populations are under extinction risk. Only through monitoring and controlling by-catch and the commercial catch of seasnakes can a sustainable yield be achieved. Efforts should focus on governmental funding to research the importance of the most harvested biological groups and assess their populations' status in different regions. Habitat destruction and pollution in rivers, estuaries, mangroves, and boat traffic are causing a reduction in population in Asia and Australia. Breeding biology remains data deficient for most species, and breeding areas and periods are lacking from scientific literature, key points to manage and protect the populations. Taxonomical data is similarly deficient, and few studies barcoding and identifying species. Genetic divergence between populations to assess key lineages worth preserving for future genetic enrichment of other less genetically rich populations is critical to address the conservation genetic management of species, especially those more harvested populations. Genetic diversity combined with taxonomical identification will elucidate pivotal information to focus harvesting on the more common species and protect other less common ones.

The most accountable and destructive practice of seasnake mortality is trawling fishing, and evidence indicates that the distance BRDs are installed from the codent drawstring and the type of net, significantly reduces bycatch or seasnakes, not affecting market table. The success of the bycatch reduction is dependent on the area (e.g., reefs) and targeted species (e.g., prawns) to harvest, and only specific studies conducted in different countries and regions through voluntary work of trawl vessels in different regions can help elucidate the methods that best suit different fishing industries. For example, knowing the size of adult seasnakes in fishing grounds can help determine the size of the net mesh, as mortality is higher in larger seasnakes than in smaller individuals, and increased mesh sizes that do not compromise target harvest could result in a significant reduction of large seasnake by-catch that likely constitutes gravid females. Trawling vessels or fishing docs would be advantageous with the presence of expert specialists (Milton et al., 2009) to conduct species counts and sex ratios as well as estimation of gravid females and breeding seasons (Fry et al., 2001). Such simple data would estimate population reproductive cycles and areas and could help establish fishing bands or a reduction in licenses throughout breeding seasons. According to Elfes et al.´s (2013) study on the distribution of seasnakes, the most critical areas identified as needing basic research are Southeast Asia and peninsular Malaysia, where the greatest concentration of Data Deficient species are found. They comment that the Data Deficient status probably reflects on high species diversity in the region, but extremely limited surveys have resulted in hardly any information in species ecology, abundance, and distribution. Future surveys should be conducted in the region to solve this lack of knowledge of these species.

Local awareness is important to reduce by-catch mortality. For example, in India, fishermen kill seasnakes intentionally when encountered as they are believed to threaten the local community. A report in 2015 showed that over only two consecutive days between around 60–80 dead seasnakes lay scattered over 20–30 meter stretch on shore due to such practice (Jamalabad 2015). At a regional scale, the impact on unnecessary seasnake mortality could make essential differences to the populations.

Species-based conservation programs are challenged in socio-economic deprived regions where water snakes are regularly harvested such as in Tonle Sap Lake in Cambodia for the last 2 to 3 decades (Stuart et al. 2000). Brooks et al. (2008) concluded that resource decline, along with the high and potentially increasing levels of poverty, are the major concerns fishing in the Tonle Sap Lake. They argue that conservation strategies that focus on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strengthening, rather than eroding the adaptive capabilities of resource users to cope with uncertainty, should be supported by increasing rather than restricting access. The nature of such markets, consumer preferences, and their drivers suggest that protection of snakes to their breeding season is likely to be the most effective tools for their conservation (Brooks et al., 2010)

Addressing effective future conservation measures for freshwater aquatic snakes is challenging. Their global distribution and the vast amounts of habitats they inhabit (swamps, marshes, lakes, rivers, estuaries, seas, etc) makes general measures unviable. In addition, the conservation and protection of freshwater biodiversity face challenges influenced by the topology of the biota, such as upstream drainage networks, surrounding lands, riparian zones and downstream reaches, making conservation management and delimitation of such areas complex. The presence of species throughout continents and their countries implies different governmental legislations to be implemented and many challenging management actions with needs for "reconciliation ecology," thus the adoption of biodiversity protection and freshwater ecosystem management. Documented threats to global freshwater biodiversity include overexploitation, water pollution, flow modification, destruction or degradation of habitat, and invasion by exotic species (Dudgeon et al., 2006), which all have an impact of aquatic snake populations in different ways. Unfortunately, because freshwater bodies are experiencing higher declines in biodiversity than most terrestrial ecosystems (Sala et al., 2000), and the human need for water will only continue to increase, species losses at even greater rates are likely to be expected.

Knowledge of species´ natural history, ecology, and distribution remains critical to protecting freshwater and marine snakes. However, data remains insufficient to estimate or predict population extinctions in many world regions accurately. Identifying major hotspots, especially for freshwater snakes, is pivotal, and will require joint efforts from non-government for organizations, research institutions, and scientific societies. Strong conservation efforts should focus on species-rich areas with high biodiversity, such as the Asian oriental region (Andaman Sea and Southeast Asia) and the neotropics (Pauwels et al., 2008). The conservation challenges of freshwater (Dudgeon et al., 2006; Hughes, 2019) and marine biota suggests the need to protect regions with high biodiversity.

On the previous page. Figure 33.1 The Tonle Sap snake harvest is the largest known snake harvest in the world. (A) Is Tonle Sap Lake when it is dry. (B) A fisher middleman who buys snakes from fishers and sells them to another middleman. (C) A collection of snakes going to market. (D) A fisher in his canoe with gill nets used to collect snakes, (E) Bags filled with snakes. (F) SNakes being cut into piecies to feed small crocodiles. (G) Crocodiles are the primary reason for the snake harvest - people buy the snakes to feed their crocodiles that they are raising for skins and meat. Photography by JCM

Table Abbreviations

CATEGORY

DD (Data Deficient), **NT** (Near Threatened), **LC** (Least Concern), **VU** (Vulnerable), **EN** (Endangered), **CR** (Critically Endangered)

POPULATION TREND

U (Unknown), **S** (Stable), **D** (Decreasing), **I,** (Increasing), **Uns** (Unspecified)

NPF, (No population severely fragmented), **PF** (Population severely fragmented), **UPD** (Unknown population fragmentation), **NAD** (No continuous decline of mature adults), **UDM** (Unknown decline of mature adults).

CONSERVATION ACTIONS

In-place land/water protection: yes **O** (yes, over the entire range), **U** (Unknown)

In place research and monitoring: **ARP**, (Action Recovery Plan), **S** (Systematic monitoring scheme)

THREATS

L (Local), **N** (National), **I** (International)

RISKS

Agriculture and Aquaculture; **AP** (Annual & perennial non-timber crops), **LR** (Livestock farming & ranching), **MA** (Marine & freshwater aquaculture), **WP** (Wood & pulp plantations).

Residential and commercial development; **TR** (Tourism and recreation areas), **HU** (Housing and urban areas), **CI** (Commercial and industrial areas)

Natural system modification; **DW** (Dams & water management/use), **OM** (Other ecosystem modifications), **F** (Fire & fire suppression)

Biological resource use; **HT** (Hunting & trapping terrestrial animals), **FH** (Fishing & harvesting aquatic resources), **LW** (Logging & wood harvesting)

Pollution; **AF** (Agricultural & forestry effluents), **DU** (Domestic & urban waste water), **IM** (Industrial & military effluents)

Transportation and service corridors; **RA** (Roads & railroads), **SL** (Shipping lanes)

Energy production and mining; **OD** (Oil & gas drilling), **RE** (Renewable energy), **MQ** (Mining & quarrying)

Climate change and severe weather; **SF** (Storms & flooding), **O** (Other impacts), **HA** (Habitat shifting & alteration), **TE** (Temperature extremes), **D** (Droughts)

Invasive and other problematic species, genes & diseases; **IAD** (Invasive non-native/alien species/diseases)

Human intrusions & disturbance; **RA** (Recreational activities)

				Conservation actions				Threats							Risks									
Species	Category	Population Trend	Assessment Year	In-place land/water protection	Included in international legislation	Subject to any international management / trade controls	In place research and monitoring	Wearing apparel accessories	Pets/display animals, horticulture	Food-animal	Food-human	Medicine - human and veterinary	Handicrafts, jewellery, etc	Venom	Agriculture and aquaculture	Residential and commercial development	Natural system modification	Biological resource use	Pollution	Transportation and service corridors	Energy production and mining	Climate change and severy weather	Invasive and other problematic species,	Human intrusions & disturbance
Ancient but Extant Lineages																								
Trachyboa boulengeri	LC	U	2016	yes	yes	yes			I															
Trachyboa gularis	CR	U	2020	no	yes	yes									AP,L									
Anilius scytale	LC	S	2013	yes													DW							
Anilius phelpsorum																								
Xenopeltis unicolor	LC	S,NPF	2014	yes				N,I	N,I									HT						
Liasis fuscus	LC	S,NPF	2017	yes	yes	yes			N,I															
Liasis olivaceus	LC	U	2017	no	no	no																		
Malayopython reticulatus	LC	U,NPF	2011	yes	yes	yes		L,N,I	L,N,I		L,N,	L,N,I			AP			HT						
Python bivittatus	VU	D,NPF	2011	yes	yes	yes		L,N,I	N,I		L,N,	L,N,I	L,N,											
Python molurus	NT	D	2019	yes	yes	yes			L,N,I		L	L,N	N		AP,L	TR		HT						
Python natalensis	LC	D	2019	yes	yes	yes		I	I		L	L,I			AP	HU, CI		HT						
Python sebae	NT	D	2019	yes	yes	yes		L,N	I		I	L,N			AP	HU		HT						
Eunectes beniensis	LC	U,NPF	2014	yes	yes	yes		L			L							HT						
Eunectes deschauenseei	LC	U,NPF	2014	yes	yes	yes		I	I						AP			HT,FH						
Eunectes murinus	LC	U	2014	yes	yes	yes		I				L			AP,L		DW	HT		RA	OD			
Eunectes notaeus	LC	S,NPF,NA	2020	yes	yes	yes		L,N,I	I	L		L			AP		DW	HT						
File Snakes																								
Acrochordus arafurae	LC	S,NPF	2017	yes				L,N,I	I		L							FH						
Acrochordus granulatus	LC	D,NPF	2020	yes				L,N,I	L,N,I		L,N	L,N			AP,M	TR		FH	DU					
Acrochordus javanicus	LC	S,NPF	2011	yes				L,N,I	L,N,I									FH						
Aquatic Pit Vipers																								
Agkistrodon conanti																								
Agkistrodon piscivorus	LC	S	2007	yes																				
Craspedocephalus malabaricus	LC	S,NPF	2010	yes											AP	HU								
The Homalopsidae																								
Brachyorrhos albus	LC	U,NPF	2019	yes																				
Brachyorrhos gastrotaenius	DD	U	2019	U																				

continued				Conservation actions				Threats							Risks									
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Brachyorrhos pygmaeus																								
Brachyorrhos raffrayi	DD	U	2019	no																				
Brachyorrhos wallacei	DD	U	2020	U																				
Calamophis jobiensis	DD	U,NPF	2009																					
Calamophis katesandersae	DD	U	2019	U																				
Calamophis ruuddelangi	DD	U	2019	U																				
Calamophis sharonbrooksae	DD	U	2019	U																				
Karnsophis siantaris																								
Bitia hydroides	LC	U,NPF	2009														OM		DU,					
Cantoria violacea	LC	U,NPF	2009	yes													OM		DU,					
Cerberus australis	LC	U,NPF	2017	yes												HU,CI,								
Cerberus dunsoni																								
Cerberus microlepis	EN	D,NPF	2009	yes											AP			LW,FH	DU					
Cerberus rynchops	LC	D,NPF	2009		yes	yes		N,I										FH						
Cerberus schneiderii																								
Dieurostus dussumieri	NT	U,NPF	2019																DU					
Djokoiskandarus annulata	DD	U,NPF	2009																					
Enhydris chanardi	DD	U,NPF	2009													HU,CI								
Enhydris enhydris	LC	U,NPF	2010	yes					L,N		L,N,I							HT						
Enhydris jagorii	DD	U,NPF	2010	yes											AP	HU,CI		FH						
Enhydris innominata	DD	U,NPF	2009	yes													DW	FH						
Enhydris longicauda	VU	D,NPF	2009	yes						L,N	L,N							HT						
Enhydris subtaeniata	LC	U,NPF	2009							N	L,N							FH						
Erpeton tentaculatum	LC	U,NPF	2010	yes						L,N	L,N							HT						
Ferania sieboldii	LC	U,NPF	2009																					
Fordonia leucobalia	LC	U,NPF	2017	yes																				
Gerarda prevostiana	LC	U,NPF	2009																					
Gyiophis maculosa	DD	U,NPF	2009																					

continued				Conservation actions				Threats								Risks									
Species	Category	Population Trend	Assessment Year	In-place land/water protection	Included in international legislation	Subject to any international management / trade controls	In place research and monitoring	Wearing apparel accessories	Pets/display animals, horticulture	Food-animal	Food-human	Medicine - human and veterinary	Handicrafts, jewellery, etc	Venom	Agriculture and aquaculture	Residential and commercial development	Natural system modification	Biological resource use	Pollution	Transportation and service corridors	Energy production and mining	Climate change and severy weather	Invasive and other problematic species	Human intrusions & disturbance
Gyiophis salweenensis																								
Gyiophis vorisi	EN	U,NPF	2009																DU,I	SL				
Heurnia ventromaculata	DD	U,NPF	2009														DW							
Homalophis doriae	LC	U,NPF	2009																					
Homalophis gyii	DD	U,NPF	2009																					
Homalopsis buccata	LC	U,NPF	2009	yes				N,I		LN	LN,I							FH						
Homalopsis hardwickii	DD	U	2019	U																				
Homalopsis mereljcoxi																								
Homalopsis nigroventralis	LC	U,NPF	2009																					
Homalopsis semizonata																								
Hypsiscopus matannensis	DD	U,NPF	2019	no																				
Hypsiscopus murphyi																								
Hypsiscopus plumbeus	LC	S,NPF	2009																					
Kualatahan pahangensis	DD	U,NPF	2009																					
Mintonophis pakistanicus	LC	U,NPF	2019	U																				
Miralia alternans	DD	U,NPF	2009														OM		DU					
Myanophis thanlyinensis																								
Myron karnsi	DD	U	2019	U																				
Myron resetari	VU	U,NPF,UD	2020	no												CI						SF		
Myron richardsonii	LC	U,NPF	2009																					
Myrrophis bennettii	DD	U,NPF	2009													HU,CL								
Myrrophis chinensis	LC	I,NPF	2009					N,I			LN							FH						
Phytolopsis punctata	DD	U,NPF	2009	yes											WP			LW			RE			
Pseudoferania polylepis	LC	S,NPF	2017	yes					N															
Raclitia indica	DD	U,NPF	2009	yes																				
Subsessor bocourti	LC	U,NPF	2009					N,I		N	N,I							FH						
Sumatranus albomaculata	DD	U,NPF	2010	yes																				
Aquatic Coral Snakes																								

continued				Conservation actions				Threats							Risks									
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Micrurus nattereri	LC	S	2014	yes															IM					
Micrurus surinamensis	LC	S	2014	yes											AP,L			HT	IM					
Aquatic Cobras (Najinae)																								
Naja annulata	LC	S	2019	yes							L							FH	AF					
Naja christyi	LC	D	2019	no							L,N													
Naja nana																								
Naja melanoleuca	LC	D	2019	yes				I	I					N,I		HU,CI		HT			OD			
Neja subfulva	LC	S	2019	yes					I															
Naja peroescobari	E	D	2020	yes				N,I							AP			HT		RA				
Naja (Boulengerina) guineensis																								
Naja (Boulengerina) savannula	LC	S,PF	2019	yes				L																
Naja kaouthia	LC	D,NPF	2011	yes	yes	yes		N,I	N		L,N	N,I						HT						
Semi-Aquatic Hydrophiinae																								
Micropechis ikaheka	LC	S	2013	yes					N,I															
Austrelaps labialis	LC	U	2017	yes																				
Austrelaps ramsayi	LC	U	2017	yes													DW							
Austrelaps superbus	LC	S	2017	yes																				
Hemiaspis damelii	EN	D,PF	2017	yes			yes								AP									
Hemiaspis signata	LC	S	2017	yes																				
Pseudechis porphyriacus	LC	U	2017	yes																			IAD	
Notechis scutatus	LC	U,NPF	2017	yes					N,I						LR		E,DW	LW					IAD	
Sea Kraits																								
Laticauda colubrina	LC	S,NPF	2009	yes							L,I	L				HU,CL	OM	FH				O		
Laticauda crockeri	VU	U,NPF	2009	yes												HU,TR		FH	DU			SF		
Laticauda schistorhyncha	VU	U,NPF	2010													HU,CL						HA,SF		
Laticauda saintgironsi	LC	S,NPF	2009													HU,CL						HA,SF		
Laticauda guineai	NT	U,NPF	2009													HU,CL		FH				HA,SF		
Laticauda frontalis	NT	U,NPF	2009													HU,CL						HA,SF		

continued				Conservation actions				Threats							Risks									
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Laticauda laticaudata	LC	S,NPF	2009	U												HU,CL						HA,SF		
Laticauda semifasciata	NT	U,NPF	2009	yes				N,I			L,N,I							FH				HA,SF		
Seasnakes																								
Aipysurus apraefrontalis	DD	U	2018	yes																				
Aipysurus duboisii	LC	D,NPF	2009	yes														FH			OD	TE		
Aipysurus eydouxii	LC	U,NPF	2009															FH						
Aipysurus foliosquama	DD	U,PF	2018	yes												HU,CI								
Aipysurus fuscus	EN	D,PF	2009	yes																		HA		
Aipysurus laevis	LC	U,NPF	2018	yes			ARP,											FH				HA		
Aipysurus mosaicus	LC	S	2018															FH				TE		
Aipysurus pooleorum	DD	U	2018															FH				TE		
Aipysurus tenuis	DD	U,NPF	2009				ARP																	
Emydocephalus annulatus	LC	D,NPF	2009				ARP											FH				O		
Emydocephalus ijimae	LC	U,NPF	2009													HU,CL		FH				O		
Emydocephalus orarius																								
Parahydrophis mertoni	DD	U,NPF	2009													HU,CL								
Ephalophis greyae	LC	U,NPF	2009													CI					MQ			
Hydrelaps darwiniensis	LC	U,NPF	2009														OM							
Hydrophis annandalei	DD	U,NPF	2009													HU,CL		FH						
Hydrophis anomalus	DD	U,NPF	2009													HU,CL						HA,O		
Hydrophis atriceps	LC	U,NPF	2009															FH						
Hydrophis belcheri	DD	U,NPF	2009					I										FH						
Hydrophis bituberculatus	DD	U,NPF	2009															FH						
Hydrophis brookii	LC	U,NPF	2009													HU,CL		FH						
Hydrophis caerulescens	LC	U,NPF	2009															FH						
Hydrophis cantoris	DD	U,NPF	2009															FH						
Hydrophis coggeri	LC	U,NPF	2009	U																		HA		
Hydrophis curtus	Lc	U,NPF	2018	yes			yes	N,I		L	L,N,I	L						FH				TE		

continued				Conservation actions				Threats							Risks									
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Hydrophis cyanocinctus	LC	U,NPF	2009	U												HU		FH						
Hydrophis czeblukovi	DD	U,NPF	2009															FH						
Hydrophis donaldi	DD	U	2013																			TE		
Hydrophis elegans	LC	S,NPF	2009				ARP											FH						
Hydrophis fasciatus	LC	U,NPF	2009													HU,CL		FH						
Hydrophis gracilis	LC	U,NPF	2009															FH						
Hydrophis hardwickii																								
Hydrophis hendersoni																								
Hydrophis inornatus	DD	U,NPF	2009																					
Hydrophis jerdonii	LC	U,NPF	2009					L								HU,CL		FH						
Hydrophis kingii	LC	U,NPF	2009				ARP											FH						
Hydrophis klossi	DD	U,NPF	2009													HU,CL		FH						
Hydrophis laboutei	DD	U,NPF	2009																					
Hydrophis lamberti	LC	U,NPF	2009	U				I			I							FH						
Hydrophis lapemoides	LC	U,NPF	2009	U				N,I										FH						
Hydrophis macdowelli	LC	U,NPF	2009				ARP											FH						
Hydrophis major	LC	U,NPF	2009	U														FH						
Hydrophis mamillaris	DD	U,NPF	2009															FH						
Hydrophis melanocephalus	DD	U,NPF	2009	U														FH						
Hydrophis melanosoma	DD	U,NPF	2009	U																				
Hydrophis nigrocinctus	DD	U,NPF	2009	U																				
Hydrophis obscurus	LC	U,NPF	2009	U														FH						
Hydrophis ornatus	LC	U,NPF	2009	U														FH						
Hydrophis ocellatus	LC	U,NPF	2009															FH						
Hydrophis pachycercos	DD	NPF	2009	U				I										FH						
Hydrophis parviceps	DD	NPF	2010	U														FH						
Hydrophis pacificus	NT	D,NPF	2009				ARP											FH						
Hydrophis peronii	LC	S,NPF	2009															FH						

continued				Conservation actions				Threats							Risks									
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Hydrophis platurus	LC	S,NPF	2009															FH	IM					
Hydrophis schistosus	LC	S,NPF	2009									N,I						FH	DU					
Hydrophis semperi	VU	D, NPF	2009													HU,CI		FH	AF					
Hydrophis sibauensis	DD	U,NPF	2009																					
Hydrophis spiralis	LC	U,NPF	2009	U				I										FH						
Hydrophis stokesii	LC	U,NPF	2009				ARP											FH						
Hydrophis stricticollis	DD	U,NPF	2009	U														FH						
Hydrophis torquatus	DD	U,NPF	2009														HU,CI	FH						
Hydrophis viperinus	LC	U,NPF	2009					L,N			L,N							FH						
Hydrophis vorisi	DD	U,NPF	2009																					
Hydrophis zweifeli	DD	U,NPF	2009	U																				
The Radiant Snakes and Gemsnakes																								
Lycodonomorphus bicolor	LC	U,NPF	2014	U														FH	AF					
Lycodonomorphus laevissimus	LC	S,NPF,NA	2009	yes	no	no											DW		DU					
Lycodonomorphus leleupi	LC	S,NPF	2019	yes																				
Lycodonomorphus mlanjensis	LC	S	2019	yes																				
Lycodonomorphus obscuriventris	DD	U,NAD	2019	yes	no	no																		
Lycodonomorphus rufulus	LC	S,NPF,NAD	2019	yes	no	no			I															
Lycodonomorphus subtaeniatus	LC	S,NPF	2019	yes																				
Lycodonomorphus whytii	LC	U,NPF	2019	yes											AP									
Boaedon upembae	LC	S	2019	yes																				
Lipholidophis sexlineatus	LC	S,NPF	2019	yes	no	no													AF					
Thamnosophis lateralis	LC	S,NPF	2011	yes	no	no																		
Thamnosophis stumpffi	VU	D,UPD	2011	yes																				
Bamboo Snakes, Pseudoxenodontidae																								
Pseudoxenodon bambusicola	LC	S,NPF	2011	yes					I															
Pseudoxenodon bannaensis	DD	U,NPF	2011																					
The Basal Dipsadids																								
Thermophis baileyi	NT	D	2011	U	no	no															RE			

continued				Conservation actions				Threats							Risks									
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Thermophis shangrila																								
Thermophis zhaoermii	EN	D,NPF	2011	yes	no	no																		
New World Mud Snakes																								
Farancia abacura	LC	S	2007	yes																				
Farancia erytrogramma	LC	S	2007	yes																				
Wetland *Coniophanes*																								
Coniophanes bipunctatus	LC	S,NPF	2012	yes O																				
Coniophanes quinquevittatus	LC	S	2012	yes																				
Neotropical Swamp Snakes																								
Hydromorphus concolor	LC	S	2012	yes														LW	DU,I					
Hydromorphus dunni	DD	U	2012												AP				DU,					
Tretanorhinus mocquardi	DD	U	2012	U												HU,CI								
Tretanorhinus nigroluteus	LC	U,NPF	2012	yes																				
Tretanorhinus taeniatus	LC	U	2013	yes											MA				IM,		MQ			
Tretanorhinus variabilis	LC	U	2016	yes											AP,L	HU							IAD	
Neotropical River Snakes																								
Hydrodynastes bicinctus	LC	U	2014	yes															IM					
Hydrodynastes gigas	LC	S	2014	yes				L																
Neotropical Fishing Snakes																								
Helicops angulatus	LC	S	2015	yes																				
Helicops apiaka	LC	U	2012	yes																				
Helicops boitata																								
Helicops carinicaudus	LC	U	2013	yes																				
Helicops cyclops	LC	U	2013	yes																				
Helicops danieli	LC	S	2013	U											AP,L			LW	DU					
Helicops gomesi	LC	U	2012	yes																				
Helicops hagmanni	LC	S	2014	yes																				
Helicops infrataeniatus	LC	S	2014	yes																				

continued				Conservation actions				Threats							Risks									
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Helicops leopardinus	LC	S	2014	yes																				
Helicops modestus	LC	S	2012	yes																				
Helicops nentur																								
Helicops pastazae	LC	U	2014	yes											AP		DW		IM	RA	MQ			
Helicops petersi	NT	U	2014	yes											AP	HU					OD			
Helicops phantasma																								
Helicops polylepis	LC	S	2014	yes																				
Helicops scalaris	LC	S,NPF	2013	yes																				
Helicops tapajonicus	LC	U	2012	yes																				
Helicops trivittatus	LC	U	2012	yes													DW							
Helicops yacu	LC	U	2014	U																				
Hydrops caesurus	LC	U,NPF	2014	yes																				
Hydrops triangularis	LC	S	2014	yes																				
Hydrops martii	LC	S,NPF	2014	yes																				
Pseudoeryx plicatilis	LC	S	2014	yes																				
Pseudoeryx relictualis	VU	U	2015	yes											AP,L									
Neotropical Bush Snakes																								
Gomesophis brasiliensis	LC	U	2012	yes																				
Ptychophis flavovirgatus	LC	U	2012	yes																				
Thamnodynastes chaquensis	LC	S	2014	yes											AP									
Thamnodynastes hypoconia	LC	S	2014	yes																				
Thamnodynastes lanei	LC	U	2014	U																				
Thamnodynastes pallidus	LC	S,NPF	2014	yes																				
Thamnodynastes ramonriveroi	LC	U	2015	U																				
Thamnodynastes strigatus	LC	U,NPF	2014	yes																				
Semi-Aquatic Painted Snakes																								
Lygophis anomalus	LC	S	2014	yes																				
Erythrolamprus miliaris	LC	S	2014	yes																				

continued				Conservation actions				Threats							Risks									
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Erythrolamprus poecilogyrus	LC	I	2014	yes																				
Erythrolamprus semiaureus	LC	S	2014	yes																				
Erythrolamprus breviceps	LC	S	2014	yes													DW							
Erythrolamprus cobellus	LC	S	2015	yes													OM							
Erythrolamprus frenatus	LC	U	2014	yes																				
Erythrolamprus jaegeri	LC	U,NPF	2014	yes																				
Erythrolamprus taeniogaster	LC	S	2013	yes																	RE			
Erythrolamprus reginae	LC	S	2014	yes																				
Erythrolamprus zweifeli	LC	S	2015	yes											AP									
Erythrolamprus macrosomus																								
Erythrolamprus epinephelus	LC	U	2018	yes																				
Erythrolamprus albiventris																								
Erythrolamprus fraseri																								
Erythrolamprus lamonae																								
Erythrolamprus melanotus	LC	S	2015	yes																				
Sordellina punctata	LC	U	2012	yes																				
Mountain Keelbacks																								
Hebius annamensis	DD	U,UPF	2011															LW						
Hebius chapaensis	DD	Uns,NPF	2011																					
Hebius craspedogaster	LC	S,NPF	2011	yes	no	no																		
Hebius deschauenseei	LC	U,UPF	2011	yes											AP		DW	LW						
Hebius modestus	LC	U,NPF	2011																					
Hebius nigriventer																								
Hebius octolineatum	LC	S,NPF	2011	yes	no	no			N,I															
Hebius popei	LC	S,NPF	2011	yes	no	no																		
Hebius parallelum	DD	U,NPF	2019	yes																				
Hebius sauteri	LC	U,NPF	2011	yes	no	no																		
Hebius taronensis	NT	U,NPF	2011	yes																				

continued				Conservation actions				Threats							Risks									
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Herpetoreas platyceps	LC	U,NPF	2019	yes	no	no																		
Herpetoreas sieboldii	CC	U,NPF	2019	yes																				
Herpetoreas tpser																								
Herpetoreas xemmi	NT	U,U	2011	yes											AP			LW						
Rhabdops aquaticus	LC	S	2019	yes																				
Rhabdops olivaceus	NT	U,PF	2019	yes	no	no	no												DU,					
Pseudoagkistrodon rudis	LC	S,NPF	2011	yes	no	no		N,I			N,I							HT						
Keeled Water Snakes																								
Amphiesma stolatum	LC	S,NPF	2019	yes				N,I											AF					
Tropidonophis doriae	LC	S	2013	yes																				
Tropidonophis elongatus	DD	U,NPF	2019	U																				
Tropidonophis mairii	LC	S,NPF	2014	yes																				
Tropidonophis multiscutellatus	LC	S	2014	yes																				
Tropidonophis negrosensis	VU	D,PF	2007	yes O											AP			HT			MQ			
Tropidonophis punctiventris	EN	U,NPF	2019	U											WP	HU		LW						
Tropidonophis truncatus	LC	S	2019	yes																				
Rhabdophis auriculatus	LC	U,UPF	2007	yes O											AP	HU	DW	LW			MQ			
Rhabdophis lineatus	LC	S,NPF,NAI	2021	no		no	no										DW				MQ			
Rhabdophis rhodomelas	LC	U,UPF	2011																					
Rhabdophis tigrinus	LC	S,NPF	2016	yes					N,I			N						HT		RA				
Rhabdophis formosanus																								
Rhabdophis lateralis	LC	S,NPF	2016	yes	no	no			N,I			N						HT		RA				
Atretium schistosum	LC	S,NPF	2019	yes	yes	yes		I										HT	AF					
Fowlea schnurrenbergeri	LC	U	2019	U												HU			DU,					
Fowlea yunnanensis	LC	D,NPF	2011	yes	no	no																		
Fowlea asperrimus	LC	S	2019	yes																				
Fowlea flavipunctata	LC	S,NPF	2011							N		N						HT	AF					

continued				Conservation actions				Threats							Risks									
Species	Category	Population Trend	Assessment Year	In-place land/water protection	Included in international legislation	Subject to any international management / trade controls	In place research and monitoring	Wearing apparel accessories	Pets/display animals, horticulture	Food-animal	Food-human	Medicine - human and veterinary	Handicrafts, jewellery, etc	Venom	Agriculture and aquaculture	Residential and commercial development	Natural system modification	Biological resource use	Pollution	Transportation and service corridors	Energy production and mining	Climate change and severy weather	Invasive and other problematic species	Human intrusions & disturbance
Fowlea melanzostus																								
Fowlea piscator	LC	S,NPF	2016	yes	no	no	no	L,N			L,N					HU		HT	DU,					
Fowlea punctulatus	LC	S,NPF	2009	yes											AP			LW						
Fowlea tytleri	LC	S	2019	yes																				
Xenochrophis bellulus	DD	U,NPF	2011												AP									
Xenochrophis cerasogaster	VU	D	2019	yes											AP	HU			DU					
Xenochrophis maculatus	LC	U,NPF	2011	yes O																				
Xenochrophis trianguligerus	LC	I,NPF	2019	yes																				
Centophallus vittatus	LC	Uns,NPF	2011						I	N,I														
Asian Stream Snakes & Relatives																								
Smithophis arunachalensis																								
Smithophis atemporalis	DD	U	2019	U																				
Smithophis bicolor	LC	U,NPF	2011	U	no	no																		
Smithophis linearis																								
Opisthotropis alcalai	EN	D,NPF	2007	yes O											AP			LW						
Opisthotropis andersonii	NT	D,NPF	2011	yes												HU								
Opisthotropis atra	DD	U	2020	U																				
Opisthotropis cheni	LC	S	2011	yes	no	no																		
Opisthotropis cucae	DD	U,UPF	2011	yes											AP			LW						
Opisthotropis daovantieni	NT	U,NPF	2011	no											AP			LW						
Opisthotropis durandi																								
Opisthotropis guangxiensis	NT	U,NPF	2011	yes	no	no															RE			
Opisthotropis hungtai																								
Opisthotropis haihaensis																								
Opisthotropis kikuzatoi	CR	D,PF	2016		yes		no											FH	AF				IAD	
Opisthotropis jacobi	DD	U,NPF	2011	yes																				
Opisthotropis kuatunensis	LC	S,NPF	2011	yes	no	no																		
Opisthotropis lateralis	LC	S,NPF	2011	yes	no	no															RE			

continued				Conservation actions				Threats							Risks									
Species	Category	Population Trend	Assessment Year	In-place land/water protection	Included in international legislation	Subject to any international management / trade controls	In place research and monitoring	Wearing apparel accessories	Pets/display animals, horticulture	Food-animal	Food-human	Medicine - human and veterinary	Handicrafts, jewellery, etc	Venom	Agriculture and aquaculture	Residential and commercial development	Natural system modification	Biological resource use	Pollution	Transportation and service corridors	Energy production and mining	Climate change and severy weather	Invasive and other problematic species	Human intrusions & disturbance
Opisthotropis latouchii	LC	S,NPF	2011	yes	no	no											DW				RE			
Opisthotropis laui																								
Opisthotropis maculosa	DD	U,NPF	2011	yes	no	no																		
Opisthotropis maxwelli	DD	U,NPF	2011	U	no	no																		
Opisthotropis rugosa	LC	Uns,NPF	2011	yes																				
Opisthotropis shenzhenensis																								
Opisthotropis spenceri	DD	Uns,NPF	2011	yes																				
Opisthotropis tamdaoensis	DD	U,UPF	2011	yes																				
Opisthotropis typicus	LC	Uns,NPF	2011	yes											AP			LW						
Opisthotropis voquyi																								
Opisthotropis zhaoermii																								
Trimerodytes aequifasciatus	LC	D,NPF	2011	yes							L				AP	HU				RA				
Trimerodytes annularis	LC	D,NPF	2011	yes	no	no		N,I			N,I							HT	AF					
Trimerodytes balteatus	DD	D,NPF	2020	yes	no	no		L,N			L,N				AP			HT	AF		RE			
Trimerodytes percarinatus	LC	S,NPF	2011	yes											AP,W									
Trimerodytes yapingi																								
Trimerodytes yunnanensis	LC	U,NPF	2011	yes O																				
Trimerodytes (=Paratapinophis) praemaxillaris	LC	U,NPF	2011	yes	no	no									AP			LW		RA				
African Water Snakes																								
Afronatrix anoscopus	LC	S,NPF	2012	yes											AP			LW						
Natriciteres bipostocularis	LC	S	2019	no																				
Natriciteres fuliginoides	LC	S,NPF	2013	yes																				
Natriciteres olivacea	LC	U,NPF	2012	yes													DW							
Natriciteres pembana	LC	U	2014	yes															AF					
Natriciteres sylvatica	LC	U	2019	yes																				
Natriciteres variegata	LC	U	2012	yes																				
Helophis schoutedeni	VU	D	2019	yes														FH						
Hydraethiops laevis	DD	U	2019	yes																				

continued				Conservation actions				Threats								Risks										
Species	Category	Population Trend	Assessment Year	In-place land/water protection	Included in international legislation	Subject to any international management / trade controls	In place research and monitoring	Wearing apparel accessories	Pets/display animals, horticulture	Food-animal	Food-human	Medicine - human and veterinary	Handicrafts, jewellery, etc	Venom	Agriculture and aquaculture	Residential and commercial development	Natural system modification	Biological resource use	Pollution	Transportation and service corridors	Energy production and mining	Climate change and severy weather	Invasive and other problematic species,	Human intrusions & disturbance
Hydraethiops melanogaster	LC	S	2019	yes																				
Limnophis bangweolicus	LC	S,NPF	2019	yes																				
Limnophis bicolor	LC	S,NPF	2019	U																				
Limnophis branchi																								
Natrix, The Paleartic Watersnakes																								
Natrix maura	LC	D,NPF	2008	yes O									N				OM	HT	DU,I					
Natrix natrix	LC	S,NPF	2016	yes	no	no			I									HT	DU,I		MQ			
Natrix helvetica																								
Natrix astreptophora																								
Natrix tessellata	LC	D,NPF	2020	yes	no	no			I							HU,CI		HT	IM,	RA			IAD	
The Thamnophiine Clade																								
Liodytes alleni	LC	S	2007	yes																				
Liodytes pygaea	LC	S	2007	yes																				
Liodytes rigida	LC	S	2007	yes																				
Clonophis kirtlandii	NT	D	2007	yes											AP	HU		HT		RA				
Regina grahamii	LC	U	2007	yes												HU,CI			IM					
Regina septemvittata	LC	S	2007	yes											AP	HU,CI			DU					
Nerodia cyclopion	LC	S	2007	yes											AP	HU								
Nerodia floridana	LC	S	2007	yes																				
Nerodia clarkii	LC	D	2007	yes											AP	HU,CL			DU,I					
Nerodia erythrogaster	LC	S	2007	yes																				
Nerodia fasciata	LC	S	2007	yes																				
Nerodia harteri	NT	S	2007	yes																				
Nerodia paucimaculata	NT	S	2007	yes													DW		DU,			D		
Nerodia rhombifer	LC	S	2007	yes																				
Nerodia sipedon	LC	S	2007	yes																				
Nerodia taxispilota	LC	S	2007	yes																				
Thamnophis atratus	LC	S	2007	yes																			IAD	

continued				Conservation actions				Threats							Risks									
Species	Category	Population Trend	Assessment Year	In-place land/water protection	Included in international legislation	Subject to any international management / trade controls	In place research and monitoring	Wearing apparel accessories	Pets/display animals, horticulture	Food-animal	Food-human	Medicine - human and veterinary	Handicrafts, jewelley, etc	Venom	Agriculture and aquaculture	Residential and commercial development	Natural system modification	Biological resource use	Pollution	Transportation and service corridors	Energy production and mining	Climate change and severy weather	Invasive and other problematic species.	Human intrusions & disturbance
Thamnophis bogerti																								
Thamnophis conanti																								
Thamnophis lineri																								
Thamnophis brachystoma	LC	S	2007	yes												HU	OM							
Thamnophis butleri	LC	S	2007	yes																				
Thamnophis chrysocephalus	LC	S	2007	yes																				
Thamnophis couchii	LC	S	2007	yes																				
Thamnophis cyrtopsis	LC	S	2012	yes																				
Thamnophis elegans	LC	S	2007	yes																				
Thamnophis eques	LC	S	2007	yes																				
Thamnophis errans	LC	U	2007	yes											AP,L	HU	F	LW						
Thamnophis exsul	LC	S	2007	yes																				
Thamnophis fulvus	LC	S	2012	yes													DW							
Thamnophis gigas	VU	D	2007	yes											AP,L	HU	OM	HT	AF	RA			IAD	
Thamnophis godmani	LC	D	2007	yes											AP,L									
Thamnophis hammondii	LC	D	2007	yes											AP,L	HU,CI	DW	HT				D	IAD	RA
Thamnophis marcianus	LC	U,NPF	2005	yes O											AP		OM		AF					
Thamnophis melanogaster	EN	D	2007	yes															IM					
Thamnophis copei	VU	D	2007	yes											AP	HU								
Thamnophis foxi	DD	U	2007													HU		LW						
Thamnophis mendax	EN	D	2007	yes											AP,L									
Thamnophis nigronuchalis	DD	U	2007												AP,L	HU		LW						
Thamnophis ordinoides	LC	S	2007	yes																				
Thamnophis postremus	LC	U	2007												AP									
Thamnophis proximus	LC	S,NPF	2005	yes O													DW							
Thamnophis pulchrilatus	LC	U	2007												AP,L	HU		LW						
Thamnophis radix	LC	S	2007	yes																				
Thamnophis rossmani	DD	U	2007																					

continued				Conservation actions				Threats							Risks									
Species	Category	Population Trend	Assessment Year	In-place land/water protection	Included in international legislation	Subject to any international management / trade controls	In place research and monitoring	Wearing apparel accessories	Pets/display animals, horticulture	Food-animal	Food-human	Medicine - human and veterinary	Handicrafts, jewelley, etc	Venom	Agriculture and aquaculture	Residential and commercial development	Natural system modification	Biological resource use	Pollution	Transportation and service corridors	Energy production and mining	Climate change and severy weather	Invasive and other problematic species.	Human intrusions & disturbance
Thamnophis rufipunctatus	LC	D	2007												LR	HU		HT					IAD	RA
Thamnophis saurita	LC	S	2007	yes																				
Thamnophis scalaris	LC	S	2007	yes											AP,L									
Thamnophis scaliger	VU	D	2007												AP,L									
Thamnophis sirtalis	LC	S	2007	yes																				
Thamnophis sumichrasti	LC	U	2007	yes																				
Thamnophis unilabialis																								
Thamnophis validus	LC	S	2007												AP	HU		LW						
Natricids of Uncertain Status																								
Anoplohydrus aemulans	DD	U,NPF	2011																					
Isanophis boonsongi	DD	U,NPF	2011	yes																				
Hydrablabes periops	DD	U	2011	yes																				
Hydrablabes praefrontalis	DD	U,NPF	2011	yes																				
African Rain Forest Water Snakes																								
Grayia caesar	LC	S	2019	yes																				
Grayia ornata	LC	S	2019	yes																				
Grayia smithii	LC	S	2014	yes							L							HT						
Grayia tholloni	LC	U	2014	yes																				
Colubridae																								
Crotaphopeltis barotseensis	LC	S	2019	yes													DW							
Crotaphopeltis degeni	LC	U	2014	yes																				
Platyceps insulanus	DD	U	2012																					
Platyceps rhodorachis	LC	S,NPF	2019	yes																				
Philothamnus angolensis	LC	U	2014	yes																				
Philothamnus hoplogaster	LC	S	2014	yes					I															
Oocatochus rufodorsatus	LC	U,NPF	2019	yes	no	no			I			N						HT	DU,					
Xenelaphis ellipsifer	LC	U,NPF	2011	yes																				
Xenelaphis hexagonotus	LC	I,NPF	2011	yes							L													

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Aquatic Snakes is an illustrated, annotated checklist of aquatic and semi-aquatic snakes in marine and freshwater environments. The biggest challenge was deciding what species to include and which to exclude. While the intent was to have accounts for all aquatic snakes, where do you draw the line on the continuum? How much evidence do you need to label a species semi-aquatic? This volume covers the range of snakes that are traditionally considered semi-aquatic. However, knowledge of some of these animals is poor or absent, while others are some of the best-studied reptiles.

ISBN 978-1-7378424-9-1
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