

Global diversity of crocodiles (Crocodylia, Reptilia) in freshwater

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Abstract Living crocodilians include the 24 species of alligators, caimans, crocodiles and gharials. These large semi-aquatic ambush predators are ubiquitous in freshwater ecosystems throughout the world's tropics and warm temperate regions. Extant crocodilian diversity is low, but the group has a rich fossil record in every continental deposit. Most populations suffered from over-hunting and habitat loss during the twentieth century and even though some species remain critically endangered others are real success stories in conservation biology and have become important economic resources.

Keywords Crocodile · Alligator · Gharial · Archosauria

Introduction

The living crocodilians belong to the order Crocodylia which is now represented by three families: the Crocodylidae, the Alligatoridae and the Gavialidae (Brochu, 2003). The 24 species of the group are all-amphibious and share morphological, anatomical,

and physiological features, which make them more adapted to water than to land (Lang, 1976).

They all live in tropical and subtropical areas in various aquatic habitats (forest streams, rivers, marshes, swamps, elbow lakes, etc.) and can be considered as the largest fresh water dwellers. They can occasionally adapt to salty waters (mangroves or estuaries) (Dunson, 1982; Mazzotti & Dunson, 1984). They are nocturnal carnivorous opportunistic predators, whose diet depends on their developmental stage, species and potential prey diversity (Magnusson et al., 1987). All crocodilian species may be considered as totally water dependent since they can only mate in water. Crocodilians appear to be very important for freshwater ecosystems as they maintain, during the dry season waterholes that are used as reservoir for many arthropods, crustacean, fishes and amphibians (Gans, 1989; Kushlan, 1974).

Species/generic diversity

With only 24 living species, the order Crocodylia is the smallest taxonomic group of the class Reptilia. The three families, Crocodylidae, Alligatoridae and Gavialidae are quite homogeneous taxa as they contain between two and four genera.

The highest level of species diversity is to be found in the genus *Crocodylus* which gathers 13 species, whereas other genera only display one or two species.

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The taxonomic place of *Tomistoma schlegelii* is also subject to debate among specialists. It used to be placed with the subfamily Crocodylinae, whereas other created the subfamily Tomistominae. Based on morphological features and on the latest DNA studies, we chose to place them together with *Gavialis* in the subfamily Gavialinae (Groombridge, 1987; Gatsby & Amato, 1992; Brochu, 2003). (Tables 1, 2)

Phylogeny and historical processes

Crocodilians belong to the great group of archosaurs which includes two extinct clades: the pterosaurs and the dinosaurs (Blake, 1982). The history of the crocodilians has been well reviewed by Buffetaud (1982), Taplin (1984), Taplin & Grigg (1989) and Brochu (2003). The very first crocodilians called Protosuchians are from the early Jurassic, whereas the Eusuchians (the modern crocodilians) appeared in the upper Triassic around 220 Million years ago under the form of terrestrial carnivores gathered in the group of Pristichampsines. The eight surviving genera of crocodilians are only a tiny rest of the past diversity of the group which has been revealed by at least 150 fossile genera (Brochu, 2003). The crocodilian diversity showed two peaks—one in the early Eocene and the other one in the early Miocene (Taplin, 1984; Markewick 1998). These fossils suggest that crocodyliomorphs were adapted to terrestrial, sub-aquatic, and even to marine environment (cf. Thalattosuchians). Until the end of the Tertiary, the geographical distribution of the crocodilians was much broader. The more restricted current distribution is due to the climatic deterioration, which

Table 1 Freshwater crocodilian species in the zoogeographical regions

	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Alligatoridae	0	1	0	5	1	0	0	0	7
Crocodylidae	2	1	3	4	5	4	0	0	14
Gavialidae	1	0	0	0	2	0	0	0	2
Total	3	2	3	9	8	4	0	0	

PA: Palaeartic, NA: Nearctic, NT: Neotropical, AT: Afrotrropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

Table 2 Freshwater crocodilian genera in the zoogeographical regions

	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Alligatoridae	0	1	0	3	1	0	0	0	4
Crocodylidae	1	1	2	1	1	1	0	0	2
Gavialidae	1	0	0	0	2	0	0	0	2
Total	2	2	2	4	4	1	0	0	8

PA: Palaeartic, NA: Nearctic, NT: Neotropical, AT: Afrotrropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

narrowed the tropical and subtropical zones (Markewick, 1998).

Present distribution and main areas of endemicity (Groombridge, 1987; Ross 1998)

Except the two *Alligator* species which are to some extend more tolerant to colder temperatures, crocodilians are distributed in inter-tropical wetlands. As shown in Table 3, most crocodilians are endemic of a zoogeographical region. Only three species of the genus *Crocodylus* (*C. niloticus*, *C. porosus* and *C. siamensis*) and a gavialid (*Gavialis gangeticus*) are found in two adjacent regions. The range of distribution of crocodilians can be very variable in size. Some species, such as the Nile crocodile (*Crocodylus niloticus*) in Africa, the saltwater crocodile, (*Crocodylus porosus*) in the indopacific region or the spectacled caiman (*Caiman crocodilus crocodilus*) in South America are widely represented at a continental level, whereas most species are living in more restricted areas. This is one of the reasons that today half of the existing crocodilian species are considered either as being endangered or threatened according to the Red List criteria of the World Conservation Union IUCN. The Chinese alligator (*Alligator sinensis*), the Siamese crocodile (*Crocodylus siamensis*), the Orinoco crocodile (*Crocodylus intermedius*) and the Philippine crocodile (*Crocodylus mindorensis*) may be considered as the most endangered crocodilians species. The first one is only found in a few spots along the lower part of Yangtze River with a remaining stronghold in the province of Anhui in People's Republic of China, the second one is restricted to five Asian countries (Cambodia, Thailand, Vietnam, Indonesia and Laos) with

Table 3 Distribution of the 24 crocodilian species in the eight zoogeographical regions

Family	Genus	Species	Sub species	Distribution region	Common name, IUCN red list
Alligatoridae (4 genera, 7 species)	<i>Alligator</i>	<i>A. mississippiensis</i>		Nearctic	American alligator/LR
		<i>A. sinensis</i>		Oriental	Chinese alligator/CR
	<i>Caiman</i>	<i>C. crocodilus</i>	<i>C. c. apaporiensis</i> , <i>C. c. crocodilus</i> , <i>C. c. fuscus</i>	Neotropical	Spectacled caiman/LR
			<i>C. c. yacare</i>		
		<i>C. latirostris</i>		Neotropical	Broad snouted caiman/LR
		<i>Melanosuchus</i>	<i>M. niger</i>	Neotropical	Black caiman/LR
	<i>Palaeosuchus</i>	<i>P. palpebrosus</i>		Neotropical	Cuvier's smooth fronted caiman/LR
			<i>P. trigonatus</i>	Neotropical	Schneider's smooth fronted caiman/LR
Crocodylidae (2 genera, 14 species)	<i>Crocodylus</i>	<i>C. acutus</i>		Nearctic; Neotropical	American crocodile/Vu
		<i>C. cataphractus</i>		Afrotropical	African slender snouted crocodile/DD
		<i>C. intermedius</i>		Neotropical	Orinoco crocodile/CR
		<i>C. johnsoni</i>		Australasia	Australian freshwater crocodile/LR
		<i>C. mindorensis</i>		Oriental	Philippines crocodile/CR
		<i>C. moreletii</i>		Neotropical	Morelet's crocodile/LR
		<i>C. novaeguineae</i>		Australasia	New guinea crocodile/LR
		<i>C. niloticus</i>		Palearctic, Afrotropical	Nile crocodile/LR
		<i>C. palustris</i>		Palearctic, Oriental	Marsh crocodile/LR
		<i>C. porosus</i>		Oriental, Australasia	Estuarine crocodile/LR
		<i>C. raninus</i>		Oriental	Borneo crocodile/DD
		<i>C. rhombifer</i>		Neotropical	Cuban crocodile/EN
		<i>C. siamensis</i>		Oriental, Australasia	Siamese crocodile/CR
	<i>Osteolaemus</i>	<i>O. tetraspis</i>	<i>O. t. tetraspis</i> & <i>O. t. osborni</i>	Afrotropical	African dwarf crocodile/ Vu
Gavialidae (2 genera, 2 species)	<i>Gavialis</i>	<i>G. gangeticus</i>		Palearctic, Oriental	Gharial/EN
	<i>Tomistoma</i>	<i>T. schlegelii</i>		Oriental	False gharial/EN

Four species CR (*Critically endangered*), three species E (*Endangered*), 14 species LR (*Low risks*), two species DD (*Data deficiency*)

scattered extremely small populations, the third one is restricted to the Orinoco water system of Venezuela and Colombia only and the fourth one is endemic to the archipelago of Philippines. The reasons for their being endangered are due to human pressure on habitat, but inversely linked to the adaptability to habitat variations. For instance the Nile crocodile is able to live in diverse aquatic environments such as streams, forest rivers, swamps, marshes, lagoons and even small desert water holes like a few known small populations lost in the Mauritanian Sahara (Pooley &

Gans, 1976; Shine et al., 2001). This species like many other Crocodylidae and Alligatoridae are able to walk long distances on dry land. When necessary during long periods of drought they are able to migrate to find new water spots. Other species such as the mugger crocodile (*Crocodylus palustris*) will dig burrows during the dry season to protect themselves from the sun and wait in the shade the next raining season (Rao, 1994). Other crocodilian species adapt at burrowing are *Alligator sinensis* and *Osteolaemus tetraspis*. According to IUCN criteria, out of 24

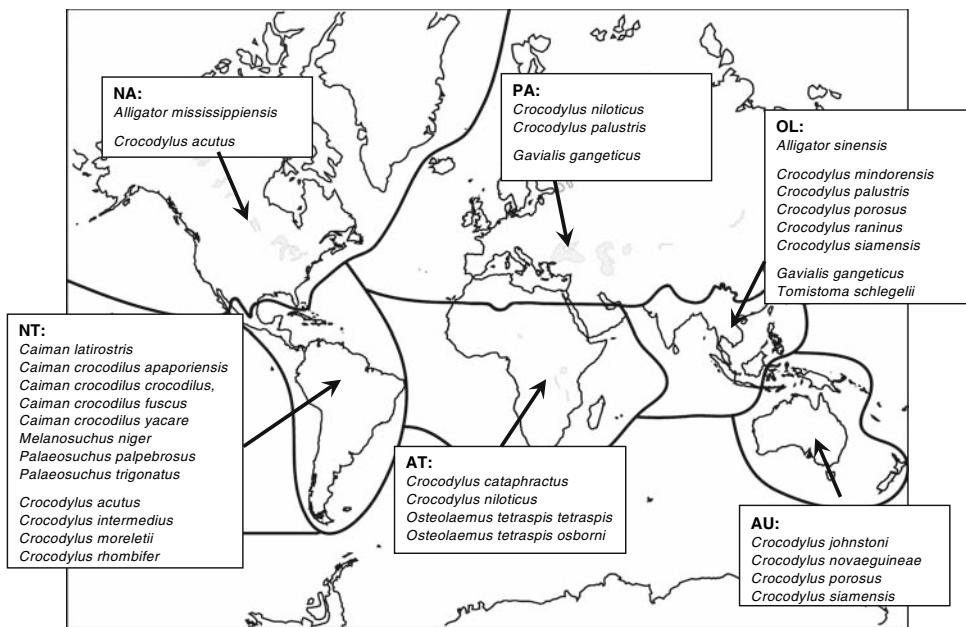


Fig. 1 Distribution of the 24 crocodilian species in the eight zoogeographical regions. PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

crocodilian species, four are critically endangered, three endangered and two species are considered as vulnerable (IUCN red list of threatened species, 2004) (Fig. 1).

Human related issues

Humans and crocodilians have been interacting since the dawn of civilization. Large crocodilians are potentially dangerous to man as they can prey on humans. Their populations have been depleted until the mid 60's because the high prices paid for their hides. In order to limit harvesting of wild populations, farming and ranching programs have been set up (Blake, 1982). Today several hundreds of farms around the world are breeding and raising crocodilians for leather and meat production (Brazaitis et al., 1998). Despite these efforts, some wild crocodilian populations are still depleting due to competition with humans for habitat and food. Dam construction on water streams has blocked seasonal migration of aquatic species when their prey was going down-stream during the rainy season and upstream when the water level lowers (Gans, 1989). The draining of swamps for agricultural purposes

has increased drastically habitat fragmentation and pollution. On a worldwide scale, the Crocodile Specialist Group of the I.U.C.N. Species Survival Commission coordinates crocodilian conservation programmes. The most successful ones are based on local community involvement combined with education (Ross, 1998).

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