Evolution / Évolution

Emergence of Hippopotamidae: new scenarios

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Abstract

Molecular data analyses blew the problem of hippo origins up to the level of a broader question: cetacean and artiodactyl relationships. Recently, new morphology-based studies strongly supported a hippo origin within Miocene bothriodontines, which are selenodont anthracotheres. Based on these results, two new scenarios for hippo emergence are proposed here. Palaeoenvironmental and evolutionary issues related to these scenarios are discussed. *To cite this article: J.-R. Boisserie, C. R. Palevol 5 (2006)*.
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Résumé

Émergence des Hippopotamidae : nouveaux scénarios. Les analyses des données moléculaires ont placé la question de l'origine des hippopotames au centre d'un vaste débat, celui des relations entre les cétacés et les artiodactyles. Récemment, de nouvelles analyses de la morphologie suggèrent que l'origine des hippopotames se situait au sein des bothriodontinés miocènes, qui sont des anthracothères sélénodontes. À partir de ces résultats, deux nouveaux scénarios sur l'émergence des hippopotames sont proposés dans ce travail. Les implications évolutives et paléoenvironnementales liées à ces scénarios sont discutées. *Pour citer cet article : J.-R. Boisserie, C. R. Palevol 5 (2006)*.
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Introduction

Bien que la famille Hippopotamidae soit apparue récemment [3], son origine reste discutée. Depuis deux décennies, des analyses de données moléculaires ont proposé les cétacés comme groupe frère de cette famille, contredisant la monophylie des artiodactyles défendue sur des bases morphologiques (voir [5] pour une liste de références liées à ce débat). De nouveaux travaux, basés sur la morphologie, sont toutefois venus soutenir cette relation [16,19]. Dans ce contexte, les hypothèses paléontologiques de l'origine des Hippopotamidae ont été récemment révisées [5,6]. Cette note a pour objectif de proposer de nouveaux scénarios de l'émergence des Hippopotamidae en adéquation avec les résultats de cette révision et de discuter les paramètres contraignant ces scénarios sur le plan évolutif et environnemental.

Cadre phylogénétique et chronologique

Les résultats obtenus récemment sur l'origine des Hippopotamidae [5,6] (Fig. 1) soutiennent fortement l'hypothèse d'une origine au sein des Anthracotheriidae [11,14,17] et s'opposent à une origine au sein des Suidés [23,24,27]. Deux groupes frères possibles ont été proposés [5,6] pour les Hippopotamidae (Fig. 1), tous deux au sein des Bothriodontinae néogènes (anthracothères à denture sélénodonte). De plus, un clade (Cetacea (Anthracotheriidae + Hippopotamidae)) a été obtenu [6], permettant de réduire la lacune fossile supposée entre les premiers cétacés et les premiers hippopotamidés.

L'apparition des Hippopotamidae est discutée. Sur la base de matériel fragmentaire et non décrit, elle est plus souvent considérée comme ayant eu lieu au Miocène moyen : soit vers 18 Ma [12], soit, plus vraisemblablement, vers 16 Ma, avec le genre *Kenyapotamus* [3,18,23,25]. Néanmoins, les premiers restes de *Kenyapotamus* [23] appartenant clairement aux Hippopotamidae datent du Miocène récent. Une vision conservatrice de l'ensemble de ce matériel plaiderait donc en faveur d'une première apparition vers 10 Ma (Fig. 2).

Nouveaux scénarios pour l'émergence des hippopotames

En tenant compte de la distribution chronostratigraphique et géographique des bothriodontinés et des hip-

popotamidés miocènes (Fig. 2), ainsi que des incertitudes sur le groupe frère de ces derniers et sur leur première apparition, il est possible de proposer deux scénarios pour leur émergence.

Le premier scénario propose une émergence tardive et se base sur un groupe frère monogénérique : *Libycosaurus*. Il implique, entre ce genre africain et les Hippopotamidae, une divergence plus ancienne que 12 Ma, à partir d'une forme proche du genre asiatique *Merycopotamus* [22]. Cette forme serait arrivée en Afrique peut-être après 15 Ma, au moment du rétablissement des échanges fauniques, lié à la fermeture définitive du corridor marin Indo-Méditerranéen [1,28,29].

Le second scénario est celui d'une émergence précoce des Hippopotamidae à partir d'un ancêtre commun avec le clade (*Libycosaurus*, *Merycopotamus*) (Fig. 1B). Les anthracothères les plus proches de ce clade sont notamment des bothriodontinés connus en Afrique entre 18 et 15 Ma (Fig. 2) [22]. Ce scénario reste peu détaillé, notamment à cause des incertitudes sur les relations de parenté entre ces animaux et les lacunes du registre fossile.

Contraintes évolutives et environnementales

Évolution de la denture jugale

L'apparence bunodonte des molaires des Hippopotamidae diffère fortement de celle des molaires sélénodontes des Bothriodontinae, s'opposant, selon certains auteurs [17,23], à une émergence des premiers à partir des seconds. Néanmoins, les trois lobes formant les cuspides des Hippopotamidae sont positionnés comme les cristas et cuspides des bothriodontinés miocènes. Des modifications relativement simples de ces cristas (principalement raccourcissement) pourraient donner une morphologie similaire à celle observée chez les Hippopotamidae. Selon les scénarios décrits plus haut, ceci aurait dû toutefois se produire rapidement. Cette hypothèse est plausible, car des travaux récents [21] ont montré que des modifications génétiques mineures pouvaient résulter en des modifications importantes de l'aspect des crêtes des molaires de certains mammifères. De plus, une simple augmentation de l'épaisseur d'émail peut contribuer fortement à la simplification du schéma occlusal des molaires [20]. Le scénario d'émergence précoce décrit plus haut, plus long et impliquant des bothriodontinés moins sélénodontes que *Merycopotamus*, semble plus compatible avec des modifications importantes de l'aspect des molaires.

Contexte environnemental

Entre 16 et 12 Ma, une dégradation marquée du climat a affecté, entre autres, l'Afrique, résultant en un accroissement de l'aridité [15,30]. L'importance de ces événements pour l'évolution des mammifères africains a été récemment montrée [13]. Il a pu en résulter une fragmentation et un isolement des populations de mammifères semi-aquatiques (bothriodontinés, hippopotamidés), favorisant une évolution rapide. Ces paramètres ont donc pu être un facteur majeur dans l'émergence des Hippopotamidae (Fig. 2). Un autre facteur pourrait être lié à l'expansion des herbacées dans les biotopes africains. Les hippopotamidés sont devenus particulièrement abondants à la fin du Miocène [8], en même temps que les plantes en C_4 (Fig. 2) [10]. Or, le régime alimentaire de ces animaux [7,9] suggère une forte relation avec ces végétaux. Une corrélation identique est observée entre la plus vieille occurrence des végétaux en C_4 en Afrique et la date d'apparition des hippopotames la plus fréquemment citée [3].

Conclusion

Il est possible de tester les deux nouveaux paléoscénarios et les questions évolutives et environnementales qui leur sont liées, notamment par le réexamen ou la description du matériel publié et non publié attribué à *Kenyapotamus*, en le comparant aux bothriodontinés miocènes et en effectuant des analyses paléoécologiques de ces formes. Toutefois, une compréhension complète de la question de l'émergence des Hippopotamidae nécessite aussi de combler les lacunes du registre fossile du Miocène moyen.

1. Introduction

The family Hippopotamidae is unique among artiodactyls. Anatomically, it is distinguished by trilobate molar cusps and skeletal adaptations to intraspecific competition (large and robust skull, hypertrophied and hypselodont front teeth). Ecologically, hippos are the only extant semiaquatic large herbivores. Phylogenetically, their origin, yet recent [3], is controversial. During the last 20 years, molecular data analyses enhanced the magnitude of this question by giving the hippos a surprising sister group: cetaceans (see [5] for a list of most of these works). This hypothesis, contradicting artiodactyl monophyly, was first denied by anatomists (again, see [5]). Nevertheless, it gained considerable credibility after the discovery of artiodactyl main apomorphy (distal trochlea on the astragalus) in archaic cetaceans [19]. Consequently, a new morphology ana-

lysis provided support to a clade including exclusively cetaceans and hippos [16].

However, such a result implied a ca. 50 Ma gap in the fossil record of Hippopotamidae, between their first occurrence in Africa and their hypothetical divergence with cetaceans assessed at 64.5 Ma [2]. Moreover, it did not consider the hypotheses previously built on the Neogene fossil record (e.g., [11,23]). For this reason, two recent studies re-examined these hypotheses [5,6]. They strongly support the rooting of Hippopotamidae within Anthracotheriidae. The present goal is to assess, from these new results, the possible scenarios of the appearance of Hippopotamidae during the Neogene, as well as to discuss the evolutionary and environmental factors that may constrain them.

2. Phylogenetic and chronological framework

2.1. Affinities of Hippopotamidae within the Cetartiodactyla

Similarities between anthracotheriids and hippopotamids were pointed out early [14], notably on the skull (elevated orbits, wide mandibular symphysis, developed angular process). This led Colbert [11] to place hippo origin within those diversified artiodactyls of almost global distribution from Middle Eocene to Late Pliocene. However, the advanced selenodonty of the Bothriodontinae, the stem group proposed by Colbert, induced Gentry and Hooker [17] to link hippos with less selenodont forms, the Anthracotheriinae. It also favoured the alternative hypothesis developed by Pickford [23,24,27] of a hippopotamid origin within Tayassuidae, a family closely related to Suidae and known since the Eocene. This was based first on anatomical similarities between peccaries and extant hippos (developed angular process, covered palatine groove, fused mandibular symphysis [23]), second on a fossil lineage linking the oldest known hippopotamid, *Kenyapotamus* Pickford, 1983, to *Doliochoerus*, an Oligocene tayassuid from Europe [24,27].

Recently, 37 morphological features used to support the former or the latter hypotheses were re-examined in details and revised [5]. This allowed comparison of each hypothesis for 21 taxa (hippopotamids, anthracotheriids, and tayassuids). This work was pursued in a broader analysis [6] considering other artiodactyls (suoids, ruminants, entelodonts), some cetaceans, and 43 additional features. These studies converged on excluding Suoidea from a close relationship with Hippopotamidae (Fig. 1A). On the contrary, they placed the
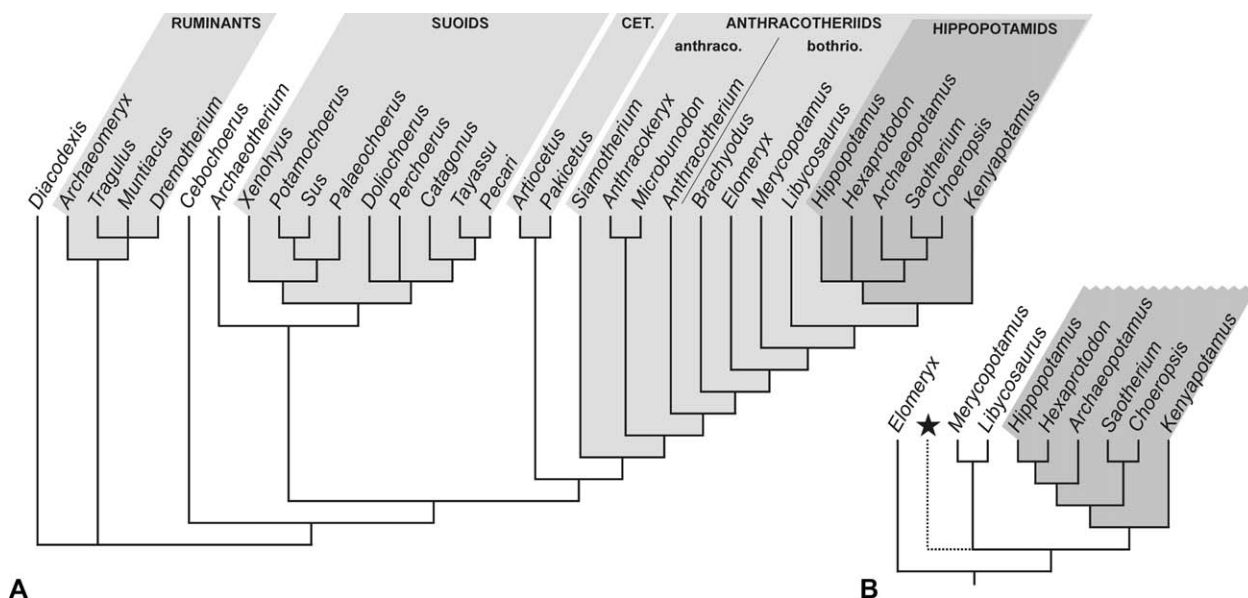
Fig. 1. Relationships of Hippopotamidae within Cetartiodactyla, following [6]. (**A**) Consensus of 18 equally parsimonious trees (cladistic analysis: 80 characters, 32 taxa). (**B**) Topology change induced by a constrained phylogeny for Hippopotamidae. The star indicates the other Miocene bothriodontines. CET.: cetaceans; anthraco.: anthracotheriines; bothrio.: bothriodontines.

Fig. 1. Relations de parentés des Hippopotamidae au sein des Cetartiodactyla, d'après [6]. (**A**) Cladogramme consensus de 18 arbres également parcimonieux (analyse cladistique : 80 caractères, 32 taxons). (**B**) Changement topologique induit par une phylogénie des Hippopotamidae contrainte. L'étoile indique les autres bothriodontinés miocènes. CET. : cétacés ; anthraco. : anthracotheriinés ; bothrio. : bothriodontinés.

sister group of Hippopotamidae within the Mio-Plio-cene bothriodontines, in agreement with Colbert [11]. Moreover, a clade Cetacea (Anthracotheriidae + hippo-potamidae) was recognized (Fig. 1A). The oldest known anthracotheriids are Middle Eocene, consider-ably reducing the gap between the first cetaceans and the lineage that lead to extant hippos.

2.2. Affinities of Hippopotamidae within Anthracotheriidae

The raw character analysis made by Boisserie et al. [6] indicated a first possible sister group for Hippo-potamidae (Fig. 1A): *Libycosaurus*. This African genus appeared near the end of the Middle Miocene (Fig. 2). Within Anthracotheriidae, only *Libycosaurus* exhibits, like all hippopotamids, an intercanine palatine groove and lower incisors with prolonged to permanent growth. It notably differs by the remarkable presence of five upper premolariform teeth [22].

Of the similarities between *Libycosaurus* and hippo-potamids, some character states are only known in ad-vanced hippopotamids (chiefly *Hippopotamus*), but ab-sent in archaic forms from Late Miocene: facial crest with a marked angle or a facial tubercle; relatively ro-bust zygomatic arch; lachrymal–nasal contact; elevated

orbits; anteroposteriorly compressed tympanic bulla; compressed basicranium. These convergences, at least some being related to amphibious specialization, in-duced basal position for the most derived hippopota-mids within their own family (Fig. 1A), and could have biased the relationships of *Libycosaurus*. For these rea-sons, two secondary analyses of the same matrix were performed (1) excluding these features, (2) constraining the relationships within Hippopotamidae following the most recent phylogenetic hypothesis [4]. Only the sec-ond test resulted in a change of hippo sister group (Fig. 1B), which became the putative clade (*Libyco-saurus*, *Merycopotamus*) [6].

2.3. The first appearance datum of Hippopotamidae

The oldest hippopotamids, known by fragmentary remains, are African and were attributed to the genus *Kenyapotamus* [23]. Two species were identified: *K. coryndoni*, known from 10 to 9 Ma in Kenya, Tuni-sia, and maybe Ethiopia [18,23,25]; *K. ternani*, known from 15.7 to 14 Ma in Kenya [3,23], and representing the FAD of Hippopotamidae (Fig. 2).

Nevertheless, the fragmentary status of the material used for describing *Kenyapotamus* calls for caution. In *K. coryndoni*, only few specimens indicate indisputably
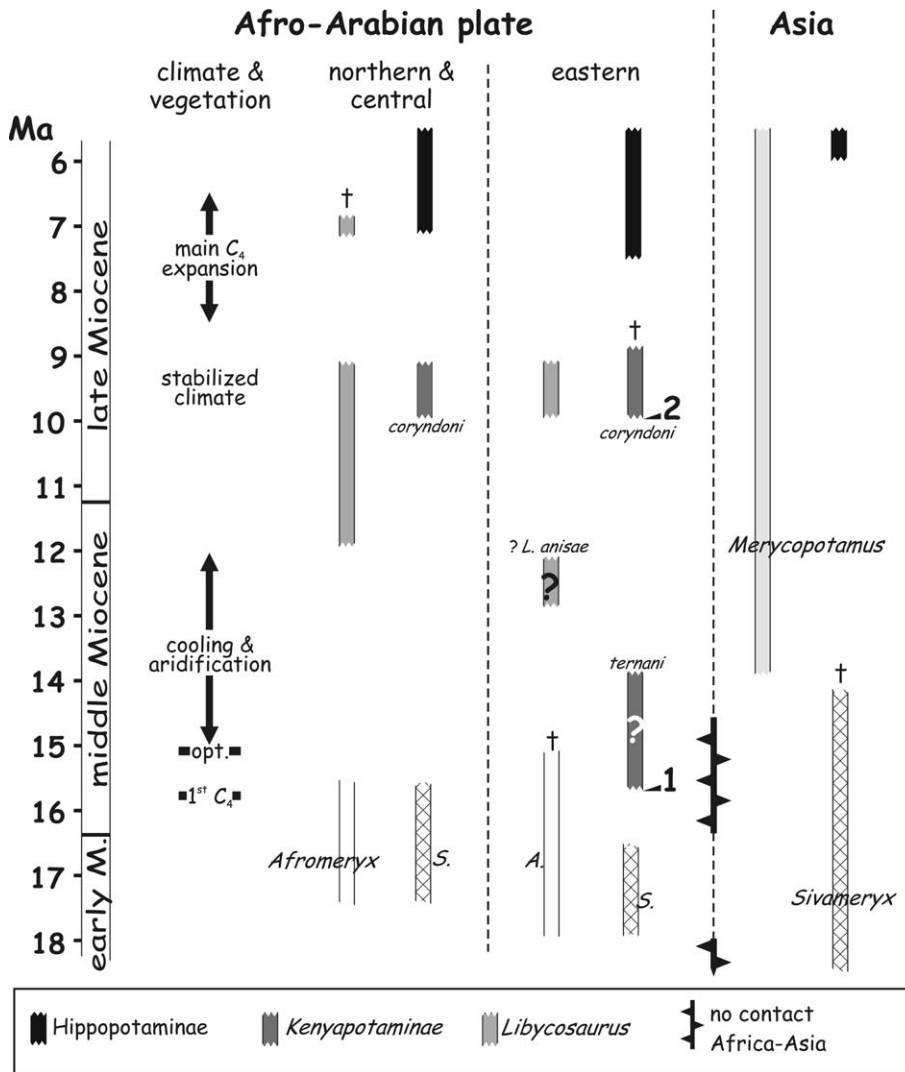
Fig. 2. Spatio-temporal distribution of the bothriodontines and hippopotamids during the Miocene in Africa and Asia, and environmental context: ?, forms with uncertain affinities; 1, 2, alternative FADs for Hippopotamidae; opt., climatic optimum.

Fig. 2. Répartition spatio-temporelle des bothriodontinés et des hippopotamidés au Miocène en Afrique et en Asie et contexte environnemental : ?, formes d'affinités incertaines ; 1, 2, premières apparitions (FAD) possibles pour les Hippopotamidae ; opt., optimum climatique.

its identification as a hippopotamid: some cylindrical and ever-growing lower incisors, and the astragalus. The trilobate wear pattern characteristic of the later hippopotamids is poorly expressed in *K. coryndoni*, yet recognizable on some molars [23]. On the contrary, a trilobate pattern is not apparent on the two isolated molars from Fort Ternan attributed to a different species, *K. ternani* [23]. Thus, Coryndon [12] did not acknowledge the presence of hippopotamids at Fort Ternan, but indicated their presence around 18 Ma at Rusinga (Kenya) on the basis of an isolated M^2, elsewhere identified as that of a bunodont anthracotheriid [23]. The inclu-

sion of *K. ternani* within Hippopotamidae seems therefore uncertain and needs to be re-examined. Accordingly, a FAD more recent around 10 Ma (Fig. 2) cannot be discarded for the time being.

3. New scenarios for hippo emergence

By taking into account the chronostratigraphical and geographical distribution of the Miocene bothriodontines (Fig. 2) and the uncertainties on the FAD and the sister group of Hippopotamidae, it is possible to propose two scenarios for hippo origination.

3.1. Late emergence

This first scenario is based on a monogeneric sister group of Hippopotamidae: *Libycosaurus*. The spatio-temporal distributions of this genus and of the first hippopotamids place their divergence in Africa at an age older than 12 Ma, which is the age of the first specimens indisputably identified as *Libycosaurus* (Fig. 2). Among bothriodontines, the closest relative of *Libycosaurus* is *Merycopotamus* [22], a genus initially thought related to hippos [11,14]. The first representative of the clade (*Libycosaurus*, Hippopotamidae) (Fig. 1A) would therefore be a form related to the Asian *Merycopotamus* (see Fig. 2 for distribution). This relationship implies the divergence *Libycosaurus*–Hippopotamidae from an anthracotheriid having Asian forerunners older than 14 Ma. The dispersion of this anthracotheriid toward Africa would be probably younger than 15 Ma. Indeed, at the beginning of the Middle Miocene, the Indo-Mediterranean sea corridor was open [28] and constituted an obstacle to faunal dispersions between Africa and Eurasia until ca. 15 Ma [1,29]. Moreover, the first African anthracotheriids related to *Merycopotamus* and/or *Libycosaurus* are known between 13 Ma and 12 Ma from the Kisegi Formation in Uganda [22,26]. Such a scenario is weakly compatible with the recognition of *K. ternani* as a hippopotamid (Fig. 2).

3.2. Early emergence

The second scenario is based on a sister group of Hippopotamidae, including both *Libycosaurus* and *Merycopotamus* (Fig. 1B). The origin of this clade should be looked for among an assemblage of Miocene bothriodontines of yet unresolved phylogenetical relationships (Fig. 2). This assemblage of Asian origin is known in Africa from 18 Ma (Fig. 2), as part of the first Neogene main faunal interchange between Africa and Eurasia [22,28,29]. Thus, hippos could have derived between 18 and 15 Ma from an African anthracotheriid linked to those Asian migrants. This scenario is congruent with both possible FADs proposed for the hippos. However, the analyses performed until now do not allow more precise determination of the relationships between those Early to Middle Miocene bothriodontines such as *Sivameryx* or *Afromeryx* with the hippos and their sister group (Fig. 1B). This scenario implies a gap in the fossil record of the first hippopotamids of at least 4 Ma.

4. Evolutionary and environmental constraints

4.1. Cheek tooth evolution

Hippopotamid molars are characterized by trilobate cusps, the wear pattern being triangular to trifoliate following lobe development. The bunodont appearance of these cusps was cited in favour of a hippo origin within groups with less selenodont dentition than Bothriodontinae [17,23]. However, the relations between hippopotamid cusp lobes are similar to those between the cristas and cusps of bothriodontine molars. Therefore, admitting that lobes and cristas are homologous, the hippopotamid dental pattern could have derived from that of a bothriodontine by reduction of crista and reorientation following the mesio-distal axis. Hence, the bothriodontine mesostyle would have become an isolated ectoconule, which is frequently observed in Miocene hippopotamids [17]. In our opinion, this modification would be sufficient to explain most of the differences between the cheek teeth of these taxa. According to the above-proposed scenarios, it should have occurred within a relatively short period for such an alteration of the molar cusp pattern. This can be considered a serious possibility.

Kangas et al. [21] recently showed that crest development in mouse cheek teeth were strongly affected by the variations of a factor involved in epithelial growth and differentiation: the expression level of ectodysplasin [21]. Although it is necessary to remain cautious with the extension of these results to ungulates, this indicates the possibility that some minor genotype changes can induce major changes in mammalian tooth cusp pattern.

At a different level, Miocene hippopotamid cheek tooth enamel is proportionally much thicker than in bothriodontines. This slight difference can contribute to significant changes of the wear pattern, conferring a more bunodont appearance to the dentition [20]. Evolution of enamel thickness is known for various mammalian taxa and can occur relatively fast.

The scenario of early hippo emergence better agrees with the constraints related to dental evolution, given the less advanced selenodonty in the Early to Middle Miocene bothriodontines than in *Merycopotamus* and *Libycosaurus*. However, this scenario also implies the parallel evolution of incisor prolonged growth and of an intercanine palatine groove in *Libycosaurus* and the first hippopotamids or, less likely, the reversal of these character states in *Merycopotamus* [6]. Finally, one can note that the possible occurrence with *Sivameryx* and

Afromeryx of a rather bunodont anthracotheriid at Rusinga (Kenya) at 18 Ma [12,23] could indicate a simple solution to the apparent incongruence between hippopotamid and bothriodontine dental morphologies.

4.2. Environmental context

The Middle Miocene was marked by a dramatic climatic and environmental shift. A major cooling of oceanic waters occurred progressively between 16/15 Ma and 12 Ma [30]. This cooling (Fig. 2) is generally correlated to the restoration of the East Antarctic ice sheet and to an increase of continental environment aridity, notably in Africa [15]. Recently, Douady et al. [13] enlightened the influence of this increasing aridity on Miocene mammal evolution, notably the role of the Sahara as a vicariant agent. An even greater influence can be considered on the populations of bothriodontines and hippopotamids strongly dependent on aquatic habitats. Increasing aridity may have resulted in altered and fragmented habitats, favouring isolations of limited populations. In these circumstances, fast evolution and morphological innovations such as the unique dental cusp pattern of the Hippopotamidae or the five premolariform teeth of *Libycosaurus* could have been favoured by exacerbated ecological pressures and the effects of genetic drift and founding populations. These climatic conditions may therefore have been a major factor in the emergence of Hippopotamidae, regardless of the considered hypothesis (Fig. 2).

Another important parameter to consider in relation to hippo origin is the expansion of grasses in African biotopes, notably that of grasses with a photosynthetic cycle in C_4. At the end of the Miocene, the hippopotamines (i.e. all Hippopotamidae except *Kenyapotamus*) arose in extreme abundance and high diversity [8]. This happened contemporaneously (Fig. 2) with the main expansion phase of C_4 grasses in Africa [10]. The diet of these first hippopotamines included a large proportion of these plants [7,9], suggesting an hypothetical co-evolution between hippopotamids and C_4 grasses [7]. A correlation in time and space is also observed between the oldest occurrence of C_4 vegetation in Africa at 15.9 Ma in Kenya [3] and the most frequently cited hippo FAD (Fig. 2).

5. Conclusion

Testing of the two proposed palaeoscenarios and their evolutionary and environmental aspects can now be implemented through:

- a thorough re-examination of the published material attributed to *Kenyapotamus* and of the isolated specimens from Maboko and Rusinga;
- the description of the unpublished material, notably from Kipsaramon;
- the comparison of these specimens with the Miocene bothriodontines;
- palaeoecological analyses of all this material (carbon and oxygen stable isotopes and dental microwear).

However, it is likely that the emergence of Hippopotamidae will not be fully understood without filling the gaps of the fossil record with more fossils from the Middle Miocene deposits of Africa.

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References

[1] P. Andrews, T. Harrison, L. Martin, E. Delson, R. Bernor, Systematics and biochronology of European Neogene catarrhines, in: R. Bernor, V. Fahlbusch (Eds.), Evolution of Neogene continental biotopes in Europe and the eastern Mediterranean, Columbia University Press, New York, 1996, pp. 168–207.

[2] S. Bajpai, P.D. Gingerich, A new Eocene archaeocete (Mammalia, Cetacea) from India and the time of origin of whales, Proc. Natl. Acad. Sci. USA 95 (1998) 15464–15468.

[3] A.K. Behrensmeyer, A.L. Deino, A. Hill, J.D. Kingston, J.J. Saunders, Geology and geochronology of the Middle Miocene Kipsaramon site complex, Muruyur Beds, Tugen Hills, Kenya, J. Hum. Evol. 42 (2002) 11–38.

[4] J.-R. Boisserie, The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): a review based on morphology and cladistic analysis, Zool. J. Linn. Soc. 143 (2005) 1–26.

[5] J.-R. Boisserie, F. Lihoreau, M. Brunet, Origins of Hippopotamidae (Mammalia, Cetartiodactyla): towards resolution, Zool. Scr. 34 (2005) 119–143.

[6] J.-R. Boisserie, F. Lihoreau, M. Brunet, The position of Hippopotamidae within Cetartiodactyla, Proc. Natl. Acad. Sci. USA 102 (2005) 1537–1541.

[7] J.-R. Boisserie, A. Zazzo, G. Merceron, C. Blondel, P. Vignaud, A. Likius, H.T. Mackaye, M. Brunet, Diets of modern and Late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel, Palaeogeogr. Palaeoclimatol. Palaeoecol. 221 (2005) 153–174.

[8] J.-R. Boisserie, A. Likius, P. Vignaud, M. Brunet, A new Late Miocene hippopotamid from Toros-Ménalla, Chad, J. Vertebr. Paleontol. 25 (2005) 665–673.

[9] T.E. Cerling, J.M. Harris, M.G. Leakey, Isotope paleoecology of the Nawata and Nachukui Formations at Lothagam, Turkana Basin, Kenya, in: J.M. Harris, M.G. Leakey (Eds.), Lothagam. The dawn of humanity in eastern Africa, Columbia University Press, New York, 2003, pp. 587–597.

[10] T.E. Cerling, J.M. Harris, B.J. MacFadden, M.G. Leakey, J. Quade, V. Eisenmann, J.R. Ehleringer, Global vegetation change through the Miocene/Pliocene boundary, Nature 389 (1997) 153–158.

[11] E.H. Colbert, The phylogeny of the Indian Suidae and the origin of the Hippopotamidae, Am. Mus. Nov. 799 (1935) 1–24.

[12] S.C. Coryndon, Hippopotamidae, in: V.J. Maglio, H.B.S. Cooke (Eds.), Evolution of African Mammals, Harvard University Press, Cambridge, 1978, pp. 483–495.

[13] C.J. Douady, F. Catzeflis, J. Raman, M.S. Springer, M.J. Stanhope, The Sahara as a vicariant agent, and the role of Miocene climatic events, in the diversification of the mammalian order Macroscelidea (elephant shrews), Proc. Natl. Acad. Sci. USA 100 (2003) 8325–8330.

[14] H. Falconer, P.T. Cautley, Note on the fossil hippopotamus of the Siwalik Hills, Asiat. Res. Calcutta 19 (1836) 39–53.

[15] B.P. Flower, J.P. Kennett, The Middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling, Palaeogeogr. Palaeoclimatol. Palaeoecol. 108 (1994) 537–555.

[16] J.H. Geisler, M.D. Uhen, Morphological support for a close relationship between hippos and whales, J. Vertebr. Paleontol. 23 (2003) 991–996.

[17] A.W. Gentry, J.J. Hooker, The phylogeny of the Artiodactyla, in: M.J. Benton (Ed.), The phylogeny and classification of the Tetrapods, Volume 2: Mammals, Clarendon Press, Oxford, 1988, pp. 235–272.

[18] D. Geraads, Z. Alemseged, H. Bellon, The Late Miocene mammalian fauna of Chorora, Awash Basin, Ethiopia: systematics, biochronology, and the ^{40}K–^{40}Ar ages of the associated volcanics, Tertiary Res. 21 (2002) 113–122.

[19] P.D. Gingerich, M.U. Haq, I.S. Zalmout, K.I. Hussain, M.S. Malkani, Origin of whales from early artiodactyls: hand and feet of Eocene Protocetidae from Pakistan, Science 293 (2001) 2239–2242.

[20] J. Jernvall, Mammalian molar cusp patterns: developmental mechanisms of diversity, Acta Zool. Fenn. 198 (1995) 1–61.

[21] A.T. Kangas, A.R. Evans, I. Thesleff, J. Jernvall, Non-independence of mammalian dental characters, Nature 432 (2004) 211–214.

[22] F. Lihoreau, Systématique et paléoécologie des Anthracotheriidae [Artiodactyla; Suiformes] du Mio–Pliocène de l'Ancien Monde : implications paléobiogéographiques, PhD thesis, université de Poitiers, France, 2003.

[23] M. Pickford, On the origins of Hippopotamidae together with descriptions of two species, a new genus and a new subfamily from the Miocene of Kenya, Geobios 16 (1983) 193–217.

[24] M. Pickford, Update on hippo origins, C. R. Acad. Sci. Paris, Ser. II 309 (1989) 163–168.

[25] M. Pickford, Découverte de *Kenyapotamus* en Tunisie, Ann. Paleontol. 76 (1990) 277–283.

[26] M. Pickford, Anthracotheriidae from the Albertine Rift Valley, in: B. Senut, M. Pickford (Eds.), Geology and palaeobiology of the Albertine Rift Valley, Uganda–Zaïre, CIFEG Orléans, 1994, pp. 309–319.

[27] M. Pickford, J. Morales, On the tayassuid affinities of *Xenohyus* Ginsburg, 1980, and the description of new fossils from Spain, Est. Geol. 45 (1989) 233–237.

[28] F. Rögl, Circum mediterranean Miocene paleogeography, in: G.E. Rössner, K. Heissig (Eds.), The Miocene land mammals of Europe, Verlag Dr. Friedrich Pfeil, Munich, Germany, 1999, pp. 39–48.

[29] H. Thomas, The Early and Middle Miocene land connection of the Afro–Arabian plate and Asia: a major event for hominoid dispersal?, in: E. Delson (Ed.), Ancestors: the hard evidence, Alan R. Liss Inc, 1985, pp. 42–50.

[30] J. Zachos, M. Pagani, L. Sloan, E. Thomas, K. Billups, Trends, rhythms, and aberrations in global climate 65 Ma to present, Science 292 (2001) 686–693.