



## SYMPOSIUM

### Marine Invasions by Non-Sea Snakes, with Thoughts on Terrestrial–Aquatic–Marine Transitions

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**Synopsis** Few species of snakes show extensive adaptations to aquatic environments and even fewer exploit the oceans. A survey of morphology, lifestyles, and habitats of 2552 alethenophidian snakes revealed 362 (14%) that use aquatic environments, are semi-aquatic, or aquatic; about 70 (2.7%) of these are sea snakes (Hydrophiinae and Laticaudinae). The ancient and aquatic family Acrochordidae contains three extant species, all of which have populations inhabiting brackish or marine environments, as well as freshwater. The Homalopsidae have the most ecologically diverse representatives in coastal habitats. Other families containing species exploiting saline waters with populations in freshwater environments include: the Dipsadidae of the western hemisphere, the cosmopolitan Natricidae, the African Grayinae, and probably a few Colubridae. Species with aquatic and semi-aquatic lifestyles are compared with more terrestrial (fossorial, cryptozoic, and arboreal) species for morphological traits and life histories that are convergent with those found in sea snakes; this may provide clues to the evolution of marine snakes and increase our understanding of snake diversity.

#### Introduction

Oceans cover 71% of the earth's surface with a minimum of 356,000 km of coastline, yet only 2.5% (about 86 species) of the 3364 extant snakes are known to inhabit the oceans on a regular basis (Earle 2001; Uetz 2011). The major snake lineages holding marine and fresh water taxa are listed in Table 1, and a list of species known and suspected to use brackish water and marine habitats is provided in Table 2 with supporting references. It is unclear whether most of these snakes are spending substantial amounts of time in salt water and are well adapted for life in saline waters, or whether they use behavioral osmoregulation, shuttling between marine and freshwater environments while remaining dependent upon sources of freshwater. Given the low percentage of snake species in the oceans, the physical environment appears to provide challenges for snakes (Dunson and Mazzotti 1989; Rasmussen et al. 2011). A survey of lifestyles (habitat use + foraging mode + daily activity pattern + reproductive mode) of 2552 alethenophidian snakes in 459

genera revealed about 362 (14%) species using aquatic environments to varying degrees; only 70 (2.7%) of these are sea snakes (Hydrophiinae and Laticaudinae). Another 65 or more species appear to use brackish water or the ocean.

The ancient Acrochordidae contains three extant species, all of which have populations in brackish, marine, and freshwater environments. The Homalopsidae containing terrestrial, semi-aquatic, and aquatic snakes has about 14 species that have invaded brackish and marine waters. The speciose Dipsadidae of the western hemisphere has at least seven species with coastal–marine populations, the cosmopolitan Natricidae has about 24 species with populations using brackish waters but most of these also have populations that primarily inhabit freshwater. The semi-aquatic, African Grayiinae has at least one species that uses brackish water (Heatwole 1999; Luiselli and Akani 2002; Murphy 2007). However, any aquatic or semi-aquatic snake with a coastal population is likely to visit brackish water on occasion. Flooding may move snakes downstream into estuaries, while

**Table 1** The phylogenetic distribution of semi-aquatic, aquatic, and marine snakes

Higher taxa	Genera	Species	Saline species	Freshwater species	Date of origin
Hydrophiinae	20	61	58	3	6.2 <sup>a</sup>
Laticaudinae	2	8	7	2	13 <sup>a</sup>
Pseudaspidinae	1	2	0	0	28.9
Lamprophiinae	10	65	0	7	28.90
Aparallactinae	10	50	0	0	30.29
Atractaspidinae	2	21	0	0	30.29
Viperidae	42	297	1	1	30.39
Grayiinae	1	4	1	4	30.42
Calamariinae	6	84	0	1	30.42
Dipsadidae	92	731	7	34	33.65
Pseudoxenodontinae	3	13	0	2	33.65
Pseudoxyrhopiinae	23	86	0	1	34.86
Elapidae	56 <sup>c</sup>	347	70+	4+	34.86
Psammophiinae	8	50	0	0	34.87
Colubrinae	102	677	0	1+	35.36
Natricidae	31	210	24	66	38.28
Scaphiodontophiinae	1	2	0	0	39.71
Anomochilidae	1	3	0	0	44.45
Cylindrophiiidae	1	10	0	1	44.45
Prosymninae	1	16	0	0	44.51
Erycinae	4	15	0	0	45.02
Boinae	7	34	0	5	45.02
Pythonidae	10	40	0	6	47.12
Loxocemidae	1	1	0	0	47.21
Homalopsidae <sup>b</sup>	12	55	14	30	53.38
Uropeltidae	8	51	0	0	56.84
Pareatidae	14	4	0	0	65.39
Bolyeridae	2	2	0	0	68.4
Xenodermatidae	5	17	0	1	76.08
Xenopeltidae	1	2	0	1	77.0
Acrochordidae	1	3	3	3	84.66
Aniliidae	1	1	0	1	91.8
Tropidophiidae	3	25	0	0	91.8

Dates are in millions of years. Data from Pyron and Burbrink (2011), <sup>a</sup>Sanders et al. (2010), and <sup>b</sup>our unpublished data; <sup>c</sup>number highly controversial.

storm surges, high tides, and rising sea levels (pre-historic marine incursions) may move saline water inland.

What follows is a survey of alethenophidian snakes using brackish and marine water (excluding the Hydrophiinae and Laticaudinae), an examination of their geographic and phylogenetic distributions, and an analysis to see which species are most convergent with the true sea snakes.

## Methods

The literature and museum specimens were surveyed for information on life history and morphology of snakes. Of 2552 alethenophidian snakes, 362 species were described as using aquatic environments, as semi-aquatic, or aquatic. Finding literature and museum specimens to document habitat, life history and morphology for 27 traits for each species was possible for only 261 (72%) of the 362 species. Thus, species with incomplete data were excluded from the database. Of the remaining 261 (listed in Appendix 1), 48 were considered aquatic, 175 semi-aquatic, 11 were fossorial, and 27 were terrestrial–arboreal. Species listed as fossorial or terrestrial–arboreal had some mention of using wetland habitats in the literature descriptions of their habitat or habits. The data were compiled in an Excel file, and analyzed with a PCA using Data Lab.

## Results

Figure 1 illustrates the distribution of non-sea snake genera using brackish water and marine environments in relationship to their geographic distribution and the diversity of mangroves. Table 2 shows the phylogenetic distribution of brackish and marine species. Species convergent with sea snakes based on the PCA results are shown in Fig. 2. While no known freshwater/brackish water snakes have a paddle-like tail, there are freshwater/brackish snakes that share most of the other morphological and life-history traits of the Laticaudinae and Hydrophiinae. Table 3 summarizes some of these traits and the frequency of their occurrence in the species sampled.

## Discussion

Fossils suggest there have been snakes in the oceans since the Cretaceous. The limbed snakes like *Pachyrhachis* were marine, and fossil evidence from the Eocene suggests that some spectacular marine species, such as *Palaeophis grandis* and *Pterosphenus schucherti*, were present during the greenhouse conditions of the time (Lee and Caldwell 1997; Holman 2000). Despite evidence for early invasions of the oceans, however, snakes have apparently had difficulty in adapting to marine environments.

The greatest diversity of extant snakes occurs in Southeast Asia. Of the 32 lineages listed in Table 1, 18 (56%) are represented in Asia, and Cadle (1987) reported a similar Asian diversity (61%, 20 of 33 lineages) based on a slightly different classification. Therefore, it is not surprising that the largest number of aquatic and marine species is associated with the

**Table 2** Species of snakes (excluding the Laticaudinae and Hydrophiinae) that use brackish water and marine environments

Species	Habitat	Geography	References
Acrochordidae			
<i>Acrochordus arafurae</i>	FBM	Australia	Lillywhite and Ellis (1994)
<i>Acrochordus granulatus</i>	FBM	Asia/AUA	Lillywhite and Ellis (1994)
<i>Acrochordus javanicus</i>	FBM	Asia	Lillywhite and Ellis (1994)
Colubridae			
<i>Coluber constrictor</i> <sup>a</sup>	T	e NA	Neil (1958)
<i>Coluber hippocrepis</i> <sup>a</sup>	T	N. Africa	Schleich et al. (1996)
<i>Oocatochus rufodorsatus</i> <sup>a</sup>	TF	Asia	Schulz (1996)
<i>Stegonotus sp.</i> <sup>a</sup>	T	Asia	McDowell (1972)
Elapidae			
<i>Pseudonaja ellioti</i> <sup>a</sup>	TF	AUA	WoRMS Database (2011)
<i>Toxicocalamus mintoni</i> <sup>a</sup>	TF	AUA	WoRMS Database (2011)
<i>Toxicocalamus pachysomus</i> <sup>a</sup>	TF	AUA	WoRMS Database (2011)
<i>Tropidechis sadleri</i> <sup>a</sup>	TF	AUA	WoRMS Database (2011)
Dipsadidae			
<i>Farancia abacura</i>	FB	NA	Linzey and Crawford (1981)
<i>Farancia erythrogrammus</i>	FB	NA	Neil (1958)
<i>Helicops angulatus</i>	FB	SA	our unpublished data
<i>Helicops infrataeniatus</i>	FB	SA	Lacomba et al. (2001)
<i>Helicops scalaris</i>	FB	SA	Barros (2001)
<i>Hydrops triangularis</i>	FB	SA	Ford and Ford (2002)
<i>Leptodeira rubricate</i>	TA, Man	CA	Dunn (1939)
<i>Pseudoeryx relictuialis</i>	FB	SA	Schargel et al. (2007)
<i>Tretanorhinus nigroluteus</i>	FBM	CAR	Barbour and Nobel (1915)
<i>Tretanorhinus variabilis gaigeae</i>	FBM	CAR	Neil (1958)
<i>Tretanorhinus variabilis lewisi</i>	FBM	CAR	Neil (1958), Grant (1946)
Grayiidae			
<i>Grayia smythii</i>	FB	Africa	Luiselli and Akani (2002)
Homalopsidae			
<i>Bitia hydroides</i>	BM	Asia	Jayne et al. (1995)
<i>Cantoria violacea</i>	FBM	Asia	Karns et al. (2002)
<i>Cerberus australis</i>	FBM	Aus	Kinghorn (1929)
<i>Cerberus microlepis</i>	F?B	Phil	Taylor (1922)
<i>Cerberus rynchops</i>	FBM	Asia	Annanadale (1907)
<i>Cerberus sp. A</i>	FBM	Asia	Jayne et al. (1988)
<i>Cerberus sp. B</i>	BM	Micronesia	Gyi (1970)
<i>Djokoiskandar annulatus</i>	BM	AUA	Parker (1982)
<i>Enhydris bennetti</i>	FBM	Asia	Smith (1943)

(continued)

**Table 2** Continued

Species	Habitat	Geography	References
<i>Erpeton tentaculatus</i> <sup>a</sup>	F?B	Indochina	Neil (1958)
<i>Fordonia leucobalia</i>	FBM	Asia/AUA	Kopstein (1931)
<i>Gerarda prevostiana</i>	BM	Asia	Karns et al. (2002)
<i>Homalopsis buccata</i> <sup>a</sup>	FB	Asia	Hagen (1890)
<i>Myron richardsonii</i>	BM	AUA	Parker (1982), O'Shea (1986)
<i>Myron karnsi</i>	BM	Indonesia	Murphy (2011)
<i>Myron resetari</i>	BM	AUA	Murphy (2011)

<sup>a</sup>Species are suspected of using brackish waters based, but without confirmation in the literature; their placement is based upon use of wetland habitats, known localities, and distribution.

WoRMs Database can be found at: <http://www.marinespecies.org/>  
 Habitat codes: A = arboreal, F = freshwater, B = brackish water, M = marine, MAN = mangroves, Sm = saltmarsh, T = terrestrial.  
 Geographic codes: AF = Africa, AUA = Australasia, CAR = Caribbean, EUR = Europe, NA = North America, Phil = Philippines, SA = South America.

Sunda Shelf and surrounding area. Diversity of coastal aquatic snakes coincides with diverse mangrove communities in Southeast Asia and Australasia (Fig. 1), and mangroves have undoubtedly acted as the transitional ecological setting for snakes moving from freshwater to salt water.

The 1.85 million square kilometer Sunda Shelf encompasses freshwater, brackish, and saltwater habitats and provided the environments that made the evolution of the marine and brackish water snakes possible. The evolution of the diverse aquatic and semi-aquatic snake fauna that evolved in this vast wetland complex are likely due to the coincidence of its geographic size, the extensive interdigitation of land and sea, the dynamic historical changes, and the presence of multiple ancestral snake lineages in the region.

Using data from Pauwels et al. (2008) about 64 (41.8%) of all 153 freshwater snake species occur in the Oriental region (inclusive of the Sunda Shelf), while 39 (25.4%) occur in the Neotropics, and 22 (14.3%) and 19 (12.4%) occur in the Nearctic and Afrotropical regions, respectively. This is a pattern that follows the biogeographic regions with the greatest numbers of brackish water and marine snakes (see Table 2).

The superfamily Acrochordoidea is represented by three living species of *Acrochordus*, relics of an ancient, more widespread lineage inclusive of the extinct families Paleophiidae and Nigerophiidae as well as the Acrochordidae (Nessov 1995). Perhaps, the most specialized marine acrochordoid was the palaeophiid genus *Pterosphenus*; with a ribbon-like body several meters long, its anatomy was so well



**Fig. 1** The distribution of snakes found in brackish water environments. Note that the number of genera is correlated with the greatest mangrove diversity, the largest geographic area occupied by mangroves and wetlands, and the greatest geographic concentration of snake lineages. Snakes from left to right: *Helicops angulatus*, *Hydrops triangularis*, *Farancia abacura*, *Liophis cobella*, *Grayia smythii*, *Natrix natrix*, *Xenochrophis piscator*, *Cerberus rynchops*, *Fordonia leucobalia*, *Acrochordus javanicus*, *Cantoria violacea*.

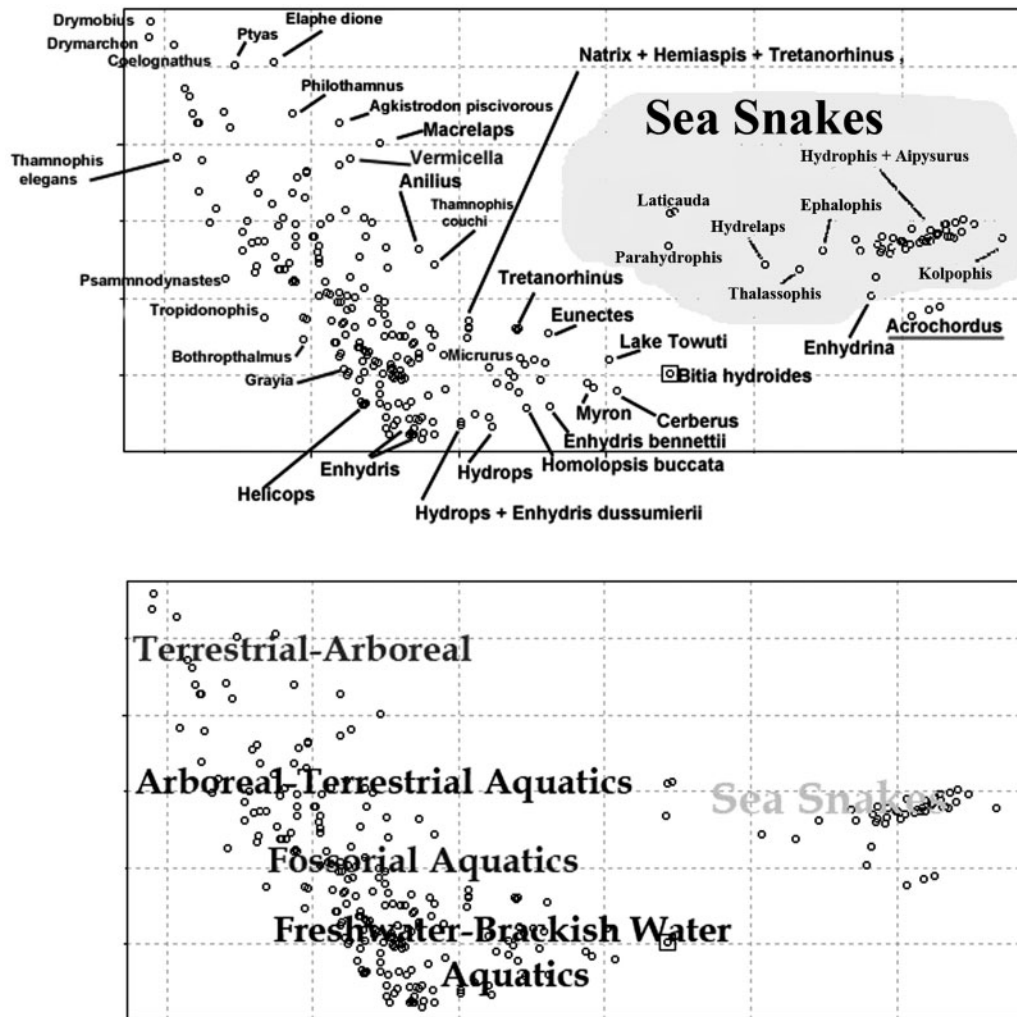
adapted to the marine environment it was unable to move on land (Nessov 1995; Rage et al. 2003). Fossil remains of *Pterospheenus schucherti* are known from coastal regions extending from New Jersey to Texas. The vertebrae are narrow, lightly constructed (with large marrow cavities) and, have long neural spines, suggesting that the snake was incapable of terrestrial locomotion. Hutchinson (1985) reported fossils of *P. schucherti* from Florida associated with whales' remains deposited >300 km from land in the Middle Eocene. Holman (2000) hypothesized this large sea-going snake had a lifestyle similar to modern sea snakes: drinking seawater (but see Lillywhite and Brischoux, this issue), using salt glands, and a viviparous reproductive mode. He reports 24 mm long vertebrae which, assuming 270 vertebrae, suggests this snake may have exceeded 6 m.

Some of the extant Homalopsidae are known for their marine lifestyles (*Bitia*, *Cantoria*, *Cerberus*, *Djokoiskandarus*, *Enhydriis bennettii*, *Fordonia*, *Myron*) and others members of the family (*E. dussumierii*, *E. maculosa*, *E. pakistantica*, *E. sieboldii*, *E. vorisi*, *Homalopsis* sp.) are likely exposed to brackish water on occasion based upon their distributions in river deltas and coastal flood plains as well as anecdotal literature (see Table 2). While Gyi (1970) recognized 10 genera and 37 species; the current number of homalopsids is 55 species in 14 genera (our unpublished data). This suggests they are not simply remnants of an ancient lineage, but a significant radiation of snakes with species that have been misplaced within other lineages. The family contains the fangless fossorial-terrestrial, vermivorous

*Brachyorrhos* Kuhl (Murphy et al. 2011) and *Calamophis* Meyer (our unpublished data), as well as many semi-aquatic and aquatic species with rearfangs and an associated venom gland. Homalopsids lack a fossil record, and the number of extant species and genera in this family will likely continue to increase. While some homalopsids appear salt tolerant, others are quite sensitive to saline conditions (Murphy 2007).

The cosmopolitan Natricidae (or Natricinae) are speciose (more than 200 species) and more recently evolved than the homalopsids (Pyron and Burbrink 2011). The family contains fossorial, terrestrial, arboreal, and aquatic species with a few adapted to brackish and marine waters. These include *Natrix* and *Xenochrophis* in Eurasia and *Nerodia*, *Liodytes* (formerly *Regina* in part, see Alfaro and Arnold 2001), *Seminatrix*, and *Thamnophis* in the western hemisphere. While most natricids are temperate, a few lineages have invaded the tropics in Africa: *Afronatrix*, *Limnophis*, *Natriciteres*; in Asia: *Rhabdophis*, *Tropidonophis*, *Xenochrophis*; in the Neotropics: *Thamnophis* and *Nerodia*; and in the Neotropics: *Nerodia* and *Thamnophis*. With the exception of *Nerodia clarkii* and *N. fasciata* (Gibbons and Dorcas 2004; Babonis and Evans 2011), the natricids using marine environments are few in number and poorly known.

The Dipsadidae primarily comprises a Neotropical radiation with a few representatives in North America; they too are speciose (more than 700 species) and of relatively recent origin (Vidal et al. 2010; Pyron and Burbrink 2011). The family contains



**Fig. 2** Above. Results of a PCA to identify which species of freshwater and brackish water snakes are most convergent with sea snakes. The Hydrophiinae and *Laticauda* (sea snakes and sea kraits, respectively) are shown in the shaded area, *Acrochordus* are closest to the sea snakes but *Bitia*, an undescribed homalopsid species from Lake Towuti, Sulawesi, *Eunectes*, and *Tretanorhinus* were nearby. The cluster near the bottom left is composed mostly of brackish water and freshwater homalopsids and dipsadids. Body size, the presence or absence of a paddle tail, dorsal pattern, dorsal scales (number of rows and ornamentation), and number of ventrals accounted for 63.1% of the variation. Below. The same plot with species categorized based on habitats used.

extant coastal species in the genera *Farancia*, *Helicops*, *Hydrops*, *Liophis*, and *Tretanorhinus* that inhabit brackish and marine water (see for species and references in Table 2). There are likely more species in this clade using brackish water environments given the recent description of *Pseudoeryx relictualis* by Schargel et al. (2007) from Lake Maracaibo, Venezuela. The mostly freshwater lake is a remnant of the Orinoco changing course, and has a direct flow of water from the Caribbean through the Strait of Maracaibo and Tablazo Bay. Under favorable tidal conditions, salt water intrudes into the lake elevating salinity (Findikakis et al. 2001). The endemic freshwater/brackish water *Helicops scalaris* also inhabits the lake (Barros 2001). Most of the

aquatic dipsadid lineages likely evolved in the Miocene's Pebas wetland that underwent at least a partial marine incursion in what are now the Orinoco and Llanos basins of Venezuela.

Salinity levels in the Pebas are controversial. Wesselingh and Ramos (2010) reported evidence for a brackish water mollusk and ostracod fauna in the Pebas system (now western Amazonia). Lundberg et al. (2010) portrayed the Amazonian Neogene fish fauna as strictly freshwater, but acknowledged the presence of carchariform sharks and lamniform rays similarly, Riff et al. (2010) examined the Neogene crocodylian and turtle fauna and suggested that fully marine conditions in the Miocene were excluded from the continent's interior. Thus aquatic

**Table 3** Life history and morphological traits associated with aquatic and semiaquatic snake

Traits	N = 261 (%)
Lifestyles	
Aquatic	49 (18.8)
Semiaquatic	136 (52.1)
Burrowing	39 (14.9)
Terrestrial	27 (10.3)
Arboreal	10 (3.8)
Dorsal patterns	
Uniform	87 (33.3)
Banded	79 (30.3)
Blotched	45 (17.2)
Striped	49 (18.8)
Foraging strategies	
Ambush	21 (8.0)
Searching	198 (75.9)
Both	42 (16.1)
Salinity of habitat	
Marine	61 (23.4)
Brackish	89 (34.1)
Reproductive modes	
Oviparous	125 (47.9)
Viviparous	136 (52.1)
Diets	
Goo	15 (5.7)
Arthropods	26 (10.0)
Fish	171 (65.5)
Amphibians	105 (40.2)
Reptiles	37 (14.2)
Birds	21 (8.0)
Mammals	15 (5.7)
Tail/body ratios	
<10%	27 (10.3)
11–20%	81 (31.0)
21–30%	102 (39.1)
31–40%	29 (11.1)
41–50%	10 (3.8)
>50%	12 (4.5)
Range of dorsal scale rows at midbody	
<20	142 (54.4)
21–30	78 (29.8)
31–40	19 (7.2)
41–50	16 (6.1)
>50	6 (2.3)
Ventral ranges	
100–200	219 (84)

(continued)

**Table 3** Continued

Traits	N = 261 (%)
201–300	23 (8.8)
301–400	13 (4.9)
>400	6 (2.3)

Note that many of these categories are not mutually exclusive.

boids and dipsadids, particularly those living close to coastal areas in Venezuela, Trinidad, and Guyana, were exposed to extended periods of increased salinity. This may explain the salt tolerance these snakes show today. The cohort of dipsadids and natricids capable of inhabiting salt water on the coastal plain of North America (*Farancia abacura*, *F. erythrogramma*, *N. clarkii*, *N. fasciata*, *Nerodia sipedon*, *Liodytes rigida*, and *L. alleni*) may also be the result of selection during marine incursions of the Oligocene–Miocene highstands, and subsequent Pleistocene sea-level fluctuations.

Only anecdotal information is available on dipsadids using salt water. However, preliminary investigation in Trinidad's Caroni Swamp, a mangrove forest reported to have three species of aquatic dipsadids (*Helicops angulatus*, *Hydrops triangularis*, and *Liophis cobella*) (Murphy 2007), found these snakes absent at salinities between 28 and 31 ppt. In Trinidad's Narvia swamp, a marsh forest/mangrove complex, both *L. cobella* and *H. angulatus* were found in water that was 8–12 ppt (J. C. Murphy, unpublished data).

Aquatic snakes, marine and freshwater, have evolved the ability to compress their bodies for increased swimming performance; this has been documented in *N. sipedon* (Pattishall and Cundall 2008) as well as the Hydrophiinae and Laticaudinae (Brischoux and Shine 2011). Freshwater and brackish-water snakes with laterally compressed bodies, small ventrals, dorsally oriented valvular nostrils, and other morphology found in sea snakes are known, but no freshwater or brackish-water snake known to date has a paddle-like tail, such as those found in sea snakes. There is no readily available answer to the absence of paddle tails in fresh water and brackish-water snakes, although clearly paddle tails evolved twice in extant marine snakes (Rasmussen et al. 2011). Sea kraits and the freshwater *Regina* both forage in the water but are otherwise quite terrestrial, so why does *Regina* lack a paddle tail while *Laticauda* have one? Both are active foragers that hunt crevices. The absence of coral reefs, or their ecological equivalent in freshwater, combined with the increased buoyancy of snakes

in saltwater, may be the answer. The paddle-tail may allow the snake to maintain a position in the water column while it probes crevices for food, as would *Laticauda* or *Hydrophis*, while experiencing increased buoyancy.

The only sea snake described as an ambush predator is *Pelamis platura* (Heatwole 1999); all other sea snakes with known habits are active foragers. *Pelamis* is filling a unique niche as a pelagic ambush specialist, floating in the debris fields of the open ocean and ambushing prey while afloat. The tentacled snake, *Erpeton*, is also a dedicated ambush predator, but it is suspended in the water column of shallow, freshwater swamps while hunting, anchored to vegetation with a long prehensile tail, its foraging strategy and lifestyles quite different from that of *Pelamis*.

An examination of phylogenetic studies suggests that aquatic–marine snakes frequently have sisters or proximal relatives that are fossorial. Burrowing snakes may be good candidates for evolving aquatic–marine habits (the reverse may also be true). Historical changes in sea levels, daily tides, storm surges in mangroves and salt marshes, and seawater incursions into freshwater wetlands would expose coastal fossorial snakes to increased salinities. Terrestrial and arboreal snakes of many groups would be able to move away from salt water, but most burrowing species would be expected to be limited in this ability.

Keogh (1998) recovered a clade composed of *Laticauda*, *Loveridgelaps*, and *Salomonelaps*. Scanlon and Lee (2004) also found that *Laticauda* and the terrestrial elapids of the Solomon Islands were basal to the remaining hydrophiines. All the poorly known elapids from the Solomon Islands are described as cryptozoic, fossorial, and semi-aquatic (O’Shea 1996; Shine and Keogh 1998). Sanders et al. (2010) recovered *Hemiaspis* (an aquatic–fossorial genus) as the sister to the sea snakes.

The terrestrial–fossorial, fangless Moluccan genus *Brachyorrhos* is the sister to all of the other homalopsids (Murphy et al. 2011). Additionally, *Enhydris plumbea*, a basal-fanged homalopsid and the sister to all other fanged homalopsids, exploits the mud-root tangle and leads a fossorial–aquatic life (Voris and Karns 1996; Alfaro et al. 2008).

The Dipsadidae contains several clades that are primarily aquatic and associated with fossorial cryptozoic sisters. Within the North American dipsadids is a lineage (the Carphophiinae of Zaher et al. 2009 or the Heterodontinae of Vidal et al. 2010) that forms the sister to the highly aquatic North American *Farancia*; it is a clade composed of *Carphophis*, *Diadophis*, and *Contia* (fossorial cryptozoic snakes).

The sister to the aquatic Hydropsini is the Tachymenini, a clade of semi-aquatic, and aquatic fossorial snakes. Within the Dipsadini, the highly aquatic *Tretanorhinus* and the fossorial cryptozoic *Trimetopon* form the sisters to the fossorial, cryptozoic, and highly speciose genus *Atractus* (Vidal et al. 2010).

Within the North American natricid tribe Thamnophiinae, the fossorial *Clonophis* and *Virginia* form a clade with the aquatic *Liodytes* (formerly *Regina* in part) *alleni*, *L. rigida* and *Seminatrix*; and the fossorial *Tropidoclonion* forms a clade with the aquatic *Nerodia*, *Regina septemvittata*, and *R. grahamii* (Alfaro and Arnold 2001).

Many homalopsid snakes appear adapted for burrowing (*Bitia*, *Cantoria*, *Enhydris alternans*, *E. indica*, *E. plumbea*, *Fordonia*, and *Gerarda*) with small eyes, smooth scales, and short tails. *Bitia* is known to feed on bottom-dwelling gobies (Jayne et al. 1995), *Cantoria* feeds on the burrow-inhabiting *Alpheus* shrimp (Voris and Murphy 2002), and *E. plumbea* is known to eat fish and anuran larva in the mud-root tangle (Voris and Karns 1996). The diets of *E. alternans* and *E. indica* remain unknown (Murphy 2007). Both *Fordonia* and *Gerarda* feed on crustaceans in mangroves and on mud flats and use the intertidal burrow system (Karns et al. 2002).

*Erpeton*’s use of brackish water is speculative (Neil 1958), but it forms a clade with *Cerberus* (brackish water/marine snakes) and *Homalopsis* (mostly freshwater snakes) and it has a highly derived morphology: ventrals about twice the size of dorsal scales, an exceptionally long prehensile tail, and rostral sensory tentacles. *Erpeton* shares heavily keeled, striated scales in numerous dorsal rows (more than 23), a tendency for fragmentation of the head scales, and a relatively long tail with *Cerberus* and *Homalopsis*. *Erpeton*, however, has the largest eyes of any homalopsid and they are decidedly lateral in orientation, while *Cerberus* and *Homalopsis* tend to have more dorsally oriented eyes. The position and size of the eyes, as well as the long tail may be derived for its strategy of ambush hunting.

Anecdotal evidence and morphology suggests some dipsadids (*Hydrops*, *Helicops*, *Hydrodynastes*, *Liophis*, *Pseudoeryx*, *Tretanorhinus*) are highly aquatic (Barbour and Ramsden 1919; Dunn 1939; Villa 1969; Ford and Ford 2002; Scartozzoni 2009), but habitat use by these snakes remains poorly studied.

Freshwater and brackish-water snakes are on trajectories that converge with aspects of the lifestyles and morphology of the true sea snakes (Hydrophiinae and Laticaudinae) and by more closely examining the behavior, ecology, physiology, and morphology of these snakes we may find clues to

the evolution of the Hydrophiinae and Laticaudinae and, more importantly, expand our view of snake diversity.

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## Appendix 1

Species used in the PCA analysis:

*Acalyptophis perionii*, *Acrochordus arafurae*, *Acrochordus granulatus*, *Acrochordus javanicus*, *Afronatrix anoscopus*, *Agkistrodon piscivorus*, *Ahaetulla prasinus*, *Aipysurus apraefrontalis*, *Aipysurus duboisii*, *Aipysurus eydouxii*, *Aipysurus foliosquama*, *Aipysurus fuscus*, *Aipysurus laevis*, *Aipysurus tenuis*, *Amphiesma beddome*, *Amphiesma craspedogaster*, *Amphiesma flavifrons*, *Amphiesma flavifrons*, *Amphiesma frenatum*, *Amphiesma modestum*, *Amphiesma octolineatum*, *Amphiesma sarawacense*, *Amphiesma venningi*, *Amphiesma vibakari*,

*Amphisima stolatum*, *Anilius scytale*, *Astrotia stokesii*, *Atractus elaps*, *Atrretium schistosum*, *Bitia hydroides*, *Bothrophthalmus lineatus*, *Boulengerina annulata*, *Boulengerina christyi*, *Brachyorrhos albus*, *Bungarus caeruleus*, *Calamaria limbricoidae*, *Cantoria violacea*, *Causus bilineatus*, *Cerberus australis*, *Cerberus microlepis*, *Cerberus rynchops*, *Charina bottae*, *Coelognathus radiate*, *Coluber rhodorachis*, *Coniophanes bipunctatus*, *Crotaphopeltis barotseensis*, *Crotaphopeltis degeni*, *Crotaphopeltis hippocrepis*, *Crotaphopeltis hotamboeia*, *Cylindrophis ruffus*, *Dasyplectis scabra*, *Dinodon rufozonatum*, *Dipsadoboa unicolor*, *Disteria kingie*, *Disteria majori*, *Disteria nigrocincta*, *Djokoiskandarum annulata*, *Drymarchon corais*, *Drymobius margaritiferus*, *Elaphe dione*, *Emydocephalus annulatus*, *Emydocephalus ijimae*, *Enhydrina schistosa*, *Enhydris albomaculata*, *Enhydris alternans*, *Enhydris bennettii*, *Enhydris bocourti*, *Enhydris chanardi*, *Enhydris chinensis*, *Enhydris doriae*, *Enhydris dussumierii*, *Enhydris enhydris*, *Enhydris gyii*, *Enhydris indica*, *Enhydris innominata*, *Enhydris jagorii*, *Enhydris longicauda*, *Enhydris maculosa*, *Enhydris matannensis*, *Enhydris pahangensis*, *Enhydris pakistanica*, *Enhydris plumbea*, *Enhydris polylepis*, *Enhydris punctata*, *Enhydris sieboldii*, *Enhydris subtaeniata*, *Enhydris vorisi*, *Ephalophis greyi*, *Erpeton tentaculatus*, *Eunectes beniensis*, *Eunectes deschauenseei*, *Eunectes murinus*, *Eunectes notaeus*, *Farancia abacura*, *Farancia erythrogramma*, *Fordonia leucobalia*, *Gerarda prevostiana*, *Grayia Caesar*, *Grayia ornata*, *Grayia smythii*, *Grayia tholoni*, *Helicops angulatus*, *Helicops carinicaudus*, *Helicops danieli*, *Helicops hagmanni*, *Helicops infrataeniatus*, *Helicops leopardinus*, *Helicops pastazae*, *Helicops polylepis*, *Helicops scalaris*, *Hemiaspis signata*, *Heurnia ventromaculata*, *Homalopsis buccata*, *Homalopsis nigroventralis*, *Hydrablades periops*, *Hydrablades praefrontalis*, *Hydraethiops melanogaster*, *Hydrelaps darwiniensis*, *Hydrodynastes bicinctus*, *Hydrodynastes gigas*, *Hydromorphus concolor*, *Hydrophis atriceps*, *Hydrophis belcheri*, *Hydrophis bituberculatus*, *Hydrophis brookii*, *Hydrophis caerulescens*, *Hydrophis cantoris*, *Hydrophis cyanocinctus*, *Hydrophis elegans*, *Hydrophis fasciatus*, *Hydrophis gracilis*, *Hydrophis klossi*, *Hydrophis nigrocinctus*, *Hydrophis obscurus*, *Hydrophis ornatus*, *Hydrophis spiralis*, *Hydrophis stricticollis*, *Hydrophis torquatus*, *Hydrops martii*, *Hydrops triangularis*, *Kerilia jerdonii*, *Kolpophis annandalei*, *Lamprophis aurora*, *Lapemis curtus*, *Laticauda colubrina*, *Laticauda laticaudata*, *Leptodeira annulata*, *Limnophis bicolor*, *Liophis*

*cobella*, *Lycodonomorphus bicolor*, *Lycodonomorphus laevisimus*, *Lycodonomorphus leleupi*, *Lycodonomorphus rufulus*, *Lycodonomorphus whytii*, *Macrelaps microlepidotus*, *Macropisthodon flaviceps*, *Micrurus surinamensis*, *Myron richardsonii*, *Naja melanoleuca*, *Naja naja*, *Natriciteres olivacea*, *Natriciteres variegata*, *Natrix maura*, *Natrix megaloccephala*, *Natrix natrix*, *Natrix tessellatus*, *Neelaps calonotus*, *Nerodia clarkii*, *Nerodia compressicauda*, *Nerodia cyclopion*, *Nerodia erythrogaster*, *Nerodia fasciata*, *Nerodia floridana*, *Nerodia harteri*, *Nerodia rhombifera*, *Nerodia sipedon*, *Nerodia taxispilota*, *Notechis ater*, *Notechis scutatus*, *Oocatochus rufodorsata*, *Opisthotropis alcalai*, *Opisthotropis andersonii*, *Opisthotropis balteatus*, *Opisthotropis boonsongi*, *Opisthotropis cheni*, *Opisthotropis daovantieni*, *Opisthotropis Jacobi*, *Opisthotropis kikuzatoi*, *Opisthotropis kuatunensis*, *Opisthotropis lateralis*, *Opisthotropis latouchii*, *Opisthotropis maculosus*, *Opisthotropis maxwelli*, *Opisthotropis rugosus*, *Opisthotropis spenceri*, *Opisthotropis typicus*, *Parahelicops annamensis*, *Parahydrophis mertoni*, *Paratapinophis praemaxillaris*, *Pelamis platurus*, *Philothamnus angolensis*, *Praescutata viperine*, *Psammodynastes pictus*, *Psammodynastes pulverulentus*, *Psammophis lineatus*, *Pseudoeryx plicatilis*, *Ptyas fuscus*, *Rabdops olivacea*, *Regina (Liodytes) alleni*, *Regina grahamii*, *Regina (Liodytes) rigida*, *Regina septemvitta*, *Rhabdophis chrysargos*, *Rhabdophis murudensis*, *Rhabdophis subminiatus*, *Rhabdophis tigrinus*, *Lake Towuti homalopsid*, *Seminatrix pygaea*, *Sinonatrix aequifasciata*, *Sinonatrix annularis*, *Sinonatrix percarinata*, *Sordellina punctata*, *Stegonotus cucullatus*, *Stegonotus parvus*, *Stoliczkaia borneensis*, *Thalassophis anomalus*, *Thamnophis atratus*, *Thamnophis brachystoma*, *Thamnophis butleri*, *Thamnophis chrysocephalus*, *Thamnophis couchii*, *Thamnophis cyrtopsis*, *Thamnophis elegans*, *Thamnophis eques*, *Thamnophis gigas*, *Thamnophis hammondii*, *Thamnophis marciannus*, *Thamnophis melanogaster*, *Thamnophis ordinoides*, *Thamnophis proximus*, *Thamnophis radix*, *Thamnophis rufipunctatus*, *Thamnophis sauritus*, *Thamnophis sirtalis*, *Thamnophis validus*, *Tretanorhinus lateralis*, *Tretanorhinus mocquardi*, *Tretanorhinus nigroluteus*, *Tretanorhinus taeniatus*, *Tropidechis carinatus*, *Tropidonophis mairii*, *Uropeltis ocellatus*, *Vermicella annulata*, *Vipera ursinii*, *Xenelaphis ellipsifer*, *Xenochrophis melanzostus*, *Xenochrophis piscator*, *Xenodermis javanicus*, *Xenopeltis hainanensis*, *Xenopeltis unicolor*.