

Global diversity of mammals (Mammalia) in freshwater

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Abstract Species that are dependant on, or adapted to, freshwater environments are found in almost all mammalian orders, and two orders, the Cetacea and the Sirenia, are strictly aquatic and include some freshwater-dependant species. Overall, the aquatic and freshwater-dependant species represent around 70 of the more than 1,200 living or recent genera of mammals, and occur in all continents except Antarctica. They include some of the most

endangered species of mammals, and several have gone extinct or become critically endangered in recent decades. One of the main threats is habitat loss or degradation. This chapter provides an overview of the freshwater species within each order of mammals, their evolutionary history, their relations to humans and their conservation status.

Keywords Mammalia · Freshwater · Diversity · Conservation

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Introduction

The mammals are tetrapod vertebrates characterized by their jaw articulation (between the dentary and the squamosal), presence of three bones in the middle ear (malleus, incus, and stapes), mammary glands that produce milk, and presence of hair. Living forms are divided into three clades, the monotremes (Monotremata), the marsupials (Metatheria), and the placentals (Eutheria). Mammals have adapted to most kinds of habitat and have assumed various modes of existence—terrestrial, arboreal, aerial, fossorial, and aquatic, and inhabit all regions of the world. At least some forms in most of the orders depend on water for habitat and food, many also for protection from predators. Two orders, the Cetacea and the Sirenia, are strictly aquatic. For most partially or semi-aquatic mammals, at least giving birth or rearing of the young takes place outside the water.

Species diversity and geographical distribution

Freshwater mammals occur on all continents except Antarctica, some species widely distributed but many with very restricted ranges (Fig. 1). Many are threatened and these are listed in Table 1 with information on their distribution.

Order Monotremata (2 families; Groves, 2005)

Among the five species of living monotremes, the duck-billed platypus (*Ornithorhynchus anatinus*) lives in streams, lakes and lagoons in eastern Australia and Tasmania, but it has been extirpated from much of its range due to hunting and habitat degradation, river fragmentation from dams, and entrapment or entanglement in fishing gear (Nowak, 1999).

Metatheria (or Marsupialia) (7 Orders, 22 families; Wilson & Reeder, 2005)

Among the 331 species of metatherians, the only truly semi-aquatic species is the South American

water opossum (*Chironectes minimus*). It possesses webbed feet and differs from other marsupials in having its rear-facing pouch equipped with a sphincter muscle to make it watertight for the attached young (Marshall, 1978). The thick-tailed opossum (*Lutreolina crassicaudata*) is an excellent swimmer that exploits wetlands for food and nesting habitat (Nowak, 1999).

Eutheria (placental mammals)

Order Chiroptera (1116 species in 18 families; Simmons, 2005): Many bats are associated with fresh water but one group, the fishing bats (*Noctilio albiventris* and *Noctilio leporinus*), belonging to the family Noctilionidae, feed on aquatic insects, and *N. leporinus* also eats fish, frogs, and crustaceans. Like other bats, they use echolocation to locate prey, detecting the ripples on the water surface (Schnitzler et al., 1994). They can swim and take flight from the water (Revenga & Kura, 2003). Several species of vesper bats (Vespertilionidae) share the enlarged hind legs and claws of noctilionids, including *Myotis (Pizonyx) vivesi* of Mexico, *Myotis adversus* of

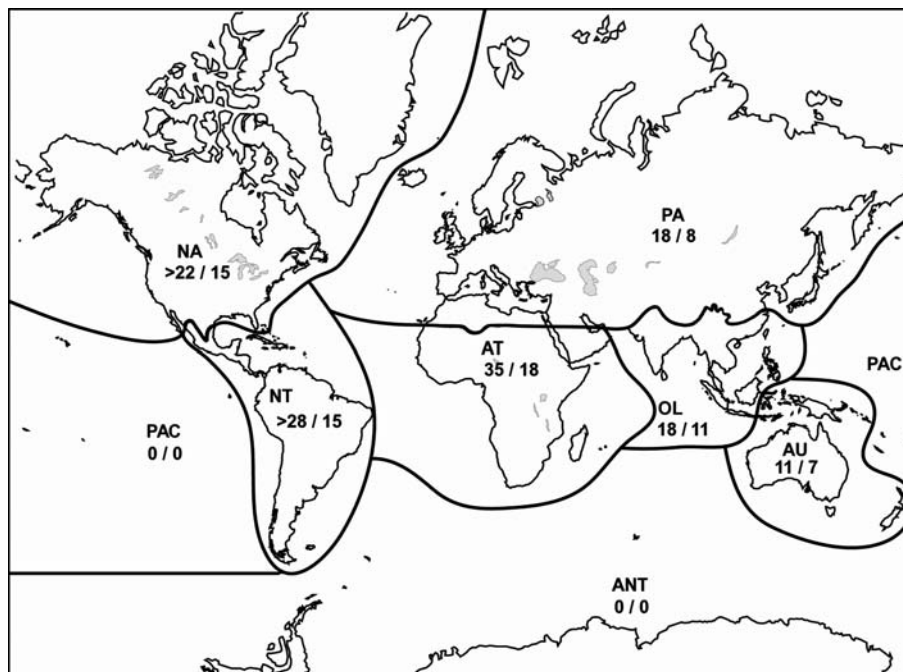


Fig. 1 Species and genus number of freshwater (aquatic and water dependent) mammals by zoogeographic region : species number/genus number. PA: Palearctic Region; NA: Nearctic

Region; AT: Afrotropical Region; NT: Neotropical Region; OL: Oriental Region; AU: Australasian Region; PAC: Pacific Region and oceanic islands, ANT: Antarctic Region

Table 1 The most threatened freshwater mammals (2006 IUCN Red List, including species in categories higher than lower risk; subspecies and subpopulations are not included)

Taxon	IUCN Red List status	Distribution
Order Didelphimorphia		
<i>Chironectes minimus</i>	Near threatened	Central and South America
Order Soricomorpha		
<i>Chimarrogale hantu</i>	Critically endangered	South East Asia (tropical forest of Malay peninsula)
<i>Chimarrogale phaeura</i>	Endangered	South East Asia (tropical forest of Borneo)
<i>Chimarrogale sumatrana</i>	Critically endangered	South East Asia (tropical forest of Sumatra)
<i>Desmana moschata</i>	Vulnerable	Central Eurasia
<i>Galemys pyrenaicus</i>	Vulnerable	West Europe (Pyrenees and Northern mountains of Iberian Peninsula)
Order Afrosoricida		
<i>Potamogale velox</i>	Endangered	Tropical Africa
<i>Micropotamogale lamottei</i>	Endangered	West Africa (Mount Nimba in Guinea, Liberia, Ivory Coast)
<i>Micropotamogale ruwenzorii</i>	Endangered	Central Africa (Uganda, Zaire)
<i>Limnogale mergulus</i>	Endangered	East Madagascar
Order Lagomorpha		
<i>Bunolagus monticularis</i>	Critically endangered	South Africa (Cape Province)
Order Rodentia		
<i>Castor fiber</i>	Near threatened	Eurasia
<i>Dasymys foxi</i>	Vulnerable	Africa (endemic to South plateau of Nigeria)
<i>Dasymys montanus</i>	Vulnerable	Africa (endemic to Ruwenzori Mountains, Uganda)
<i>Dasymys nudipes</i>	Near threatened	Africa (S Angola, South West Zambia, North East Namibia, North Botswana)
<i>Pelomys hopkinsi</i>	Vulnerable	Africa (Rwanda, Uganda, South West Kenya)
<i>Pelomys isseli</i>	Endangered	Africa (endemic to islands of Lake Victoria, Uganda)
<i>Nectomys parvipes</i>	Critically endangered	South America (known only from Comte River, French Guiana)
<i>Ichthyomys pittieri</i>	Vulnerable	South America (North Venezuela)
<i>Neusticomys mussoi</i>	Endangered	South America (known only from Paso Hondo, Rio Potosi, Venezuela)
<i>Neusticomys oyapocki</i>	Endangered	South America (known only from Trois sauts, French Guyana)
<i>Neusticomys peruviansis</i>	Endangered	South America (known only from Balta, Peru)
<i>Nectomys parvipes</i>	Critically endangered	South America (known only from Cacao, Comte River, French Guyana)
<i>Mesocapromys angelcabrerai</i>	Critically endangered	Cuba
<i>Mesocapromys auritus</i>	Critically endangered	Cuba
<i>Mesocapromys nanus</i>	Critically endangered	Cuba
<i>Mesocapromys sanfelipensis</i>	Critically endangered	Cuba
Order Carnivora		
<i>Mustela lutreola</i>	Endangered	Europe (in isolated small populations)
<i>Aonyx congicus</i>	Data deficient	Equatorial Africa (distribution scarce and not fully known)
<i>Lutra lutra</i>	Near threatened	Eurasia
<i>Lontra longicaudis</i>	Data deficient	Central and South America

Table 1 continued

Taxon	IUCN Red List status	Distribution
<i>Lutra provocax</i>	Endangered	South America (Patagonia)
<i>Pteronura brasiliensis</i>	Endangered	South America
<i>Lutra sumatrana</i>	Data deficient	South-East Asia
<i>Lutrogale perspicillata</i>	Vulnerable	Asia and Middle East
<i>Aonyx cinerea</i>	Near threatened	Asia
<i>Herpestes palustris</i>	Endangered	Asia (West Bengal, India)
<i>Cynogale bennettii</i>	Endangered	South-East Asia
<i>Genetta piscivora</i>	Data deficient	Africa (Zaire)
<i>Prionailurus viverrinus</i>	Vulnerable	Asia
<i>Prionailurus planiceps</i>	Vulnerable	South East Asia
Order Sirenia		
<i>Trichechus manatus</i>	Vulnerable	Southeastern North America, Central America and northern South America
<i>Trichechus inunguis</i>	Vulnerable	South America (Amazon basin)
<i>Trichechus senegalensis</i>	Vulnerable	West Africa
Artiodactyla		
<i>Hexaprotodon liberiensis</i>	Vulnerable	West Africa
<i>Hippopotamus lemerlei</i>	Extinct	Madagascar
<i>Hippopotamus laloumena</i>	Extinct	Madagascar
<i>Hexaprotodon madagascariensis</i>	Extinct	Madagascar
<i>Bubalus bubalis</i>	Endangered	Asia (formerly India to Indochina)
<i>Elaphurus davidianus</i>	Critically endangered (extinct in the wild)	Asia (formerly North East China)
<i>Blastocerus dichotomus</i>	Vulnerable	South America
<i>Hyemoschus aquaticus</i>	Data deficient	West and Central Africa
Cetacea		
<i>Lipotes vexillifer</i>	Critically endangered	Asia (Yangtze and Qiantang rivers, China)
<i>Neophocaena phocaenoides</i>	Data deficient	Asia
<i>Platanista gangetica</i>	Endangered	Asia (major rivers of South Asian subcontinent)
<i>Orcaella brevirostris</i>	Data deficient	South East Asia and Australasia
<i>Inia geoffrensis</i>	Vulnerable	Amazon, Madeira and Orinoco systems of central and northern South America
<i>Sotalia fluviatilis</i>	Data deficient	Central and northern South America

Australia, and *Myotis ricketti* of China, and are known to eat fish (Ma et al., 2003), often being included among the fishing bats.

Order Afrosoricida (51 species in 2 families; Bronner & Jenkins, 2005): The Tenrecidae includes some semi-aquatic forms. The otter shrews are represented by three African species (giant otter shrew, *Potamogale velox*, Nimba otter shrew *Micropotamogale lamottei*, and Ruwenzori otter shrew *Micropotamogale ruwenzorii*) with restricted distributions in the Congo Basin and Equatorial Africa. The remaining Tenrecidae are endemic to

Madagascar. Some species live in marshy areas or burrow in banks of rice paddies, while the aquatic or web-footed tenrec (*Limnogale mergulus*) lives along large fast-flowing rivers and feeds mainly on aquatic invertebrates (Benstead & Olson, 2003, Fig. 2, Tables 2 and 3).

Order Soricomorpha (428 species in 4 families; Hutterer, 2005): The water shrews live in boreal North America (*Blarina brevicauda*, *Sorex palustris*, *Sorex bendirii*, and *Sorex alakanus*), in Southeast Asia (*Nectogale elegans*, *Chimarrogale*, six species), and in the Palearctic (*Neomys*, three species). Water



Fig. 2 Web-footed tenrec *Limnogale mergulus* from Ranomafana National Park in Madagascar, Dec 1996. Photo by S. Zack & B. D. Patterson

shrews are found along streams and lakes and in wet forests; many other shrews also exploit mesic microhabitats yet are not water-dependent. The desmans are specialized aquatic insectivores living in Europe. The Russian desman, *Desmana moschata*, prefers quiet lakes and streams while the Pyrenean desman, *Galemys pyrenaicus*, requires fast-flowing streams. Among several American moles that frequent damp habitats, the star-nosed mole (*Condylura cristata*) is semi-aquatic, living in wet meadows and marshes and near streams. It is an accomplished diver and swimmer, eating aquatic insects, crustaceans, small fish, and earthworms (Nowak, 1999).

Order Lagomorpha (92 species in 3 families; Hoffmann & Smith, 2005): 2 of 61 species of Leporidae are closely associated with water, living in marshes, swamps, lake margins, and coastal waterways in North America (*Sylvilagus palustris* and *Sylvilagus aquaticus*). The riverine rabbit (*Bunolagus monticularis*) inhabits dense riverine scrub along seasonal rivers in South Africa but is entirely terrestrial.

Order Rodentia: This is the largest order of mammals, including 2277 species in 33 families (Wilson & Reeder, 2005). The Holarctic beavers, *Castor canadensis* and *Castor fiber*, are two of the best-known semi-aquatic mammals because of their former economic importance and their visible effects on the environment (Veron, 1992a,b). By building dams and lodges, they impound water, converting streams and rivers into wetlands. Beavers are the prototypical “landscape engineers.”

Other water-dependent rodents include many of the common rats and mice (Muroidea; 1518 species,

Musser & Carleton, 2005). Among the voles and lemmings (Arvicolinae), some are associated with water-dependent habitats (e.g., three species of Palearctic *Arvicola* and Nearctic *Microtus richardsoni*) and others are more strongly aquatic or semi-aquatic; the muskrats (*Ondatra* and *Neofiber*) live and forage in freshwater habitats. The American marsh rats (*Holochilus*), water rats (*Nectomys* and *Amphinectomys*), and some species of rice rats (*Oryzomys*) also inhabit marshy or swampy habitats, although they often forage in adjacent grasslands and forests. One tribe of Cricetidae [fish-eating mice or Ichthyomyini; *Anotomys* (1 sp) *Chibchanomys* (2 sp), *Ichthyomys* (4 sp), *Neusticomys* (5 sp), and *Rheomys* (4 sp)] lives mainly in streams and rivers of tropical America, foraging on aquatic invertebrates and small vertebrates (Voss, 1988), and the two species of Neotropical swamp rats (*Bibimys*) are accomplished swimmers well adapted to aquatic life. In Australasia, a parallel radiation has produced eight species of semi-aquatic murines: *Hydromys* (4 sp, among which 1 sp in Australia), *Parahydromys* (sp), *Crossomys* (1 sp), and *Baiyankamys* (2 sp), the New Guinea waterside rat (*Parahydromys asper*), and the earless water rat (*Crossomys moncktoni*). In Africa, the lone species of *Nilopegamys* is the only murid that seems to fill this swimming, pursuit-predator niche (Kerbis Peterhans & Patterson, 1995), although *Colomys* (1 sp), *Dasymys* (9 sp), *Malacomys* (3 sp), and *Pelomys* (5 sp) also live in close association with fresh water, some even foraging for aquatic organisms in shallow pools.

Members of several families of porcupine relatives have become aquatic or semi-aquatic. In Central and South America, one of the best-known aquatic rodents is the capybara (*Hydrochaeris hydrochaeris*), which grazes on vegetation near rivers, lakes, ponds, and wetlands. Another Neotropical rodent, the paca (*Cuniculus*), feeds on seeds and vegetation in riverine forest and is an accomplished swimmer, taking refuge from predators in water. The nutria or coypu (*Myocastor*), native to Patagonia but introduced worldwide to control weeds and provide food, is consummately adapted to life in fresh water. The five species of hutia (*Mesocapromys spp.*) inhabit the wetlands of Cuba. The African greater cane rat (*Thryonomys swinderianus*) lives near water in swamps, reed beds, and tall, dense grass and is a proficient swimmer.

Order Carnivora (286 species in 15 families, Wozencraft, 2005): All seals are carnivores highly

Table 2 Number of species of freshwater (aquatic and freshwater-dependent) mammals

	PA		NA		AT		NT		OL		AU		PAC		ANT		World FW Species number FW	Total mammal species number
	FW aq	FW depdt	FW aq	FW depdt	FW aq	FW depdt	FW aq	FW depdt	FW aq	FW depdt	FW aq	FW depdt	FW aq	FW depdt	FW aq	FW depdt		
Monotremata												1					1	3
Metatheria				1?				1									2	331
Eutheria																		
Chiroptera				2													2	1,116
Insectivora	2	3		4				4		7							20	479
Insectivora-	2	3		4					7								16	428
Soricomorpha (water shrews, desmans, moles)																		
Insectivora-								4									4	51
Afrosoricida (otter shrews)																		
Lagomorpha				2				1									3	92
Rodentia	2	3	5	>3	2	18	>20					9					>60	2,277
Rodentia-castor	2		2														2	
Rodentia-Muroidea		3		>3	1	18	>20					9					>54	1,518
Rodentia-others			3		1												4	
Carnivora	6	2	2	2	7	3	5	2									25	286
Carnivora-seals	2		1														3	
Carnivora-otters	2	2	1	2	4	3	3		3								17	
Carnivora- mongooses					2				1								3	
Carnivora-Viverrids					1				1								2	
Carnivora-felids	2									2							2	
Sirenia						1	1	1									3	4
Artiodactyla					2												2	220
Cetacea							2	4				1					6	~80
Total	10	8	7	>15	9	26	>27	1	9	9	11	0	0	0	0	0	>124	~5,500

PA: Palearctic, NA: Nearctic, AT: Afrotropics, NT: Neotropics, OL: Orient, AU: Australasia, PAC: Oceanic Islands Pacific, ANT: Antarctic

Table 3 Genera of freshwater (aquatic and freshwater-dependent) mammals

	PA	NA	AT	NT	OL	AU	PAC	ANT	World FW genus number
Monotremata						1			1
Metatheria		1		1					2
Eutheria									
Chiroptera		1							1
Insectivora	3	2	3		2				10
Insectivora-Soricomorpha (water shrews, desmans, moles)	3	2			2				7
Insectivora-Afrosoricida (otter shrews)			3						3
Lagomorpha		1	1						2
Rodentia	2	7	6	8		4			26
Rodentia-castor	1	1							1
Rodentia-Muroidea	1	3	5	8		4			21
Rodentia-others		3	1						4
Carnivora	3	3	5	3	5	1			14
Carnivora-seals	1	1							2
Carnivora-otters	2	2	3	2	3				8
Carnivora-mongoose			2		1				2
Carnivora-Viverrids				1		1			2
Carnivora-felids					1				1
Sirenia			1	1					1
Artiodactyla			2						2
Cetacea				2	4	1			6
Total	8	15	18	15	11	7	0	0	65

PA: Palearctic, NA: Nearctic, AT: Afrotropics, NT: Neotropics, OL: Orient, AU: Australasia, PAC: Oceanic Islands Pacific, ANT: Antarctic

modified for aquatic life. Most are marine, but several live in fresh water. The Baikal seal (*Pusa sibirica*) is the only species of seal restricted to fresh water. The Caspian seal (*Pusa caspica*) is endemic to the Caspian Sea, a saline lake. Two subspecies of ringed seal (*Pusa hispida*), the Ladoga seal (*P. h. ladogensis*), and the Saimaa seal (*P. h. saimensis*), are endemic to freshwater lake systems in Russia and Finland, respectively, and the Ungava seal (*Phoca vitulina mellonae*), a subspecies of the widely distributed harbor seal (*Phoca vitulina*), inhabits a network of rivers and lakes in Quebec's Ungava Peninsula (Reijnders et al. 1993). Other harbor seals are primarily marine and estuarine, but sometimes wander far up rivers and visit lakes, occasionally remaining in fresh water year-round.

Many other carnivores fish in rivers and lakes, but spend more time on land. All otters (subfamily Lutrinae) other than *Enhydra lutris* and *Lontra felina*,

which are principally marine (also some individuals of *Lontra canadensis* forage in near-shore marine waters), are completely dependent on fresh water; their morphology and behavior reflects their aquatic way of life. Otters live in Africa (*Aonyx capensis*, *Aonyx congicus*, *Lutra lutra*, *Lutra maculicollis*), Central and South America (*Lontra longicaudis*, *Lontra provocax*, *Pteronura brasiliensis*), Eurasia (*Lutra lutra*, *Lutra nippon*), southeast Asia (*Lutra sumatrana*, *Lutrogale perspicillata*, *Aonyx cinerea*) and North America (*Lontra canadensis*). Their terrestrial relatives, the American mink (*Neovison vison*) and the European mink (*Mustela lutreola*), are also closely associated with freshwater ecosystems, as is the polecat (*Mustela putorius*).

Other groups of carnivores show lesser degrees of dependence on fresh water. The raccoons (*Procyon spp.*) and many mongooses (Herpestidae) live in marshy and riverine habitats and feed on freshwater

animals; the Marsh mongoose (*Atilax paludinosus*) and the long-snouted mongoose (*Herpestes naso*) are among the most water-dependent. Two viverrids are adapted to freshwater habitats and have morphological adaptations for semi-aquatic life. One lives in Congo tributaries (the aquatic genet, *Genetta piscivora*), whereas the other (the otter civet, *Cynogale bennettii*) lives in south-east Asian streams and swamps (Veron et al., 2006). Two species of Asian felids, the fishing cat (*Prionailurus viverrinus*) and the flat-headed cat (*Prionailurus planiceps*), are strongly associated with wetlands and hunt aquatic animals. The jaguar (*Panthera onca*) also feeds on aquatic prey like turtles and caimans, and the jungle cat (*Felis chaus*) can dive to catch fish.

Order Sirenia (2 families, Shoshani, 2005): Sirenians are fully aquatic herbivores that live in coastal marine and fresh waters of the tropics. There are four living species in the order, the dugong (marine) and three species of manatees (*Trichechus* spp). All three manatee species occur to some extent in fresh water and those manatees that live primarily in marine environments may depend on at least occasional access to fresh water for drinking. The Amazonian manatee (*T. inunguis*) is an obligate freshwater species confined to lakes and rivers of South America. The West African (*T. senegalensis*) and West Indian (*T. manatus*) manatees are riverine, estuarine, and marine, respectively occurring in central-west Africa and in northern South America, eastern Central America, south-eastern North America, and the Caribbean islands.

Order Artiodactyla (240 species in 10 families; Grubb, 2005): The best-known freshwater artiodactyls are the two living hippopotamuses (the common hippopotamus, *Hippopotamus amphibius* and the pygmy hippopotamus, *Hexaprotodon liberiensis*), both of which live in Africa (Fig. 3). Other ungulates forage in and around fresh water but cannot be considered semi-aquatic: the moose or elk (*Alces alces*) in the Holarctic region, the South American marsh deer (*Blastocerus dichotomus*), the Chinese water deer (*Hydropotes inermis*), the Père David's deer (*Elaphurus davidianus*), the Asian water buffalo (*Bubalus bubalis*) in tropical Asia, Africa's sitatunga (*Tragelaphus spekei*), the five species of the genus *Kobus* (waterbuck, lechwes, kob, puku), and the African water chevrotain (*Hyemoschus aquaticus*).



Fig. 3 A pod of hippos (*Hippopotamus amphibius*) rests on the banks of the Mara River in SW Kenya. Remaining in or close to water throughout the day, hippos emerge at night to graze on nearby vegetation. Photo by B. D Patterson

Order Cetacea (84 species in 11 families; Mead & Brownell, 2005): The cetaceans are strictly aquatic; most of the species are marine but a few live in fresh water. There are two obligate freshwater species in Asia: the Yangtze River dolphin or baiji (*Lipotes vexillifer*) and the blind South Asian species *Platanista gangetica* in the Indus, Ganges, Brahmaputra, Meghna, and Karnaphuli river systems. The Irrawaddy dolphin (*Orcaella brevirostris*) and finless porpoise (*Neophocaena phocaenoides*) are considered facultative freshwater cetaceans as they have populations living in major river systems (e.g., Irrawaddy, Mekong, Yangtze) as well as estuaries and coastal marine waters (Jefferson & Smith, 2002). South America has two species of river dolphin, the Amazon dolphin or boto (*Inia geoffrensis*) and the tucuxi (*Sotalia fluviatilis*). An estuarine and coastal marine form of tucuxi (*S. guianensis*) also exists, and it occurs far up some major rivers such as the Orinoco (Cunha et al., 2005). Another so-called “river dolphin,” the La Plata dolphin or franciscana (*Pontoporia blainvillei*), actually lives in coastal waters and estuaries of eastern South America.

Phylogeny and historical process

The earliest representative of the Eutherian mammals is about 125 millions years old, but the ecomorphological diversification of placental mammals began in earnest with the demise of dinosaurs 65 millions years ago (Rose & Archibald, 2005).

The approximate ages of the two strictly aquatic orders of mammals are 52 million years for the cetaceans and 61 million years for the sirenians (Rose & Archibald, 2005). Within the Artiodactyla, the specialized freshwater family Hippopotamidae arose in the middle Miocene (ca 15 million years ago) (Rose & Archibald, 2005). Within the carnivores, the otters split from other Mustelidae between 15 and 8 million years ago (Marmi et al 2004). Within the Rodentia, the beavers were believed to be related to the Sciuridae, while recent studies now place them close to the Geomyoidea (pocket gophers and allies) with a possible Eocene origin in North America (Huchon et al., 2002). There are only two extant species, but the family was more diverse in the past, with species not adapted to aquatic life, including a species living underground (Miocene), and giant species during the Pleistocene (Müller-Schwarze & Sun, 2003). The Ichthyomyine forms a diversified group of freshwater rodents within the neotropical muroids; their ecomorphological adaptation to a semi-aquatic way of life and carnivory is peculiar among rodents (Voss, 1988).

In some cases, the morphological differentiation of an aquatic form has occurred in a short time, within a group of terrestrial forms. The aquatic genet is a specialized genet, and recent phylogenetic results (Gaubert et al., 2004) show that this species is included within the genet clade, suggesting its rapid adaptation to piscivory and freshwater habitat occurred via extreme morphological modification.

Human related issues

Many of the freshwater mammals are threatened (IUCN Red List species; IUCN, 2006), both by the destruction of their habitat and by direct or specific menaces. Also, very little is known about many of the species and there are insufficient data to determine the status of their populations. The status of threatened freshwater mammals is given in Table 1.

The major threats to the freshwater mammals are the modification or destruction of their habitat (deforestation, canalisation of rivers, removal of bankside vegetation, dams, draining of wetlands), pollution, trapping, and hunting.

Among the threatened freshwater mammals, the European mink suffers from competition with the

American mink (escaped from fur farms) and from over-hunting and habitat loss. In France, an additional threat comes from unintentional poisoning and trapping. The American mink is not the only invasive species in Europe to cause serious threats to indigenous wetland species. The South American nutria, for instance, escaped from fur farms, and feral populations have become established in North America, Europe, and Asia, causing damage to river banks and feeding on wetland plants.

In Africa and Asia, otters are killed for skins and meat and they are considered responsible for poultry losses. Bush clearing and deforestation have destroyed or modified their habitat. Otters also suffer from canalisation of rivers, removal of bankside vegetation, dams, draining of wetlands, and other man-made habitat changes. Pollution is another major threat, as are trapping and hunting.

Some more specific threats affect the hippopotamus. The historical range of the common hippopotamus extended throughout Africa, but is now limited, with an estimated total population in 2004 of only 120,000–148,000 individuals (IUCN/SSC Hippo Specialist Group, 2006). The numbers in some countries are unknown. Common hippos have probably disappeared from Liberia and Mauritania. Major threats are habitat loss and illegal hunting for meat and ivory, which have been increasing in recent years. The trade ban on elephant ivory has increased illegal hunting of hippos for their teeth—annual exports of hippopotamus teeth increased by 530% within 2 years following the ivory ban (IUCN/SSC Hippo Specialist Group, 2006). The pygmy hippopotamus (*H. liberiensis*) also suffers from hunting and habitat loss and its total population was estimated in 2004 at no more than 2,000–3,000 individuals in the wild (IUCN/SSC Hippo Specialist Group, 2006). Three species of hippopotamus are recently extinct (*Hippopotamus lemerlei*, *Hippopotamus laloumena* and *Hexaprotodon madagascariensis*), but dating of their remains and times of extinction are debated.

Most of the water-dependent ungulates are threatened. Wild Asian buffalo suffer from interbreeding with feral and domestic buffalo and habitat loss and degradation. Transmission of diseases and parasites by domestic livestock and competition with them are also serious threats.

Certain of the river dolphins and porpoises are among the most threatened mammals of the world.

The Yangtze River dolphin has been regarded for many years as the world's most endangered cetacean (IWC, 2001; Reeves et al., 2003) and the results of a range-wide survey in late 2006 suggest that it already may be extinct. River cetaceans suffer from the loss or fragmentation of habitat (land 'reclamation', channelization, impoundment, diversion, etc.), pollution, depletion of food resources by fishing, incidental mortality from fishing operations (entanglement in nets, electrocution, snagging on hooks, etc.), boat collisions, and disturbance or displacement by intensive vessel traffic.

The beaver played a very important economic and historical role during the 16th to 18th century, particularly in North America. Competition for fur trade among the European powers resulted in conflict over territory and trade hegemony (Müller-Schwarze & Sun, 2003). As a consequence of trapping and hunting, by the end of the 19th century the populations of beavers in both North America and Eurasia had been reduced and even extirpated from large areas portions of their range (Veron, 1992a,b).

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