

Evolution of the Sirenia: An Outline

The order Sirenia is closely associated with a large group of hoofed mammals known as Tethytheria, which includes the extinct orders Desmostylia (hippopotamus-like marine mammals) and Embrithopoda (rhinoceros-like mammals). Sirenians probably split off from these relatives in the Palaeocene (65-54 mya) and quickly took to the water, dispersing to the New World. This outline attempts to order all the species described from the fossil record in chronological order within each of the recognized families of Prorastomidae, Protosirenidae, Dugongidae, and Trichechidae. This outline began as an exercise in preparation for my Ph. D. preliminary exams and is primarily based on decades of research and peer-reviewed literature by Dr. Daryl P. Domning, to whom I am eternally grateful. It has been recently updated with the help of Dr. Jorge Velez-Juarbe. However, this document continues to be a work-in-progress and not a peer reviewed publication!

Ancestral line: *Eritherium*

Order Proboscidea

- Elephantidae (elephants and mammoths)
- Mastodontidae
- Deinotheriidae
- Gomphotheriidae

Ancestral line: *Behemotops*

Order Desmostylia (only known extinct Order of marine mammal)

Order Sirenia Illiger, 1811

- Prorastomidae
- Protosirenidae
- Dugongidae
- Trichechidae

With only 5 species in 2 families known to modern man, you might be surprised to learn that the four extant species represent only a small fraction of the sirenians found in the fossil record. As of 2012, ~60 species have been described and placed in 4 families. Sirenians, as well as the sea grasses (their primary food item) probably originated in the Tethys Sea area, the ancient sea that separated Gondwanaland from Laurasia. Morphologically and molecularly they are grouped with proboscideans (elephants) and desmostylians in a taxon called Tethytheria. Sirenians probably share an Old World origin with these and other orders such as the Embrithopoda and Hyracoidea (hyraxes). After returning to the sea, they quickly

“dispersed throughout the Tethyan realm and have remained pantropical ever since with the notable exception of the lineage leading to Steller’s seacow (Hydrodamalis), which adapted to the temperate and cold waters of the North Pacific. This persistent tropicality very likely accounts for the depleted diversity of the Sirenian, given the global cooling of the last few million years.” (Domning 2001b).

Sirenians first appear in the fossil record about 50 mya in the Middle Eocene Epoch (image above is (c) Christopher Scotese, <http://www.scotese.com>), early Cenozoic Era. The Cenozoic is the most recent of three major subdivisions of animal history; a convenient Epoch Key is found in the footer of this document (PDF and DOC versions). Prior to the Cenozoic, there were the Paleozoic Era (age of the invertebrates, fishes, & amphibians) and the Mesozoic Era (age of the reptiles & dinosaurs). The Cenozoic Era is short, relative to the two previous Eras, spanning only about 65 million years, from the end of the Cretaceous Epoch (marked by the extinction of non-avian dinosaurs) to the present. The Cenozoic Era is often called the Age of Mammals, but it could just as easily be called the Age of the Birds, Insects, Flowering Plants, or Teleost Fish.

Nomenclature omitted from this outline (because I could not place them within a family based on my readings):

Sirenavus hungaricus Kretzoi, 1941 possibly referred to the Prorastomidae (Domning 1978) and *Anisosiren pannonica* Kordos, 1979 are both from the Middle Eocene Hungary, *Paralitherium tarkanyense* Kordos 1977 Late Eocene Hungary, *Ishatherium subathuensis* Sahni and Kumar, 1980 (Domning, Morgan & Ray 1982); *nomen nudum Trachypleurotherium* (Domning 1982a.); *Florentinoameghinia mystica* Simpson, 1932a from the Early Eocene of Patagonia, referred to the Sirenia



Dr. Daryl Domning, Howard University, November 2007
with *Metaxytherium* skull. Photo © Caryn Self-Sullivan

<u>Palaeocene</u>	<u>Eocene</u>	<u>Oligocene</u>	<u>Miocene</u>	<u>Pliocene</u>	<u>Pleistocene</u>	<u>Holocene</u>
64-54 mya	54-38 mya	38-23 mya	23-5 mya	5-1.8 mya	1.8-0.012 mya	12kya-Present

by Sereno (1982), is considered *Mammalia incertae sedis* (Domning 2001a); *Lophiodolodus chaparralensis* is best regarded as *Mammalia incertae sedis*, possibly Sirenia (Domning 1982a); *Thalattosiren petersi* (Abel, 1904) may represent merely immature *Metaxytherium* (Domning 1994); *Prohalicore*?

1. **Family Prorastomidae** Cope, 1889 (Middle Eocene): Oldest fossil records of sirenians, the taxonomic family of prorastomids, were amphibious quadrupeds that resembled Paleocene and Eocene condylarths, but had aquatic specializations such as retracted nasal openings, absence of paranasal air sinuses, and dense and swollen ribs. The most primitive prorastomids had adequate support of body weight through the sacroiliac joint to provide for terrestrial locomotion. Shared characteristics included: (1) undeflected, laterally compressed, anterior skull and mandible; and (2) well-developed hind legs. Prorastomids had almost straight (undeflected) rostra, whereas all later sirenians had more or less down turned snouts (for bottom feeding).
 - 1.1. *Pezosiren portelli* Domning, 2001 (from Jamaica)¹: Oldest known sirenian in the fossil record; named and described by Domning in 2001. “This animal was fully capable of locomotion on land, with four well-developed legs, a multivertebral sacrum, and a strong sacroiliac articulation that could support the weight of the body out of water as in land mammals. Aquatic adaptations show, however, that it probably spent most of its time in the water. Its intermediate form thus illustrates the evolutionary transition between terrestrial and aquatic life. Similar to contemporary primitive cetaceans, it probably swam by spinal extension with simultaneous pelvic paddling, unlike later sirenians and cetaceans, which lost the hindlimbs and enlarged the tail to serve as the main propulsive organ. Together with fossils of later sirenians elsewhere in the world, these new specimens document one of the most marked examples of morphological evolution in the vertebrate fossil record.” Domning, D. P. 2001. The earliest known fully quadrupedal sirenian. *Nature* 413:625-627.
 - 1.2. An un-named genus and species of Prorastomidae from the Late Early or early Middle Eocene, Jamaica Guys Hill Member, Chapelton Formation (Domning et al., 1995, 1996 as reported in Domning 2001a)
 - 1.3. *Prorastomus sirenoides* Owen, 1855 (Middle Eocene from Jamaica): Reduced sacroiliac articulation, but could probably still support its body weight out of the water. *Image at right is artist's conception of Prorastomus sirenoides submitted by Daryl P. Domning*
 - 1.4. An unknown genus and species of Prorastomidae from the early middle Eocene of Senegal (Hautier et al., 2012)
2. **Family Protosirenidae** Sickenberg 1934: Middle Eocene Protosirenids, the next most primitive sirenian family, retained well-developed (through reduced) hind limbs, but had weak sacroiliac joints (interpreted as unable to support body via hind limbs on land?). The genus Protosiren represents one of the more widely distributed Eocene genera, ranging across the southern part of the eastern Tethys Sea from North Africa (Egypt) to South Asia (Indo-Pakistan). Compare image below to Eocene map on previous page. Protosiren is known from skulls and partial skeletons (Abel, 1907; Domning and Gingerich, 1994; Gingerich et al., 1994, 1995, Zalmout et al., 2003). They were mainly aquatic animals that probably spent little if any time on land. Shared characteristics included: (1) well-developed hind legs; (2) more or less down-turned rostrum suitable for bottom feeding; (3) broadened mandibular symphysis indicative of less selective grazing; and (4) reduction and eventual loss of incisors and canines (except tusks). Both prorastomids and protosirenids were evidently extinct by the end of the Eocene, ~38 mya.
 - 2.1. Genus *Protosiren* Abel, 1907 (from Egypt, North America?, Europe, Asia)
 - 2.1.1. *P. eoethene* (Zalmout et al. 2003, from early middle Eocene deposit in Pakistan)
 - 2.1.2. *P. fraasi* Abel, 1907 (Early Middle Eocene, India, Egypt, Hungary?)
 - 2.1.3. *P. sattaensis* (Gingerich et al. 1995; late middle Eocene, 39-40 Ma, Pakistan)
 - 2.1.4. *P. smithae* (Domning & Gingerich, 1994; direct descendent from *P. fraasi*; Late Middle Eocene, Egypt)
 - 2.1.5. *P. minima* Desmarest, 1822 (Middle-late Eocene, France – not mentioned in Zalmout et al. 2003, current classification unknown?)
 - 2.2. A new genus and species of protosirenid from Florida and North Carolina Avon Park, Inglis, and Castle Hayne formations and possibly another from Florida Late Eocene Crystal River Formation (Domning 2001a)
 - 2.3. Genus *Ashokia* Bajpai et al., 2009 (from Asia)
 - 2.3.1. *A. antiqua* (Bajpai et al., 2009; early Middle Eocene of India)

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64-54 mya	54-38 mya	38-23 mya	23-5 mya	5-1.8 mya	1.8-0.012 mya	12kya-Present

3. **Family Dugongidae** Gray, 1821 (Middle and Late Eocene to Recent): Early members of the taxonomic family of dugongids were fully aquatic, with only vestigial hind limbs (i.e., loss of functional hind limbs). Dugongids went on to become the most diverse and successful sirenian family, and also may have given rise to the trichechid family. The Oligocene Epoch (38-23 mya) was dominated by the dugongids, including the genera *Halitherium*, *Metaxytherium*, *Caribosiren*, (ALL subfamily Halitheriinae), *Crenatosiren*, *Dioplotherium*, and probably *Corystosiren* and *Rytiodus*, (ALL subfamily Dugonginae) which have Early Miocene (and thereafter) fossil records.

Subfamily Halitheriinae Carus, 1868: Halitheriines are not known in the Caribbean after the Miocene, which ended 5 mya.

- 3.1. Genus *Eotheroides* Palmer, 1899 (Synonymous with *Eotherium* Owen 1875, *nec* Leidy 1853, *Eosiren* Andrews 1902, *Archaeosiren* Abel 1913, *Masrisiren* Kretzoi 1941): Mid Eocene, Mediterranean. Contained 5 nominal species? Domning 1978.
- 3.1.1. *E. aegyptiacum* Owen, 1875: Middle Eocene, near Cairo, Egypt, later discoveries from the late Eocene marine beds of Fayum.
- 3.2. Genus *Prototherium* de Zigno, 1887 (Mid to Late Eocene, Mediterranean)
- 3.2.1. *P. veronense* de Zigno, 1875 Late Eocene dugongid from Italy. (includes *Protosiren dolloi* Abel 1904 = *Mesosiren* Abel 1906) The most primitive sirenian in which the juvenile dentition is adequately known, with 5 being the primitive number of premolars in sirenians, the last 4 of which are presumably homologous to those in other placental mammals (Domning 1982a). There is no fossil record of the juvenile dentitions of the manatees, making it all the more striking to find in the Recent *Trichechus* a pattern almost identical to that of *P. veronense*.
- 3.2.1.1. "*P.*" *intermedium* Bizzotto, 1983
- 3.3. Genus *Eosiren* Andrews, 1902 (Mid to Late Eocene, Mediterranean)
- 3.3.1. *E. abeli* Sickenberg, 1934 (?synonymous w/ *E. imenti*, see Domning 1994; Early Oligocene, Egypt)
- 3.3.2. *E. libyca* (*Eotheroides libycum*?) Andrews, 1902 (see Domning 1994; Late Eocene)
- 3.3.3. *E. stromeri* (*Eotherium stromeri*?) Sickenberg, 1934
- 3.4. Genus *Halitherium* Kaup, 1838 (extends to Late Oligocene in Europe, and apparently the western Atlantic and Caribbean, where it gave rise to the genus *Metaxytherium*)
- 3.4.1. *H. schinzii* Kaup, 1838
- 3.4.2. *H. christolii* Fitzinger, 1842 (here includes *H. abeli* Spillman, 1959 and *H. pergense* Toula, 1899)
- 3.4.3. *H. antillense* Matthew (1916): Early to Late Oligocene, Puerto Rico Juana Díaz and San Sebastián formations. May be synonymous w/ *Metaxytherium*)
- 3.4.4. *H. alleni*
- 3.4.5. *H. taulannense* Sorbi, 2001 (late Eocene of France)
- 3.5. Genus *Caribosiren* Reinhart, 1959
- 3.5.1. *Caribosiren turneri* Reinhart, 1959 (Late Oligocene, Puerto Rico)
- 3.6. Genus *Metaxytherium* de Christol, 1840 (prominently represented in the Miocene & Pliocene, sympatric with *Crenatosiren* and *Dioplotherium* in northern Florida, and sympatric with *Dusisiren* and *Dioplotherium* in Baja; the taxon *Hesperosiren* has been placed in the synonymy of *Metaxytherium*)
- 3.6.1. *M. krahuletzii* Depéret, 1895 (Early Miocene in Europe, probably direct ancestor to all other Old World *Metaxytherium*; relationship to New World *Metaxytherium* is unclear)
- 3.6.2. *M. medium* Desmarest, 1822 (Europe, direct descendent of *M. krahuletzii*)²
- 3.6.3. *M. serresii* Gervais, 1847 (Europe, direct descendent of *M. medium*)²
- 3.6.4. *M. subapenninum* Bruno, 1839 (Europe, direct descendent of *M. serresii*; synonymous w/ *M. forestii* Capellini, 1872)²

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64-54 mya	54-38 mya	38-23 mya	23-5 mya	5-1.8 mya	1.8-0.012 mya	12kya-Present

- 3.6.5. *M. crataegense* (= *M. calvertense* Kellogg, 1966, = *M. riveroi*, American Atlantic, dispersed to eastern Pacific Middle Miocene Baja California, Mexico, and Orange County California (Aranda-Manteca et al. 1994).
- 3.6.6. *M. floridanum* Hay, 1922 (American Atlantic). *Metaxytherium floridanum* skeleton and artist conception below are on display at the Smithsonian Museum of Natural History in Washington, D.C. Photo submitted by Caryn Self-Sullivan
- 3.6.7. *M. arctodites* (Aranda-Manteca Francisco J. et al. 1994; direct link to new subfamily, the Hydrodamalinae)
- 3.6.8. *M. albifontanum* (Velez-Juarbe, Jorge, and Daryl P. Domning. 2014. Journal of Vertebrate Paleontology 34(2)). Abstract: We describe a new species of the halitheriine dugongid genus *Metaxytherium* from the late Oligocene of Florida and South Carolina. The new species is represented by cranial and postcranial material, including parts of the axial and appendicular skeleton. *Metaxytherium albifontanum*, sp. nov., differs from other species of *Metaxytherium* by the following unique combination of plesiomorphic and derived characters: posterior end of nasal process of premaxilla broad and flat relative to what is observed in most other members of the genus (somewhat resembling *M. subapenninum*); ventral extremity of jugal under posterior edge of orbit (character 85[1]) (shared with *M. krahuletzii*); exoccipitals separated in dorsal midline (character 66[1]) (shared with all other species in the genus, except some *M. krahuletzii*); and innominate with acetabulum (nearly lost or lost in *M. crataegense*, *M. floridanum*, *M. serresii*). This new species was sympatric with two dugongines, *Crenatosiren olseni* and *Dioplotherium manigaulti*. The small tusks and cranial morphology of *M. albifontanum*, sp. nov., indicate that it was likely a consumer of small seagrasses. Our phylogenetic analysis is consistent with previous ones in placing Hydrodamalinae within a paraphyletic *Metaxytherium* spp. and placing the *Metaxytherium* spp. + Hydrodamalinae clade as the sister group to Dugonginae. *Metaxytherium albifontanum*, sp. nov., is the oldest known member of its genus; this might indicate that the group originated in the West Atlantic and Caribbean region and later dispersed to the Old World Tethys region.

Subfamily Dugonginae Gray, 1821 (here includes Rytiodontinae Abel, 1914): early Oligocene to Late Pliocene. The subfamily Dugonginae are the only dugongines known from the Caribbean region's Pliocene deposits. By this time the halitheriines have disappeared from the Caribbean fossil record. *Corystosiren* is present in Early Pliocene, and *Xenosiren* (descendent from *Dioplotherium*) may have been contemporaneous with it (*Corystosiren*). The ONLY Late Pliocene dugongid known in the Caribbean region is a Dugong-like dugongine with large tusks (# 8 Unnamed, below). Its immediate ancestry is unclear, but may have stemmed from one of the un-described small dugongines mentioned above. By the end of the Pliocene, 1.8 mya, dugongids seem to have died out in the western Atlantic altogether. Dugonginae had the tendency to evolve large and often blade-like tusks, in contrast to the smaller, sub-conical tusks of Oligocene and Miocene halitheriines, and may have fed preferentially on the rhizomes of more robust sea grasses. This sub-family probably arose in the Caribbean-West Atlantic region and underwent an adaptive radiation and pantropical dispersal in the Late Oligocene and Early Miocene.

- 3.7. Genus *Crenatosiren* Domning, 1991 (Early-Late Oligocene, SE USA)
 - 3.7.1. *C. olseni* Reinhart, 1976
- 3.8. Genus *Dugong* Lacépède, 1799
 - 3.8.1. *Dugong dugon* Müller, 1776. This is the only extant dugong. Its modern distribution includes 37 countries, from SW Africa and Madagascar around the Indian Ocean coastline, including the Red Sea, Gulf of Mannar between Indian and Sri Lanka, and Shark Bay, Western Australia; to the Indo-Pacific islands, Torres Strait; and in the Pacific it's found south to Hervey and Moreton Bay and north to Okinawa.
- 3.9. Genus *Dioplotherium* Cope, 1883
 - 3.9.1. *D. manigaulti* Cope, 1883 (Late Oligocene, Florida, divergently specialized and contemporary with *Crenatosiren*)
 - 3.9.2. *D. allisoni* (Kilmer, 1965): Early Miocene, Brazil, California and Baja; Middle Miocene, Argentina; in California this species was sympatric with *H. gigas* ancestor, *Dusisiren* Kilmer, 1965
- 3.10. Genus *Xenosiren* Domning, 1989

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64-54 mya	54-38 mya	38-23 mya	23-5 mya	5-1.8 mya	1.8-0.012 mya	12kya-Present

3.10.1. *X. yucateca* Domning, 1989 (Late Miocene/Early Pliocene, Yucatan, a direct descendant of *Dioplotherium*)

3.11. Genus *Corystosiren* Domning, 1990

3.11.1. *C. varguezi* Domning, 1990: Early Pliocene in Yucatan and Florida, only, but lineage probably in the region throughout the Miocene; unique in its extremely massive skull roof

3.12. Genus *Rytiodus* Lartet, 1866 (Europe, North Africa, and in Brazil sympatric with *D. allisoni* and *Metaxytherium*)

3.12.1. *R. capgrandi* Lartet, 1866

3.12.2. *R. heali* Domning & Sorbi, 2011 (early Miocene of Libya)

3.13. Genus *Bharatisiren* (India)

3.13.1. *B. kachchhensis* Bajpai, Singh, and Singh 1987: Probably arose in the Caribbean-western Atlantic region and underwent adaptive radiation and pantropical dispersal in the late Oligocene and early Miocene (Bajpai and Domning 1997). Sympatric in the late early Miocene of India with *Domningia* and *Kutchisiren* (Velez-Juarbe et al., 2012).

3.13.2. *B. indica* Bajpai et al., 2006 (late Oligocene of India)

3.14. Genus *Nanosiren* Domning in Domning & Aguilera, 2008 (late early Miocene-early Pliocene of the Western Atlantic, Caribbean and eastern Pacific regions); sympatric with *Corystosiren* and *Dioplotherium* in the early Pliocene of Mexico (Velez-Juarbe et al., 2012).

3.14.1. *Nanosiren garciae* JVP 28(2):479-500; New undescribed Genus (early Pliocene, Florida and Mexico, close to living Indo-Pacific *Dugong*, latest dugongid known in West Atlantic-Caribbean region.

3.14.2. *Nanosiren sanchezi* (late Miocene of Venezuela)

3.15. Genus *Domningia* Thewissen & Bajpai, 2009 (Asia)

3.15.1. *D. sodhae* Thewissen & Bajpai, 2009 (late early Miocene of India)

3.16. Genus *Kutchisiren* Bajpai et al., 2010 (Asia)

3.16.1. *K. cylindrica* Bajpai et al., 2010 (late early Miocene of India)

Subfamily Hydrodamalinae Palmer, 1895 (1833): Distinction due to new adaptive direction; departed from bottom-feeding, increased body size, expanded into temperate to cold climates; adaptations attributed to general cooling in the Pacific and replacement of seagrasses with kelps. See “Sea Cow Family Reunion”, Daryl P. Domning, Natural History, April 1987.

3.17. Genus *Dusisiren* Domning, 1978

3.17.1. *D. jordani* (Kellogg, 1925): Middle Miocene (10-12 mya), California, ancestor of *D. dewana*; sympatric with *Metaxytherium* and *Dioplotherium* in California. Length of one specimen = 4.3 m.

3.17.2. *D. dewana* Takahashi, Domning, and Saito, 1986 (Middle Miocene (9-10 mya), Japan, perfect morphological and chronological “link” between *Dusisiren* and *Hydrodamalis*; see Domning 1987)

3.18. Genus *Hydrodamalis* Retzius, 1794

3.18.1. *H. cuetae* Domning, 1978 (here includes *H. spissa* Furusawa, 1988. Upper Pliocene Pismo Formation California, California & Baja; immediate ancestor to Steller’s seacow; largest sirenian skull on record; *H. cuetae* represents the largest sirenians at up to 10 meters, they are larger than the remnant population of *H. gigas* in the Commander Islands)

3.18.2. *H. gigas* (Zimmermann, 1780)³: Steller’s seacow; Late Pleistocene-Recent. Extant in the North Pacific Commander Islands during modern times; extirpated by humans for food. Last known kill in 1768. See note 4 for details.

4. **Family Trichechidae** Gill, 1872 (1821): This family arose in the Late Eocene or Early Oligocene, about 38 mya, possibly from within Dugongidae. During the Pliocene (5-1.8 mya), trichechids in the form of *Ribodon* are known in the Caribbean/Western Atlantic region from North Carolina and had apparently expanded their range outside South America

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(where the family originated) by the late Pliocene and with the end of the Pliocene Epoch, had become the only surviving western Atlantic-Caribbean sirenians. *Ribodon* and its descendant *Trichechus* are characterized by supernumerary molars, which continue to be replaced horizontally throughout the animal's life; this is an adaptation to eating the abrasive true grasses (Gramineae), which constitute the principal diet of manatees in South American rivers, their ancestral home. Nutrient runoff from the rising Andes during the Late Tertiary is assumed to have greatly increased the abundance of these true grasses and the biomass of freshwater plants in general (note: seagrasses are not true grasses, but angiosperms). Trichechids may have been restricted to coastal rivers and estuaries of South America until the Late Miocene. Here they fed on freshwater plants, while dugongids inhabited the West Atlantic and Caribbean marine waters and exploited seagrass meadows. "The Mio-Pliocene Andean orogeny (5-10 mya) dumped large quantities of silt and dissolved nutrients into many South American rivers, stimulating growth of aquatic macrophytes, particularly true grasses. Manatees adapted to this newly abundant but abrasive food source by evolving supernumerary molars continually replaced throughout life, as in the Mio-Pliocene form *Ribodon* from Argentina." DPD 1982. Prior to the Andean orogeny, most of the western and central Amazon basin drained in the Pacific and was separated (as it remains today) from the Magdalena (*Potamosiren*), Orinoco, and La Plata basins by drainage divides. The Miocene orogeny closed off the Pacific entrance, temporarily creating (in Mio-Pliocene times) an initially brackish lake system with interior drainage.

Subfamily Miosireninae Abel, 1919: "The Miosireninae are the sister group of the Trichechidae and are now placed in that family. The Trichechidae in this broader sense appear to have arisen somewhat later than previously supposed (late Eocene or early Oligocene rather than middle Eocene) and are rooted well within the Dugongidae instead of being derived separately from the Protosirenidae" (Domning 1994); no further literature is available on these genera)

4.1. Genus *Anomotherium* Siegfried, 1965

4.1.1. *A. langewieschei* Siegfried, 1965

4.2. Genus *Miosiren* Dollo, 1889: Middle Miocene, Europe, aberrant, possibly molluscivorous. Previously placed (with its own subfamily, Miosireninae) within the Dugongidae, though a separate descent from protosirenids was considered an alternate possibility (Domning 1978).

4.2.1. *M. kocki* Dollo, 1889

4.2.2. *M. canhami* (a and b are probable synonyms)

Subfamily Trichechinae Gill, 1872 (1821) [new rank] (see Domning 1982a, 1994) Tertiary trichechids or possible trichechids occur in estuarine and riverine deposits on three sides of the present Amazon region: *Sirenotherium* on the coast of Para in the east, *Potamosiren* in the Magdalena River basin to the north, and *Ribodon* in the Parna River to the south (as well as in North America). At least by the Late Miocene, manatees must have occurred widely along the Caribbean and tropical Atlantic coasts of South America and since the Central American seaway was open, could have reached the Pacific coast as well (Domning 1982a). Competition was from Miocene *Metaxytherium* and they probably remained mostly in coastal rivers and lagoons to exploit expanding resources of freshwater vegetation.

4.3. Genus *Sirenotherium* Possible Early Miocene trichechid described by Paula Couto (1967) on the basis of 2 teeth and some postcranial fragments from Brazil.

4.3.1. *Sirenotherium pirabense* is allocated to Trichechidae or Dugongidae *incertae sedis* (Domning 1982a)

4.4. Genus *Potamosiren* Reinhart, 1951: Colombia, Middle Miocene (Friasian); earliest known probable trichechid. Another species not listed below from one tooth probably represents a large species of manatee either contemporaneous and sympatric with or immediately derived from *P. magdalenensis*; and another possible species from an atlas (Domning 1982a).

4.4.1. *P. magdalenensis* Reinhart, 1951 (here includes "*Metaxytherium*" *ortegense* Kellogg 1966, earliest and most primitive known trichechine or true manatee. Earliest specimens from Middle Miocene (Friasian 10-15 mya) Colombia, synonymous with "*Metaxytherium*" *ortegense*; lacked the horizontally-replaced supernumerary teeth characteristic of all later manatees, suggesting that siliceous true grasses (Gramineae) had not yet become an important part of its diet)

4.5. Genus *Ribodon* Ameghino, 1883: Late Miocene/Early Pliocene, ~ 5-6 mya, Argentina and North Carolina; only one species known; probably gave rise to *Trichechus*; evolution of unlimited horizontal tooth replacement appears in *Ribodon* and continues in modern manatees ⁴

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64-54 mya	54-38 mya	38-23 mya	23-5 mya	5-1.8 mya	1.8-0.012 mya	12kya-Present

4.5.1. *R. limbatus* Ameghino, 1883 Argentina

- 4.6. Genus *Trichechus* Linnaeus⁴, 1758 (Modern manatees⁶): Plio-Pleistocene – Recent (1.8 mya): Diversification of the New World *Trichechus* into the ancestors of the modern Amazonian and West Indian species, followed by dispersal of members of the latter stock to West Africa, probably occurred in the Late Pliocene to Pleistocene. Trichechids, probably initially distributed mostly in brackish and/or fresh water expanded their niche following the Later Tertiary Andean orogeny into fresh water and gave rise to the Amazonian manatee. After the end-Pliocene extinction of the last Caribbean dugongids, West Indian manatees invaded the salt-water ecological vacuum.
- 4.6.1. *T. inunguis* (Natterer in von Pelzeln 1883): Amazonian manatee. Probably evolved when the Amazon basin was isolated from both Pacific and Atlantic. Perhaps entered the basin prior its closure during the Andean orogeny from the Pacific (*Ribodon*) or later during intermittent connections or stream capture events on the other sides of the basin (*Trichechus*). In adapting to the new environment, *T. inunguis* evolved more rapidly than did the populations remaining in the coastal regions, and hence exhibits **more derived** characters including smaller and more complex molars, loss of nails, increased diploid chromosome numbers (54 vs. 48 in *T. m.*).
- 4.6.2. *T. manatus* Linnaeus 1758: West Indian manatee; appears about 1.3 mya, Early Pleistocene in Florida, Late Pleistocene - subrecent in Jamaica, Louisiana, Ohio, Arkansas, Florida, South Carolina, North Carolina, Maryland, New Jersey
- 4.6.2.1. *T. m. manatus* Linnaeus, 1758: Antillean manatee
- 4.6.2.2. *T. m. bakerorum* (Domning 2005): North America Pleistocene
- 4.6.2.3. *T. m. latirostris* (Harlan, 1824): Florida manatee
- 4.6.3. *T. senegalensis* Link 1795: West African manatee - dispersed across the Atlantic from South America to Africa in the Late Pliocene or Pleistocene; distributed from Senegal to Angola, this is the **least studied extant** species.
- 4.6.4. cf. *Trichechus* sp. Plio-Pleistocene, western Amazon basin of Brazil, which resembled the modern *T. manatus* rather than *T. inunguis*.
- 4.6.5. *T. m.* unnamed subspecies (120,000-125,000 ya; SE USA, Florida, North Carolina, Louisiana. ?_Is this *T. m. bakerorum*_?

Notes

- 1 See National Geographic Magazine April 2003 for popular account and extraordinary images of *Pezosiren portelli*.
- 2 In the Pliocene, these were the only sirenians left in the Mediterranean; they were extinct by the end of the Pliocene – representing the last sirenians in the European-North African segment of the former Tethyan realm (Domning 1982). Large shark fossils (*Carcharodon megalodon*) are found almost exclusively in association with *M. serresii* bones in the Sahabi Formation, Libya; the sirenian bones bear small scratches or grooves, which could have been made by shark teeth, indicating that shark predation and/or scavenging played an important role in this system.
- 3 *Hydrodamalis gigas* is commonly known as Steller’s sea cow⁵ and is lumped with modern sirenians because it was extant during modern times. A remnant population (~2000 animals living near what are today known as Copper and Bering Islands) of this giant sea-cow was discovered and described by Georg Wilhelm Steller in 1741.
- 4 Unlimited horizontal tooth replacement has been found only in *Ribodon* and *Trichechus*. This evolutionary oddity appears in the marsupial *Peradorcas concinna* (convergent evolution) but not in other sirenian or mammal, not even elephants despite a widespread misunderstanding. Elephants have neither an increased number of teeth nor true horizontal replacement. Like dugongs and many mammals, elephants have forward movement of cheek teeth, AKA “mesial drift”, and the eruption of successive teeth is spaced out over time, but they have no supernumerary molars and do not replace teeth continuously throughout their life like manatees (Domning and Hayek 1984). Dugongs have tusks and also exhibit root hypsodonty.

<u>Palaeocene</u>	<u>Eocene</u>	<u>Oligocene</u>	<u>Miocene</u>	<u>Pliocene</u>	<u>Pleistocene</u>	<u>Holocene</u>
64-54 mya	54-38 mya	38-23 mya	23-5 mya	5-1.8 mya	1.8-0.012 mya	12kya-Present



Photo from Helsinki Museum, submitted by Ari Lampinen, University of Jyväskylä, Finland. *H. gigas* had no phalanges (finger/toe bones), but this mount included man-made ones when the photo was taken; the phalanges have since been removed. There is also a full skeleton on display at the Smithsonian in Washington, DC. Other skeletons have been reported from Kamchatka. Steller's sea cow is the only known Sirenian to have lived in extremely cold, sub-polar waters. For an excellent reconstruction of how Steller's sea cow came to be, see *Sea Cow Family Reunion*, by Daryl Domning (1987).

- 5 *Hydrodamalis gigas*, formerly classified as *Rytina gigas*, was first seen by modern humans when Captain Vitus Bering and his comrades discovered an uninhabited island (later named Bering Island) in 1741. Bering and his two ships, St. Peter and St. Paul, were on their way home to Kamchatka following an expedition to map the coast of Alaska for Tsar Peter I the Great of Russia. The ships were separated during a storm and Captain Bering, the St. Peter, and her crew were stranded on the island. Although Bering died on the island during the winter of 1741, Georg Wilhelm Steller (a German-born naturalist), and about half of the ship's crew survived. Steller described a giant sea cow and its habits, but was vague in his accounts of abundance and distribution. He said he found it numerous and in herds, leaving future researchers to guess at exactly how many. Stejneger (1887) estimated the number at less than 1500 and hypothesized that they were the last survivors of a once more numerous and widely distributed species which had been spared because man had not yet reached their last resort. Upon the survivors' return to Kamchatka in 1742, new hunting expeditions were formed almost every year. They returned to Bering Island where they spent 8-9 months hunting fur-animals and eating sea cow meat to survive. Indeed, many of the expeditions are reported to have wintered on Bering Island for the express purpose of collecting sea cow meat for the remainder of their 3-4 year journey to the Aleutian Islands and America. The last sea cow was reported killed in 1768, just 27 years after the island had been discovered by modern man. From Steller's description, these huge herbivores are believed to have numbered around 1500-2000 in the Bering Island and Copper Island areas of the North Pacific (circa 1741). The largest animals were 4-5 fathoms long (1 fathom = 6 feet), 3.5 fathoms thick around, and weighed 200 puds or 80 short hundredweight (up to about 8,000 pounds). They had no teeth, but two flat white bones, the one above fixed to the palate, and the one below on the inside of the lower jaw. Both were furrowed and had raised ridges with which they masticated kelp. The sea cows were found in herds close to shore. They drifted just below the surface of the water; a single animal resembled an overturned boat. Steller and Waxell both noted large midsections and very small heads.
- 6 The evolutionary history of trichechids is not as well defined as it is for the dugongids. Rather than interpret what I've read, I've selected an excerpt from the expert below. Enjoy!

Evolution of manatees: a speculative history, by Daryl P. Domning. *Journal of Paleontology* 56(3):599-619 May 1982

“Conclusions”

A Primitive sirenians (*Protosiren* or related form) were present in the New World by the Middle Eocene and presumably colonized coastal rivers and estuaries of the then-isolated South American continent. The descendants of these colonists (the Trichechidae), though paralleling contemporary dugongids in reduction of dental formula, remained morphologically conservative in other respects down to *Potamosiren* in the Middle Miocene. They probably continued to occupy a fluvioestuarine niche in contrast to the dugongids in adjacent marine waters; whereas most Oligocene to Miocene Caribbean dugongids had strongly downturned snouts evidently adapted to feeding on marine seagrass beds, Tertiary trichechids (like protosirenids) had slight rostral deflections more suited to a diet of floating or emergent aquatic plants.

<u>Palaeocene</u>	<u>Eocene</u>	<u>Oligocene</u>	<u>Miocene</u>	<u>Pliocene</u>	<u>Pleistocene</u>	<u>Holocene</u>
64-54 mya	54-38 mya	38-23 mya	23-5 mya	5-1.8 mya	1.8-0.012 mya	12kya-Present

B Mio-Pliocene Andean orogeny, with resultant erosion and runoff of dissolved nutrients in South American river systems, greatly increased the productivity of these waters and the abundance of floating macrophytes, especially grasses (Gramineae). Trichechids adapted to this major new food resource, first by evolving horizontally-replaced supernumerary molars (in *Ribodon*) and later by reducing the size of the molars (to increase length of enamel ridge per unit of occlusal area), complicating their enamel folds, and increasing the number of teeth in the toothrow (in *Trichechus*).

C Pliocene trichechids gained entrance to the interior of the Amazon basin, at that time temporarily isolated by drainage reorientation resulting from the Andean orogeny. Cut off from marine waters, they adapted to feed on the floating meadows of nutrient-rich Amazonian lakes, and gave rise to the most derived living species, *T. inunguis*.

D The onset of continental glaciation and the eustatic fall in sea level during the Pliocene cause worldwide rejuvenation of drainage systems and increased silt runoff into nearshore marine waters. Bottom-feeding brachyodont dugongids probably underwent selective pressure for more wear-resistant teeth; in the Indopacific this resulted in the evolution of root hypsodonty in *Dugong*. West Atlantic dugongids might have evolved comparable adaptations, but for the presence of trichechids already possessing highly resistant dentitions. *Ribodon* and primitive *Trichechus* then spread into marine waters as far as North America, replacing the dugongids, broadening their feeding niche to include seagrass meadows, and giving rise to the modern *T. manatus*. *Trichechus* very similar to *T. manatus* dispersed to West Africa, where as *T. senegalensis*, they continue to occupy a fluvioestuarine niche.

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<u>Palaeocene</u>	<u>Eocene</u>	<u>Oligocene</u>	<u>Miocene</u>	<u>Pliocene</u>	<u>Pleistocene</u>	<u>Holocene</u>
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