The position of Hippopotamidae within Cetartiodactyla

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The origin of late Neogene Hippopotamidae (Artiodactyla) involves one of the most serious conflicts between comparative anatomy and molecular biology: is Artiodactyla paraphyletic? Molecular comparisons indicate that Cetacea should be the modern sister group of hippos. This finding implies the existence of a fossil lineage linking cetaceans (first known in the early Eocene) to hippos (first known in the middle Miocene). The relationships of hippos within Artiodactyla are challenging, and the immediate affinities of Hippopotamidae have been studied by biologists for almost two centuries without resolution. Here, we compare opposing hypotheses implicating several “suiform” families. This morphological analysis of a comprehensive set of taxa and characters offers a robust solution to the origins of Hippopotamidae. This family appears to be deeply nested within the otherwise extinct artiodactyl family Anthracotheriidae, most precisely within the most advanced selenodont forms. The proposed sister group of hippos is the middle to late Miocene African semiaquatic Libycosaurus. Any close relationships of hippos with suoids, particularly with Tayassuidae, are rejected. Furthermore, the clade (Hippopotamidae, Anthracotheriidae) is proposed as the sister group of the Cetacea, offering broad morphological support for a molecular phylogeny, such support being also consistent with the fossil record. Corroborated of this relationship requires an exploration of anthracothere affinities with other Paleogene artiodactyls. Among those, the position of Ruminantia is a central question, still to be solved. Further progress in this debate is likely to come from morphological studies of paleontological data, whether known or still to be discovered.

Although anatomists had strongly claimed the monophyly of Artiodactyla for 150 years, during the last two decades, molecular-based phylogenies told a very different story. Indeed, analyses of a substantial diversity of molecular data repeatedly pointed out that cetaceans should be included among artiodactyls, most probably as the sister group of the Hippopotamidae (1–20). The independence of those results provides a strong support to the clade Cetartiodactyla (cetaceans plus artiodactyls, ref. 7). On the contrary, most previous morphology-based studies designated a non-artiodactyl stem group for cetaceans: the Paleogene paraxonian mesonychians (21–26). This disagreement between morphology and genes gave rise to criticisms of both methods (27, 28). However, the discovery of Pakistani early cetaceans recently brought some conclusive anatomical support to the clade Cetartiodactyla (29). Indeed, the astragal of these fossil forms exhibit a distal trochlea, seen until now as an unequivocal synapomorphy uniting all artiodactyls and absent in mesonychians. As a consequence, the debate is now ready to refocus on the relationships within the Cetartiodactyla. Morphologists have already offered a variety of hypotheses, cetaceans alternatively being assumed to be the sister group of all artiodactyls (30, 31), of the “anthracotherioids” (29, 32), or of the Hippopotamidae (33), of the entelodonts (figure 2a in ref. 28), or of the ruminants (figure 2b in ref. 28).

This study proposes to tackle the problem differently. Because genes more frequently distinguish the Hippopotamidae as the modern sister group of the Cetacea, the unresolved question of hippo origins has become central to the phylogeny of the cetartiodactyls. On the one hand, hippos could actually be the closest modern and fossil relatives of cetaceans, but this would imply that the known fossil record suffers a gap of ~40 million years between the oldest known hippopotamids and their last common ancestor with Cetacea (34, 35). On the other hand, hippos may have derived from one or another Neogene artiodactyl lineage, but there is no consensus after a >150-year dispute over the identification of such close relatives. In fact, paleontologists are still divided between two mutually exclusive candidates: the extinct Anthracotheriidae and the Suoidea (most particularly the Tayassuidae, which include modern peccaries). Although the resolution of this question would provide a precious indication about where to look for early cetacean relatives, the last decade has been marked by the lack of attempts to do so. Therefore, the present morphological analysis aims to clarify the phylogenetic position of the Hippopotamidae among artiodactyls.

Materials and Methods

Taxa. Diacodexis pakistaniensis, the oldest known and most primitive cetartiodactyl (36, 37), was used as outgroup taxon. Ingroup taxa were selected according to the different hypotheses formulated on hippo origins. The oldest one was mostly elaborated by Colbert (38, 39) and was based on the many potential similarities between derived anthracotheres (Bothriodontinae) and hippos (Fig. 1A). Gentry and Hooker (40) suggested, on the contrary, that some primitive anthracotheres (among the Anthracotheriinae) could be a better sister group for the Hippopotamidae (Fig. 1A). Since this work, no thorough examination of this hypothesis has been undertaken. To span the large morphological, temporal, and geographical diversity of this family, the present study included eight Paleogene to Neogene anthracotheriids from Africa, Eurasia, and northern America (for details on these taxa, see supporting information, which is published on the PNAS website).

Against an anthracotheriid origin, Pickford (41, 42) put forth his own hypothesis based on the discovery of the oldest hippopotamid in the middle Miocene of Kenya and on anatomical similarities between modern hippos and peccaries. He proposed a lineage that would nest the Hippopotamidae within the Dolichochoerinae, the Old World stem of the Tayassuidae (Fig. 1B). As a consequence, the taxa involved in this lineage (Xenotyus, Dolichochoerus), the three modern peccaries, and the primitive tayassuid Perchoerus were sampled by the present study.

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along with two modern suids, the Paleogene suoid Palaeochor¬
erus, and the entelodont Archaeotherium (see supporting in¬
formation). Indeed, together with the Tayassuidae, Suidae have
been also frequently placed in the sister group of the Hip¬
opotamidae (most recently in refs. 26 and 31), occasionally
put together with the peculiar Entelodontidae (25, 43). Another
“suiform,” the dichobunid Eocene Cebochoerus from western
Europe, was also seen >70 years ago as a close relative of the
hippos on the basis of its basicranial anatomy (44). This hy¬
thesis was, in a way, resurrected by Pickford (42), who saw in the
Cebochoeridae a possible stem group for the Tayassuidae and
Suidae. This observation justified the addition of Cebochoerus
to the sample of taxa.

Representatives of two other groups were considered with
respect to their positions within Cetartiodactyla following mo¬
luscular phylogenies: cetaceans and ruminants. Two early ar¬
chaeocetes, Pakicetus (early Eocene) and Archaeotherium (mid¬
dle Eocene), were selected according to their completeness and
their primitive anatomy. Close relationships between cetaceans,
hippos, and ruminants have also been postulated (5, 6, 8, 12–14,
15, 16, 17, 19, 20). Therefore, two extant and two well preserved
extinct primitive ruminants were included in this study (see
supporting information).

Finally, an exhaustive sampling of the Hippopotamidae was
made by selecting six taxa (see supporting information); the two
modern species, the only one to have been considered by most
recent works (but see ref. 27); two Mio-Pliocene species that may
offer a better approximation for earliest hippotamoids than the
modern Choeropsis (45); Kenyapotamus, the oldest identified
hippotamapid, although poorly known; and the Asian Hexp¬
opotodon that Colbert (38, 39) compared to the anthracotheriid
Merycopotamus.

Characters. About half of the 80 used osteological characters
(for character definitions, see supporting information) were derived
from the “classic” literature (38–42, 44, 46). They were carefully
reviewed and, frequently, modified according to our own ob¬
servations. Other characters were adapted from more recent
works (mainly refs. 45 and 47, but also refs. 31 and 33), or
elaborated during the comparative work. Cranio-mandibular
characters were more frequently represented (59% of the data
matrix) than postcranial and dental characters (10% and 31%,
respectively). Among the latter, 14 features describe the cheek
teeth. Character states were coded between 0 and 4 and gathered
unordered and unweighted for each taxa. In the resulting data
matrix (see supporting information), the missing data percent¬
age is 12.6%.

Results
A heuristic parsimony analysis was performed by using PAUP*
(version 4.0β10) (48) on the data matrix of 80 characters for 32
 taxa. All characters are parsimony informative. A total of 18
equally parsimonious phylogenetic trees were obtained, with a
length of 287 steps, a consistency index (CI) = 0.3937 and a
retention index (RI) = 0.7171. Branch support was assessed by
using computation of Bremer support (49) and bootstrap re¬
sampling (Fig. 2). The trees are listed in the supporting in¬
formation. These trees differ by the position of Dolicho¬
choerus and Perchoerus relative to the modern tayassuids, the position
of Hippotomus and Hexaprotodon relative to the other Hippo¬
otaminae, and the relationships between Dremotherium, Mun¬
tiacus, and Tragulus. According to literature, tree number 7, for
which all character changes are given in the supporting in¬
formation, show the most plausible topology. In this tree, Dolio¬
choerus is the sister group of the New World tayassuids (50–52),
Hippopotamus and Hexaprotodon form a clade (45), and Dre¬
motherium and Muntiacus form a clade (40).

The monophyletic Ruminantia appears to be close to the
outgroup Diacodexis pakanstenis. Cebochorus is equally re¬
lated to suoids (Tayassuidae, Suidae) and anthracotheriids (Fig.
2). Archaeotherium and the sister families Tayassuidae and
Suidae (the latter including Xenohyus) form a clade. The sister
group of this clade associates the archaeocetes to the Anthra¬
cotheriidae and the Hippotominae. This association is weakly
supported (Fig. 2) by high orbits at least at the level of the cranial
roof (character 18) and a snout or hidden tympano-hyal sulcus
(character 35). The Hippotominae are deeply nested in the
paraphyletic Anthracotheriidae. The former notably share with
all anthracotheres the loss of lachrymal foramen (character 14)
and an anterior digital fossa on the astragalus (character 75).
They share with Anthracotherium and the Bothriodontinae an
expanded mandible angular process (character 46), a pustulate
and/or wrinkled dental enamel (character 60), a central keel on
the distal trochlea of the astragalus (character 76); and they
share with Merycopotamus and Libycosaurus a high orbit (char¬
acter 18), small randomly distributed supraorbital foramina
(character 23), a widened mandibular symphysis (character 43),
loss of the paracone (character 65), and loss of the manubt first
digit (character 79). With Libycosaurus, hippos share an inter¬
canine depression (character 6) and prolonged to permanent
growth of the lower incisors (character 54). The family Hip¬
notominae is a monophyletic taxon in which the Hippopotami¬
nae is defined as the sister group of Kenyapotamus (in accord
with ref. 41). Alone in the family, the latter retains a poorly
expressed triboliat cusp pattern (character 69). Among hippo¬
tomines, Hexaprotodon sivalensis and Hippopotamus am¬
phibius, the most derived hippos included in this study, occupy
a basal position (unlike in ref. 45). Correlatively, 17 of the 23
caracter state changes defining relationships between the hippo¬
tomines are reversions.

Discussion and Conclusions
Although hippos have been considered as extant relatives of
anthracotheres since the pioneer suggestions of Falconer and
Cautley (53), which were enhanced by Colbert (38, 39), several
authors doubted or rejected this “aging” hypothesis (41,
54–58), notably because the anthracotheres that exhibit the
most hippo-like cranial anatomy were also the most selendet. Meanwhile, the work of Pickford (41, 42, 50), who advocated a tayassuid origin of the hippos (Fig. 1B), might have appeared to be an appealing alternative (27). However, our morphological analysis unambiguously indicates that the stem group of the Hippopotamidae should not be sought among the suoids. Indeed, on the basis of the selected characters, 19 extra steps would be required to obtain any clade grouping the Tayassuidae–Suidae with the Hippopotamidae, increasing to 34 extra steps to validate the hypothesis of Pickford (41), or even to 40 extra steps if Cebochoerus is included (as in Fig. 1B). A thorough review of this “tayassuid hypothesis” (59) showed that, in fact, most of its supporting characters (41, 42) were either plesiomorphic within artiodactyls (e.g., rounded postcanine muzzle transversal section, character 9), highly variable within the studied families (e.g., the relative height of the glenoid cavities, character 31), or even, sometimes, erroneous (e.g., postulated lack of canine sexual dimorphism in hippos similar to that of modern peccaries, character 52) or meaningless (e.g., comparison of relative molar cingulum height in Xenohyus and Kenyapotamus; ref. 42). Moreover, Pickford (41, 42) ignored the synapomorphies of the Tayassuidae and Suidae (e.g., fusion of the postglenoid and posttympanic processes of the squamosal, character 26). Therefore, although the limited development of the mandible angular process (character 46) and the partially buried palatine groove (character 7) of modern peccaries (not found in Dolichochoerus) are reminiscent of the conditions seen in hippos, they would be better interpreted as convergences. In addition, Xenohyus (42, 50, 60), the purported transitional tayassuid between the doliochoeres and Kenyapotamus, appears here more closely related to the suids (Fig. 2), in agreement with refs. 52 and 61–63. Similarly, the role of Cebochoerus in suoid origins, suggested by Pickford (42), is not supported by this analysis (consistent with ref. 51), no more than any close relationships of this genus with the Hippopotamidae (in agreement with refs. 38–40, but contrary to ref. 44).

In opposition to several recent morphology-based phylogenies excluding an immediate link between hippos and anthracotheres (25, 26, 31, 33), the nesting of the Hippopotamidae within the advanced Bothriodontinae constitutes one of the most robust relationships found in this analysis (see Fig. 2 and character state

![Fig. 2. Temporal distribution and phylogenetical relationships of the studied taxa, based on the strict consensus of the 18 most parsimonious trees (L = 287 steps, CI = 0.3937, RI = 0.7171) obtained after analysis of the data matrix (see supporting information) of 80 characters and 32 taxa. At each node, indices are Bremer support/bootstrapping percentages >50%.](image-url)
relationships (see also ref. 31). To conclude, the absence of any between molecular and morphological data bearing on cetacean than classically suspected, therefore often found to be homoplasious, i.e., that mammalian teeth could be more plastic and favor here. This finding echoes the suggestions of Naylor and Adams (28), although it is weakly supported (Fig. 2), is congruent with molecular data linking modern whales and hippos. This result also provides a broader morphological support to previous suggestions of a close relation between anthropothe, hippos, and cetaceans (11, 29, 35, 64). It disagrees with Geisler and Uhen (33), who obtained a clade (Hippopotamidae, Cetacea) that excludes all other artiodactyls. In fact, the latter result is not strongly consistent with paleontological data. Indeed, the time gap between the earliest hippos (at most 15.7 million years, according to ref. 65) and the oldest known cetaceans (~35.5 million years, ref. 66) implies that, during its first 35–40 million years, the hippo lineage failed to leave any fossil record. On the contrary, the phylogenetic hypothesis advocated here dramatically reduces this gap to <12 million years (35) because the oldest known anthrochothereids are from the upper middle Eocene from southeastern Asia (67). In fact, according to several authors (58, 68, 69, 70), the Helophyidae could be the sister group of the Anthracotheriidae. Given that Helophus was found in northern America in the lower middle Eocene (69), the time discrepancy between the oldest cetaceans and this potential oldest known representative of the hippo-anthrochotherid lineage could be no more than 3 million years.

The position of the ruminants found here is incongruent with a close link suggested between Cetacea, Hippopotamidae, and Ruminantia by some molecular phylogenies (5, 6, 8, 12–14, 16, 17, 19, 20). On the contrary, this position, close to Diacodexis pakistanensis, fits previous suggestions (figure 2a in ref. 28, and ref. 40). In agreement with Geisler and Uhen (33), these contradictory results mostly indicate that the position of Ruminantia within Cetartiodactyla remain a major question that requires further phylogenetic work to be properly resolved.

Finally, these results indicate that the relationships between basal anthrochothere and early cetaceans constitute major tracks to follow regarding the exact position of Cetacea within Cetartiodactyla. On the one hand, the morphological specialization of the most primitive known archaeocete show that some additional discoveries of more primitive early cetaceans are needed to clarify these relationships. On the other hand, the emergence of the Anthrochothereidae is yet to be fully understood. To fully understand this emergence, in addition to the Helophyidae, other extinct primitive artiodactyls, including the Hoplobunodontidae, the Raelloidae, the Oreodontidae, and some dichobunoids, should be included in future morphological studies of this basal radiation of the artiodactyls. Integration of these paleontological data with a large corpus of modern soft anatomy and ethological data, in the way initiated by some authors (33, 71), will most probably result ultimately in a conclusive consensus with molecular studies.

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