Superfamily Hippopotamoidea

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*Jan van der Made**

The superfamily Hippopotamoidea includes two families, the Anthracotheriidae and the Hippopotamidae. Hippopotamoidea are "suiform" animals. This term refers mostly to retention of primitive artiodactyl characters such as separate metapodials (usually four metapodials; in some anthracotheres five metacarpals), the lateral metapodials being relatively large, navicular and cuboid not fused, astragalus with proximal and distal trochlea making an angle, complete fibula, presence of upper incisors, etc. The enamel of the cheek teeth is generally crenelated. Anthracotheres have selenodont or buno-selenodont molars: the lingual cusps in the upper molars and the buccal cusps in the lower molars have the shape of a crescent. Hippo molars have trefoil shaped cusps, which resulted as a modification of the anthracothere selenodont pattern. Incisors and canines became very large in hippos. The crowns of the incisors wear off rapidly, but the teeth keep growing.

Most hippos have the orbita in an elevated position, as an adaptation to an aquatic lifestyle. The same character evolved parallel in the later anthracotheres. Living species of hippos tend to spend large parts of the day in the water. During the night they leave water to graze, but usually are not more than some kilometres away from the nearest river or lake. More or less similar habits are usually assumed for the anthracotheres.

Anthracotheriidae are first known from the Eocene of Asia and Europe and the Oligocene of Africa and America. During the Early Miocene they went extinct in America and the mainland of Europe, but lived on till the Late Miocene in Africa and till the Plio-Pleistocene in southern Asia. In Europe they reappeared once again, during the Early Miocene another form seems to have lived on on a Mediterranean island.

The Hippopotamidae evolved in Africa during the Early Miocene. They reached southern Asia and Europe during the latest Miocene. In Europe they went extinct, but re-entered during the Pleistocene. There were several Pleistocene endemic species on several Mediterranean islands and on Madagascar. There are two living species in Africa (CORYNDON 1978).

Most workers agree that hippos evolved from the anthracotheres. PICKFORD (1983) assumed that hippos evolved from *Xenohyus* (Suidae), which in turn evolved from *Doliochoerus* (Palaeochoeridae), all Tayassuidae (= Dicotylidae) in his opinion. This would place the hippos in the superfamily Suoidea and the anthracotheres in the Anthracotherioidea. However, numerous dental, cranial and postcranial characters, as well as characters of the soft tissues argue against this model.

Evolutionary history of the Miocene European Hippopotamoidea GRAY, 1821

Anthracotheriidae LEIDY, 1869: Anthracotheriidae were common in Europe during the Oligocene. The most common forms were the large buno-selenodont *Anthracotherium*, the much smaller selenodont *Elomeryx*, and the very small buno-selenodont *Microbunodon*. *Elomeryx* persisted into the earliest part of the Miocene.

***Elomeryx* MARSH, 1894:** The genus *Elomeryx* contains small selenodont anthracotheres with complete dentition, upper molars with distinct protopreconule (nomenclature of VAN DER MADE 1996) or protoconule, large canines, all incisors incisiform, small diastemata, low elongate skulls with orbitae not or not much elevated. *E. borbonicus* (GERVAIS, 1849) is known from three Miocene localities. The specimens from Pyrimont were initially described as the variety *minor* of the species *E. borbonicus*. SCHAUB (1948) described material of two other Aquitanian localities and elevated *minor* to species rank on the basis of small skull size and the small size of the premolars compared to the molars. HELLMUND (1991) revised the genus and did not recognize the subspecies. However, the premolars of the Miocene form are indeed smaller than those of the Oligocene form and I am inclined to recognize the subspecies *E. borbonicus minor*.

***Brachyodus* DEPÉRET, 1895:** The genus *Brachyodus* is characterized by selenodont molars with a distinct protopreconule, reduced first upper incisors and either caniniform and enlarged third (DINEUR & GINSBURG 1986) or second (HELLMUND 1991) lower incisors, reduced other incisors, low elongate skulls with long diastemata and orbitae not or not much elevated.

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* Dr. Jan van der Made, Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal, 2, E-28006 Madrid, Spain

The Miocene Land Mammals of Europe. – pp. 203-208.

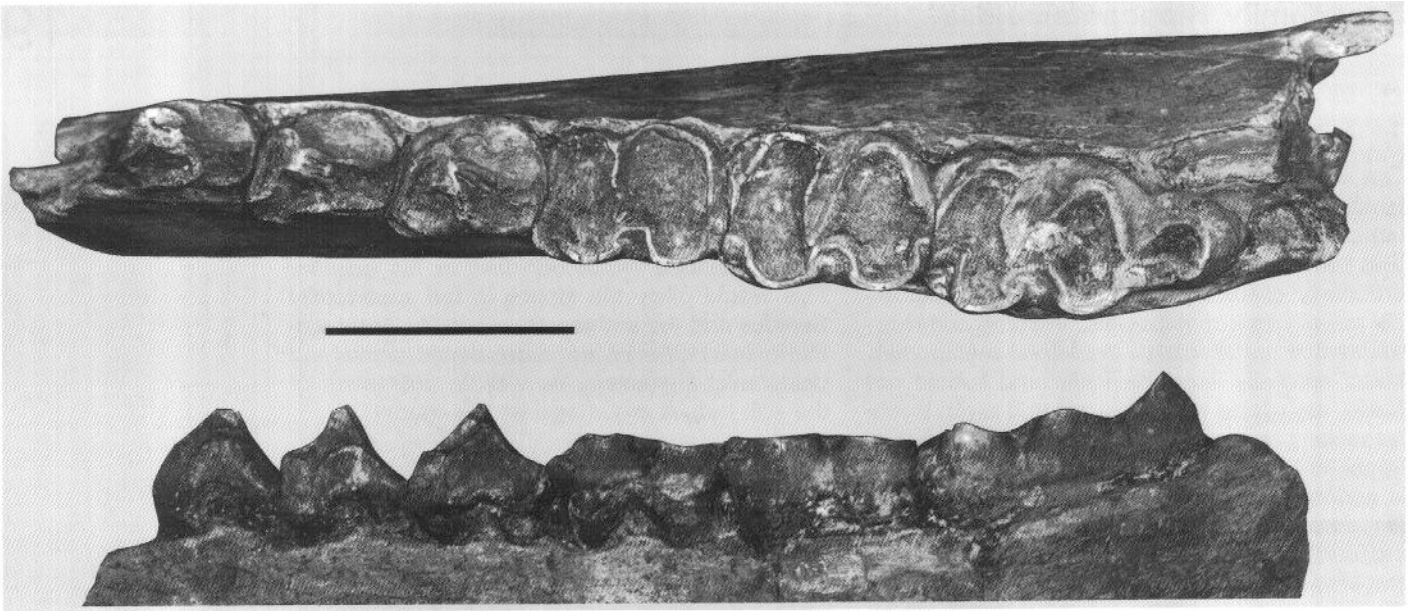

Fig. 19.1. Right mandible with P_2-M_3 of *Brachyodus onoideus* from Neuville-aux-Bois (MSNO 914), holotype. The bar represents 5 cm.

There seems to be a consensus that *Brachyodus* evolved from the Oligocene anthracotheres known from the Fayum in Egypt (PICKFORD 1991). When, after a long period of isolation, in the Early Miocene (MN 3) Africa became connected to Eurasia *Brachyodus* dispersed to Europe (DINEUR & GINSBURG 1986), the Indian Subcontinent (PICKFORD 1987), Asia north of the Himalayas (VISLOBOKOVA 1994) and Japan (TAKAI 1954, as cited by TASSY 1990).

In Europe, *Brachyodus* is represented by a lineage that is characterized by increase in size, the small *B. intermedius* (early MN 3) evolved into the larger *B. onoideus* (late MN 3 and MN 4) (DINEUR & GINSBURG 1986).

***Anthracotherium* CUVIER, 1822?**: HÜRZELER (1982) states that a lower third molar from Casteani, that WEITHOFER (1888, as cited by HÜRZELER) assigned to a species of suid, in reality belongs to an anthracothere of the size of a large *Microbunodon*.

The locality of Casteani is in the lower levels of the Bacinello basin (Italy). Faunas from these levels are late Miocene and their composition indicates that central Italy at that time was an island (ENGESSER 1989). The faunas are poor in species, with few carnivores and no perissodactyls, and the species present show adaptations that are typical of endemic island species. The island may have been large including central Italy as well as Corsica and Sardinia.

ENGESSER (1989) assumed a migration from Africa during the early Late Miocene bringing the primate *Oreopithecus* and the anthracothere to the island. HÜRZELER referred to *Microbunodon*, a bunodont anthracothere. The tooth (labelled as from Ribolla) is indeed bunodont. All later anthracotheres are selenodont. The last bunodont anthracotheres from Europe are from the Oligocene: the very small *Microbunodon* and the very large *Anthracotherium*. In India *Anthracotherium* survived into the the Early Miocene (PICKFORD 1987) and a small bunodont anthracothere is known from Middle Miocene strata of the Chinji Formation (COLBERT 1935). All Neogene anthracotheres described by PICKFORD (1991) from Africa are selendont. However, a tooth from Malembe that HOOIJER (1963) made the type of *Hyotherium dartevellei* was recognized by PICKFORD (1986) as anthracothere. This tooth is bunodont and small and is probably from the Lower Miocene. Morphologically the tooth from Italy fits best *Anthracotherium*. Large mammals tend to reduce their size in endemic island environments (SONDAAR 1986), in the case of suiforms this may be as much as some 25% (VAN DER MADE 1988). All bunodont anthracotheres mentioned are smaller than the animal from Casteani, save for *Anthracotherium*.

A calcaneum from the early Miocene of Oschiri (Sardinia) might be an anthracothere. It suggests an animal roughly of the same size as the tuscan anthracothere. The fauna from Oschiri is supposed to be earliest Miocene (De BRUIJN &

RÜMKE 1974). Corsica and Sardinia were first connected to the mainland of France, but more or less during the Late Oligocene, they became islands (compare RÖGL & STEININGER 1983 and DERCOURT et al. 1986). Later these islands moved towards the island formed by central Italy. The presence of *Oreopithecus* on Sardinia (CORDY & GINESU 1994) suggests that during the Late Miocene Sardinia and central Italy were connected and formed one large island.

In any case, we have to assume that a bunodont anthracothere survived millions of years isolated on an island, while the mainland bunodont anthracotheres went extinct. It is possible that *Anthracotherium* was present on Sardinia when this area separated from southern France and became an island, or that it got to Sardinia shortly after it became an island. The animal reduced its size and possibly aquired other adaptations that are typical of island species. When Sardinia became connected to the central Italian island, the anthracotheres dispersed into that area as well.

Hippopotamidae GRAY, 1821: The oldest hippo known, is a tooth from Rusinga in East Africa (CORYNDON 1978). Deposits at Rusinga are about 18 Ma old (PICKFORD 1986). *Kenyapotamus* from deposits that are slightly younger is the earliest well known hippo (PICKFORD 1983). The genus *Hexaprotodon* appeared some 7 Ma ago. The name refers to the number of incisors in the lower jaw, three on each side; there is an equal number of incisors in the upper jaw. Later species of this genus may have as few as two incisors in each upper and one in each lower jaw. During the Late Miocene, hippos dispersed to Europe and southern Asia. In the Indian Subcontinent and Indonesia, *Hexaprotodon* (with a full set of incisors) lived and evolved well into the Pleistocene. The form that migrated to Europe is currently placed in *Hexaprotodon*, but is different from the southern Asian lineage in being tetraprotodont (with only four incisors in the lower jaw). The living *Hexaprotodon liberiensis* is the last representative of the genus. *Hippopotamus* evolved in Africa from *Hexaprotodon*. All species in this genus are tetraprotodont. This genus dispersed during the Pleistocene to Europe, but not to southern Asia. The living representative is *Hippopotamus amphibius*.

***Hexaprotodon* FALCONER & CAUTLEY, 1836?:** Several hippos were described from the circum Mediterranean area: *Hippopotamus pantanellii* JOLEAUD, 1920 from Casino in Italy, *Hippopotamus*

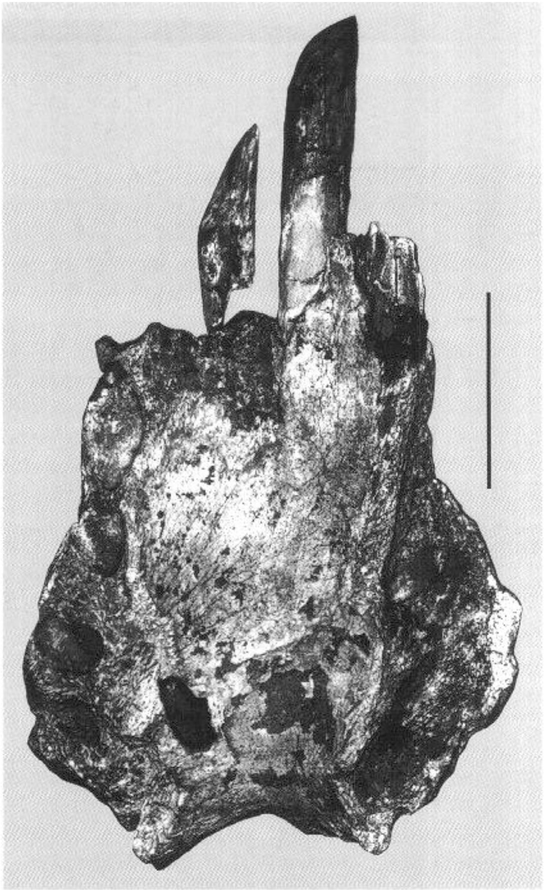

Fig. 19.2. Symphysis with $I_{1\text{-}2}$ of *Hexaprotodon? pantanellii* from La Portera (MNCN). The bar represents 5 cm.

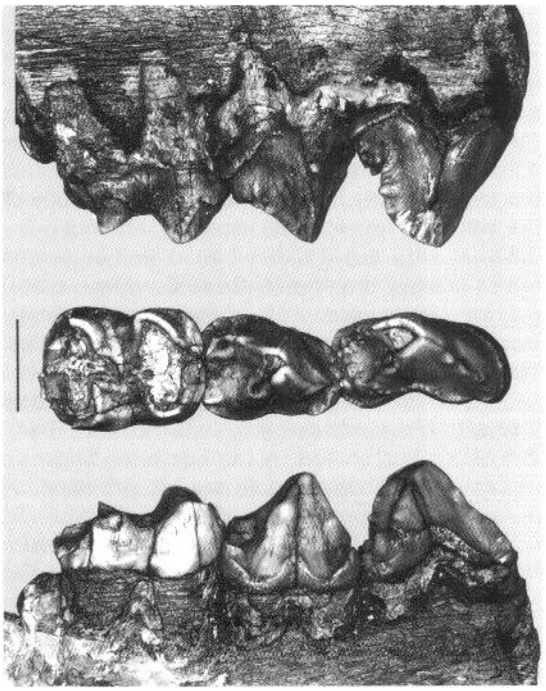

Fig. 19.3. Left mandible with P_3-M_1 of *Hexaprotodon? pantanellii* from La Portera (MNCN). The bar represents 2 cm.

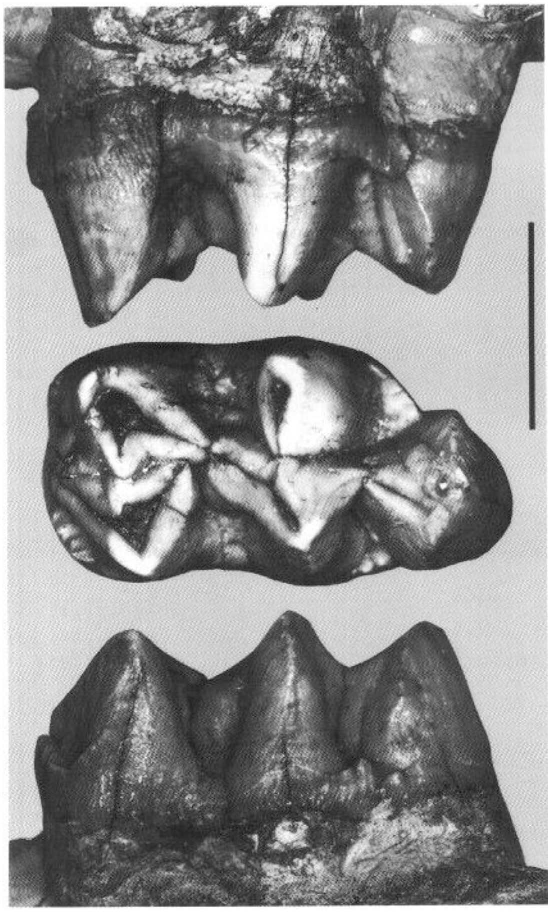

Fig. 19.4. Left M_3 of *Hexaprotodon? pantanellii* from La Portera (MNCN). The bar represents 2.5 cm.

siculus HOOIJER, 1946 from Gravitelli in Italy, *Hippopotamus crusafonti* AGUIRRE, 1963 from Arenas del Rey in Spain, and *Hexaprotodon primaevus* CRUSAFONT, ADROVER & GOLPE, 1963 from El Arquillo de la Fontana in Spain. All these localities are placed in MN 13. The size and morphology of the remains from these localities are not very different (AGUIRRE 1963, table 1) and it seems rather unlikely that the Miocene European material, from few geographically and stratigraphically close localities belongs to more than one species. The name that has precedence is *H. pantanellii*.

The small hippos from Europe are currently placed in *Hexaprotodon* (MORALES ROMERO 1984). The characters shared by the European Miocene hippos and *Hexaprotodon* are all primitive. A revision of hippo evolution is badly needed and might reveal affinities of the European form with *Hippopotamus*. It is of interest to note that the loss of an incisor in the lower jaw first occurred in *Hippopotamus* and only much later in *Hexaprotodon*. A mandible from Spain shows the early loss of the third lower incisor (fig. 19.2; LACOMBA et al. 1986). This shows that the hippos that dispersed during the late Miocene to Europe and Asia were different; the Indian and Indonesian hippos had three incisors in both jaws.

The dispersal from Africa to Europe occurred during the Messinian "Salinity Crisis" when, the Mediterranean became isolated from the Atlantic Ocean and partially desiccated (HSÜ et al. 1977).

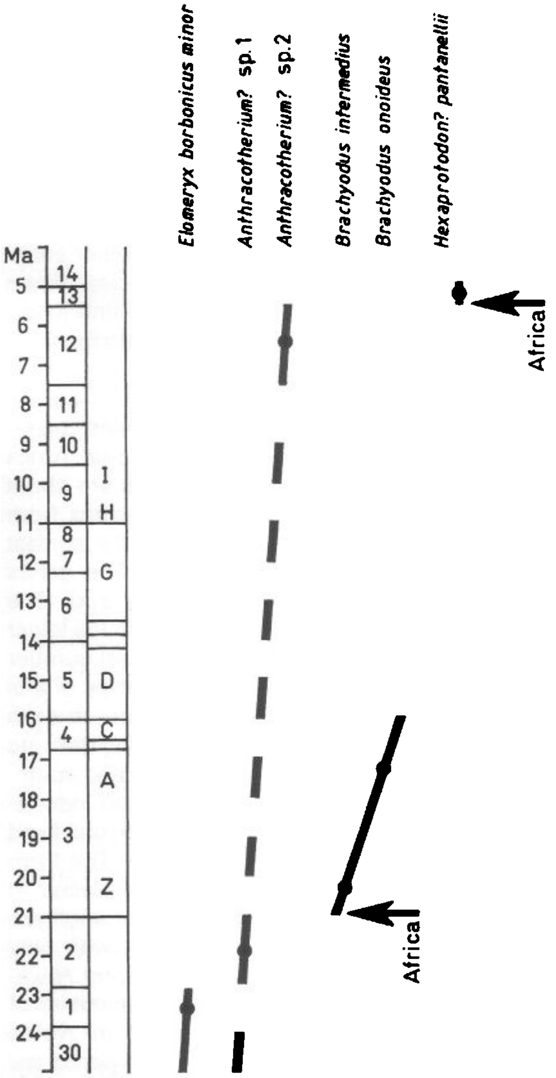

Fig. 19.5. Stratigraphical distribution of the European Hippopotamoidea. On the left age in millions of years (Ma), Paleogene and Neogene Mammal Units (MP 30 and MN 1-14) and the zones of the Ramblian, Aragonian and Vallesian (Z-I). Dots indicate the stratigraphical position of type material or, if no species is defined, of the material in question. Oblique lines connecting dots indicate gradual evolution from one species to the other. Arrows indicate dispersal events; Africa is the area of origin of the dispersing taxa.

Material

species	locality	age	collection	literature
Elomeryx borbonicus (GERVAIS, 1848-1852)	Wischberg (Switzerland)	MN 1	NMB	SCHAUB 1948
	Zürchersmühle (Switzerland)	MN 1?		SCHAUB 1948
	Pyrimont-Challonges (France)	MN 1	UCBL	HELLMUND 1991, DEPÉRET & DOUXAMI 1902
Brachyodus intermedius MAYET, 1908	Chitenay (France)	MN 3		MAYET 1908
	Brüttelen (Switzerland)	MN 3	NMBe	STUDER 1896
	Chilleurs aux Bois (France)	MN 3	MSNO	MAYET 1908
	Tuchorice (Czechia)	MN 3	IPUW	
	Eggenburg (Austria)	MN 3	IPUW	DAXNER-HÖCK 1971
Brachyodus onoideus (GERVAIS, 1869)	Neuville-aux-Bois (France)	MN 3	MSNO	MAYET 1908
	Horta das Tripas (Portugal)	MN 3	MHNL	ROMAN 1907
	Artenay (France)	MN 4, B		MAYET, 1908
	Quinta da Noiva (Portugal)	MN 4, C	MHNL	
	Quinta do Narigao (Portugal)	MN 4, C	MHNL	
	Pont Boutard (France)	MN 4, C		DINEUR & GINSBURG, 1986
Anthracotherium? sp. 1	Oschiri (Italy)	MN 2	IVAU	
Anthracotherium? sp. 2	Casteani/Ribolla (Italy)	MN 12	IGF	HÜRZELER 1982
Hexaprotodon? pantanellii (JOLEAUD, 1920)	El Arquillo (Spain)	MN13	IPMC, MNCN	CRUSAFONT et al. 1964, ALCALÁ MARTÍNEZ 1994
	Las Casiones (Spain)	MN13	MNCN	ALCALÁ MARTÍNEZ 1994
	La Portera (Spain)	MN13	MNCN	LACOMBA et al. 1986
	Venta del Moro (Spain)	MN13	MNCN	AGUIRRE et al. 1973, MORALES ROMERO 1984
	Arenas del Rey (Spain)	MN13	MNCN	MORALES ROMERO 1984
	Villastar (Spain)	MN13		MEIN et al. 1990
	Casino (Italy)	MN13		
	Gravitelli (Italy)	MN 13	lost	SEGUENZA 1902
	Scirpi (Italy)	MN 14	lost	SEGUENZA 1902
	La Masson (Spain)	MN 14		FAURE & MÉON 1984

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