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Global diversity of snakes (Serpentes; Reptilia) in freshwater

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Abstract A list of the snake species inhabiting freshwaters is provided. It includes 153 species, which represents about 5% of all known snakes. These freshwater snakes belong to 44 genera distributed among the families Acrochordidae, Boidae, Colubridae, Elapidae, Homalopsidae and Viperidae. The highest diversities in freshwater snakes are found in the Oriental (64 species) and Neotropical (39 species) Regions. Conservation actions are needed for several overcollected species with a limited distribution.

Keywords Snakes · Serpentes · Freshwater · Biodiversity

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Introduction

With about 3000 species known so far, snakes are a successful group of predatory vertebrates that occupy a wide range of environments in tropical and temperate areas, from deserts and mountain summits to oceans. Many snake species live close to water and often venture into it; probably all can swim, but only a limited number can be considered strictly aquatic. One can regard the truly aquatic snakes as those foraging in water and which are unable to survive without aquatic prey and frequent to constant submersion. Subtle external anatomical characters betray aquatic habits in freshwater snakes. These morphological specializations include position of nostrils on the snout top, allowing the snake to breath at the surface without being seen by birds and other predators; a banded pattern, useful for camouflage; valvular nostrils; dorsolaterally oriented eyes; keeled scales; etc. However none of these characters are common to all freshwater snakes, and some of these characters, like a banded pattern, are shared with many strictly terrestrial as well as with many exclusively marine species. Many freshwater species

belong to genera also including marine or terrestrial species. Only the combination of morphology and natural history data can reveal if a species is a freshwater dweller, and much work remains to be done in these fields. Hereafter we briefly present the results of a thorough study of the literature and our experience in the field to provide a list as accurate as possible of the freshwater snakes of the World. The list must be regarded as provisional, since biological information which could confirm freshwater habits is lacking for many genera and species (Fig. 1).

Species diversity and distribution

Details on freshwater snake systematics, distribution and natural history are to be found in the works of, a.o., Anonymous (no date) (World), Boulenger (1913) (Palaearctic), Manthey & Grossmann (1997), Pauwels et al. (2001), Cogger et al. (1987), Murphy & Voris (2005), Vogel et al. (2004), Voris et al. (2002) (Australasian and Oriental), do Amaral (1978), Cei (1993) and Roze (1996) (Nearctic and Neotropical). Familial and subfamilial allocations of colubroid genera mostly follow Lawson et al. (2005) (Fig. 2).

Australasian Region

Among the most specialized aquatic snakes are the acrochordids, containing three species found in brackish and/or freshwater. Their morphological adaptations towards aquatic life are so radical (a.o. absence of enlarged ventral scales) that these snakes are unadapted for terrestrial locomotion. One freshwater *Acrochordus* species (*A. arafurae*) lives in the Australasian Region. *Laticauda crockeri*, endemic to Rennell Island (Solomon Archipelago), is the only known freshwater member of this marine elapid genus. The freshwaters of the region are also home to four homalopsid snakes: *Enhydris polylepis*, *Cantoria annulata*, *Cerberus rynchops* and *Heurnia ventromaculata*. The Australasian Region shares one freshwater snake species with the Oriental Region: *Cerberus rynchops*, which actually mainly lives in brackish and sea water. The Australasian freshwater snake diversity is as poor as that of the Palearctic Region, and about nine times less rich than that of the neighbouring Oriental Region.

Afrotropical Region

Relatively few aquatic snakes live in the Afrotropical Region's continental waters. They are distributed among the families Colubridae and Elapidae. Several genera are specialized towards aquatic life and contain exclusively freshwater species: *Afronatrix*, *Grayia* (*sensu lato*, including *Xenurophis*), *Helophis*, *Hydraethiops* (including two species, one, *H. laevis*, being known so far by only three specimens) and *Limnophis* (Colubridae), *Boulengerina* and *Lycodonomorphus* (including a.o. *L. bicolor*, endemic to Lake Tanganyika) (Elapidae). Madagascar houses only two freshwater species, both endemic to the island, *Liopholidophis lateralis* and *L. sexlineatus*. It is interesting to note the extreme colour and habitus

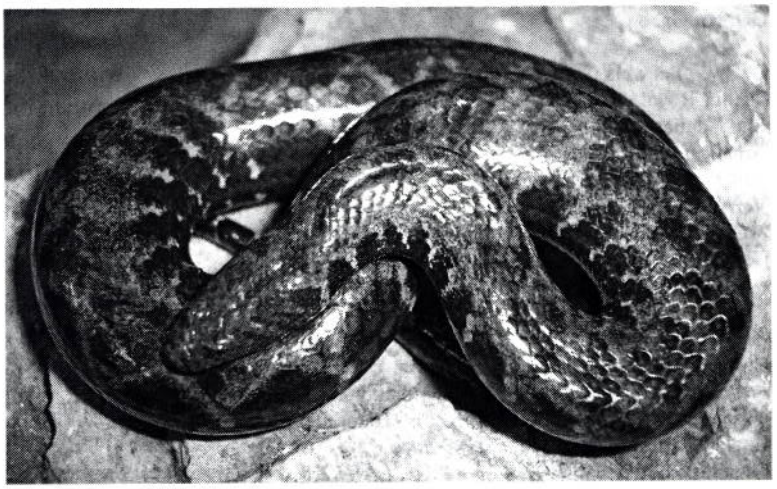

Fig. 1 *Enhydris jagori* (photo credit: Olivier S.G. Pauwels)

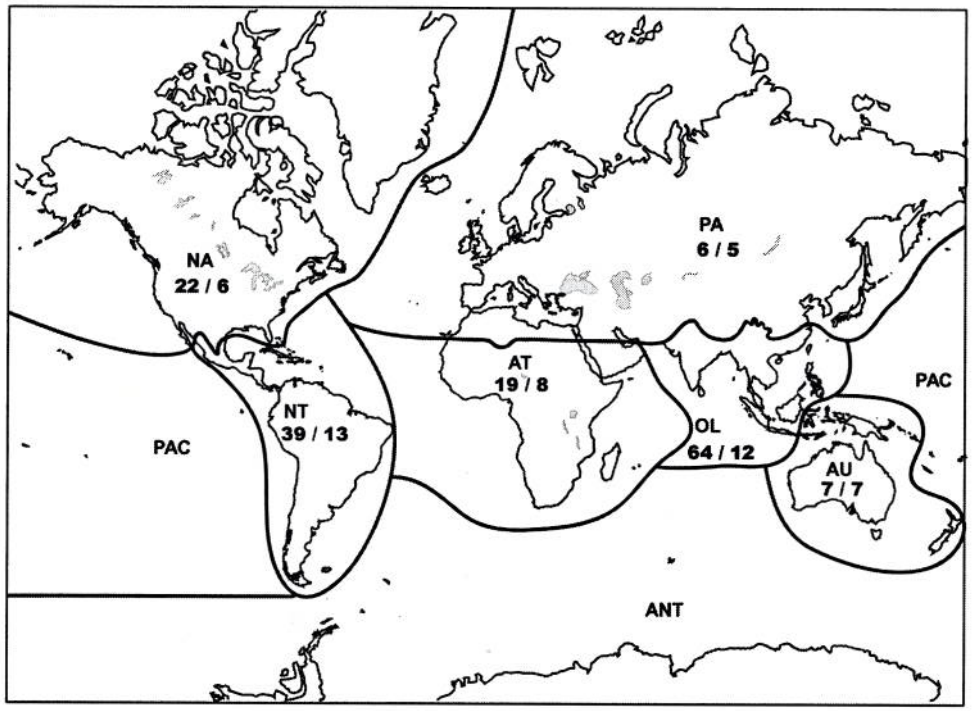

Fig. 2 Distribution of freshwater snake species and genera per biogeographic region (species number/genus number). PA: Palaearctic Region, NA: Nearctic Region, NT: Neotropical Region, AT: Afrotropical Region, OL: Oriental Region, AU: Australasian Region, PAC: Pacific Region and oceanic islands, ANT: Antartic Region

resemblance between the harmless *Grayia ornata* and the *Boulengerina* cobras, with which they share most of their distribution. In contrast with the Australasian Region, Afrotropical brackish waters do not house any specialized mangrove-dwelling species, although mangroves are widespread there. Besides the strictly freshwater Afrotropical taxa, a number of mostly terrestrial snakes use aquatic systems as hunting fields, at least occasionally, including: *Dromophis lineatus*, *Natriciteres* spp. (Colubridae), *Naja* spp., *Pseudohaje goldii* (Elapidae) and *Python* spp. (Pythonidae). None of the Afrotropical freshwater snake species is shared with another Region.

Nearctic Region

Nearctic freshwater snakes belong to the Colubridae, Elapidae and Viperidae. The colubrid genera *Farancia*, *Nerodia*, *Regina* and *Seminatrix* include only freshwater dwellers. The natricine genus *Thamnophis* includes 34 species, of which only four are freshwater dwellers. The Nearctic Region is home to a single venomous freshwater species, the pitviper *Agkistrodon piscivorus*. No Nearctic aquatic species is shared with the Neotropical Region. The diversity is relatively low and comparable to that of the Afrotropical Region.

Neotropical Region

The most remarkable Neotropical freshwater snakes are the anacondas (Boidae: *Eunectes* spp.), with *E. murinus* being one of the world's longest snakes, with official records of specimens above 8 m long. The venomous New World elapid genus *Micrurus* includes 70 species; a single species (*M. surinamensis*) being aquatic. All other Neotropical freshwater snakes belong to 11 xenodontine colubrid genera. Some of these genera exclusively contain aquatic species (e.g., *Helicops*); in others aquatic species are the exception (e.g., *Echinanthera*). None of the New World freshwater snake species is shared with the Old World. The Neotropical freshwater snake diversity is the world's second highest, although still much lower than the Oriental one.

Oriental Region

Among the two acrochordids inhabiting the Oriental Region, only *Acrochordus javanicus* penetrates freshwaters. The genus *Hydrablabes* is composed of two freshwater species, both endemic to Borneo. The genera *Opisthotropis* and *Parahelicops*, sometimes considered to be synonymous but here regarded as two distinct genera, comprise a total of 16 species from the Oriental Region, and one (*O. kikuzatoi*) from Japan. Many are restricted to unpolluted fast streams in undisturbed montane forest. All four *Sinonatrix* species, a genus endemic to the Oriental Region, are living in freshwater. The genus *Xenochrophis* includes 11 species, all freshwater dwellers and belonging to the Oriental Region, except one, *X. vittatus*, whose distribution extends east to Sulawesi, and is thus shared with the Australasian Region. Besides sea snakes, the most aquatic snakes are the Homalopsidae, which include 10 genera and 33 species, living in sea, mangroves or freshwater. They are mainly distributed in the Oriental Region, but some inhabit the Australasian Region. *Enhydris pakistanica* occurs at the limit between the Oriental and the Palaearctic Regions. Only one of the two known *Cerberus* inhabits freshwaters, and this species (*C. microlepis*) is endemic to Lake Buhi, Luzon, Philippine Islands. The most morphologically peculiar homalopsid is the genus *Erpeton*, characterized by two soft nasal appendices, the role of which is still unclear. The marine elapid snake *Hydrophis torquatus diadema* often penetrates into Tonle Sap Lake in Cambodia (Ineich, 1996). The "sea snake" *Hydrophis semperi* seems endemic to the freshwater lake Taal in the Philippines. *Hydrophis sibauensis* is known from Sibau River in Borneo. No information on the biology of the monotypic genera *Anoplohydrus*, *Fimbrios* and *Iguanognathus* (Colubridae; future morphological studies might attribute *Anoplohydrus* to homalopsids) are currently available, which would allow to list them with certainty among the freshwater snakes.

Palaearctic Region

In Europe, only two strictly aquatic snakes occur, both being harmless colubrids: *Natrix maura*, found in Europe and north Africa, and *N. tessellata*, which has a wide Eurasian distribution. Besides the latter species, Palaearctic Asia is home to four other natricine freshwater snakes. Two of them (*Sinonatrix annularis* and *Xenochrophis piscator* [including *X. sanctijohannis*]) are shared with the Oriental Region. The distributions of some of the species of *Opisthotropis* extend to the limits between the Oriental and the Palaearctic Regions. None of the Palaearctic freshwater species or genera are shared with the Afrotropical Region.

A total of 153 freshwater snake species, i.e., *circa* 5% of all currently known snakes, is found in the Australasian, Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions (see Table 1). No snakes are known from the Antarctic Region. The most specialized species towards aquatic life are the elapid sea snakes, of which two genera contain species living in freshwater, and Homalopsidae. All homalopsids show strong morphological adaptations to aquatic life (all notably have dorsolaterally oriented eyes and valvular nostrils) and contain marine as well as brackish and freshwater species. Most of the remaining freshwater snakes belong to the colubrid Natricinae and Xenodontinae, but these subfamilies contain terrestrial as well as freshwater species. Freshwater snakes are found in various groups in six families: Acrochordidae, Boidae, Colubridae, Elapidae, Homalopsidae and Viperidae. Except the Acrochordidae and Homalopsidae, no freshwater species belong to strictly aquatic snake families. Among the 44 genera including freshwater species, 13 (29.5%) include non-freshwater species, i.e. terrestrial or marine (compare total number of species in each genus *versus* number of freshwater species per Region in Table 1).

Human related issues

Few works on freshwater snake–human interactions are available, but field studies might reveal locally important links. For instance, some homalopsids are intensively collected for food or skin trade, as is happening in Tonle Sap Lake in Cambodia, where they are also used to feed crocodiles in neighbouring breeding farms; this overcollection notably puts at risk *Enhydris longicauda*, endemic to the lake (Stuart et al., 2000). In China, snakes like *Sinonatrix annularis*, some *Enhydris* spp. and *Homalopsis* are sold in large numbers in food markets and restaurants (Zhou & Jiang, 2005). Fuchs & Fuchs (2003) documented the

Table 1 Global distribution of freshwater snake species per Region

Taxa/Region	PA	NA	NT	AT	OL	AU	WORLD
ACROCHORDIDAE							
Acrochordus (3)					1	1	2
BOIDAE							
Boinae							
Eunectes (4)			4				4
COLUBRIDAE							
Colubrinae							
Grayia (4)				4			4
Natricinae							
Afronatrix (1)				1			1
Atretium (2)					2		2
Hydrablabes (2)					2		2
Hydraethiops (2)				2			2
Limnophis (1)				1			1
Natrix (4)	2						2
Nerodia (10)		10					10
Opisthotropis (15)	1				14		15
Parahelicops (2)					2		2
Regina (4)		4					4
Seminatrix (1)		1					1
Sinonatrix (4)	1				4		4
Thamnophis (34)		4					4
Xenochrophis (11)	1				11	1	11
Pseudoxyrhophiinae							
Liopholidophis (9)				2			2
Xenodontinae							
Coniophanes (12)			1				1
Echinanthera (6)			1				1
Farancia (2)		2					2
Gomesophis (1)			1				1
Helicops (17)			17				17
Helophis (1)				1			1
Hydrodynastes (2)			2				2
Hydromorphus (2)			2				2
Hydrops (3)			3				3
Liophis (44)			1				1
Pseudoeryx (1)			1				1
Sordellina (1)			1				1
Tetranorhinus (4)			4				4
Thermophis (1)	1						1
ELAPIDAE							
Boodontinae							
Lycodonomorphus (6)				6			6
Elapinae							
Boulengerina (2)				2			2

Table 1 continued

Taxa/Region	PA	NA	NT	AT	OL	AU	WORLD
Micrurus (70)			1				1
Hydrophiinae							
Hydrophis (29)					3		3
Laticauda (7)						1	1
HOMALOPSIDAE							
Cantoria (2)						1	1
Cerberus (2)					1	1	1
Enhydris (23)					22	1	23
Erpeton (1)					1		1
Heurnia (1)						1	1
Homalopsis (1)					1		1
VIPERIDAE							
Crotalinae							
Agkistrodon (4)		1					1
Total species	6	22	39	19	64	7	153
Total genera	5	6	13	8	12	7	44

Genera are followed between brackets by the total number of species they contain. Brackish and sea water species are considered if they also tolerate pure freshwater. PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical ; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic

use in leather trade of not less than ten freshwater snake species. In western central Africa, *Grayia ornata* plays an important role in local culture, food, traditional medicine and magic (Pauwels et al., 2002). Besides local overcollecting, the main threats to conservation might come from intensive logging and freshwater habitat degradation. Field studies on the most localized species (e.g., some *Enhydris* spp.) would be necessary to evaluate specific threats. Most freshwater snakes are harmless, but some are poisonous among the Elapidae, Homalopsidae and Viperidae. *Boulengerina* venoms have not been studied so far, and there thus exists no specific antivenom, although the venom might have a strong neurotoxic action (Spawls & Branch, 1995), like *Micrurus surinamensis*, *Hydrophis* spp. and *Laticauda* spp. Although venomous, Homalopsidae are rear-fanged and do not represent a medical problem; none is deadly. *Agkistrodon piscivorus*'s bite is potentially lethal to humans.

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