

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. Corroboration 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.

hippo origin | phylogeny | Anthracotheriidae | suoids | archaeocetes

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 astragali 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), 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 pakistanensis*, 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 web site).

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 Doliochoerinae, the Old World stem of the Tayassuidae (Fig. 1B). As a consequence, the taxa involved in this lineage (*Xenohyus*, *Doliochoerus*), the three modern peccaries, and the primitive tayassuid *Perchoerus* were sampled by the present study,

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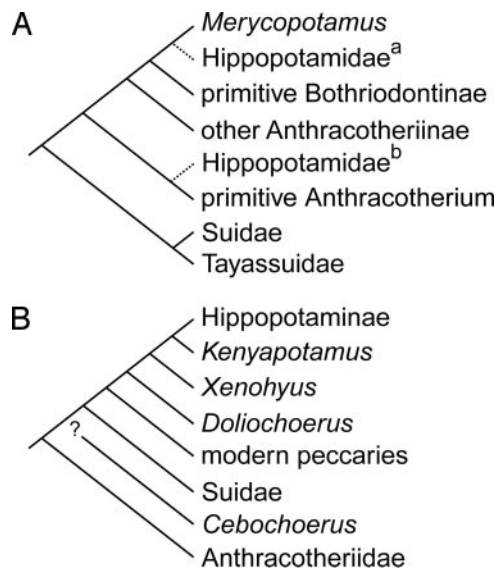


Fig. 1. Cladograms representing the two main hypotheses previously formulated on the origins of the Hippopotamidae. (A) Anthracotheriid hypothesis, with two alternative positions for the Hippopotamidae: a, according to refs. 38 and 39; b, according to ref. 40. (B) Tayassuid hypothesis, modified from refs. 42 and 50.

along with two modern suids, the Paleogene suoid *Palaeochoerus*, and the entelodont *Archaeotherium* (see supporting information). Indeed, together with the Tayassuidae, Suidae have been also frequently placed in the sister group of the Hippopotamidae (most recently in refs. 26 and 31), occasionally together with the peculiar Entelodontidae (25, 43). Another “suiform,” the dichobunoid 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 hypothesis 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 molecular phylogenies: cetaceans and ruminants. Two early archaeocetes, *Pakicetus* (early Eocene) and *Artiocetus* (middle 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, 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 hippopotamids than the modern *Choeropsis* (45); *Kenyapotamus*, the oldest identified hippopotamid, although poorly known; and the Asian *Hexaprotodon* 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 observations. 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 percentage 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 resampling (Fig. 2). The trees are listed in the supporting information. These trees differ by the position of *Doliochoerus* and *Perchoerus* relative to the modern tayassuids, the position of *Hippopotamus* and *Hexaprotodon* relative to the other Hippopotaminae, and the relationships between *Dremotherium*, *Muntiacus*, and *Tragulus*. According to literature, tree number 7, for which all character changes are given in the supporting information, show the most plausible topology. In this tree, *Doliochoerus* is the sister group of the New World tayassuids (50–52), *Hippopotamus* and *Hexaprotodon* form a clade (45), and *Dremotherium* and *Muntiacus* form a clade (40).

The monophyletic Ruminantia appears to be close to the outgroup *Diacodexis pakistanensis*. *Cebochoerus* is equally related 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 Anthracotheriidae and the Hippopotamidae. This association is weakly supported (Fig. 2) by high orbits at least at the level of the cranial roof (character 18) and a small or hidden tympano-hyal sulcus (character 35). The Hippopotamidae 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 (character 18), small randomly distributed supraorbital foramina (character 23), a widened mandibular symphysis (character 43), loss of the paraconule (character 65), and loss of the manus first digit (character 79). With *Libycosaurus*, hippos share an intercanine depression (character 6) and prolonged to permanent growth of the lower incisors (character 54). The family Hippopotamidae is a monophyletic taxon in which the Hippopotaminae is defined as the sister group of *Kenyapotamus* (in accord with ref. 41). Alone in the family, the latter retains a poorly expressed trilobate cusp pattern (character 69). Among hippopotamines, *Hexaprotodon sivalensis* and *Hippopotamus amphibius*, the most derived hippos included in this study, occupy a basal position (unlike in ref. 45). Correlatively, 17 of the 23 character state changes defining relationships between the hippopotamines 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

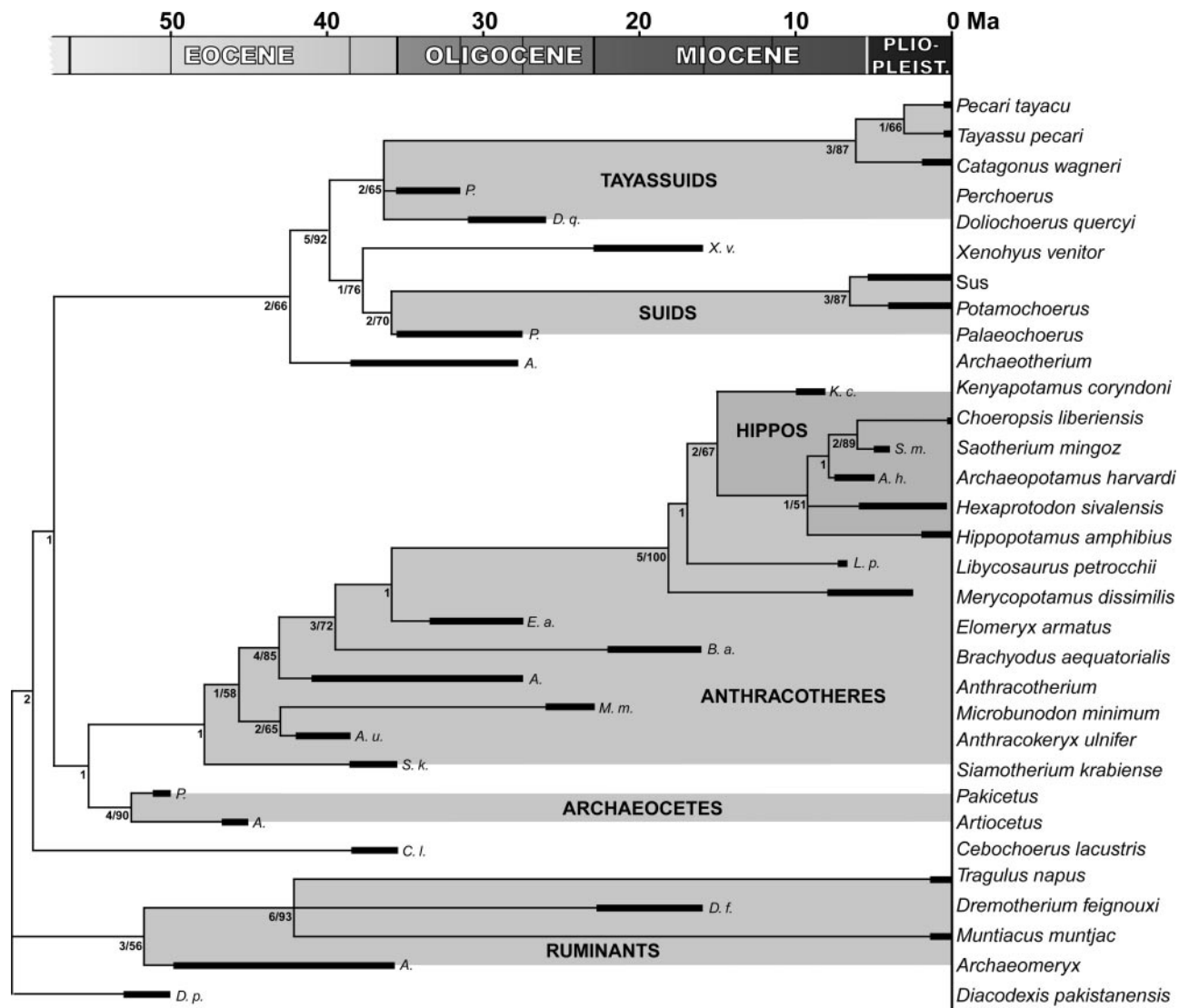


Fig. 2. Temporal distribution and phylogenetical relationships of the studied taxa, based on the strict consensus of the 18 most parsimonious trees ($L = 287$ steps, $CI = 0.3937$, $RI = 0.7171$) obtained after analysis of the data matrix (see supporting information) of 80 characters and 32 taxa. At each node, indices are Bremer support/bootstrapping percentages $>50\%$.

most hippo-like cranial anatomy were also the most selenodont. 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 *Doliochoerus*) 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

changes in supporting information), providing the strongest support to the “anthracotheriid” hypothesis since Colbert’s works (38, 39). The recent identification of two exclusive apomorphies of the Bothriodontinae (47) agrees with this relationship. First, their position of the anterior palatine foramen, anterior to the P², is more similar to the condition seen in the Hippopotamidae than to other anthracotheres. Secondly, the bucco-distal crest bearing one or two accessory cusps on upper premolars (P¹⁻³) is frequent in the late Miocene hippopotamids, although somewhat variable. Among the Bothriodontinae, the sister group of the Hippopotamidae is *Libycosaurus* (Fig. 2), an upper middle to upper Miocene African anthracother. This genus exhibits many similarities with the most advanced hippopotamids (notably *Hippopotamus*), including adaptations to a semiaquatic way of life (47). Those character states that are not found in primitive Hippopotaminae (45) should be interpreted as convergences between *Libycosaurus* and advanced Hippopotaminae (characters 11, 13, 16, 18, 34, and 38; in *Kenyaipotamus*, these data are lacking; see supporting information). To the contrary, in this analysis, these characters appear as synapomorphies of *Libycosaurus* and Hippopotamidae, whereas the most primitive hippos exhibit reversed states for them. In fact, the phylogeny of the Hippopotaminae obtained here (Fig. 2) is reversed compared to the most recent hypothesis (45). Therefore, it has been suspected that these characters could have inaccurately induced the clade (*Libycosaurus*, Hippopotamidae). The withdrawal of these six characters from the analysis reestablished advanced hippos in a terminal position, in agreement with ref. 45, but did not change the position of *Libycosaurus*. Therefore, the Hippopotamidae and *Libycosaurus* would have shared a common ancestor closely related to the Asian *Merycopotamus* that probably arrived in Africa during the middle Miocene. An alternative test was conducted by analyzing the whole set of characters, but keeping only the trees compatible with the most recent hippo phylogeny (45). In this case, a new hippo sister group was found, including both *Libycosaurus* and *Merycopotamus* (see supporting information). This finding would mean that the common ancestor of these clades could be looked for in the closest relatives of *Libycosaurus* and *Merycopotamus*, i.e., the African *Afromeryx*, the Asian *Hemimeryx*, and the Afro-Asian *Sivameryx* (47). The divergence of hippos and anthracotheres could then be traced back to the early Miocene. Unfortunately, little is known about the cranial morphology of these genera. Moreover, this hypothesis implies that the intercanine depression of the palate (character 6) and the lower incisors with prolonged to permanent growth (character 50) and absence of crown contacts (character 51) that are shared by *Libycosaurus* and the Hippopotamidae would have been lost in *Merycopotamus* or convergent in *Libycosaurus*. For this reason, this hypothesis is somewhat less parsimonious than the former.

In any case, a close relationship between the Hippopotamidae and the basal Anthracotheriinae (40) is contradicted. This hypothesis was essentially based on dental morphology, basal anthracothere cheek teeth being close to that of hippos in their poorly developed selenodonty. In contrast, hippo cheek tooth derivative from selenodont teeth of the Bothriodontinae would necessitate a spectacular reversion, i.e., the reorientation of cristas and cristids, turning into the mesio-distally oriented “lobes” of hippo cusps/ids (character 68), as well as a dramatic reduction of the mesostyle (character 70). Although these important changes of dental morphology seem poorly parsimonious, according to the cranio-mandibular evidences, they are favored here. This finding echoes the suggestions of Naylor and Adams (28), i.e., that mammalian teeth could be more plastic than classically suspected, therefore often found to be homoplastic, and therefore notably responsible for the discrepancies between molecular and morphological data bearing on cetacean relationships (see also ref. 31). To conclude, the absence of any

known anthracotheriid lineage that also gradually and simultaneously developed hippo-like cranial and dental morphologies is not a decisive argument to reject the strongly supported relationship between Hippopotamidae and Anthracotheriidae. A serious alternative to that hypothesis is yet to be formulated.

Although the main focus of this study was the immediate relationships of the Hippopotamidae, the inclusion of two archaeocetes in the analysis constituted an attempt to verify the position of Cetacea within artiodactyls. The obtained clade [archaeocetes, (Anthracotheriidae, Hippopotamidae)], even though 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 anthracotheres, 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 (\approx 53.5 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 anthracotheriids are from the upper middle Eocene from southeastern Asia (67). In fact, according to several authors (58, 68, 69, 70), the Helohyidae could be the sister group of the Anthracotheriidae. Given that *Helohyus* 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-anthracotheriid 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 anthracotheres 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 archaeocetes show that some additional discoveries of more primitive early cetaceans are needed to clarify these relationships. On the other hand, the emergence of the Anthracotheriidae is yet to be fully understood. To fully understand this emergence, in addition to the Helohyidae, other extinct primitive artiodactyls, including the Haplobunodontidae, the Raoellidae, 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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- Boyden, A. A. & Gemeroy, D. G. (1950) *Zoology* **35**, 145–151.
- Sarich, V. (1985) in *Evolutionary Relationships Among Rodents: A Multidisciplinary Approach*, eds. Luckett, W. & Hartenberger, J. L. (Plenum, New York), pp. 423–452.
- Graur, D. & Higgins, D. G. (1994) *Mol. Biol. Evol.* **11**, 357–364.
- Irwin, D. M. & Arnason, U. (1994) *J. Mamm. Evol.* **2**, 37–55.
- Gatesy, J., Hayashi, C., Cronin, M. A. & Arctander, P. (1996) *Mol. Biol. Evol.* **13**, 954–963.
- Gatesy, J. (1997) *Mol. Biol. Evol.* **14**, 537–543.
- Montgelard, C., Catzeflis, F. M. & Douzery, E. (1997) *Mol. Biol. Evol.* **14**, 550–559.
- Shimamura, M., Yasue, H., Ohshima, K., Abe, H., Kato, H., Kishiro, T., Goto, M., Munechikak, I. & Okada, N. (1997) *Nature* **388**, 666–670.
- Gatesy, J. (1998) in *The Emergence of Whales*, ed. Thewissen, J. G. M. (Plenum, New York), pp. 63–111.
- Milinkovitch, M., Bérubé, M. & Paslball, P. (1998) in *The Emergence of Whales*, ed. Thewissen, J. G. M. (Plenum, New York), pp. 113–131.
- Ursing, B. M. & Arnason, U. (1998) *Proc. R. Soc. London B* **265**, 2251–2255.
- Gatesy, J., Milinkovitch, L., Waddell, V. & Stanhope, M. (1999) *Syst. Biol.* **48**, 6–20.
- Nikaido, M., Rooney, A. P. & Okada, N. (1999) *Proc. Natl. Acad. Sci. USA* **96**, 10261–10266.
- Nomura, O. & Yasue, H. (1999) *Mamm. Genome* **10**, 526–527.
- Shimamura, M., Abe, H., Nikaido, M., Ohshima, K. & Okada, N. (1999) *Mol. Biol. Evol.* **16**, 1046–1060.
- Ursing, B. M., Slack, K. E. & Arnason, U. (2000) *Zool. Scr.* **29**, 83–88.
- Matthee, C. A., Burzlaff, J. D., Taylor, J. F. & Davis, S. K. (2001) *Syst. Biol.* **50**, 367–390.
- Nikaido, M., Matsuno, F., Abe, H., Shimamura, M., Hamilton, H., Matsubayashi, H. & Okada, N. (2001) *Mamm. Genome* **12**, 909–915.
- Madsen, O., Willemsen, D., Ursing, B. M., Arnason, U. & de Jong, W. W. (2002) *Mol. Biol. Evol.* **19**, 2150–2160.
- Amrine-Madsen, H., Koep, K. P., Wayne, R. K. & Springer, M. S. (2003) *Mol. Phylogenet. Evol.* **28**, 225–240.
- Van Valen, L. (1966) *B. Am. Mus. Nat. Hist.* **132**, 1–128.
- Geisler, J. H. & Luo, Z. (1998) in *The Emergence of Whales*, ed. Thewissen, J. G. M. (Plenum, New York), pp. 163–212.
- O'Leary, M. A. (1998) in *The Emergence of Whales*, ed. Thewissen, J. G. M. (Plenum, New York), pp. 133–161.
- Luo, Z. & Gingerich, P. D. (1999) *Univ. Michigan Papers Paleont.* **31**, 1–98.
- O'Leary, M. A. & Geisler, J. H. (1999) *Syst. Biol.* **48**, 455–490.
- Geisler, J. (2001) *Am. Mus. Nov.* **40**, 1–53.
- Luckett, W. P. & Hong, N. (1998) *J. Mamm. Evol.* **5**, 127–182.
- Naylor, G. J. P. & Adams, D. C. (2001) *Syst. Biol.* **50**, 444–453.
- Gingerich, P. D., Haq, M. U., Zalmout, I. S., Hussain, K. I. & Malkani, M. S. (2001) *Science* **293**, 2239–2242.
- Thewissen, J. G. M. & Madar, S. I. (1999) *Syst. Biol.* **48**, 21–30.
- Thewissen, J. G. M., Williams, E. M., Roe, L. J. & Hussain, S. T. (2001) *Nature* **413**, 277–281.
- Rose, K. D. (2001) *Science* **293**, 2216–2217.
- Geisler, J. H. & Uhen, M. D. (2003) *J. Vertebr. Paleontol.* **23**, 991–996.
- Arnason, U., Gullberg, A., Solweig, G., Ursing, B. & Janke, A. (2000) *J. Mol. Evol.* **50**, 569–578.
- Theodor, J. M. (2004) *J. Paleontol.* **78**, 39–44.
- Thewissen, J. M. G., Russell, D. E., Gingerich, P. D. & Hussain, S. T. (1983) *Proc. Koninkl. Nederland Acad. Wetenschap.* **86**, 153–180.
- Thewissen, J. M. G. & Hussain, S. T. (1990) *Anat. Histol. Embryol.* **19**, 37–48.
- Colbert, E. H. (1935) *Trans. Am. Philos. Soc.* **26**, 278–294.
- Colbert, E. H. (1935) *Am. Mus. Nov.* **799**, 1–24.
- Gentry, A. W. & Hooker, J. J. (1988) in *The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals*, ed. Benton, M. J. (Clarendon, Oxford), Vol. 35B, pp. 235–272.
- Pickford, M. (1983) *Géobios* **16**, 193–217.
- Pickford, M. (1989) *C. R. Acad. Sci.* **309**, 163–168.
- O'Leary, M. A. (2001) *Am. Zool.* **41**, 487–506.
- Pearson, H. S. (1927) *Philos. Trans. R. Soc. London* **215**, 389–460.
- Boisserie, J.-R. (2005) *Zool. J. Linn. Soc.*, in press.
- Lydekker, R. (1876) *Rec. Geol. Surv. India* **9**, 144–153.
- Lihoreau, F. (2003) Ph.D. thesis (Université de Poitiers, Poitiers, France).
- Swofford, D. L. (1998) PAUP*: *Phylogenetic Analysis Using Parsimony (*and Other Methods)* (Sinauer, Sunderland, MA), Version 4.
- Bremer, K. (1994) *Cladistics* **10**, 295–304.
- Pickford, M. (1993) *Paleontol. Evol.* **26–27**, 237–269.
- Ducrocq, S. (1994) *Palaeontology* **37**, 765–779.
- Hünemann, K. A. (1999) in *The Miocene Land Mammals of Europe*, eds. Rössner, G. E. & Heissig, K. (Verlag Dr. Friedrich Pfeil, München), pp. 209–216.
- Falconer, H. & Cautley, P. T. (1847) *Fauna Antiqua Sivalensis* (Smith, Elder, and Co., London).
- Matthew, W. D. (1929) *Bull. Am. Mus. Nat. Hist.* **56**, 437–560.
- Matthew, W. D. (1929) *Bull. Geol. Soc. Am.* **40**, 403–408.
- Viret, J. (1961) in *Traité de Paléontologie*, ed. Piveteau, J. (Masson, Paris), Vol. 6, pp. 963.
- Coryndon, S. C. (1972) in *Actes du 6^{ème} Congrès Panafricain de Préhistoire, Dakar 1967* (Les Imprimeries Réunies de Chambéry, Chambéry, France), pp. 350–352.
- Kron, D. G. & Manning, E. (1998) in *Evolution of Tertiary Mammals of North America*, eds. Janis, C. M., Scott, K. M. & Jacobs, L. L. (Cambridge Univ. Press, Cambridge, U.K.), pp. 381–388.
- Boisserie, J.-R., Lihoreau, F. & Brunet, M. (2005) *Zool. Sci.*, in press.
- Pickford, M. & Morales, J. (1989) *Est. Geol.* **45**, 233–237.
- Ginsburg, L. (1980) *Géobios* **13**, 861–877.
- Ginsburg, L., Huin, J. & Locher, J. P. (1988) *Bull. Mus. Nat. Hist. Nat.* **10**, 197–207.
- van der Made, J. (1990) *Paleontol. Evol.* **23**, 99–104.
- Milinkovitch, M. C. & Thewissen, J. G. M. (1997) *Nature* **388**, 622–624.
- Behrensmeier, A. K., Deino, A. L., Hill, A., Kingston, J. D. & Saunders, J. J. (2002) *J. Hum. Evol.* **42**, 11–38.
- Bajpai, S. & Gingerich, P. D. (1998) *Proc. Natl. Acad. Sci. USA* **95**, 15464–15468.
- Holroyd, P. A. & Ciochon, R. L. (1995) *Ann. Carnegie Mus.* **64**, 177–183.
- Coombs, W. P., Jr., & Coombs, M. C. (1977) *N. Jb. Geol. Paläont. Abh.* **10**, 584–599.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V. & Jaeger, J. J. (1997) *C. R. Acad. Sci.* **325**, 367–372.
- Tsubamoto, T., Takai, M., Egi, N., Shigehara, N., Tun, S. T., Aung, A. K., Soe, A. N. & Thein, T. (2002) *Paleontol. Res.* **6**, 363–384.
- Lusseau, D. (2003) *J. Evol. Biol.* **16**, 531–535.