1

Introduction

ON BECOMING AQUATIC

J. G. M. Thewissen and Sirpa Nummela

Vertebrate life became terrestrial about 370 million years ago when a lobe-finned fish evolved into the giant-salamander-like shape of a labyrinthodont amphibian. The transition is well documented in the fossil record, and important discoveries continue to fill out its details. Over the eons subsequent to the water-to-land transition, vertebrates became more and more independent from water. The new land vertebrates are called tetrapods, a group that includes modern amphibians, reptiles, birds, and mammals. The term refers to their extremities: the replacement of four paired fins by four paired legs. Amphibians still return to the water to avoid dehydration of their eggs and larvae and have skin that is permeable to water, restricting them to live in humid environments. With the origin of amniotes (reptiles, birds, and mammals) around 320 million years ago, the transition to land was complete: the embryo is protected from dehydration by being bathed in a fluid bubble surrounded by membranes. Moreover, amniote skin is covered by keratin, a waterproof protein that minimizes water loss through evaporation, allowing amniotes to live away from humidity. Dry land offered a host of opportunities and challenges to the newly terrestrial tetrapods.

In the period since the origin of tetrapod land life, many vertebrates have returned to the water. Some, such as crocodiles, became amphibious and never left these transitional habitats. Others, such as whales, returned to the oceans completely and are unable to live on land. In spite of their deep watery roots, these secondarily aquatic vertebrates started their evolutionary journey with bodies that were adapted to live on land and in air. Occasionally they evolved adaptations similar to those of their fish ancestors, such as the multirayed, multisegmented forelimbs of ichthyosaurs. In most cases, though, their amniote body plan was specialized and did not revert to its ancestral state. Most amniotes evolved solutions for the challenges of aquatic life that were different from those of their fishlike ancestors.

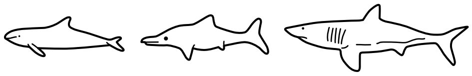

FIGURE 1.1. A cetacean, an ichthyosaur, and a shark. These animals are textbook examples of convergent evolution in locomotor and foraging behavior. However, their main sensory organs differ greatly: toothed whales (odontocete cetaceans) hunt mostly with their ears, ichthyosaurs with their eyes, and sharks with a combination of chemical, electric, and tactile senses.

NATURAL EXPERIMENTS

The entire range of secondarily aquatic tetrapods adapted to handle similar problems inflicted by their new environment. They commenced their journey to the water with different phylogenetic backgrounds and body plans. This makes becoming aquatic one of the greatest natural experiments: evolutionary hypotheses about specific adaptations can be tested in other aquatic groups that are not closely related phylogenetically. This book focuses on the aquatic adaptations in some of the most complex organ systems of a vertebrate's body, the sense organs. Though often not the first organ to change in the journey from land to water, most sense organs had to change pervasively to adapt to the new environment. In many cases, a clade that relied on one sense organ for gathering information about the outside world changed to another organ after entering the water. The origin of echolocation in toothed whales is an example of such a change. At other times, it was the dominant sense that was retained and improved in order to meet the challenges of living in water. Vision in penguins is an example of this phenomenon. Maybe most interestingly, vertebrates from varying phylogenetic backgrounds that are ecologically similar may have vastly different sensory specializations. For instance, toothed whales, sharks, and ichthyosaurs are all predators and are a classic example of adaptive convergence in body form and locomotor behavior: all have sleek and streamlined bodies and are fast pursuit predators (Fig. 1.1). Sensorywise, they could hardly be more different. Dolphins and porpoises use hearing as their main sense organ in locating prey, ichthyosaurs used vision, and in sharks mechanoreception, electroreception, and chemoreception are all important. The sense organs are excellent examples of natural experiments: they are complex and functionally well understood, most fossilize well, and there are well established procedures for experimenting with the senses in modern animals.

AQUATIC TETRAPODS

Vertebrates have become secondarily aquatic many times in their evolution. The timing of origin of the back-to-the-water events varied greatly among these forms, and Figure 1.2 summarizes the approximate time of the return to the water for some of the major clades, as well as the amount of time it took to become obligately aquatic. Figures 1.3 to 1.7 and Tables 1.1 to 1.4 summarize the phylogeny and diversity of the major groups of secondarily aquatic tetrapods, focusing on those animals that are discussed in the chapters of this book.

Amphibians (Fig. 1.3; Table 1.1) assume a special position in this book, because most of them never completely left the water, and they retained an aquatic larval stage. On the other hand, evolutionarily, modern amphibians are probably derived from a terrestrial ancestor, more terrestrial than most modern forms. In this volume, they are included for those sense organs that form a useful comparison to those of amniotes (such as chemical senses and hearing), but not when their sense organs resemble those of fishes and may represent a

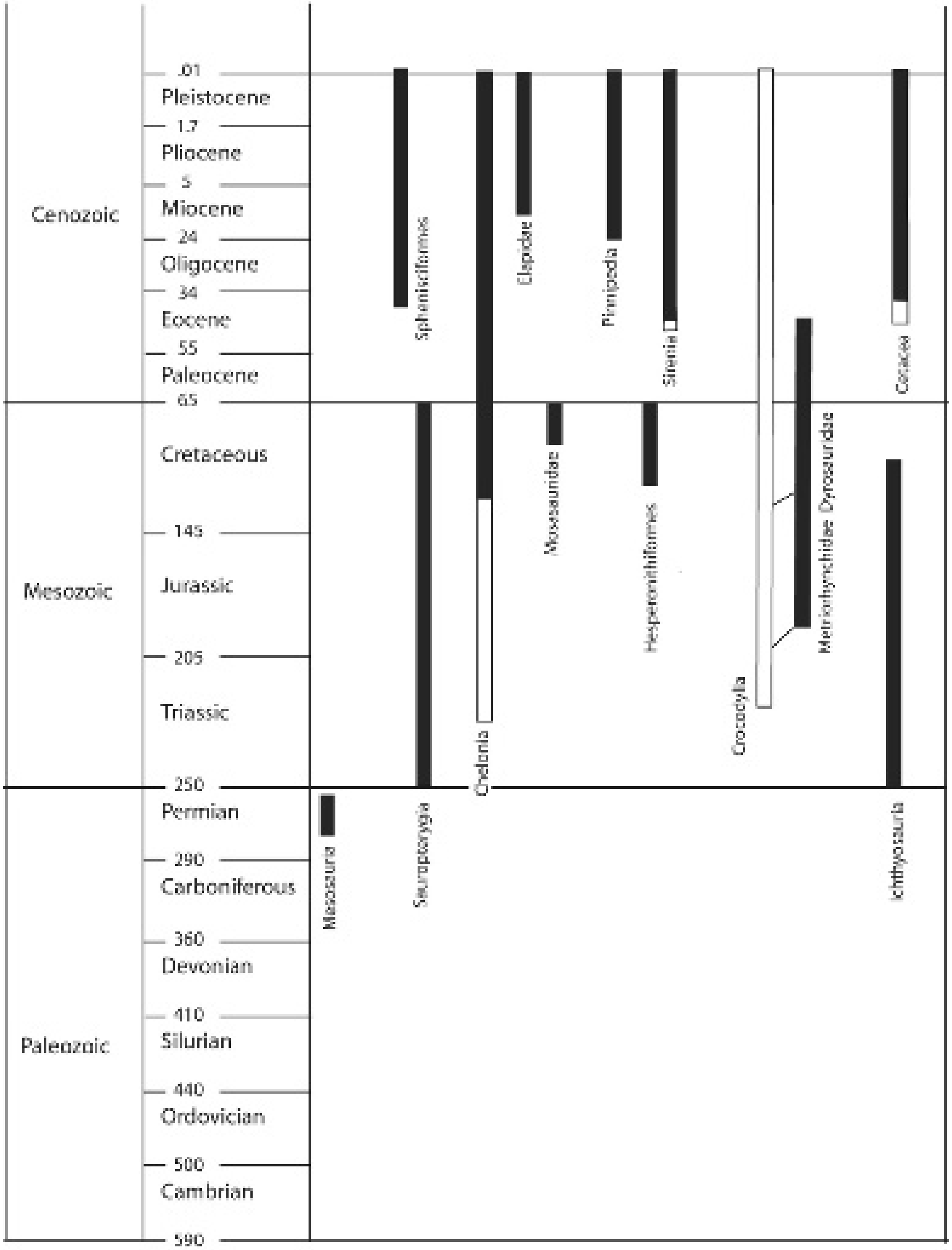

FIGURE 1.2. Temporal ranges of some important groups of aquatic tetrapods. *White bars* indicate that most members of a clade were transitional or amphibious, *black bars* indicate that the clade was mostly fully aquatic. Terms such as amphibious, semiaquatic, and transitional cannot be unambiguously defined, making figures such as this suggestive of a pattern rather than explicit statements.

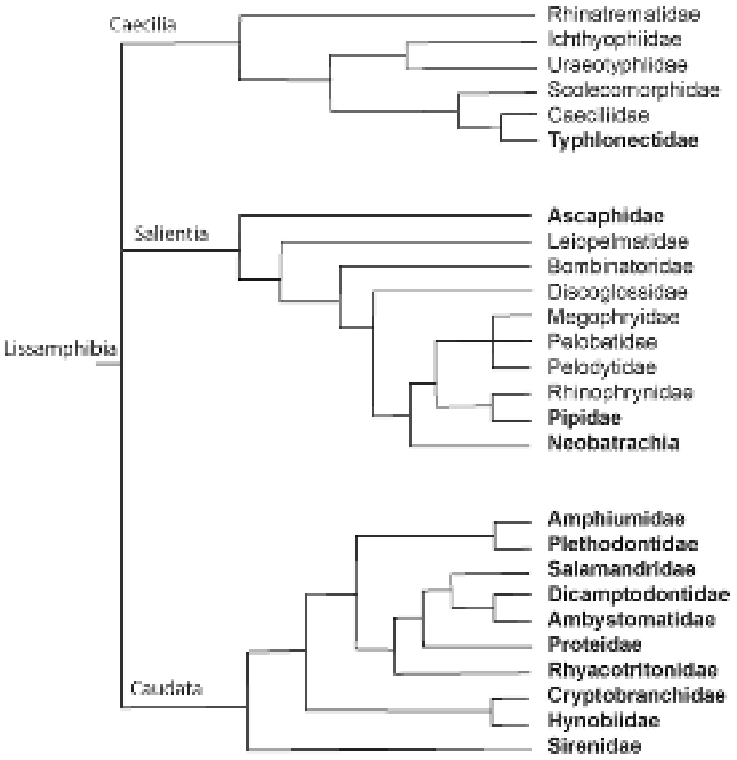

FIGURE 1.3. Generalized phylogeny of extant amphibians emphasizing taxa discussed in this volume. *Bold* indicates amphibians with aquatic adult stages. See Table 1.1 for details. By T. Hetherington.

primitive retention from a larval form (such as mechanoreception and balance).

SENSES IN EVOLUTION

Sensory biology is a large field positioned on the crossroads of neurobiology, physiology, and cell biology. Research in sensory biology is rich and multidisciplinary, and many questions about the basic function of the sense organs are asked and answered. However, evolutionary studies of the sense organs are less common. The reason for this is may be that most sensory scientists are not trained in evolution and most evolutionary scientists lack background in sensory systems. We believe that the senses offer a remarkable opportunity to study evolution in action, and we hope that this book will help in the cross-fertilization of evolutionary and sensory biology.

GOAL AND SCOPE

The purpose of this book is then to bring together basic information about the comparative evolutionary aspects of all the sense organs in secondarily aquatic tetrapods. For the sense organs that have been studied extensively from a comparative perspective, the focus has been on summarizing past research, whereas for sense organs that have received less attention, primary research is reported here. However, as editors, we felt strongly that this book should form a coherent work that covers all the basics, allowing those newly interested in sensory evolution to use it as a primer for boosting their background knowledge and as a sounding board for determining where new research would be most fruitful. We have encouraged authors to be explicit about where new research will answer important questions, as well as to boldly generalize evolutionary patterns, thus generating new hypotheses that

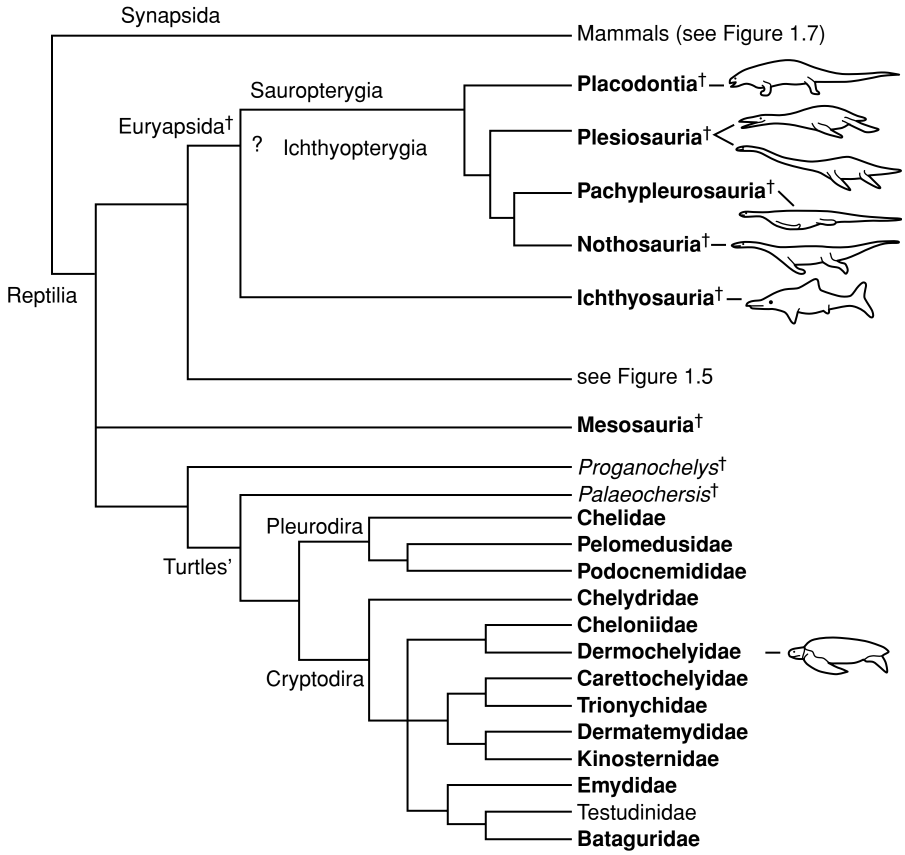

FIGURE 1.4. Generalized phylogeny of some reptiles (euryapsids and turtles) emphasizing taxa discussed in this volume. *Crosses* indicate extinct groups, *bold* indicates groups with aquatic representatives. See Table 1.2 for details. By Kurt Schwenk and J. G. M. Thewissen.

can be tested by future generations. We have also encouraged them to not get lost in details and jargon; this is a book for those interested in biology in the broadest sense of the word.

The sense organs can be understood only if their stimulus is understood, and the difference between stimuli in air and water is of great importance. For this reason, for most of the senses in this book, there is a chapter that discusses the difference between how they are stimulated in air and water.

Finally, it is our belief that all evolutionary studies need to be done against a systematic background, and we therefore have included simplified phylogenetic information in this chapter and have encouraged authors to propose daring hypotheses of sensory evolution in their chapters. These hypotheses are explicit and can therefore be tested relatively straightforwardly. The phylogenetic information in this chapter is condensed so that finding information about unfamiliar taxa does not distract from the central theme of the book: the sense organs as they move on either side of the threshold between land and water.

We will consider this volume a success if it is used by those sensory biologists who are interested in evolution, and by those evolutionary researchers that are interested in the senses. In addition, we hope that it will form the basis for much research in the future, facilitating the entry of young people into this field.

AMPHIBIANS

Thomas Hetherington and J. G. M. Thewissen

There are three modern groups of amphibians, often referred to as Lissamphibia (Fig. 1.3):

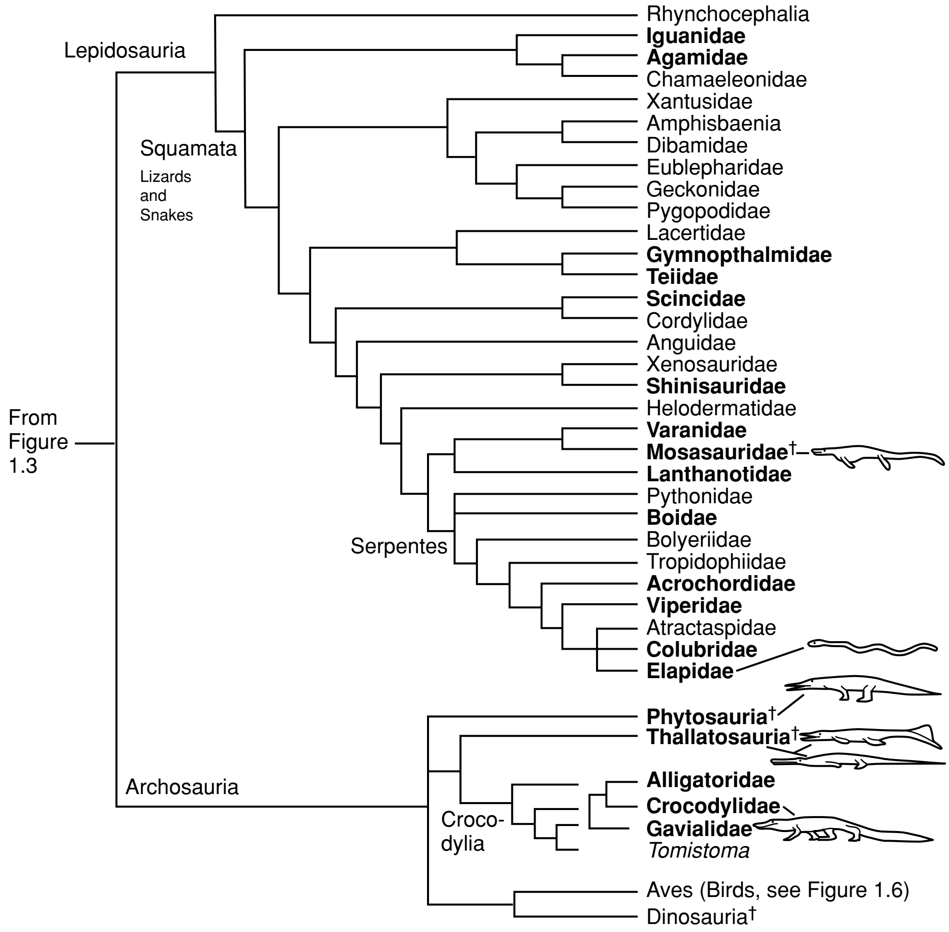

FIGURE 1.5. Generalized phylogeny of some reptiles (lepidosaurs and archosaurs excluding birds) emphasizing taxa discussed in this volume. *Crosses* indicate extinct groups, **bold** indicates groups with aquatic representatives. See Table 1.2 for details. By Kurt Schwenk and J. G. M. Thewissen.

Anura (toads and frogs), Caudata (or Salientia, salamanders and newts), and Gymnophiona (caecilians). All three of these have representatives whose adults are aquatic. During the Paleozoic Era tetrapods radiated into several lineages, many of which are called "amphibians" but are not closely related to the surviving modern amphibians (Lissamphibia). Lissamphibians usually are considered to form a monophyletic group (Trueb and Cloutier, 1991; Hedges and Maxson, 1993; Feller and Hedges, 1998). They are not closely related to the other surviving lineage of tetrapods, the amniotes. Lissamphibians and amniotes last shared a common ancestor more than 300 million years ago and possibly even arose independently from different fishlike ancestors.

Living amphibians and amniotes, therefore, do not share a long history of common terrestrial ancestors. Although the oldest fossil lissamphibians are late Triassic in age, lissamphibians likely share a common ancestor that lived more than 270 million years ago (Clack, 2002). The earliest lissamphibians lived in relatively dry environments and likely had terrestrial adult stages (Bolt, 1991), so it is appropriate to consider the more aquatic modern amphibians as secondarily aquatic. The first known largely aquatic representatives appeared approximately 200 million years ago.

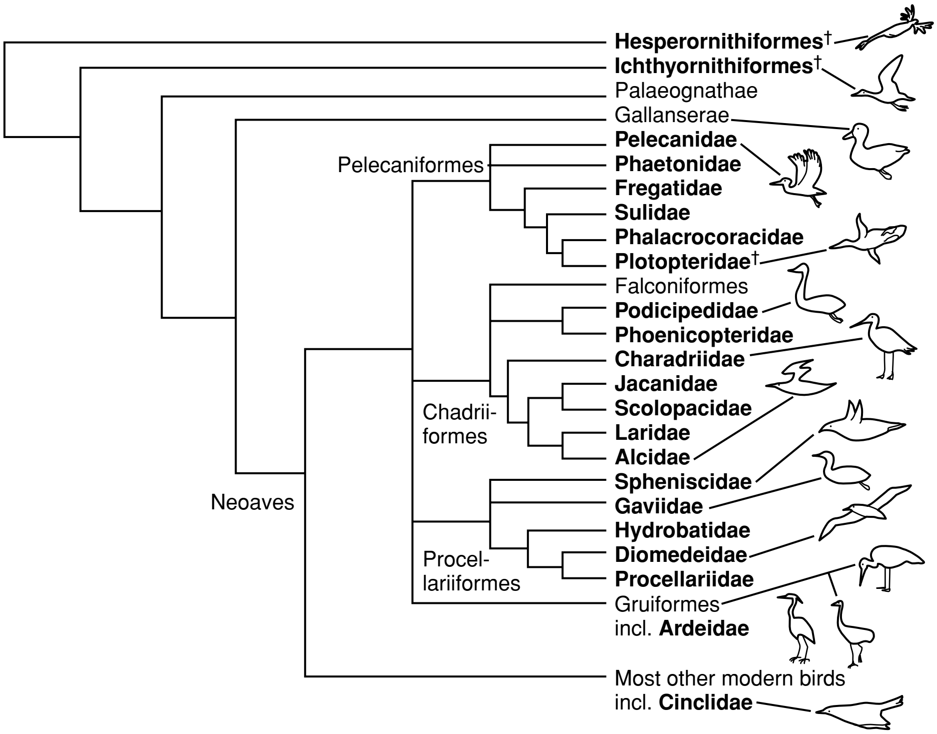

FIGURE 1.6. Generalized phylogeny of aquatic birds *(bold)* emphasizing taxa discussed in this volume. *Crosses* indicate extinct groups. See Table 1.3 for further details. By J. G. M. Thewissen and Tobin Hieronymus.

Most lissamphibians return to the water to lay eggs that hatch into aquatic larvae. Some amphibians, however, have no aquatic larval stage but rather lay terrestrial eggs that hatch into fully terrestrial juveniles. In many amphibians that have aquatic larval stages, the larvae usually metamorphose into more terrestrial forms, but in several taxa the adults remain completely or largely aquatic (Table 1.1). Except for a few species of frogs that live in brackish water (Duellman and Trueb, 1994), amphibians are restricted to freshwater habitats.

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AQUATIC AND SEMIAQUATIC REPTILES

Kurt Schwenk and J. G. M. Thewissen

The reptiles comprise a diverse and phylogenetically ancient group of amniote vertebrates (Figs. 1.4 and 1.5; Table 1.2). Reptiles are a paraphyletic group if birds are excluded. Phylogenetically,

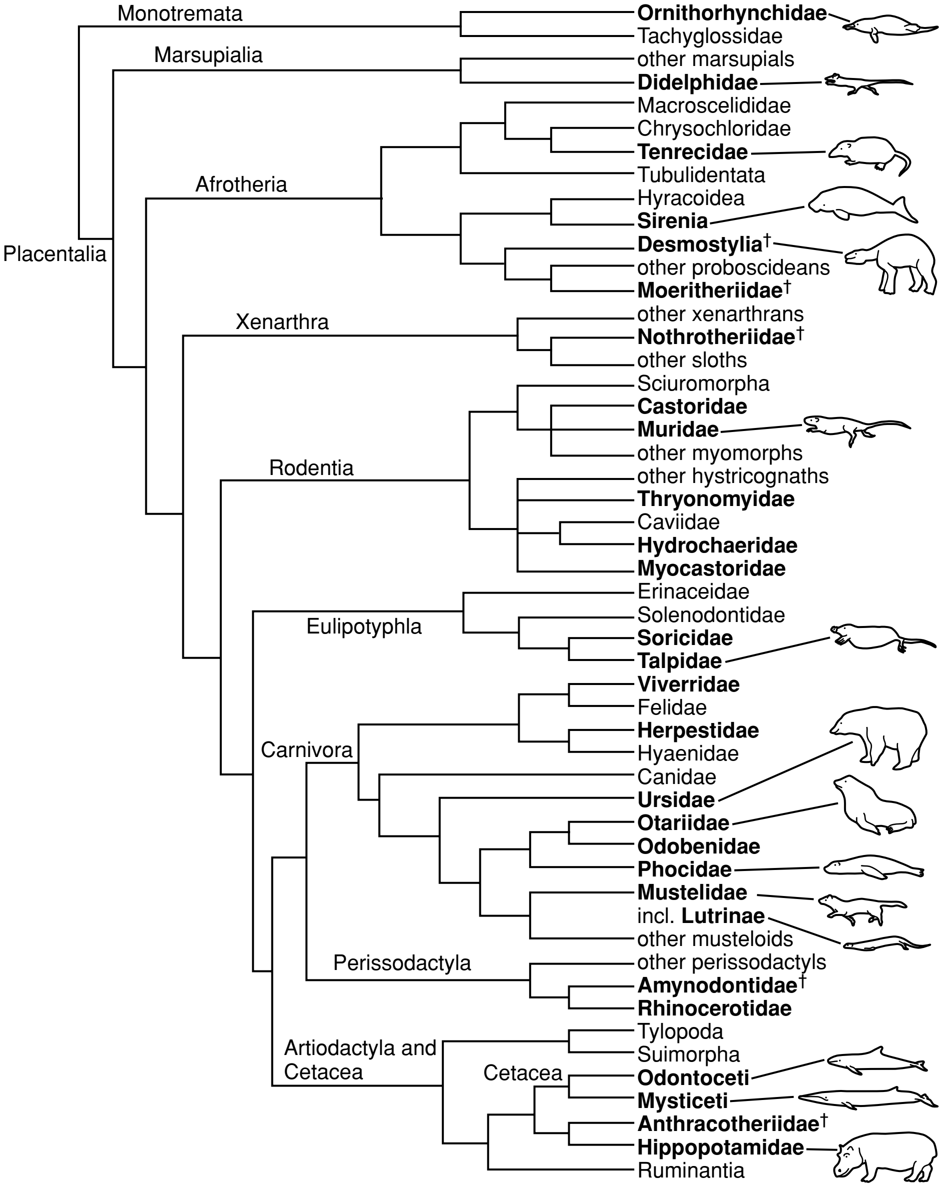

FIGURE 1.7. Generalized phylogeny of mammals *(aquatic in bold)* emphasizing taxa discussed in this volume. *Crosses* indicate extinct groups. See Table 1.4 for details. By Henry Pihlström.

birds are included with the dinosaurs. There are three principal lineages of reptiles with extant representatives: Chelonia (turtles), Lepidosauria (tuatara, lizards, and snakes), and Archosauria (crocodylians and birds). Each of these major extant clades of modern reptiles contains aquatic taxa, including some of the most fully water adapted species among tetrapod vertebrates. Nonetheless, aquatic forms constitute only about 8% of living species. Indeed, the major aquatic reptile lineages, turtles and crocodylians, are also the least speciose. Most reptile diversity (in terms of species numbers) is represented by the Squamata (lizards and snakes), and within this group, specialized aquatic habits have arisen infrequently and are phylogenetically dispersed (with several notable exceptions; see below). In addition to

TABLE 1.1

Overview of Amphibians in Which the Adults Have Aquatic Habits, and Other Taxa Discussed in This Volume

CLASSIFICATION	EXAMPLES OF AQUATIC GENERA	HABITAT	DEGREE	NOTES
Caudata (salamanders and newts)				
Sirenidae	*Siren*	F	1	
Hynobiidae	*Ranodon, Onychodactylus*	F	1, 2, 3	
Cryptobranchidae	*Andrias, Cryptobranchus*	F	1	Includes giant form
Ambystomatidae	*Ambystoma*	F	1, 3	Terrestrial adults except for completely aquatic neotenic forms such as the axolotl
Dicamptodontidae	*Dicamptdon*	F	1, 3	Aquatic neotenic adults common
Rhyacotritonidae	*Rhyacotriton*	F	2	
Salamandridae	*Cynops, Notophthalmus, Pleurodeles, Triturus*	F	1, 2, 3, 4	
Amphiumidae	*Amphiuma*	F	1	
Proteidae	*Proteus, Necturus*	F	1	
Plethodontidae	*Desmognathus, Eurycea, Gyrinophilus, Pseudotriton, Stereochilus*	F	1, 2, 3, 4	Fully aquatic species are neotenic. Listed are aquatic genera (1, 2), most plethodontid genera are fully terrestrial (4).
Gymnophiona (caecilians)				
Typhlonectidae	*Typhlonectes*	F	1	Live-bearing
Anura (frogs and toads)				
Ascaphidae	*Ascaphus*	F	2	
Pipidae	*Hymenochirus, Pipa, Xenopus*	F	1	Capable of moving on land but rarely do
Discoglossidae	*Bombina*	F	2	
Leptodactylidae	*Telmatobius*	F	1, 2, 3, 4	Most leptodactylids are 4 and lay directly developing eggs on land, *Telmatobius* is 1 or 2.
Ranidae	*Rana*	C, F	2, 3	

NOTE: Habitat; F, freshwater; C, coastal. Degree to which aquatic: 1, never leave water; 2, forage both on land and in water; 3, forage mostly on land; 4, completely terrestrial; lay eggs on land that hatch into terrestrial juveniles or give birth to terrestrial juveniles. Table by Thomas Hetherington and J. G. M. Thewissen.

TABLE 1.2

Overview of Aquatic Reptiles, Focusing on Taxa Discussed in This Volume

	EXAMPLE AQUATIC TAXA	HABITAT	DEGREE	NOTES
Mesosauria	*Mesosaurus*	MC?	2?	Extinct, Permian of South America and Africa. Limb structure indicates that mesosaurs could walk on land.
Placodontia	*Placodus*	MC	2?	Extinct, Triassic of Europe and Africa.
Pachypleurosauria	*Pachypleurosaurus*	MC	2?	Extinct, Triassic of Europe. Sometimes included in Nothosauria.
Nothosauria	*Nothosaurus* *Ceresiosaurus*	M	2?	Extinct, mostly Triassic of Europe and Asia.
Plesiosauria	*Cryptocleidus* *Liopleurodon*	M	2?	Extinct, Mesozoic. Well known skeletally. Morphological intermediates between nothosaurs and plesiosaurs are known.
Ichthyosauria	*Mixosaurus* *Cymbospondylus* *Ophthalmosaurus* *Temnodontosaurus*	M	1	Extinct, Mesozoic. Well known skeletally, but all fully aquatic.
Chelonia				
Chelidae	*Chelodina* *Chelus* *Elusor* *Platemys* *Rheodytes*	FP, FS	2, 3	*Elusor* and *Rheodytes* are highly aquatic, rarely leaving the water; no terrestrial representatives.
Pelomedusidae	*Pelomedusa* *Pelusios*	FP, FS	3	Often forage by bottom-walking; no terrestrial representatives.
Podocnemididae	*Erymnochelys* *Peltocephalus* *Podocnemis*	FS	3	Sometimes considered a subfamily of Pelomedusidae; primarily stream and river turtles; no terrestrial representatives.
Chelydridae	*Chelydra* *Macrochelys* *Platysternon*	FP, FS	2, 3	*Chelydra* rarely leaves water except to lay eggs; *Macrochelys* uses a wormlike lingual lure to capture prey underwater; no terrestrial representatives.
Cheloniidae	*Caretta* *Chelonia* *Eretmochelys* *Lepidochelys*	M	2	The sea turtles; the most aquatic of all turtles; pelagic, often swim at depth; no terrestrial representatives.

TABLE 1.2 (*continued*)

	EXAMPLE AQUATIC TAXA	HABITAT	DEGREE	NOTES
Dermochelyidae	*Dermochelys*	M	2	The leatherback sea turtle; pelagic, often swim at depth; no terrestrial representatives.
Carettochelyidae	*Carettochelys*	FS	2	The pig-nosed turtle has a snorkellike nose and forelimbs modified as flippers, like sea turtles; no terrestrial representatives.
Trionychidae	*Lissemys* *Amyda* *Apalone* *Aspideretes* *Trionyx*	FP, FS	2	Many with snorkellike snouts; spend most of their time on the bottom; no terrestrial representatives.
Dermatemydidae	*Dermatemys*	FP, FS	2	Monotypic; highly aquatic, restricted to slow-moving water.
Kinosternidae	*Kinosternon* *Sternotherus*	FP, FS	2, 3	Musk glands may be used for communication, as well as for defense; no terrestrial representatives.
Emydidae	*Chrysemys* *Clemmys* *Emys* *Graptemys* *Malaclemys* *Pseudemys*	BE, FP, FS	3	Highly variable in aquatic habits—some species highly aquatic, some completely terrestrial; most are semiaquatic pond and stream turtles; only *Malaclemys* is estuarine.
Bataguridae	*Batagur* *Cuora* *Chinemys* *Heosemys* *Kachuga* *Mauremys* *Rhinoclemmys*	BE, FP, FS	3	Sometimes included within Emydidae; similarly variable in aquatic habits.
Crocodylia				
Crocodylidae	*Crocodylus* *Osteolaemus* *Tomistoma*	MC, BE, FP, FS	3	The saltwater crocodile, *C. porosus*, often estuarine, sometimes travels long distances in the ocean; no terrestrial representatives.
Alligatoridae	*Alligator* *Caiman* *Melanosuchus* *Paleosuchus*	FP, FS	3	All amphibious; no terrestrial representatives.
Gavialidae	*Gavialis*	FS	2	The most aquatic of the crocodylians, gharials rarely leave the water; no terrestrial representatives.
		M	2	Extinct marine crocodylians that left the water only to reproduce.

(*continued*)

TABLE 1.2 (*continued*)

	EXAMPLE AQUATIC TAXA	HABITAT	DEGREE	NOTES
Metriorhynchidae				
Squamata, snakes				
Boidae	*Eunectes*	FS	2, 3	Green anacondas, *E. murinus*, are highly aquatic, spending most time submerged; with dorsal eyes and nostrils; most boids are terrestrial.
Acrochordidae	*Acrochordus*	MC, BE, FP, FS	1	Rarely observed outside of water, file snakes are some of the most aquatic-adapted snakes; exceptionally long tines of the forked tongue, dorsal nostrils; tongue-flick underwater; coastal species swim at depth; no terrestrial representatives.
Colubridae	*Bitia* *Erpeton* *Helicops* *Homalopsis* *Hydrodynastes* *Liophis* *Lycodonomorphus* *Natrix* *Nerodia* *Regina* *Thamnophis*	BE, FP, FS	2, 3	Natricines, homolopsines, and some xenodontines are among the most aquatic of the colubrids; some homolopsines, in particular, are highly aquatic and inhababit coastal areas—*B. hydroides* resembles a true seasnake (Elapidae) in body form and coloration; *Erpeton* has two mechanoreceptive tentacles it probably uses to locate fish prey; most colubrids are terrestrial.
Elapidae	*Emydocephalus* *Enhydrina* *Enhydris* *Hydrelaps* *Hydrophis* *Pelamis* *Laticauda*	BE, MC, M	1, 2	Laticaudinae (seakraits) and Hydrophiinae (seasnakes) are sometimes elevated to family status (Hydrophiidae); some species are the most aquatic of any reptile, never leaving the water; frequently tongue-flick underwater; many species swim at depth; most elapids are terrestrial.
Viperidae	*Agkistrodon*	BE, FP, FS	3	The cottonmouth, *A. piscivorus*, is highly aquatic and is tolerant of brackish water; all other viperids are terrestrial.

TABLE 1.2 (*continued*)

	EXAMPLE AQUATIC TAXA	HABITAT	DEGREE	NOTES
Squamata, Lizards				
Iguanidae	*Amblyrhynchus* *Basiliscus*	MC, FP, FS	3	*A. cristatus* is the only marine lizard; it often grazes on submerged algae at depth; *Basiliscus* use water as an avenue of escape; occasionally catch prey in water; usually run or swim across surface of water; occasional water escape in other iguanid species, but most are terrestrial.
Agamidae	*Hydrosaurus* *Physignathus*	FP, FS	3	Water as escape; good swimmers; *Hydrosaurus* with laterally compressed tail and tail fin; most agamids are terrestrial.
Scincidae	*Eulamprus* *Tropidophorus*	FP, FS	3	*Eulamprus* known as the "water skinks"; most scincids are terrestrial.
Teiidae	*Crocodilurus* *Dracaena*	FP, FS	3	Swim or walk on bottom, foraging; *Dracaena* observed tongue-flicking underwater; most teiids are terrestrial.
	Alopoglossus	FS	3	Swim through water; most gymnopthalmids are terrestrial.
Gymnophthalmidae Xenosauridae	*Neusticurus* *Shinisaurus*	FS	3	Sometimes placed in its own family; water as escape; the other genus in the family, *Xenosaurus* is terrestrial.
Lanthanotidae	*Lanthanotus*	FP, FS	3	Monotypic; highly aquatic, but very poorly known; sometimes collected in fish seins.
Varanidae	*Varanus*	FP, FS	3	Many species enter the water readily, where they swim and forage or spend time submerged; some species specialize on aquatic prey; most varanids are terrestrial.
Mosasauridae	*Clidastes* *Tylosaurus* *Plotosaurus*	MC	2	Extinct, Cretaceous, well known skeletally. A possible intermediate between the fully aquatic mosasaurs and terrestrial lepidosaurs are the aigialosaurs, which combine terrestrial and aquatic features.

(*continued*)

TABLE 1.2 (*continued*)

	EXAMPLE AQUATIC TAXA	HABITAT	DEGREE	NOTES
Phytosauria	*Phytosaurus* *Rutiodon*	MC	2?	Extinct, mostly Triassic of Northern Hemisphere.
Thalattosauria	*Askeptosaurus*	MC	2?	Extinct, Triassic of Europe and North America.

SOURCES: Neill, 1971; Carroll, 1988; Ernst and Barbour, 1989; Greer, 1989; Glasby et al., 1993; Greene, 1997; Cann, 1998; Zug et al., 2001; Pianka and Vitt, 2003; and see text.
NOTE: Habitat: M, marine; MC, marine, coastal; BE, brackish/estuarine; FP, freshwater, ponds, lakes, marshes; FS, freshwater, streams, rivers. Degree to which aquatic: 1, fully aquatic, never returns to land; 2, mostly aquatic, returns to land only to reproduce; 3, semiaquatic, spends time on land for purposes other than reproduction, e.g., foraging, basking. Table by Kurt Schwenk and J. G. M. Thewissen.

the extant clades, there are several diverse groups of extinct reptiles, some with predominantly or exclusively aquatic members.

Members of the crown group Reptilia probably arose during the Middle to Late Pennsylvanian (approximately 290 million years ago). However, the split between the stem groups Sauropsida and Synapsida (Fig. 1.4) occurred earlier, during the Early Pennsylvanian (approximately 300 to 320 million years ago) (Carroll, 1988). Interestingly, many basal reptiles are aquatic, such as mesosaurs, chelonians, and euryapsids. Seymour (1982) suggested that low metabolic rate and body temperature, and a tolerance of low-oxygen conditions are useful features in aquatic animals and may have facilitated life in water among early reptiles.

MESOSAURS The affinities of mesosaurs are unclear; they are usually included with the sauropsids but may have instead branched off before the sauropsid-synapsid split (Rossman, 2000). They were up to 1 meter long with a long snout and long teeth, possibly for filter-feeding, and a bilaterally flat tail (Huene, 1941).

TURTLES Living turtles comprise approximately 300 extant species that are divided into two lineages: the Pleurodira, or side-necked turtles, and the Cryptodira, or hidden-neck turtles (Shaffer et al., 1997; Zug et al., 2001). The origin of turtles is contentiously debated. The traditional view is that turtles are basal sauropsids that exhibit the ancestral anapsid amniote skull condition (i.e., lacking a temporal fenestra) (Carroll, 1988). Reisz and Laurin (1991) suggested that turtles might not be reptiles in the cladistic sense. However, recent studies are divided on whether turtles are primitively anapsid reptiles that arose within a basal group known as parareptiles (Lee, 1995, 1996), or whether they are primitively diapsid (having two temporal fenestrae), allied with either lepidosaurs or archosaurs (Rieppel, 1994/1995; Rieppel and deBraga, 1996; deBraga and Rieppel, 1997; Rieppel and Reisz, 1999; Zardoya and Meyer, 2001).

Although the earliest turtle ancestors must have been terrestrial, it is now well established that the common ancestor of all living turtles was aquatic (Gaffney et al., 1987; Rieppel and Reisz, 1999; Joyce and Gauthier, 2003). Nearly all extant turtles are semi- or fully aquatic. The sea turtles (Cheloniidae and Dermatochelyidae) are highly adapted for marine life and emerge from the water only to lay eggs. Several freshwater lineages are almost as specialized, including the Carettochelyidae and Trionychidae. The only fully terrestrial family is the Testudinidae (the tortoises). Systematic study of chelonians argues that terrestriality in testudinids must have evolved secondarily from an aquatic ancestry. A recent mitochondrial DNA study also suggested that the terrestrial box turtles (Terrepene), of the diverse family Emydidae, arose from within a wholly aquatic or semiaquatic

TABLE 1.3

Overview of Aquatic Birds (English Names are Generalized), Focusing on Taxa Discussed in This Volume

	SELECTED GENERA	HABITAT	DEGREE	NOTES
Galloanserae				Mostly terrestrial forms, such as fowl.
Anatidae (ducks, geese)	*Somateria, Histrionicus, Anas*	C, F	2, 3	Some species are partly pelagic *(Somateria)*.
Pelecaniformes Pelecanidae (pelicans)	*Pelecanus*	C, F	2	Most species gather food while surface swimming and bill dipping; one species plunge-dives *(P. occidentalis)*.
Phaethontidae (tropic birds)	*Phaethon*	M	4	*Phaeton* gathers food in flight over water; can barely walk and is poor diver.
Fregatidae (frigate birds)	*Fregata*	M	4	*Fregata* gathers food flying over water and rarely dives.
Sulidae (boobies, gannets)	*Morus, Papasula, Sula*	C	2	Plunge-divers.
Phalacrocoracidae (cormorants)	*Phalacrocorax*	C, F	2	Surface divers.
Anhingidae	Anhinga	C, F	2	Surface divers.
Plotopteridae		C, M	2?	Extinct birds strongly resembling penguins, but unrelated. Known only from the North Pacific.
Podicipediformes				
Podicipedidae (grebes)	Around 10 species	C, F	2	Mostly pursuit divers from position on surface freshwater.
Phoenicopteriformes				
Phoenicopteridae (flamingos)	*Phoenicopterus Phoeniconaias Phoenicoparrus*	C, F	2	Use their bill to filter feed while wading.
Charadriiformes				Mostly nonaquatic birds.
Charadriidae (plovers)		C, F	3	Some species probe wet sand with their bills feeding in the intertidal zone, most not aquatic.
Jacanidae (Jacanas)	*Jacana*	F	3	
Scolopacidae (sandpipers)	Many genera	C, F	3	Some species wade while probing bottom for buried food.
Laridae (gulls and terns)	*Larus* *Sterna* (tern)	M, C, F C	2–3	Not all gull species are aquatic. Gulls are dietary opportunists. *Sterna* plunge-dives for food.
Rhynchopidae	*Rhynchops*	F	4	Skim water, dipping lower jaw.
Alcidae (auks)	*Alca, Uria, Fratercula*	C	2	Excellent pursuit divers, stay under water for minutes.
Falconiformes	*Haliaeetus, Pandion*	F	4	Hunt swimming prey.

(*continued*)

TABLE 1.3. (*continued*)

	SELECTED GENERA	HABITAT	DEGREE	NOTES
Sphenisciformes				
Spheniscidae (penguins)	Six genera	M	2	The most aquatic birds, some species spend months without leaving the water. No species fly, all are fast pursuit divers, and land locomotion is poor.
Gaviiformes				
Gaviidae (loons)	*Gavia*	C, F	2	Pursuit divers from water surface.
Procellariiformes				All live on the open ocean and feed mostly while flying closely over the water surface.
Hydrobatidae (storm petrels)	*Oceanites, Fregetta, Hydrobates*	M	4	Occasional divers.
Diomedeidae (albatroses)	*Diomedea, Phoebetria*	M	4	
Procellariidae (shearwaters, petrels)	*Pterodroma, Puffinus*	M	2, 4	*Pelecanoides* is a wing-propelled diver.
Gruiformes				Mostly nonaquatic birds.
Ardeidae (Herons)		F	3	Striker hunters, breaking the water surface with their bill after spotting prey.
Passeriformes				Mostly nonaquatic birds.
Cinclidae (dippers)		F	3	Forage while walking on the bottom of streams, fully submerged.
Coraciiformes				Mostly nonaquatic birds.
Alcedinidae (Kingfishers)	*Ceyx, Alcedo*	F	3	Plunge divers.

NOTE: Habitat: M, marine (coastal for reproduction); C, coastal; F, freshwater. Degree to which aquatic: 2, highly aquatic, always feed in water, return to land only for reproduction; 3, moderately aquatic, occasionally forage on land; flying; 4, usually feed over water, but remain airborne. Table by J. G. M. Thewissen and T. Hieronymus.

clade (Feldman and Parham, 2002), once again supporting the secondary derivation of terrestrial habits in living turtles.

SAUROPTERYGIA The sauropterygians are a diverse group of extinct marine reptiles known only from the Mesozoic (250 to 65 million years ago), with the well-known genus *Claudiosaurus* near its base (Carroll, 1981). *Claudiosaurus* was aquatic, as indicated by its paddlelike, weakly muscled forelimbs and its poorly ossified skeleton, and had large hind limbs with which it swam. However, it displays fewer aquatic adaptations than most sauropterygians. Later sauropterygians include nothosaurs (Kuhn-Snyder, 1963) and pachypleurosaurs (Carroll and Gaskill, 1985), which are tail-propelled forms with weak limbs. Nothosaurs had partly pachyostotic skeletons, suggesting a partly submerged life. Most plesiosaurs had a small head on a long, mobile neck with very large hands and feet, but the plesiosaur family Pliosauridae had short necks with large heads specialized for different aquatic modes of life (Brown, 1981). Placodonts were heavy, slow moving, putative mollusk-eaters (Drevermann, 1933; Peyer and Kuhn-Snyder, 1955).

TABLE 1.4

Overview of Aquatic Extant Mammals (English Names are Generalized)

CLASSIFICATION	GENERA	HABITAT	DEGREE	NOTES
Monotremata				
Ornithorhynchidae (platypus)	*Ornithorhynchus*	F	2	*O. anatinus* has an electric organ for locating prey underwater.
Didelphimorphia				
Didelphidae (American opossums)	*Chironectes*	F	3	*C. minimus* is the only extant semiaquatic marsupial.
Afrosoricida				
Tenrecidae (tenrecs)				
Oryzorictinae (rice tenrecs)	*Limnogale*	F	3	
Potamogalinae (otter shrews)	*Potamogale*	F	3	
	Micropotamogale	F	3	
Sirenia				
Dugongidae (dugongs)	*Dugong*	C	1	
	Hydrodamalis	C	1	The recently extinct *H. gigas* was the only nontropical sirenian, living near the Arctic Circle.
Trichechidae (manatees)	*Trichechus*	C, F	1	
Rodentia				
Castoridae (beavers)	*Castor*	F	3	Semiaquatic, but feed mainly on terrestrial plants.
Muridae (mice)				Largest extant mammal family, several semiaquatic lineages.
Sigmodontinae (New World rats and mice)	*Oryzomys*	F	3	This genus has 36 terrestrial and 1 semiaquatic species, *O. palustris*.
	Nectomys	F	3	
	Amphinectomys	F	3	
	Holochilus	F	3	
	Scapteromys	F	3	
	Neusticomys	F	3	
	Chibchanomys	F	3	
	Anotomys	F	3	
	Ichthyomys	F	3	
	Rheomys	F	3	
Arvicolinae (voles)	*Arvicola*	F	3	
	Microtus	F	3	This genus has 64 terrestrial and 1 semiaquatic species: *M. richardsoni*.
	Neofiber	F	3	
	Ondatra	F	3	

(*continued*)

TABLE 1.4 (*continued*)

CLASSIFICATION	GENERA	HABITAT	DEGREE	NOTES
Murinae (Old World rats and mice)	*Colomys*	F	3	
	Nilopegamys	F	3	
Hydromyinae (water rats)	*Hydromys*	F	3	This subfamily is known as water rats, although most of its genera are terrestrial.
	Crossomys	F	3	
Thryonomyidae (cane rats)	*Thryonomys*	F	3	This genus has one terrestrial and one semiaquatic species: *T. swinderianus*.
Hydrochaeridae (capybara)	*Hydrochaeris*	F	3	
Myocastoridae (nutria)	*Myocastor*	F, C	3	
Eulipotyphla				
Soricidae (shrews)	*Sorex*	F	3	This genus has 66 terrestrial and 2 semiaquatic species: *S. palustris* and *S. bendirii*.
	Neomys	F	3	
	Nectogale	F	3	
	Chimarrogale	F	3	
Talpidae (moles)	*Desmana*	F	3	
	Galemys	F	3	
	Condylura	F	3	
Carnivora				
Ursidae (bears)	*Ursus*	C	3	This genus has five terrestrial and one semiaquatic species: *U. maritimus*, the polar bear.
Mustelidae (weasels, mink, otters, etc.)	*Mustela*	F, C	3	This genus has 14 terrestrial and 3 semiaquatic species: *M. lutreola*, *M. vison*, and the recently extinct *M. macrodon*.
	Lutra	F, C	3	
	Lutrogale	F, C	3	
	Lontra	F, C	3	
	Pteronura	F	3	
	Aonyx	F, C	3	
	Enhydra	M, C	2	*E. lutris* is the most aquatic otter, some individuals apparently never come ashore.
Otariidae (fur seals, sea lions)	*Callorhinus*	M, C	2	All species in this family are semiaquatic.
	Arctocephalus	M, C	2	
	Zalophus	M, C	2	
	Phocarctos	M, C	2	
	Neophoca	M, C	2	
	Otaria	M, C	2	
	Eumetopias	M, C	2	
Odobenidae (walrus)	*Odobenus*	M, C	2	All species in this family are semiaquatic.

TABLE 1.4 (*continued*)

CLASSIFICATION	GENERA	HABITAT	DEGREE	NOTES
Phocidae (earless seals)	*Monachus*	M, C	2	All species in this family are semiaquatic.
	Lobodon	M, C	2	
	Hydrurga	M, C	2	
	Leptonychotes	M, C	2	
	Ommatophoca	M, C	2	
	Mirounga	M, C	2	
	Erignathus	M, C	2	
	Cystophora	M, C	2	
	Phoca	M, C, F	2	Some species and subspecies in this genus live permanently in freshwater.
Viverridae (civets, genets)	*Osbornictis*	F	3	
	Cynogale	F	3	
Herpestidae (mongoose)	*Atilax*	F	3	
Cetacea/Odontoceti				
Platanistidae (Indian river dolphin)	*Platanista*	F	1	Lives in murky waters; eyes small, and vision presumably poor.
Lipotidae (baji)	*Lipotes*	F	1	
Pontoporiidae (franciscana)	*Pontoporia*	C	1	
Iniidae (Amazon River dolphin)	*Inia*	F	1	
Monodontidae (narwhal, beluga)	*Delphinapterus*	M, C	1	
	Monodon	M	1	
Phocoenidae (porpoises)	*Phocoena*	M, C	1	
	Neophocaena	C, F	1	
	Phocoenoides	M, C	1	
Delphinidae (marine dolphins)	*Steno*	M	1	
	Sousa	C, F	1	
	Sotalia	C, F	1	
	Lagenorhynchus	M	1	
	Grampus	M	1	
	Tursiops	M	1	
	Stenella	M	1	
	Delphinus	M	1	
	Lagenodelphis	M	1	
	Lissodelphis	M	1	
	Orcaella	C, F	1	
	Cephalorhynchus	M, C	1	
	Peponocephala	M	1	
	Feresa	M	1	
	Pseudorca	M	1	
	Orcinus	M	1	
	Globicephala	M	1	

(*continued*)

TABLE 1.4 (*continued*)

CLASSIFICATION	GENERA	HABITAT	DEGREE	NOTES
Ziphiidae (beaked whales)	*Berardius*	M	1	This family is highly specialized for deep-sea diving.
	Ziphius	M	1	
	Tasmacetus	M	1	
	Hyperoodon	M	1	
	Indopacetus	M	1	
	Mesoplodon	M	1	
Physeteridae (sperm whales)	*Kogia*	M	1	This family is highly specialized for deep-sea diving.
	Physeter	M	1	
Cetacea/Mysticeti				This suborder includes highly specialized filter feeders.
Eschrichtiidae (gray whale)	*Eschrichtius*	M	1	
Neobalaenidae (pygmy right whale)	*Caperea*	M	1	
Balaenidae (right whales)	*Eubalaena*	M	1	
	Balaena	M	1	
Balaenopteridae (rorquals)	*Balaenoptera*	M	1	
	Megaptera	M	1	
Artiodactyla				
Hippopotamidae (hippopotami)	*Hippopotamus*	F	3	This genus has one living *(H. amphibius)* and three recently extinct species. Hippopotamids are semiaquatic but feed on terrestrial plants.
	Choeropsis	F	3	

NOTE: Habitat: M, marine; C, coastal; F, freshwater. Degree to which aquatic: 1, obligately aquatic; 2, mostly aquatic, return to land for reproduction and resting; 3, moderately aquatic, fully capable of terrestrial locomotion, may forage on land. Table by H. Pihlström.

ICHTHYOPTERYGIA Ichthyosaurs were obligate marine swimmers with short limbs, a long snout, and a tail fin (Kuhn-Snyder, 1963; Mazin, 1981). Consistent with life in water, they were live-bearing, and the external nares of many forms are located posteriorly on the snout. Even the earliest ichthyosaur genera are fully adapted for aquatic life (Shikama et al., 1978).

ARCHOSAURIANS Archosaurs include crocodylians (discussed below) and dinosaurs (including birds, which are discussed below). The radiation of extinct, Mesozoic dinosaurs is enormous, and it is surprising that only a single dinosaur has been identified with aquatic adaptations (Li et al., 2004).

CROCODYLIANS The Crocodylia (Fig. 1.5) comprises only 23 extant species (Zug et al., 2001) of aquatic reptiles arrayed within three lineages/families (Alligatoridae, Crocodylidae, Gavialidae). There is some disagreement about the relationships among these families, centering around the placement of two monotypic genera, *Tomistoma* and *Gavialis*. Although the distant archosaurian ancestors of crocodylians were terrestrial, it is clear that aquatic habits are primitive for the living species (Benton and Clark, 1988).

Among modern crocodylians, gharials (*Gavialis*) are the most highly aquatic, rarely leaving the water. Most crocodylians are freshwater species, but many can tolerate saltwater for extended periods of time. The saltwater crocodile (*Crocodylus porosus*) is especially tolerant of hyperosmotic environments and is often found in coastal areas, sometimes venturing far out to sea (Grigg and Gans, 1993; Richardson et al., 2002). Indeed, biogeographic, phylogenetic, and physiological evidence supports transoceanic migrations in crocodylian history (Brochu, 2001). One family of fossil Mesozoic crocodilians, the metriorhynchids, was fully marine and had a tailfin.

SQUAMATES There are approximately 7200 species of squamate reptiles divided almost equally between snakes and lizards (Zug et al., 2001). Snakes (Serpentes) form a monophyletic radiation that, in all likelihood, is derived from within lizards, so that the latter group is paraphyletic and not recognized in formal taxonomies (e.g., Fig. 1.5). The only extant, nonsquamate lepidosaurs are two species of terrestrial tuatara (*Sphenodon*), relicts of a once diverse group of reptiles now restricted to a few small islands off the coast of New Zealand.

Fossils that can be assigned to Recent families date from the Cretaceous (approximately 100 million years ago), but as a group, squamates arose in the Triassic, or even Late Permian (approximately 250 million years ago) (Estes, 1983; Carroll, 1988). Thus, modern squamate diversity reflects a very ancient radiation. It is thus surprising that, relatively, so few species have become specialized for aquatic environments. Even more striking is the failure of squamates and reptiles, in general, to invade marine habitats in significant numbers. Only about 75 species (approximately 1%) of all living reptiles spend time in saltwater, and more than half of these belong to a group of marine snakes in the family Elapidae (Greene, 1997). Only a few other snake groups include estuarine or marine species, and there is only one species of marine lizard. The remaining aquatic squamates are all freshwater species, and few of these evince obvious adaptations for life in water (Schwenk, chapter 5 in this volume).

At least one lineage of extinct squamates became marine predators: the mosasaurs (Russell, 1967). Mosasaurs are known only from the Upper Cretaceous and reached large sizes; some are 10 meters long. Mosasaurs are varanoid lizards (Lee, 2005), with limbs and sometimes tail modified for swimming. Although well known from many fossils, no mosasaurs are known with fetuses in their bodies, suggesting that the females hauled out of the water to lay eggs.

Relationships within the monophyletic Serpentes (snakes) are poorly resolved, although much of this controversy revolves around the relationships of the basal snake groups. Most of these taxa are fossorial and none are aquatic and therefore do not concern us here. All aquatic species, including the marine elapids, are members of the advanced snakes known as the macrostomatans, in reference to their ability to increase gape by separating the mandibular rami and swinging the quadrate bones laterally, permitting them to swallow prey that are very large relative to head size. As noted, the most highly aquatic snakes in the world, and probably the most adaptively committed aquatic reptiles of any kind, are the marine elapids belonging to the subfamilies Laticaudinae and Hydrophiinae. Two subfamilies of the diverse and speciose Colubridae are also highly aquatic, the Natricinae and Homolopsinae.Aquatic species are infrequently distributed among other taxa.

OTHER DIAPSIDS Phytosaurs (Colbert, 1947) were probably similar to crocodiles in habitat and ecology and are, in fact, related to archaic crocodiles. Thallatosauria were a small radiation of long-tailed diapsids that swam with their elongate tails. Their limbs are not specialized for aquatic locomotion (Fraas, 1902).

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AQUATIC AND SEMIAQUATIC BIRDS

J. G. M. Thewissen and Tobin Hieronymus

With the plethora of discoveries of Mesozoic birds in the last decade (reviewed in Chiappe and Dyke, 2002; Hou et al., 2003), it has become clear that early birds were nearly as diverse as modern birds and included aquatic taxa. The recent discovery that an Early Cretaceous (110 million year old) aquatic bird is closely related to modern birds (You et al., 2006) has led to speculations that modern birds (Neornithes, Fig. 1.6) had aquatic ancestors. It is also clear that many Cretaceous birds were strongly specialized for life in water and were unable to fly (e.g., the hesperornithiform *Hesperornis* [Marsh, 1880]). Even among the modern Neornithes, a large number of orders display a variety of aquatic specializations (Table 1.3).

The phylogeny of Chiappe and Dyke (2002) is used here to describe the relationships of the fossil groups to living birds (Neornithes). While the relationship of the basal modern bird groups Palaeognathae and Galloanserae (including the aquatic Anseriformes) to Neoaves are well understood, relationships within Neoaves have proved difficult to resolve (Cracraft et al., 2004). Because of this, many of the higher-order comparisons presented in Figure 1.6 are tentative and have only heuristic value. This figure uses the phylogeny of Cracraft et al. (2004) to resolve higher-order relationships within Neoaves. Relationships within groups of aquatic birds are shown after those proposed by Bertelli and Giannini (2005) for Sphenisciformes; Kennedy and Page (2002) for Procellariiformes; Kennedy et al. (2000) and Kennedy and Spencer (2004) for Pelecaniformes; Thomas et al. (2004a, 2004b) and van Tuinen et al. (2004) for Charadriiformes; and van Tuinen et al. (2001) for Podicipediformes.

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AQUATIC AND SEMIAQUATIC MAMMALS

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Table 1.4 and Figure 1.7 present an overview of orders, families, and genera of extant aquatic mammals. Table 1.4 is a consensus classification and indicates habitat and degree of aquatic specialization of these mammals, and Figure 1.7 is a cladogram. The higher-level phylogeny of Table 1.4 and Figure 1.7 are identical except that the traditional orders Cetacea and Artiodactyla have been retained in the former, which is invalid from a purist phylogenetic standpoint (Price et al., 2005). Habitat information, as well as nomenclature for genera and species, follows Nowak (1999), with these exceptions: the gray seal genus *Halichoerus* is included in the genus *Phoca* (following Arnason et al. [1995] and Davis et al. [2004]), and the genus name *Choeropsis* is used for the pygmy hippopotamus (following Boisserie [2005]).

Figure 1.7 is compiled from Murphy et al. (2001) for overall phylogeny; Cardillo et al. (2004) for marsupials; Stanhope et al. (1998), Douady et al. (2002), Clementz et al. (2003), Grenyer and Purvis (2003), and Shoshani and Tassy (2005) for afrotherians; Gaudin (2004) for xenarthrans; Adkins et al. (2001) and Huchon et al. (2002) for rodents; Grenyer and Purvis (2003) for Eulipotyphyla; Flynn et al. (2005) for Carnivora; Prothero et al. (1986) for amynodontid and rhinocerotid perissodactyls; Price et al. (2005) and Boisserie et al. (2005) for whales and artiodactyls.

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