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# The Libycosaurus (Hippopotamoidea, Artiodactyla) intercontinental dispersal event at the early late Miocene revealed by new fossil remains from Kasserine area, Tunisia

Fabrice Lihoreau, El Mabrouk Essid, Hayet Khayati Ammar, Laurent Marivaux, Wissem Marzougui, Rodolphe Tabuce, Rim Temani, Monique Vianey-Liaud, Gilles Merzeraud

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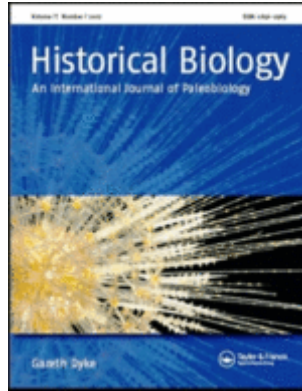
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**The Libycosaurus (Hippopotamoidea, Artiodactyla)  
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3 **The *Libycosaurus* (Hippopotamoidea, Artiodactyla) intercontinental**  
4 **dispersal event at the early Late Miocene revealed by new fossil**  
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6 **remains from Kasserine area, Tunisia**  
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14 Fabrice Lihoreau<sup>a\*</sup>, El Mabrouk Essid<sup>b</sup>, Hayet Khayati Ammar<sup>b</sup>, Laurent Marivaux<sup>a</sup>,  
15  
16 Wissem Marzougui<sup>b</sup>, Rodolphe Tabuce<sup>a</sup>, Rim Temani<sup>b</sup>, Monique Vianey-Liaud<sup>a</sup> and  
17  
18 Gilles Merzeraud<sup>c</sup>  
19  
20  
21  
22

23 <sup>a</sup>Institut des Sciences de l'Evolution de Montpellier, Univ. Montpellier CNRS IRD  
24  
25 EPHE, Montpellier, France  
26  
27

28 <sup>b</sup>Service Géologique, Office National des Mines, Tunis, Tunisia  
29

30 <sup>c</sup>Géosciences Montpellier, Univ. Montpellier CNRS, Montpellier, France  
31  
32  
33  
34

35 \*Corresponding author: Institut des Sciences de l'Evolution de Montpellier, Université  
36  
37 de Montpellier, cc064 place eugène Bataillon 34095 Montpellier cedex, France,  
38  
39 Fabrice.Lihoreau@UMontpellier.fr  
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3 **The *Libycosaurus* (Hippopotamoidea, Artiodactyla) intercontinental**  
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6 **remains from Kasserine area, Tunisia**  
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15 Anthracotheres dispersed from Asia toward Africa at least three times: at the  
16 Eocene/Oligocene transition, during early Miocene and later during the Miocene.  
17 Those dispersals are important datum events for African tertiary biochronology.  
18  
19 New fossil remains of early *Libycosaurus*, the genus implicated in the Late  
20 Miocene dispersal, are described from a new Tunisian locality of the Kasserine  
21 area. The new fossils enhance the hypodigm of *Libycosaurus algeriensis* and  
22 permit increased resolution of the phylogenetic position of this species using  
23 cladistics analysis. The inclusion of the genus *Libycosaurus* within the well-  
24 described *Merycopotamus* lineage allows us to constrain its dispersal time.  
25  
26 Dispersal of this anthracothere from the Indian sub-continent to Africa was  
27 probably facilitated by sea level decrease during the early Tortonian, just  
28 preceding the *Hipparion* dispersal event. This new age estimation refines the  
29 resolution of the succession of late Miocene deposits in the Maghreb and frames  
30 the date of the onset of the Sahara.  
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46 Keywords: *Cladistic analysis, Bothriodontinae, Merycopotamini, Sahara,*  
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48 *Tortonian, dispersal events*  
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## Introduction

Anthracotheres are an extinct family of morphologically and ecologically diverse cetartiodactyls, usually interpreted as swampy environment inhabitants. Within the superfamily Hippopotamoidea, the anthracotheres are considered closely related to the Hippopotamidae (e.g., Boisserie et al. 2011; Lihoreau, Boisserie, et al. 2015), but parts of the branching sequence within this clade are still unclear; as such the content of some anthracothere genera requires revisions. Anthracotheres are also particularly remarkable as they display unusual dispersal abilities, leading several palaeontologists to regard them as ‘ungulate pioneers’ in most of the intercontinental dispersal events (e.g., Ducrocq 1995; Lihoreau and Ducrocq 2007; Holroyd et al. 2010; Grandi and Bona 2017; Scherler et al. 2018).

The last African genus of anthracotheres, *Libycosaurus*, engaged in a form of semi-aquatic-lifestyle as indicated by the marked specialisation of its skeleton and its paleobiology (Lihoreau et al. 2006; Lihoreau et al. 2014). During the middle-late Miocene in Africa, *Libycosaurus* underwent a spectacular evolution characterized by a substantial body size change and a diet shifting (increase in C4-plant consumption), associated with social modifications notably with sexual size dimorphism and indices of fight between males (Lihoreau et al. 2014). This evolution was linked to the reduction of *Libycosaurus* habitat through change of the river system probably due to the variation of Sahara expansion. However, the evolutionary history of the genus is incomplete, as the origin of the genus remains unclear. A recent validation of the small and plesiomorphic species *Libycosaurus algeriensis* Ducrocq et al. 2001, with new material from the locality of Bir el Ater 3 (Algeria), highlighted the possibility that *Libycosaurus*

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2  
3 originated in Africa during the middle Miocene following the arrival of its ancestor  
4  
5 from the Indian subcontinent (Lihoreau, Hautier, et al. 2015).  
6

7  
8 We recently discovered new fossils attributable to *Libycosaurus algeriensis* in  
9  
10 Tunisia, from Sidi Hedri, a new locality situated near the town of Kasserine. We  
11  
12 describe here this new fossil material, which provides previously unknown elements for  
13  
14 documenting the basal morphotype of the genus. We perform a cladistic assessment  
15  
16 incorporating these new data with previously known morphological evidence, in order  
17  
18 to formalize the position of *Libycosaurus* within the anthracotheres. The original  
19  
20 phylogeny discussed in this study constrains a paleobiogeographic scenario prior to the  
21  
22 initiation of the Sahara desert and contemporaneous to a major sea-level drop. This  
23  
24 scenario refines the age estimates of some North African vertebrate fossil-bearing  
25  
26 deposits of the Miocene epoch.  
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### 33 **Materials and Methods**

#### 34 35 36 37 *Provenance of the new fossil material*

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39 The new material was discovered in the western part of central Tunisia, in the Kasserine  
40  
41 region, north of the Djebel Chambi (Fig. 1). The locality yielded three specimens  
42  
43 belonging to the same taxon, due to coherence in size and morphology. The new  
44  
45 remains consist of a right upper canine (SHI01), a right lower mandible with P/3-M/2  
46  
47 (SHI02) and a left M/3 (SHI03). These fossils were found during our 2012 field  
48  
49 expedition and come from a unique locality, Sidi Hedri, corresponding to a limited spot  
50  
51 and horizon (F4 on Fig. 1). The name locality is due to its proximity to the Marabout of  
52  
53 Sidi Hedri. The material is housed in the paleontological collections of the Museum of  
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55 Sidi Hedri. The material is housed in the paleontological collections of the Museum of  
56  
57 the Office National des Mines (ONM) in Tunis, Tunisia.  
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3 Material for comparisons is abbreviated as follows: M, material from the Natural  
4 History Museum, London, NG, material from Nagri Fm. Pakistan housed at the Utrecht  
5 University, Utrecht, Y, material from Potwar Plateau housed at the Harvard Peabody  
6 Museum, Cambridge, and CUWM material from Wadi Moghra housed at Cairo  
7 University, Cairo.  
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### 17 ***Stratigraphical context***

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19 The new Sidi Hedri fossil-bearing locality is situated in the Bir-Om-Ali stratigraphic  
20 section (Fig. 1; Vialle et al. 2013; Sweydan et al. 2018), north side of the Djebel  
21 Chambi. This section overlies laterally the late early to early middle Eocene fossil-  
22 bearing localities of Chambi locus 1 (CBI-1) and Chambi locus 2 (CBI-2), which have  
23 yielded numerous fossil remains of key taxa documenting the early evolutionary history  
24 of several vertebrates from Africa (e.g., Marivaux et al. 2015, Ravel et al. 2016,  
25 Mourer-chauviré et al. 2016, Tabuce 2018). The section contains the late Eocene  
26 locality of Bir-Om-Ali that yielded fragmentary fossil remains of the embriothopod  
27 *Arsinoitherium* (Vialle et al. 2013; F2 on Fig. 1), the fossiliferous locality of Mabrouk, a  
28 level with reworked marine fossils dated from the late Eocene-early Oligocene  
29 (Sweydan et al. 2018; F3 on Fig. 1), and a Neogene fine grained sandstone  
30 corresponding to the Sidi Hedri locality (F4 on Fig. 1). The Sidi Hedri fossiliferous  
31 horizon overlies alluvial-fan conglomerates in a unit consisting of fluvio-deltaic  
32 deposits. This unit was generally considered as belonging to the Beglia Formation (Fm.)  
33 but the definition of this formation might be taken with caution (e.g., Mannaï-Tayech  
34 2006; Mannaï-Tayech 2009; Belghithi et al. 2016). The sandstone attributed by  
35 Hartenberger et al. (2001) to the Beglia Fm. in fact corresponds to the uppermost  
36 Paleogene levels where the Mabrouk locality occurs (Sweydan et al. 2018). The  
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3 geological study made by Hartenberger *et al.* (2001) did not include the area where the  
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5 Neogene sediments outcrop. Furthermore, recent discussion of the Miocene sandstones  
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7 capping the Nementcha Fm. in Algeria (Lihoreau, Hautier, et al. 2015), only 130 km  
8  
9 southwest of Sidi Hedri, highlighted the critical role of fossil assemblage in correlating  
10  
11 between continental formations, and demonstrates that it is best to avoid using only  
12  
13 facies correlation for precise dating.  
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16  
17 The Neogene deposits in Tunisia unconformably overlie the latest Paleogene  
18  
19 deposits (Swezey 2009). The Neogene sandstones resulted from fluvial system  
20  
21 deposits in deltaic context over a long period of time, ranging from the Serravalian up to  
22  
23 the late Tortonian (Belghithi et al. 2016). They are usually gathered in formations  
24  
25 (Beglia Fm., Saouaf Fm., and Segui Fm.), but the variety of facies and the progradation  
26  
27 of the system make lithostratigraphy unreliable at a regional scale. In Tunisia, the  
28  
29 Neogene deposits yield two important fossil vertebrate faunas that provide constraints  
30  
31 on the age and chronology of associated formations. First, the locality of Bled Douarah  
32  
33 (Beglia Fm, western Tunisia) is assigned to the late Serravalian-early Tortonian in age  
34  
35 (Werdelin 2010). Bled Douarah is divided in to two sedimentological units, likely  
36  
37 corresponding to different environmental deposits and possibly climates (Mannai-  
38  
39 Tayech 2009). The faunal assemblages in each unit differ. Only the upper unit has  
40  
41 yielded equids (Robinson and Black 1969; Robinson and Black 1974) and seems to  
42  
43 represent more forested and more humid conditions (Mannai-Tayech 2009). The arrival  
44  
45 of equids in Africa is estimated close to 10.5 Ma (early Tortonian; Bernor et al. 2010).  
46  
47 Using the equid biotic marker, the earliest deposits referred to the Beglia Fm. are  
48  
49 estimated to document deposits dating near the Serravalian/Tortonian transition (Biely  
50  
51 et al. 1972; Mannai-Tayech 2009; following Hilgen et al. 2012), or near the beginning  
52  
53 of the marine regression recorded during the earliest Serravalian (13.8 Ma following  
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3 Hilgen et al. 2012; Belghithi et al. 2016). Recently, a part of the Beglia Fm. in western  
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5 Tunisia was correlated to the Saouaf Fm. in eastern Tunisia (Mannai-Tayech 2009;  
6  
7 Belghithi et al. 2016). The second fossil vertebrate fauna is from the Djebel Khechrem  
8  
9 El Artsouma (Geraads 1989) and belongs to the Segui Fm., stratigraphically overlying  
10  
11 the Beglia Fm. (Mannai-Tayech 2009; Belghithi et al. 2016). This locality is estimated  
12  
13 to be 0.5 to 1 myr more recent than the fauna from Bled Douarah (Geraads 1989).  
14  
15  
16 Several other localities from the Neogene silicoclastic deposits of Tunisia are known  
17  
18 but cannot be precisely dated due to the scarcity of the material or poorly time  
19  
20 constrained taxa (e.g., (Mannai-Tayech and Otero 2005).  
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### 26 ***Anatomy and cladistics analyses***

27  
28 The teeth description follows the dental nomenclature established for Hippopotamoidea  
29  
30 (Boisserie et al. 2010). Tooth measurements follow Lihoreau *et al.* (2014). A  
31  
32 calculation of the flattening index (fli) of the canine follows Kostopoulos *et al.* (2012),  
33  
34 which consists of a ratio at the cervix between the mesio-distal length and the labio-  
35  
36 lingual length ( $L_{md}/L_{ll} * 100$ ).  
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40 We consider the new fossil material described here as *Libycosaurus algeriensis*,  
41  
42 a species previously described in Algeria (Ducrocq et al. 2001; Lihoreau, Hautier, et al.  
43  
44 2015). Some of this material complements the hypodigm of this species. The new  
45  
46 material betters our knowledge of *L. algeriensis*, and facilitates inclusion of *L.*  
47  
48 *algeriensis* into a phylogenetic matrix incorporating recent matrices assembled for  
49  
50 deciphering internal phylogenetic relationships among taxa of the superfamily  
51  
52 Hippopotamoidea (including the “Anthracotheriidae” and the Hippopotamidae). Here,  
53  
54 we use the latest character matrices dealing with Merycopotamini (Lihoreau et al. 2016)  
55  
56 and with Hippopotaminae (Boisserie et al. 2017), as well as some updates (supp. data).  
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3 We added recent data for the species *Bothriogenys andrewsi* Schmidt, 1913, for which  
4 new material was recently published (Sileem et al. 2015), leading to better character  
5 scoring for *Bo. andrewsi* compared to previous analyses (Lihoreau, Boisserie, et al.  
6 2015). Then, we added four new characters that deal with the morphological conditions  
7 describing the genus *Libycosaurus* with respect to the other genera. We coded, on lower  
8 molars, the morphology of the postentocristid (= entoconid fold, 63, supp. data) and the  
9 pattern of incomplete hypoconulid (80, supp. data); on upper molars, the relation  
10 between the mesostyle and cingulum (139, supp. data); and on the mandible, the  
11 presence and morphology of a notch (156, supp. data). We also added the position of  
12 the main palatine foramen, a diagnostic character in *Merycopotamus* species (162;  
13 Lihoreau et al. 2004; character already used in Boisserie et al. 2005). All characters are  
14 unordered and unweighted. Parsimony analyses were performed on the new matrix (64  
15 taxa and 181 characters) with PAUP 4.0a164 (Swofford 2002) using heuristic searches  
16 with random step-wise addition (1000 replications with randomized input order of taxa)  
17 and tree-bisection-reconnection branch swapping options. We calculated the Bremer  
18 support for each node up to five supplementary steps.

## 41 **Systematic Paleontology**

42  
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46 Order Artiodactyla Owen, 1848

47  
48 Suborder Cetancodonta Arnason et al., 2000

49  
50 Superfamily Hippopotamoidea Gray, 1821 (*sensu* Gentry and Hooker 1988)

51  
52 Subfamily Bothriodontinae Scott, 1940

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54 Tribe Merycopotamini Lydekker, 1883

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56 Genus *Libycosaurus* Bonarelli, 1947  
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5 *Type-Species.* *Libycosaurus petrocchii* Bonarelli, 1947 (but see Lihoreau et al. 2014).

6  
7 *Included Species.* *Libycosaurus anisae* Black, 1972 from Bled Dourah and Djebel  
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9  
10 Kechrem el Artsouma, Tunisia (Geraads 1989), *L. bahri* Lihoreau et al., 2014 from  
11  
12 Toros-Ménalla, Chad and As Sahabi Libya (Lihoreau et al. 2014), and *L. algeriensis*  
13  
14 Ducrocq *et al.*, 2001.

15  
16 *Stratigraphic range.* Late Miocene (Tortonian to early Messinian).

17  
18 *Geographic distribution.* North and Central Africa (Libya, Algeria, Tunisia, Chad,  
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22 Uganda).

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26 *Libycosaurus algeriensis* Ducrocq *et al.*, 2001

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30 *Holotype.* Fragmentary left maxilla bearing M2/-M3/ (UONM1).

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33 *New material.* A right upper canine (SHI01), a fragment of right mandible preserving  
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35 P/3-M/2 (SHI02), and a fragment of left mandible bearing M/3 (SHI03). This material is  
36  
37 housed at the ONM, Tunis, Tunisia.

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39  
40 *Type locality.* Bir el Ater 2, Nementcha mountains, Algeria.

41  
42 *Other locality.* Bir el Ater 3, Algeria (Lihoreau, Hautier et al. 2015), Sidi Hedri, north of  
43  
44 Djebel Chambi, western part of central Tunisia (Fig. 1), and possibly Oluka, Kakara  
45  
46 Fm. Uganda (Pickford 1991a).

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48  
49 *Type horizon.* Nementcha Fm., considered to be late Serravalian/early Tortonian in age  
50  
51 (Lihoreau, Hautier, et al. 2015).

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56 *Diagnosis (emended from Lihoreau, Hautier and Mahboubi 2015).* Smallest known  
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58 species of the genus; retention of a small endometacristid on lower molars that connects  
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3 the preprotocristid; ectocristylids form cusplets in the transverse valleys near a  
4 developed labial cingulid; only one postentostylid on the posthypocristulid separated to  
5 the hypoconulid apex by a lingual groove; enamel microstructure of molars retains large  
6 and blurry Hunter Schreger Bands; shallow mandible with a weak vascular impression;  
7 retention of a lingual cingulum around the protocone in upper molars, even in worn  
8 specimen.  
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17 *Differential diagnosis.* *Libycosaurus algeriensis* differs from other species of the genus  
18 (*L. anisae* and *L. bahri*) in its smaller dimensions with shallow mandible, the presence a  
19 small endometacristid on lower molars, the ectocristylids frequently developed in  
20 cusplets in the transverse valleys, which is rare in other species, the large lingual  
21 cingulum around the protocone of upper molars (even in worn specimens), and in the  
22 preprotocristid on p/4, which is directed mesially then lingually as in most  
23 Merycopotamini and unlike in the two other species of *Libycosaurus*. It also differs  
24 from *L. anisae* in the presence of only one entostylid on the third lobe of the M/3. It also  
25 differs from *L. bahri* in the presence of a posthypocristulid on M/3, the retention of a  
26 weak vascular impression on the mandible, and in the presence of large and blurry  
27 Hunter Schreger Bands on the tooth enamel.  
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#### 46 ***Comparative descriptions***

47 *Upper canine (SHI01).* The crown apex is broken but wear facet and crown section are  
48 visible (Fig. 2). The cervix section is tear-shaped with a sharp distal keel, a swollen  
49 labial border and a flatter lingual border. The mesial border is rounded and bears the  
50 worn part of the tooth. The enamel appears thin and finely wrinkled. The whole tooth  
51 (crown plus root) is slightly inclined outward. The root is covered by cement, displays  
52 at least three constrictions toward the root apex, and remains open at its apex.  
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3 Considering the canine morphology and the enamel ornamentation, both gathered  
4 conditions expected for a bothriodontine anthracothere. In *Bothriodon velaunum* Cuvier,  
5 1824, an early Oligocene bothriodontine, the upper canine of males exhibits a clear  
6 demarcation at the cervix, with a smaller crown. On SHI01, the crown appears to be in  
7 continuity with the root. The SHI01 canine has a similar morphology of transverse  
8 section to that of *Elomeryx*, another Oligocene bothriodontine, but differs in being more  
9 transversally compressed (Flattening index = 53.6% in *E. borbonicus* (Geais, 1934; see  
10 Kostopoulos et al. 2012) and 60.9% in SHI01). SHI01 is larger than *E. borbonicus* and  
11 lacks the serration on the distal keel that is visible on the canine of *E. borbonicus*.

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Upper canines are known in few merycopotamine species. *Afromeryx zelteni*  
Pickford, 1991b, a stem Merycopotamini, displays a round and smaller upper canine  
section at the cervix (M82211). *Merycopotamus medioximus* Lihoreau et al., 2004,  
shows a canine of comparable dimension (Table 1, Fig. 2), with a similar wrinkled  
enamel characterized by longitudinal striations, and equivalent crown height proportion  
(NG104; Lihoreau et al. 2004). The labial border seems to be more swollen than in  
SHI01. There is a keel running on the distal border of the tooth, and a slight one is  
visible on the mesial border. In *Merycopotamus dissimilis* (Falconer and Cautley, 1836),  
the canine section is larger (Fig. 2), subcircular with slight distal and mesial keels in the  
three known specimens (Y49776, M16551, and M16552). The enamel covers at one  
third of the total length of the tooth. The root is closed and covered with cement in the  
only specimen where it is observable (Y49776; Lihoreau et al. 2007). Indeed, despite  
the marked similarities with the canine of *M. medioximus*, the SHI01 canine also shares  
anatomical traits with the canines of the two other species of *Libycosaurus* (*L. anisae*  
and *L. bahri*), notably in the lack of mesial keel, the presence of a lingual flattening of  
the crown section at the cervix, an open root apex, and in the presence of longitudinal

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3 grooves both on the labial and lingual sides of the root, which are not marked in canines  
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5 of *Merycopotamus* (Pickford 2006; Lihoreau et al. 2014). The SHI01 canine has smaller  
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7 dimensions at cervix than the upper canine of *L. anisae* (Black 1972; Pickford 2006)  
8  
9 and that of *L. bahri* (Lihoreau et al. 2014; Fig. 2D; Table 1). It is also more curved. A  
10  
11 similar small radius of curvature occurs in upper canines of *Merycopotamus*.  
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16  
17 *Lower premolars (P/3-4 on SHI02)*. The premolars are narrow and dominated by a  
18  
19 salient protoconid, which occupies a labial position (Fig. 3-4). A short and trenchant  
20  
21 preprotocristid joins the mesio-lingual margin of the tooth. It is adorned with three  
22  
23 successive small cusplets that decrease in height before reaching the mesial cingulid  
24  
25 (Fig. 3A-B, Fig. 4A). Such an unusual cusplets organization/striation is typical of  
26  
27 Merycopotamini, but such an amount of accessory cusps on P/3 and P/4 is only  
28  
29 known in species of *Libycosaurus* (Fig 4B-C) and in *Hemimeryx blanfordi* Lydekker,  
30  
31 1883 (Lihoreau et al. 2016; Fig. 4). The preprotocristid on P/4 has a mesial orientation  
32  
33 near the protoconid apex and turns abruptly distally, a pattern proposed as a features of  
34  
35 the Merycopotamini (Lihoreau et al. 2016; Fig. 4). This structure is less marked in the  
36  
37 latest known Merycopotamini, such as *L. anisae* and *L. bahri*, and in *M. dissimilis* (Fig.  
38  
39 4B-C, F). The postprotocristid is slightly arched and has a lingual position with respect  
40  
41 to the protoconid, also a Merycopotamini trait. The postprotocristid reaches a hypoconid  
42  
43 and then the distal cingulid in a small distostylid (Fig. 4). An endoprotocristid emerges  
44  
45 from the postprotocristid and reaches an entostylid (larger on P/4 than on P/3). The  
46  
47 premolars are narrower than those of *L. anisae* and *L. bahri* (Table 1), and equal the size  
48  
49 of *Merycopotamus nanus* Falconer, 1868 and *Sivameryx* spp. The P/4 seems slightly  
50  
51 smaller than the only known P/4 of *L. algeriensis* (Ducrocq et al. 2001). The mandibular  
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3 depth below M/1 is similar to the mean depth in *Sivameryx* spp. (Table 1) and to the  
4  
5 lowest values of *M. nanus* and *M. medioximus*.  
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10 *Lower molar.* Unfortunately, the right lower molars M/1-2 preserved on SHI02 are  
11 worn and badly preserved. The M/1 is similar in size to that of *Sivameryx* and  
12  
13 *Merycopotamus* spp. (Table 1). The left M/3 is well preserved (SHI03; Fig. 5) and  
14  
15 displays a bothriodontine pattern, which is characterized by an important development  
16  
17 of the cristids, notably the long prehypocristid that reaches the lingual margin of the  
18  
19 tooth. It also exhibits some Merycopotamini characters such as the lack of connection  
20  
21 between the premeta- and preprotocristids, and the pinched loop-like hypoconulid  
22  
23 (Lihoreau et al. 2016). Furthermore, the SHI03 M/3 lacks the premetacristid, displays a  
24  
25 pinched postentocristid between the entoconid and the posthypocristid, and a notched  
26  
27 posthypocristulid (an incomplete loop-like hypoconulid), all of which are diagnostic  
28  
29 traits of *Libycosaurus* (Lihoreau, Hautier, et al. 2015). Mesial to the posthypocristulid  
30  
31 notch, there is a marked postentostylid. This pattern is observed in all known specimens  
32  
33 of *L. algeriensis* and some *M. medioximus*. However, it differs from that characterizing  
34  
35 M/3 of *L. anisae* where there are many stylids without a clear groove separating the  
36  
37 entostylid from the rest of the posthypocristulid, and from that of *L. bahri*, where the  
38  
39 tooth lacks the posthypocristulid (Lihoreau, Hautier, et al. 2015). Lingual cuspids of  
40  
41 lower molar are more linguo-labially flattened in *L. algeriensis*, whereas they present a  
42  
43 rounded outline (in occlusal view) in other species of *Libycosaurus*. This is probably  
44  
45 due to development of sharper cristids in *L. algeriensis* than in the other species. This  
46  
47 condition also exists in early species of *Merycopotamus*.  
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56 Compared to *L. anisae* and *L. bahri*, the M/3 (SHI03) shows a blurry  
57  
58 endometacristid, not as developed as in *Sivameryx*, but similar to that observed in some  
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specimens of *Merycopotamus*. Such a very small endometacristid is observed in material of *L. algeriensis* from Algeria (Lihoreau, Hautier, et al. 2015).

There is a cusplet within the transverse valley that could be considered as an inflated ectocristilid as it joins the labial cingulid, forming small ectostylid. This pattern is known in most of specimens of *L. algeriensis* (6 of the 7 known lower molars). We also observed this structure within Merycopotamini, notably in some specimens of *M. nanus* (almost 4 of 15 molars) and in *Sivameryx* (close to 5 on 11 molars). In contrast, the ectocristilid in *L. anisae* and *L. bahri* do not form a cusplet (or rarely: 0 and 1 on at least 23 and 40 lower molars, respectively) but form an alignment of the enamel knob instead. The SHI03 M/3 is similar in size to the specimens from Bir el Ater 2 and 3 (UONM10, 9 and 14; Fig. 5; Lihoreau, Hautier, et al. 2015) and also very close to the mean value of *M. medioximus* (Table 1).

### Phylogeny

Heuristic searches have yielded 18 equally most parsimonious trees of 1226 steps each (CI= 0.30; RI= 0.64). A strict consensus tree is provided in Figure 6. The phylogenetic relationships are particularly well resolved, despite an apparent important number of homoplasies. The latter are much involved in the structure of the tree. The observed polytomies concern relationships between the two *Kenyapotamus* species and the Hippopotaminae, between *Sivameryx* spp. and *Hemimeryx*, and within the clade *Brachyodus* spp. + *Bothriogenys andrewsi*. The latter is mainly due to the small number of characters scored for *Bo. andrewsi* (few known fossil remains) and uncertainties regarding *Brachyodus*, suggesting a need for a revision of its evolutionary history. However, this study proposes *Bo. andrewsi* as a basal member of the *Brachyodus* clade, thereby representing the only Paleogene representative of that clade (this would suggest



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2  
3 a generic re-attribution of the species *Bo. andrewsi*; i.e. *Brachyodus andrewsi* following  
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5 Schmidt 1913). Our phylogenetic analyses, based on the characters used here (Lihoreau  
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7 et al. 2016), fail to discriminate the genus *Sivameryx* from *Hemimeryx*. The two genera  
8  
9 are considered phylogenetically close and differ mainly by their upper molar  
10  
11 morphologies notably the dimension of the paraconule (Lihoreau et al. 2016). In the  
12  
13 resulting tree the paraconule reduction appears as a reversion in *Sivameryx*. Further  
14  
15 phylogenetic analysis should therefore add more *Sivameryx* species to discuss this  
16  
17 particular point. Unfortunately, new material of *Sivameryx moneyi* (Fourtau, 1918) from  
18  
19 Wadi Moghra (Miller et al. 2014) cannot be included in this cladistic analysis due to the  
20  
21 lack of published description for the upper tooth. It is worth noting here that one  
22  
23 specimen of *S. moneyi* (CUWM 172) displays five upper premolars (Miller et al. 2014)  
24  
25 as in all the specimens of the two well-known species of *Libycosaurus* (Lihoreau et al.  
26  
27 2006; Pickford 2006). Therefore, unlike what is proposed by Miller et al. (2014, p.974),  
28  
29 this is not ‘a fairly common occurrence among anthracothere species in general’, and  
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31 should hence be tested in order to decipher possible close affinities between *S. moneyi*  
32  
33 and *Libycosaurus*.  
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40 The main clades depicted from this analysis, which display Bremer indices (BI)  
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42 of 3 or more (Fig. 6), are those of the suines, anthracotheriines, hippopotamids +  
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44 *Epirigenys lokonensis* Lihoreau, Boissérie, et al., 2105, hippopotamids, hippopotamins,  
45  
46 bothriodontines, *Brachyodus* spp. + *Bo. andrewsi* and merycopotamins (Fig. 6). The  
47  
48 main aim of this analysis was to assess the phylogenetic position of *L. algeriensis*  
49  
50 within the Merycopotamini. Therefore, we will here focus primarily on the description  
51  
52 of the nodes that gather the species of *Merycopotamus* and those of *Libycosaurus*.  
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56 First, the *Merycopotamus+Libycosaurus* clade (BI=5) is characterized by nine  
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58 non-ambiguous traits: the presence of a groove on the labial side on the lower canine  
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3 (12<sup>1</sup>), also observed in *Suina*, the lack of ectometafossid on lower molars (54<sup>1</sup>), a  
4  
5 character convergent with some Bothriodontinae and Hippopotaminae, an important  
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7 regression or lack of the endometacristid on lower molars (55<sup>0</sup>), which is convergent  
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9 with the Hippopotamidae, *Brachyodus* (+*Bo. andrewsi*) and stem Hippopotamoidea, the  
10  
11 lack of premetafossid on lower molars (57<sup>1</sup>), convergent with *Brachyodus*, *E.*  
12  
13 *borbonicus* and *Myaingtherium*, a reduced postectoentocristid (60<sup>1</sup>), which appears as a  
14  
15 reversion in Hippopotamoidea, a convex mesial border of P4/ (105<sup>1</sup>), also observed in  
16  
17 some Bothriodontinae (*Bothriodon*, *Aepinacodon* and *S. africanus* (Andrews, 1914), the  
18  
19 lack of postectoprotocrista (114<sup>0</sup>), as in Hippopotaminae, some microbunodontines and  
20  
21 *Siamotherium*, a maximal thickness in the middle of the sagittal section of the  
22  
23 symphysis (153<sup>0</sup>), as in Hippopotamidae and *Anthracotherium*, and the presence of a  
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25 mandibular notch with a short extension below m/3 (156<sup>2</sup>), as observed in *E.*  
26  
27 *borbonicus*.

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33 *Merycopotamus nanus* is the sister-taxon of a clade including the other species  
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35 of *Merycopotamus* (successively arranged) and the three species of *Libycosaurus*, the  
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37 latter forming a subclade. This *Merycopotamus*-*Libycosaurus* clade is supported (BI=  
38  
39 5) by six non ambiguous traits: crown of the male lower canine with a prolonged growth  
40  
41 (15<sup>2</sup>), also known in Hippopotamidae and *Suina*, the presence of a postentocristilid on  
42  
43 P/4 (42<sup>1</sup>), convergent with Hippopotamidae, *Elomeryx* spp., *S. palaeindicus* and  
44  
45 *Microbunodon minimum* (Cuvier, 1822) upper canine with prolonged growth of the root  
46  
47 (86<sup>2</sup>), convergent with *Suina*, a partial to total division of the mesostyle on upper molars  
48  
49 (140<sup>1</sup>), also observed in *Bothriodon*, *Aepinacodon* and *Elomeryx borbonicus*, a bony  
50  
51 fusion of the mandibular symphysis in adult (152<sup>1</sup>), a character highly convergent  
52  
53 within Hippopotamoidea but characteristic of several *Merycopotamini*, and the presence  
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3 of an inner radial enamel (schmelzmuster with 3 layers, 164<sup>1</sup>), which is highly  
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5 convergent within Hippopotamoidea.  
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8 *Merycopotamus dissimilis* and the three species of *Libycosaurus* form a well-  
9  
10 supported clade (BI=5) characterized by six non-ambiguous traits, including a non-  
11  
12 homoplastic apomorphy of the Hippopotamoidea. This exclusive trait is the presence of  
13  
14 an ectometacristule developed on the last upper molars (not M1/; 118<sup>2</sup>). This character  
15  
16 differs from the condition observed in other Hippopotamoidea where the  
17  
18 ectometacristule is expressed on M1/ and also from other Merycopotamini where the  
19  
20 ectometacristule is absent. The other unambiguous traits are the presence of a  
21  
22 postentocristid (62<sup>1</sup>), which is also observed in some *Bothriogenys*, Hippopotamidae,  
23  
24 Anthracotheriinae, although this postentocristid is mesio-distally oriented between the  
25  
26 posthypocristid and the entoconid (= the entoconid fold in Lihoreau et al. 2007) and  
27  
28 only observed in *S. africanus* among the Hippopotamoidea (63<sup>1</sup>), the presence of an  
29  
30 ectostylid on lower molars (72<sup>2</sup>), also known in Hippopotamidae and stem  
31  
32 Hippopotamidae, in *E. borbonicus*, *S. africanus* and in *H. blanfordi*, an incomplete  
33  
34 posthypocristulid (79<sup>1</sup>), also known in *Afromeryx zelteni* and *Chororatherium*, the  
35  
36 rostral opening of the main palatal foramen (162<sup>2</sup>), which is a character convergent with  
37  
38 Hippopotamidae and *B. onoideus* (Gervais, 1848-52).  
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45 The three species of *Libycosaurus* are gathered together (BI= 4) on the basis of  
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47 four non-ambiguous traits including two non-homoplastic apomorphies: the presence of  
48  
49 at least two accessory cusplets on the preprotocristid of all lower premolars (18<sup>2</sup>) and a  
50  
51 long postentocristilid on P/4 that reaches the distal cingulid (42<sup>2</sup>). Both character states  
52  
53 are derived condition of what is known in Merycopotamini (18<sup>1</sup>) or *Merycopotamus*  
54  
55 (42<sup>1</sup>). The other two non-ambiguous traits are the endoprotofossid on P/4 that reaches  
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57 the lingual cingulid wall (ectocristilid; 41<sup>1</sup>), a character which is convergent with *E.*  
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3 *borbonicus*, *A. zelteni* and *S. africanus* within the Bothriodontinae, and that is linked to  
4 the important development of the ectocristilid (42<sup>1-2</sup>), and finally the cingulum  
5 reduction at the mesostyle (139<sup>2</sup>), which is convergent with *Brachyodus* spp.,  
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10 *Bothriogenys fraasi* (Schmidt, 1913) and *Bo. andrewsi*, Hippopotamidae, *Bothriodon*,  
11  
12 *Aepinacodon* and *Hemimeryx*.

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15 In our cladistic analysis, *Libycosaurus algeriensis* forms the earliest offshoot of  
16 the *Libycosaurus* lineage, appearing as the sister-taxon of the two other species of the  
17 genus (*L. anisae* and *L. bahri*). The latter clade shows two non-ambiguous traits,  
18 including one non homoplastic synapomorphy: the preprotocristid direction on P/4 is  
19 lingual and then mesial (43<sup>1</sup>), whereas it is mesial then lingual in other Merycopotamini.  
20 The other non-ambiguous trait is the lack (loss) of the mandibular notch, mesial to the  
21 vertical ramus (156<sup>0</sup>), which is convergent with *Afromeryx* and the Hippopotaminae.  
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## 33 Discussion

### 34 35 36 37 *The age of Tunisian silicoclastic formations*

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39 The new anthracothere fossil remains from Sidi Hedri are the first known for the species  
40 *Libycosaurus algeriensis* in Tunisia. Based on the determination of these fossils, we can  
41 postulate that the sedimentary deposits where these fossils were found, are most likely  
42 contemporaneous with the Nementcha Fm. in Algeria, inasmuch as *Libycosaurus*  
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49 *algeriensis* was originally described from that rock unit (Fig. 1; Ducrocq et al. 2001;  
50 Mahboubi et al. 2003; Lihoreau, Hautier, et al. 2015). *Libycosaurus algeriensis* does not  
51 display some of the derived morphological traits characterizing *L. anisae* and *L. bahri*,  
52 and has so far never been found in association with those species. Evolutionary trends  
53 observed in the genus, notably general size increase and reduction of molar crests  
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3 suggest that *L. algeriensis* represents the most primitive known species of the genus  
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5 (Lihoreau, Hautier, et al. 2015). This suggests an earlier origin for *Libycosaurus*. This  
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7 view is corroborated here by the results of our phylogenetic analysis, which included  
8  
9 more characters and a better scoring of the matrix for some taxa, notably *L. algeriensis*.  
10  
11 Indeed, *L. algeriensis* was previously known only by 14 elements (upper molars, lower  
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13 molars, a fragmentary mandible, and a lower P/4 (Ducrocq et al. 2001; Lihoreau,  
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15 Hautier, et al. 2015). The new material has substantially improved the hypodigm of the  
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17 earliest species of *Libycosaurus*, and thus permitted to assess its phylogenetic  
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19 relationships. The phylogenetic results presented here recover the monophyly of the  
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21 *Libycosaurus* genus with *L. algeriensis* falling as the sister of *L. anisae* and *L. bahri*  
22  
23 (more recent species). The *Libycosaurus* clade is nested within a paraphyletic  
24  
25 *Merycopotamus* clade. The morphological characters in support of the *Libycosaurus*  
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27 clade (e.g., accessory cusplets on lower premolars) were already included in the  
28  
29 amended diagnosis of the genus (Lihoreau et al. 2014). Thanks to the new fossil  
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31 material and based on the phylogenetic results, we could add some aspects of the  
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33 morphology of the P/4 (e.g., long ectocristilid including the distal development of the  
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35 endoprotofossid) and of the upper molars (cingulum reduction at mesostyle) to the  
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37 genus diagnosis.  
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44 A key point of this discovery is the identification of two diachronous species of  
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46 *Libycosaurus* (*L. algeriensis* and *L. anisae*) in similar facies of silicoclastic deposits,  
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48 which were previously combined as Beglia Fm. We propose that either (1) that different  
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50 formations of late middle to early late Miocene sandstones were deposited in Tunisia  
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52 and therefore that all ochre sandstones should not be considered by default as  
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54 documenting (belonging to) the Beglia Fm., or (2) that the Beglia Fm. records deposits  
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3 corresponding to a long period of time, which require that they be separated into  
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5 different ages.  
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8 Within the Beglia Fm., the locality of Bled Douarah (including two levels) was  
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10 dated around 10.5 Ma (arrival in Africa of hipparions following Bernor et al. 2010). The  
11  
12 *Libycosaurus* from both levels do not show morphological discrimination (Black 1972)  
13  
14 or biometrical difference (Fig. 5). Therefore, this material may documents one unique  
15  
16 species, *L. anisae*, documenting a similar evolutionary grade. Thus, these two levels  
17  
18 might not represent a long time-span. The base of the Beglia Fm. may be early  
19  
20 Tortonian (11.6 Ma; Hilgen et al. 2012) or recording the earliest sediments  
21  
22 corresponding to the onset of the Serravalian marine regression (13.8 Ma; Hilgen et al.  
23  
24 2012). We can add here that the Beglia Fm. corresponds to a long regressive sequence,  
25  
26 and that the sediments characterizing the Sidi Hedri locality are also within regressive  
27  
28 deposits, and furthermore are older than the Bled Douarah low level.  
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33 Another important point is that the *Libycosaurus* clade shares a common  
34  
35 ancestry with *Merycopotamus dissimilis* and might originate from a *M. medioximus*-like  
36  
37 ancestral stock (Fig. 6). *Merycopotamus medioximus* is known from 10.4 Ma to 8.6 Ma  
38  
39 in deposits recorded in the Potwar Plateau (Pakistan; Fig. 7; Lihoreau et al. 2007). The  
40  
41 latter area displays successive species of *Merycopotamus*, thereby suggesting a possible  
42  
43 anagenetic lineage in this case. Some transitional form between *M. nanus* and *M.*  
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45 *medioximus* are present between 11.3 and 10.5 Ma. Therefore, a possible age for  
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47 *Libycosaurus algeriensis* could be bracketed between the earliest *M. medioximus*-like  
48  
49 ancestral stock (11.3 Ma) and the earliest level of Bled Douarah (older than 10.5 Ma).  
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56 ***The impact of the Tortonian/Serravalian marine regression on Libycosaurus***  
57  
58 ***dispersal***  
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3 The phylogenetic and geographic origins of *Libycosaurus* are deduced from results of  
4 the cladistics analysis (Fig. 6). Although *Libycosaurus* was proposed as sister-taxon of  
5 the *Merycopotamus* clade in previous analyses (Lihoreau et al. 2006; Lihoreau et al.  
6 2014), *Libycosaurus* was supposed to originate from a *M. nanus*-like ancestral stock  
7 from Asia (Lihoreau et al. 2014). From the phylogenetic results presented here,  
8 proposing that *Libycosaurus* is in fact nested within the *Merycopotamus* radiation, the  
9 arrival in Africa of the ancestor of *Libycosaurus* corroborates the hypothesis of a  
10 dispersal event from Asia to Africa as proposed by Lihoreau *et al.* (2006, 2014).  
11 However, the derivation of *Libycosaurus* would be related to a *M. medioximus-*  
12 *dissimilis* like ancestral stock, rather than a *M. nanus*-like ancestral stock. In this  
13 context, the origin of *Libycosaurus* would be viewed as more recent (later) than coeval  
14 to the *Merycopotamus* origin, as formerly suggested by earlier phylogenetic results  
15 (Lihoreau et al. 2006; Lihoreau et al. 2014). Accordingly, the genus *Merycopotamus*  
16 becomes paraphyletic in this phylogenetic context. However, in order for maintaining  
17 systematics stability, we propose here that all the species of *Libycosaurus* belong to  
18 *Merycopotamus* (following Black 1972), and that *Libycosaurus* represents an African  
19 subgenus of *Merycopotamus*. This taxonomic option requires additional paleontological  
20 evidence (documenting for instance the number of premolars in *L. algeriensis*) to  
21 further test this new systematic proposal.

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47 The new fossil material from Tunisia provides key arguments for rooting the  
48 origin of *Libycosaurus* near the origin of *Merycopotamus dissimilis*, most probably  
49 from a *M. medioximus*-like ancestral stock in Asia. The latter species, contrary to its  
50 precursors, points at widespread distribution characterized by a sudden expansion out of  
51 the Indian sub-continent, reaching South-East Asia and Middle East (Lihoreau et al.  
52 2007). This species most probably underwent disruptive evolution in different region of  
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3 Asia, with distinct populations in Thailand (a skull has been considered as a new species  
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5 *M. tachangensis* Hanta et al., 2008, which is considered as slightly derived from *M.*  
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7 *medioximus*) and in Iraq (Brunet and Heintz 1983; Lihoreau et al. 2007). We consider  
8  
9 that a population of *Merycopotamus* (close to the evolutionary degree of *M.*  
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11 *medioximus*) extended its range and shifted westward to reach Africa.  
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15 The Indian sub-continent is bordered by mountainous arc that limited the  
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17 distribution of anthracotheres outside, at least until the early Tortonian. Following  
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19 Lihoreau *et al.* (2007) and in accordance with freshwater-constrained distribution of the  
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21 anthracotheres (Lihoreau et al. 2014), the dispersal out of the Indian sub-continent  
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23 might have been facilitated by a major eustatic event (low sea-level) that would have  
24  
25 connected main river mouths in South Asia. In this province, the Tiger River and  
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27 Euphrates River, as well as the Indus River could have been involved in the connection  
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29 between Middle East and the Indian sub-continent, thus generating a possible dispersal  
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31 pathway for anthracotheres. Recent sedimentological and tectonical studies support the  
32  
33 existence of these proposed rivers connections. During the Burdigalian (early Miocene),  
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35 fan deposits of the Paleo-Indus River contact those of a river system north of the extant  
36  
37 Tiger River (Barrier et al. 2018). During this period important dispersal events  
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39 involving many mammalian species occurred between Asia and Africa. These are most  
40  
41 famously exemplified by the “*Gomphotherium* landbridge” in the Middle East (e.g. Sen  
42  
43 2013). At this time two anthracotheres genera, *Sivameryx* and *Afromeryx*, dispersed  
44  
45 from the Indian sub-continent to Africa (Holroyd et al. 2010). We suggest that this  
46  
47 Burdigalian dispersal was possible due to river mouth connections. In the same way, we  
48  
49 propose that a new connection between the same river mouths facilitated a dispersal of  
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51 anthracotheres from Indian sub-continent to Africa during Neogene (Tortonian).  
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3 The stratigraphical sequence where the earliest *Libycosaurus* (i.e., *L. algeriensis*)  
4  
5 is found corresponds to a marine regression phase. The environmental condition of  
6  
7 deposits characterizing the whole Beglia Fm., would correspond to this kind of eustatic  
8  
9 event (Belghithi et al. 2016). In contrast, the sediments of the Saouaf Fm. correspond to  
10  
11 a marine transgressive sequence (Belghithi et al. 2016). We hypothesize that first, the  
12  
13 dispersal took place during a regression event or second, at the regression maximum. A  
14  
15 main regression event is recorded between 12 Ma and 10.5 Ma in US mid-Atlantic  
16  
17 coastal plain (Kominz et al. 2008), and between 12.1 Ma and 10.9 Ma in the  
18  
19 northeastern Australian margin (John et al. 2011). This event is framed by the Mi5 and  
20  
21 Mi6 isotopic event (Haq et al. 1988; Westerhold et al. 2005; John et al. 2011). The sea  
22  
23 level drop is estimated close to 50 m, with a lowstand at 10.4-10.9 Ma (John et al. 2004;  
24  
25 Westerhold et al. 2005; Kominz et al. 2008). This event permitted the extension of the  
26  
27 hydrographical networks that may have connected temporarily the river mouths of  
28  
29 Paleo-Indus River and a paleo-river north to the Tiger River, and likely allowed semi-  
30  
31 aquatic mammals to disperse outside the Alpine arc. Following the distributions of  
32  
33 fluvio-lacustrine deposits during the Tortonian (Barrier et al. 2018), connections are  
34  
35 possible between the Tiger-Euphrate water system and the main trans-Saharan drainage  
36  
37 systems as the Nile rivers (Bussert et al. 2018) and the Sahabi rivers (Griffin 2010),  
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39 providing large dispersal pathway from Middle East to North Africa for fresh-water  
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41 aquatic mammals.  
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49 This dispersal event could therefore serve as a marker to precisely determine the  
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51 age of the first *Libycosaurus* arrival in Africa at the base of the Tortonian, between 11.3  
52  
53 Ma (the earliest occurrence of a *M. medioximus*-like representatives) and 10.9 Ma or  
54  
55 10.5 Ma (the minimal sea level). This age is crucial for dating the Nementcha Fm. in  
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57 Algeria and the early phase of deposition of the Beglia Fm. (earlier than Bled Douarah),  
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3 both of which record the occurrence of the most primitive species of *Libycosaurus* (*L.*  
4 *algeriensis*). Moreover, the record of *Libycosaurus* in the late Miocene of Oluka in  
5  
6 Uganda (Pickford 1991a), indicates that connections between North and East Africa  
7  
8 were possible for semi-aquatic mammals, thereby constraining the age of the onset of  
9  
10 the Sahara. The specimen, an upper molar, from the Kakara Fm, Uganda, was attributed  
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12 to *Libycosaurus* cf. *anisae* (Pickford 1991a) and to *L. petrocchii* (Simon et al. 2017),  
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14 even if the latter must only be restricted to its holotype (see Lihoreau et al. 2014). It is  
15  
16 difficult to discriminate *Libycosaurus* species on upper molar morphology but its small  
17  
18 size could eventually correspond to a very small specimen of *L. anisae* (Pickford 1991a)  
19  
20 or to a specimen of *L. algeriensis*. The age of this specimen is proposed to be early  
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22 Tortonian (Simon et al. 2017), and it is worth noting that this specimen was found in  
23  
24 association with *Tetralophodon*, as is the case at Bir el Ater 3 (Lihoreau, Hautier, et al.  
25  
26 2015). In sum, the Ugandan specimen, as well as the Algerian and the Tunisian  
27  
28 materials might represent evidence of the first arrival of *Libycosaurus* in Africa.  
29  
30 Besides, the apparent widespread distribution of this taxon would indicate riverine  
31  
32 connections between East and North Africa during the early Tortonian. This element  
33  
34 brackets the age of the Saharan onset after 10.5 Ma to at least a new period of near-river  
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36 connection within Sahara, near 7 Ma (Griffin 2002; Lihoreau et al. 2006; Otero et al.  
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38 2009).

## 39 40 41 42 43 44 45 46 47 48 49 **Conclusions**

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53 The evolution of *Libycosaurus* toward a more aquatic life style, a grazer diet and  
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55 gregarious habit is not a convergent history with *Merycopotamus*, but the same history  
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57 that took place in Africa. *Libycosaurus algeriensis* is here considered as  
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3 morphologically more advanced than *Merycopotamus nanus*, and thus already in course  
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5 of global ecological shift. Additional paleontological support documenting this species,  
6  
7 notably cranial elements, would be necessary for substantiating a new systematic  
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9 hypothesis according to which *Libycosaurus* would be a subgenus of *Merycopotamus*.  
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12 Our estimate regarding the dating of the new Tunisian Sidi Hedri locality, where  
13  
14 we discovered fossil remains attributable to *Libycosaurus algeriensis*, suggests an age  
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16 close to the base of Tortonian. *Libycosaurus algeriensis* represents the most ancient  
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18 record of the genus in Africa so far. *Libycosaurus algeriensis* probably documents a  
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20 species morphologically close to its Asian ancestor who probably dispersed to Africa  
21  
22 only shortly before the first appearance of *Libycosaurus* in the fossil record of Africa.  
23  
24 This corresponds to an important African event prior to the *Hipparion* Datum and thus  
25  
26 helps resolving African Neogene biochronology more precisely. A thorough review of  
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28 biostratigraphical correlations of Tunisian Neogene formations using vertebrate fossil  
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30 data should improve resolution of the local history for establishing an important scale  
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32 for the Middle-Late Miocene transition in Africa.  
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## Declaration of interest statement

## References

- Andrews CW. 1914. On the Lower Miocene Vertebrates from British East Africa, collected by Dr. Felix Oswald. *Quart Journ Geol Soc.* 70(1-4):163-NP.
- Arnason U, Gullberg A, Gretarsdottir S, Ursing BM, Janke A. 2000. The mitochondrial genome of the sperm whale and a new molecular reference for estimating eutherian divergence dates. *J Mol Evol.* 50:569–578.
- Barrier E, Vrielynck B, Brouillet JF, Brunet MF. (Contributors : Angiolini L, Kaveh F, Poisson A, Pourteau A, Plunder A, Robertson A, Shekawat R, Sosson M, Zanchi A) 2018. Paleotectonic Reconstruction of the Central Tethyan Realm. *Tectonono-Sedimentary-Palinspastic maps from Late Permian to Pliocene.* Paris: Commission for the Geological Map of the World.
- Belghithi H, Boulvain F, Yaich C, Da Silva AC. 2016. Évolution des séries silicoclastiques miocènes en Tunisie centrale : Cas de la coupe de Khechem El Artsouma. *Carnets Géologie Note Geol.* 16(23):557–568. doi:10.4267/2042/61846.
- Bernor RL, Armour-Chelu MJ, Gilbert H, Kaiser TM, Schulz E. 2010. Equidae. In: Werdelin L, Sanders WJ, editors. *Cenozoic Mammals of Africa.* Berkeley, Los Angeles, London: University of California Press. p. 685–721.

- 1  
2  
3 Biely A, Rakus M, Robinson P, Salaj J. 1972. Essai de corrélation des formations  
4 miocènes au sud de la dorsale tunisienne. Notes Serv Géologie Tunis. 38(7):73–92.  
5  
6 Black CC. 1972. A new species of *Merycopotamus* (Artiodactyla : Anthracotheriidae)  
7 from the late Miocene of Tunisia. Notes Serv Géologie Tunis. 37:5–39.  
8  
9 Boisserie JR, Fisher RE, Lihoreau F, Weston EM. 2011. Evolving between land and  
10 water: key questions on the emergence and history of the Hippopotamidae  
11 (Hippopotamoidea, Cetancodonta, Cetartiodactyla). Biol Rev. 86(3):601–625.  
12  
13 Boisserie JR, Lihoreau F, Brunet M. 2005. Origins of Hippopotamidae (Mammalia,  
14 Cetartiodactyla): towards resolution. Zool Scr. 34(2):119–143.  
15  
16 Boisserie JR, Lihoreau F, Orliac M, Fisher RE, Weston EM, Ducrocq S. 2010.  
17 Morphology and phylogenetic relationships of the earliest known hippopotamids  
18 (Cetartiodactyla, Hippopotamidae, Kenyapotaminae): *Kenyapotamus* and Hippopotamid  
19 Origins. Zool J Linn Soc. 158(2):325–366.  
20  
21 Boisserie JR, Suwa G, Asfaw B, Lihoreau F, Bernor RL, Katoh S, Beyene Y. 2017.  
22 Basal hippopotamines from the upper Miocene of Chorora, Ethiopia. J Vertebr  
23 Paleontol. e1297718. doi:10.1080/02724634.2017.1297718.  
24  
25 Bonarelli G. 1947. Dinosaurio fossile del Sahara Cirenaico. Riv Biol Colon Roma. 8:23–  
26 33.  
27  
28 Brunet M, Heintz E. 1983. Interpretation paleoecologique et relations biogéographiques  
29 de la faune de vertébrés du Miocène inférieur d’Injana, Irak. Paleogeogr Palaeoclimatol  
30 Palaeoecol. 44:283–293.  
31  
32 Bussert R, Eisawi AAM, Hamed B, Babikir IAA. 2018. Neogene palaeochannel  
33 deposits in Sudan – Remnants of a trans-Saharan river system? J Afr Earth Sci. 141:9–  
34 21.  
35  
36 Cuvier, G., 1822. Recherches sur les ossemens fossiles, où l’on rétablit les caractères de  
37 plusieurs animaux, dont les révolutions du globe ont détruit les espèces, Tome V, Paris:  
38 E. d’Ocagne.  
39  
40 Cuvier G. 1824. Recherches sur les ossemens fossiles: où l'on rétablit les caractères de  
41 plusieurs animaux dont les révolutions du globe ont détruit les espèces, Tome V, partie  
42 II. Paris: G. Dufour et E. D'Ocagne.  
43  
44 Ducrocq S. 1995. The contribution of Paleogene anthracotheriid artiodactyls in the  
45 paleobiogeographical history of southern Europe. Neues Jahrb Geol P M. 6:355–362.  
46  
47 Ducrocq S, Coiffait B, Coiffait PE, Mahboudi M, Jaeger JJ. 2001. The Miocene  
48 Anthracotheriidae (Artiodactyla, Mammalia) from the Nementcha, eastern Algeria.  
49 Neues Jahrb Geol P M. 3:145–156.  
50  
51 Falconer H. 1868. Palaeontological memoirs. London: R. Hardwicke.  
52  
53 Falconer H, Cautley PT. 1836. Note on the fossil Hippopotamus of the Siwalik hills.  
54 Asiatic Res. 19: 39-53.  
55  
56  
57  
58  
59  
60

- 1  
2  
3 Fourtau R. 1918. Contributions à l'étude des Vertébrés Miocènes de l'Égypte. Cairo:  
4 Geological Survey of Egypt.  
5
- 6 Geais G. 1934. Le *Brachyodus borbonicus* des argiles de St Henri (près Marseille). Trav  
7 Lab Géol Fac Sci Lyon Mém. 21:1-54.  
8
- 9 Gentry AW, Hooker JJ. 1988. The phylogeny of the Artiodactyla. In: Benton MJ, editor.  
10 The phylogeny and classification of the Tetrapods, Volume 2: Mammals, vol. 35B.  
11 Systematics Association Special Volume. Oxford: Clarendon Press; p. 235–272.  
12
- 13 Geraads D. 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem et  
14 Artsouma (Tunisie centrale). Comparaisons biostratigraphiques. Geobios. 22(6):777–  
15 801.  
16
- 17 Gervais P. 1848-52. Zoologie et paléontologie françaises: nouvelles recherches sur les  
18 animaux vivants et fossiles de la France. Paris: A. Bertrand.  
19
- 20 Grandi F, Bona F. 2017. Prominatherium dalmatinum from the late Eocene of Grancona  
21 (Vicenza, NE Italy). The oldest terrestrial mammal of the Italian peninsula. Comptes  
22 Rendus Palevol. 16(7): 738–745.  
23
- 24 Gray JE. 1821. On the natural arrangement of vertebrate animals. London Med Reposit.  
25 15: 296–310.  
26
- 27 Griffin DL. 2002. Aridity and humidity: two aspects of the late Miocene climate of  
28 North Africa and the Mediterranean. Paleogeogr Palaeoclimatol Palaeoecol. 2808:1–27.  
29
- 30 Griffin DL. 2011. The late Neogene Sahabi rivers of the Sahara and the hamadas of the  
31 eastern Libya–Chad border area. Paleogeogr Palaeoclimatol Palaeoecol. 309:176–185.  
32
- 33 Hanta R, Rathanastien B, Kunimatsu Y, Saegusa H, Nakaya H, Nagaoka S, Jintasakul  
34 P. 2008. A new species of Bothriodontinae, *Merycopotamus thachangensis*  
35 (Cetartiodactyla, Anthracotheriidae) from the late Miocene of Nakhon Ratchasima,  
36 Northeastern Thailand. J Vertebr Paleontol. 28(4):1182–1188.  
37
- 38 Haq BU, Hardenbol J, Vail PR. 1988. Mesozoic and Cenozoic chronostratigraphy and  
39 cycles of sea level change. In: Wilgus CK, Posamentier C, Ross CA, Kendall CG,  
40 editors. Sea level changes-An integrated approach. Vol. 42. Tulsa: Society of Economic  
41 Paleontologist and Mineralogist, special publication. p. 71–109.  
42
- 43 Hartenberger JL, Crochet JY, Martinez C, Marandat B, Sigé B. 2001. The Eocene  
44 mammalian fauna of Chambi (Tunisia) in its geological context. In: Gunnell GF, editor.  
45 Eocene Biodiversity. Vol. 18. Boston, MA: Springer US. p. 237–250.  
46
- 47 Hilgen FJ, Lourens LJ, Van Dam JA. 2012. The Neogene Period. In: Gradstein FM,  
48 Ogg JG, Schmitz M, Ogg G. The Geologic Time Scale. Amsterdam: Elsevier. p. 923–  
49 978.  
50
- 51 Holroyd PA, Lihoreau F, Gunnell GF, Miller ER. 2010. Anthracotheriidae. In: Werdelin  
52 L, Sanders WJ. Cenozoic mammals of Africa. Berkeley: University of California press.  
53 p. 843–851.  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 John CM, Karner GD, Browning E, Leckie RM, Mateo Z, Carson B, Lowery C. 2011.  
4 Timing and magnitude of Miocene eustasy derived from the mixed siliciclastic-  
5 carbonate stratigraphic record of the northeastern Australian margin. *Earth Planet Sci*  
6 *Lett.* 304(3–4):455–467.  
7  
8 John CM, Karner GD, Mutti M. 2004.  $\delta^{18}\text{O}$  and Marion Plateau backstripping:  
9 combining two approaches to constrain late middle Miocene eustatic amplitude.  
10 *Geology.* 32(9):829–832.  
11  
12  
13 Kominz MA, Browning JV, Miller KG, Sugarman PJ, Mizintseva S, Scotese CR. 2008.  
14 Late Cretaceous to Miocene sea-level estimates from the New Jersey and Delaware  
15 coastal plain coreholes: an error analysis. *Basin Res.* 20(2):211–226.  
16  
17  
18 Kostopoulos DS, Koufos GD, Christanis K. 2012. On some anthracotheriid  
19 (Artiodactyla, Mammalia) remains from northern Greece: comments on the  
20 palaeozoogeography and phylogeny of *Elomeryx*. *Swiss J Palaeontol.* 131(2):303–315.  
21  
22  
23 Lihoreau F, Alloing-Séguier L, Antoine PO, Boisserie JR, Marivaux L, Métais G,  
24 Welcomme JL. 2016. Enamel microstructure defines a major Paleogene hippopotamoid  
25 clade: the Merycopotamini (Cetartiodactyla, Hippopotamoidea). *Hist Biol.* 29(7):947–  
26 957.  
27  
28 Lihoreau F, Barry J, Blondel C, Brunet M. 2004. A new species of Anthracotheriidae,  
29 *Merycopotamus medioximus* nov. sp. from the Late Miocene of the Potwar Plateau,  
30 Pakistan. *Comptes Rendus Palevol.* 3(8):653–662.  
31  
32  
33 Lihoreau F, Barry J, Blondel C, Chaimanee Y, Jaeger JJ, Brunet M. 2007. Anatomical  
34 revision of the genus *Merycopotamus* (Artiodactyla; Anthracotheriidae): its significance  
35 for Late Miocene mammal dispersal in Asia. *Palaeontology.* 50(2):503–524.  
36  
37  
38 Lihoreau F, Boisserie JR, Blondel C, Jacques L, Likius A, Mackaye HT, Vignaud P,  
39 Brunet M. 2014. Description and palaeobiology of a new species of *Libycosaurus*  
40 (Cetartiodactyla, Anthracotheriidae) from the Late Miocene of Toros-Menalla, northern  
41 Chad. *J Syst Palaeontol.* 12(7):761–798.  
42  
43  
44 Lihoreau F, Boisserie JR, Manthi FK, Ducrocq S. 2015. Hippos stem from the longest  
45 sequence of terrestrial cetartiodactyl evolution in Africa. *Nat Commun.* 6:6264.  
46 doi:10.1038/ncomms7264.  
47  
48  
49 Lihoreau F, Boisserie JR, Viriot L, Coppens Y, Likius A, Mackaye HT, Tafforeau P,  
50 Vignaud P, Brunet M. 2006. Anthracothere dental anatomy reveals a late Miocene  
51 Chado-Libyan bioprovince. *Proc Natl Acad Sci USA.* 103(23):8763–8767.  
52  
53  
54 Lihoreau F, Ducrocq S. 2007. The Family Anthracotheriidae. In: Protero DR, Foss SE,  
55 editors. *The evolution of Artiodactyls.* John Hopkins University Press. p.89-105.  
56  
57  
58 Lihoreau F, Hautier L, Mahboubi M. 2015. The new Algerian locality of Bir el Ater 3:  
59 validity of *Libycosaurus algeriensis* (Mammalia, Hippopotamoidea) and the age of the  
60 Nementcha Formation. *Palaeovertebrata.* 39 (2):e1. doi:10.18563/pv.39.2.e1.

Lydekker R. 1883. Siwalik selenodont Suina. *Palaeontol Indica.* 10:143–177.



- 1  
2  
3 Mahboubi M, Tabuce R, Mebrouk F, Coiffait B, Coiffait PE, Jaeger JJ. 2003. L'écène  
4 continental à vertébrés de la bordure sud des monts des Nementcha (Atlas saharien  
5 oriental, Algérie). Bull Serv Géologique Algér. 14(1):27–35.  
6  
7  
8 Mannaï-Tayech B. 2006. Les séries silicoclastiques miocènes du Nord-Est au Sud-  
9 Ouest de la Tunisie : une mise au point. Geobios. 39(1):71–84.  
10  
11 Mannaï-Tayech B. 2009. The lithostratigraphy of Miocene series from Tunisia,  
12 revisited. J Afr Earth Sci. 54(3–4):53–61.  
13  
14 Mannaï-Tayech B, Otero O. 2005. Un nouveau gisement miocène à ichthyofaune au sud  
15 de la chaîne des Chotts (Tunisie méridionale). Paléoenvironnement et  
16 paléobiogéographie. Comptes Rendus Palevol. 4(5):405–412.  
17  
18 Marivaux L, Essid EM, Marzougui W, Khayati Ammar H, Merzeraud G, Tabuce R,  
19 Vianey-Liaud M. 2015. The early evolutionary history of anomaluroid rodents in  
20 Africa: new dental remains of a zegdomyid (Zegdomyidae, Anomaluroidea) from the  
21 Eocene of Tunisia. Zool Scri. 44:117–134.  
22  
23  
24 Miller ER, Gunnell GF, Gawad MA, Hamdan M, El-Barkooky AN, Clementz MT,  
25 Hassan SM. 2014. Anthracotheres from Wadi Moghra, early Miocene, Egypt. J  
26 Paleontol. 88(5):967–981.  
27  
28  
29 Mourer-Chauviré C, El Mabrouk E, Khayati H, Marivaux L, Marzougui W, Temani R,  
30 Vianey-Liaud M, Tabuce R. 2016. New remains of the very small cuckoo,  
31 *Chambicuculus pusillus* (Aves, Cuculiformes, Cuculidae) from the late Early or early  
32 Middle Eocene of Djebel Chambi, Tunisia. Palaeovertebrata. 40(1):e2.  
33 doi:10.18563/pv.40.1.e2.  
34  
35 Owen R. 1848. The archetype and homologies of the vertebrate skeleton. London: J.  
36 van Voorst.  
37  
38  
39 Otero O, Pinton A, Mackaye HT, Likius A, Vignaud P, Brunet M. 2009. Fishes and  
40 palaeogeography of the African drainage basins: relationships between Chad and  
41 neighbouring basins throughout the Mio-Pliocene. Palaeogeogr Palaeoclimatol  
42 Palaeoecol. 274(3–4):134–139.  
43  
44  
45 Pickford M. 1991a. Late Miocene anthracothere (Mammalia, Artiodactyla) from  
46 tropical africa. Comptes Rendus Académie Sci Paris. 313:709–715.  
47  
48  
49 Pickford M. 1991b. Revision of the Neogene Anthracotheriidae of Africa. In: Salem  
50 MJ, Busrewil MT, editors. The geology of Libya, vol. 4. New York: Academic press;  
51 p.1491-1525.  
52  
53  
54 Pickford M. 2006. Sexual and individual morphometric variation in *Libycosaurus*  
55 (Mammalia, Anthracotheriidae) from the Maghreb and Libya. Geobios. 39(2):267–310.  
56  
57  
58 Pickford M. 2008. *Libycosaurus petrocchii* Bonarelli, 1947, and *Libycosaurus anisae*  
59 (Black, 1972) (Anthracotheriidae, Mammalia): nomenclatural and geochronological  
60 implications. Ann Paléontol. 94(1):39–55.



1  
2  
3 Ravel A, Adaci M, Bensalah M, Charruault AL, Essid EM, Khayati Ammar H,  
4 Mahboubi M, Marzougui W, Mebrouk F, Merzeraud G, Vianey-Liaud M, Tabuce R,  
5 Marivaux L. 2016. Origine et radiation initiale des chauves-souris modernes : nouvelles  
6 découvertes dans l'Éocène d'Afrique du Nord. *Geodiversitas*. 38:355–434.

7  
8  
9 Robinson P, Black CC. 1969. Note préliminaire sur les vertébrés fossiles du  
10 vindobonien (formation Béglia), du Bled Douarah, Governorat de Gafsa, Tunisie. *Notes*  
11 *Serv Géologie Tunis*. 31:67–70.

12  
13 Robinson P, Black CC. 1974. Vertebrate faunas from the Neogene of Tunisia. *Ann Geol*  
14 *Surv Egypt*. 4:319–332.

15  
16 Scherler L, Lihoreau F, Becker D. 2018. To split or not to split *Anthracotherium*? A  
17 phylogeny of Anthracotheriinae (Cetartiodactyla; Hippopotamoidea) and its  
18 paleobiogeographic implications. *J Linn Soc*. 1–24. doi :10.1093/zoolinnean/zly052

19  
20  
21 Schmidt M. 1913. Über Paarhufer des fluviomarinen Schichten des Fajum,  
22 odontographisches und osteologisches Material. *Geol Paläontol Abh*. 11:153–264.

23  
24 Scott WB. 1940. The mammalian fauna of the White River Oligocene, part IV.  
25 Artiodactyla. *Trans Am Phil Soc*. 28:363–746.

26  
27 Sen S. 2013. Dispersal of African mammals in Eurasia during the Cenozoic: ways and  
28 whys. *Geobios* 46(2): 159–172.

29  
30  
31 Sileem AH, Sallam HM, Hewaidy AGA, Gunnell GF, Miller ER. 2015. Anthracotheres  
32 (Mammalia, Artiodactyla) from the upper-most horizon of the Jebel Qatrani formation,  
33 latest Early Oligocene, Fayum depression, Egypt. *Egypt J Paleontol*. 15:1–11.

34  
35  
36 Simon B, Guillocheau F, Robin C, Dauteuil O, Nalpas T, Pickford M, Senut B, Lays P,  
37 Bourges P, Bez M. 2017. Deformation and sedimentary evolution of the Lake Albert  
38 Rift (Uganda, East African Rift System). *Mar Pet Geol*. 86:17–37.

39  
40  
41 Sweydan S, Merzeraud G, Essid EM, Marzougui W, Temani R, Ammar HK, Marivaux  
42 L, Vianey-Liaud M, Tabuce R, Adnet S. 2018 Aug. A reworked elasmobranch fauna  
43 from Tunisia providing a snapshot of Eocene-Oligocene Tethyan faunas. *J Afr Earth*  
44 *Sci*. doi:10.1016/j.jafrearsci.2018.08.008. [accessed 2018 Aug 29].

45  
46 Swezey CS. 2009. Cenozoic stratigraphy of the Sahara, Northern Africa. *J Afr Earth*  
47 *Sci*. 53(3):89–121.

48  
49 Swofford DL. 2002. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other  
50 Methods). Sinauer Associates. Sunderland, Massachusetts.

51  
52  
53 Tabuce R. 2018. New remains of *Chambius kasserinensis* from the Eocene of Tunisia  
54 and evaluation of proposed affinities for Macroscelidea (Mammalia, Afrotheria). *Hist*  
55 *Biol*. 30(1–2):251–266.

56  
57  
58 Vialle N, Merzeraud G, Delmer C, Feist M, Jiquel S, Marivaux L, Ramdarshan A,  
59 Vianey-Liaud M, Essid EM, Marzougui W, et al. 2013. Discovery of an embrithopod  
60 mammal (*Arsinoitherium*?) in the late Eocene of Tunisia. *J Afr Earth Sci*. 87:86–92.

1  
2  
3 Werdelin L. 2010. Chronology of Neogene Mammal localities. In: Werdelin L, Sanders  
4 WJ, editors. Cenozoic Mammals of Africa. Berkeley: University of California Press. p.  
5 27–43.  
6

7  
8 Westerhold T, Bickert T, Röhl U. 2005. Middle to late Miocene oxygen isotope  
9 stratigraphy of ODP site 1085 (SE Atlantic): new constrains on Miocene climate  
10 variability and sea-level fluctuations. *Palaeogeogr Palaeoclimatol Palaeoecol.* 217(3–  
11 4):205–222.  
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Table 1. Teeth measurements of specimens from Sidi Hedri compared to mean values of some Merycopotamini species (Mean value $\pm$ SD from Lihoreau et al. 2004, 2007, 2014 and new measurements of *L. bahri* from CNRD, N'djaména)

		SHI	<i>L. algeriensis</i>	<i>L. anisae</i>	<i>L. bahri</i>	<i>M. nanus</i>	<i>M. medioximus</i>	<i>M. dissimilis</i>	<i>S.palaeindicus</i>	<i>S. africanus</i>
Upper C	L	18.4		23.9 $\pm$ 3.4	37.8 $\pm$ 2.6		e. 16	21.0 $\pm$ 2.9		
	l	11.2		17.3 $\pm$ 1.8	25.1 $\pm$ 1.3		11.1	17.4 $\pm$ 2.9		
	Fi	60.9		73.0 $\pm$ 4.4	66.0 $\pm$ 2.8		69.4	82.6 $\pm$ 6.3		
P/3	L	15		21.1 $\pm$ 1.4	24.7 $\pm$ 2.0	15.7 $\pm$ 1.2	17.7 $\pm$ 1	18	16.4	15.2 $\pm$ 1
	l	10		17.8 $\pm$ 1.4	18.8 $\pm$ 2.0	10.1 $\pm$ 0.9	10.6 $\pm$ 1	10	10.2	9.9 $\pm$ 1.2
P/4	L	17.5	19.4	20.5 $\pm$ 2.0	24.7 $\pm$ 2.2	17.1 $\pm$ 1.7	18.2 $\pm$ 1.7	20.6	17.4 $\pm$ 1.2	15.8 $\pm$ 1.3
	l	10.6	14.2	17.0 $\pm$ 1.6	19.5 $\pm$ 1.6	11.5 $\pm$ 1.2	11.3	14.6	11.2 $\pm$ 2.3	9.9 $\pm$ 0.9
M/1	L	18.5		24.9 $\pm$ 1.5	32.0 $\pm$ 2.4	19.7 $\pm$ 1.3	20.7 $\pm$ 2	20.7	17.1 $\pm$ 2.1	18.6
M/3	L	37.1	36.2 $\pm$ 0.8	44.3 $\pm$ 2.7	59.4 $\pm$ 4.6	33.2 $\pm$ 1.2	36.6 $\pm$ 3.7	39.2 $\pm$ 2.2	34.3 $\pm$ 2.1	32.7 $\pm$ 2.2
	l	16.4	17.6 $\pm$ 0.5	23.9 $\pm$ 1.6	30.7 $\pm$ 2.8	15.9 $\pm$ 1.7	17.3 $\pm$ 1.9	20.1 $\pm$ 2.1	15.5 $\pm$ 1.1	14.8 $\pm$ 1.1
mandible	H <sub>P4-M1</sub>	33.5		66.1 $\pm$ 7.6	104.8 $\pm$ 18	42.5 $\pm$ 3	44 $\pm$ 9.4	60.9 $\pm$ 4.8	31	32.2 $\pm$ 3.4
	Min	33.5		57.1	72	38	37	47.9	31	27.2

## Figure Captions

Figure 1. Geographical location of Sidi Hedri and other localities that have yielded *Libycosaurus* remains in Algeria and Tunisia (full black circle), position in regard of other fossiliferous localities (F1-4) from the Djebel Chambi area in Tunisia, and their stratigraphical relations.

Figure 2. Upper canine comparisons. Lingual views of (A) left upper canine of *L. bahri* from Toros-Ménalla (TM257-04-08, reversed), (B) left upper canine of *L. anisae* from Bled Douarah (T271, reversed) and, (C) right upper canine of *L. algeriensis* from Sidi Hedri (SHI01). (D) Compared dimensions at cervix of upper canines of *Merycopotamus* and *Libycosaurus* species.

Figure 3. New mandibular material with right P/3-M/2 from Sidi Hedri (SHI02) in (A) lingual, (B) occlusal, and (c) labial views.

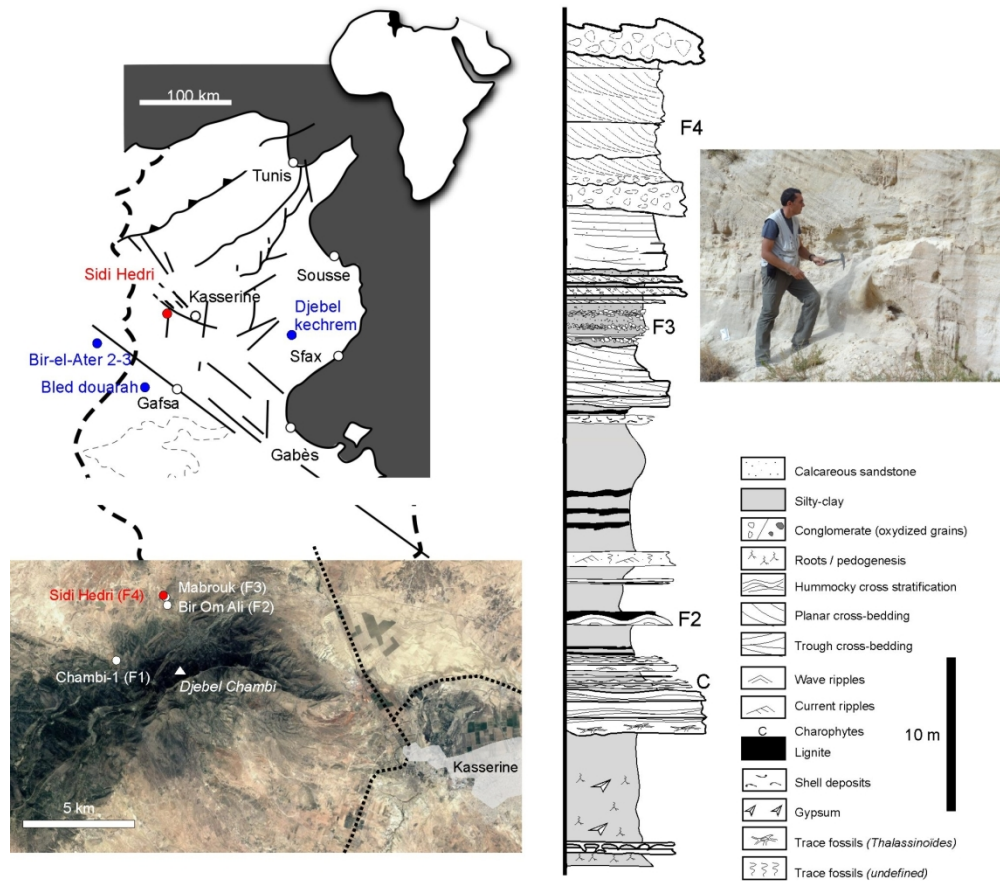
Figure 4. Comparisons of occlusal pattern of lower P/4 in Merycopotamini. (A) *Libycosaurus algeriensis*, Sidi Hedri (SHI02). (B) *Libycosaurus anisae* Bled Douarah (Holotype T356G). (C) *Libycosaurus bahri*, Toros-Menalla (TM258-01-13). (D) *Merycopotamus nanus*, Potwar Plateau (AMNH 94616, reversed). (E) *Merycopotamus medioximus*, Potwar Plateau (HGSP14969, reversed). (F) *Merycopotamus dissimilis* Potwar Plateau (HGSP16418, reversed). (G) *Sivameryx africanus* Gebel Zelten (NHM No N° reversed). (H) *Afromeryx zelteni*, Gebel zelten (M82233). (I) *Hemimeryx blanfordi*, Bugti Hills (M12026). Abbreviations: Proto<sup>d.</sup>, protoconid; Ento<sup>std.</sup>, entostylid; Hypo<sup>d.</sup>, hypoconid; 1, preprotocristid; 2, postprotocristid; 3, endoprotocristid.

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Figure 5. Left m/3 from Sidi Hedri (SHI03) in (A) labial, (B) lingual and, (C) occlusal views with scheme. Comparisons of m/3 dimensions of *Libycosaurus* species by origin. Abbreviations: Proto<sup>d</sup>., protoconid; Meta<sup>d</sup>., metaconid; Hypo<sup>d</sup>., hypoconid; Ento<sup>d</sup>., entoconid; Hypo<sup>ulid</sup>., hypoconulid; 1, preprotocristid; 2, postprotocristid; 3, prehypocristid; 4, posthypocristid; 5, prehypocristulid; 6, posthypocristulid; 7, postectometacristid; 8, postmetacristid; 9, postectoentocristid; 10, preentocristid; 11, postentocristid.

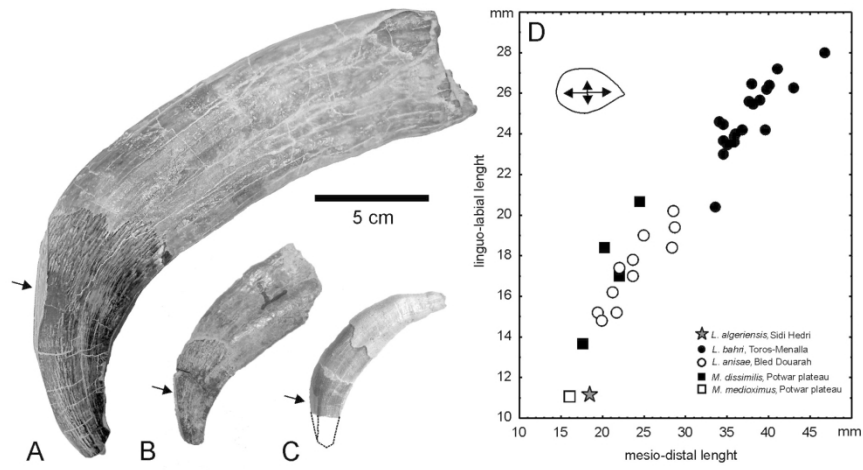
Figure 6. Phylogenetic results. Strict consensus tree of 18 equally most parsimonious trees of 1266 steps each (CI=0.30; RI=0.64). Bremer indices (> 1) are indicated at nodes.

Figure 7. Paleobiogeographical scenario for Merycopotamini implied by new phylogeny with paleocological inferences from Lihoreau *et al.* (2014). The geochronological time scale is from Hilgen *et al.* (2012).



Geographical location of Sidi Hedri and other localities that have yielded *Libycosaurus* remains in Algeria and Tunisia (full black circle), position in regard of other fossiliferous localities (F1-4) from the Djebel Chambi area in Tunisia, and their stratigraphical relations.

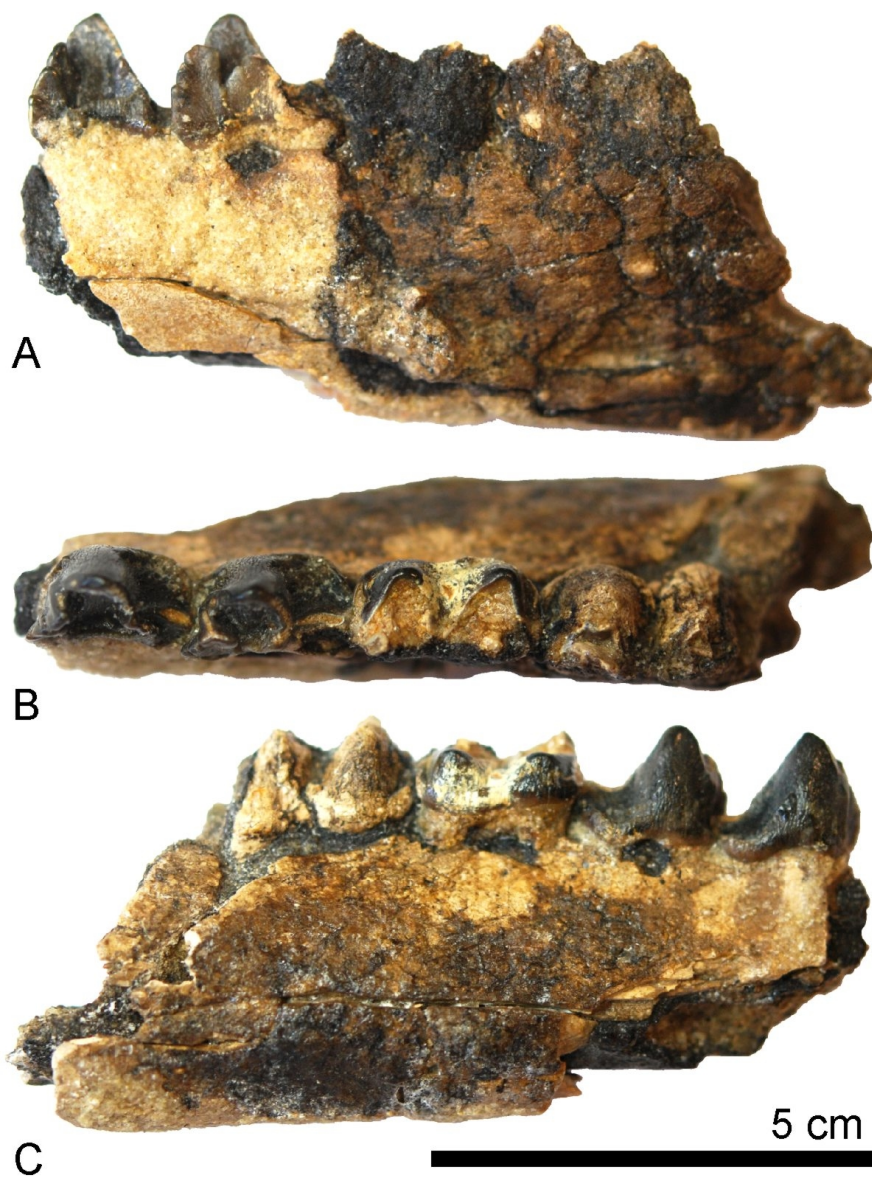
173x157mm (300 x 300 DPI)



Upper canine comparisons. Lingual views of (A) left upper canine of *L. bahri* from Toros-Ménalla (TM257-04-08, reversed), (B) left upper canine of *L. anisae* from Bled Douarah (T271, reversed) and, (C) right upper canine of *L. algeriensis* from Sidi Hedri (SHI01). (D) Compared dimensions at cervix of upper canines of *Merycopotamus* and *Libycosaurus* species.

185x92mm (300 x 300 DPI)





45 Figure 3. New mandibular material with right P/3-M/2 from Sidi Hedri (SHI02) in (A) lingual, (B) occlusal,  
46 and (c) labial views.

47 102x137mm (300 x 300 DPI)



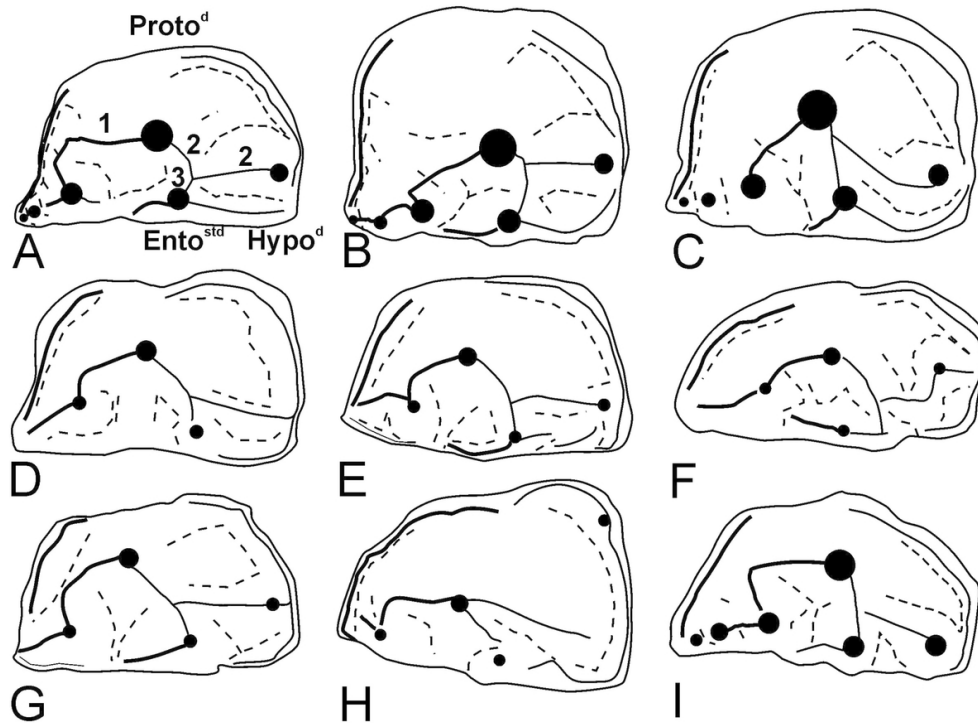


Figure 4. Comparisons of occlusal pattern of lower P/4 in Merycopotamini. (A) *Libycosaurus algeriensis*, Sidi Hedri (SHI02). (B) *Libycosaurus anisae* Bled Douarah (Holotype T356G). (C) *Libycosaurus bahri*, Toros-Menalla (TM258-01-13). (D) *Merycopotamus nanus*, Potwar Plateau (AMNH 94616, reversed). (E) *Merycopotamus medioximus*, Potwar Plateau (HGSP14969, reversed). (F) *Merycopotamus dissimilis* Potwar Plateau (HGSP16418, reversed). (G) *Sivameryx africanus* Gebel Zelten (NHM No N° reversed). (H) *Afromeryx zeltani*, Gebel zelten (M82233). (I) *Hemimeryx blanfordi*, Bugti Hills (M12026). Abbreviations: Proto., protoconid; Entostd., entostylid; Hypod., hypoconid; 1, preprotocristid; 2, postprotocristid; 3, endoprotocristid.

102x75mm (300 x 300 DPI)

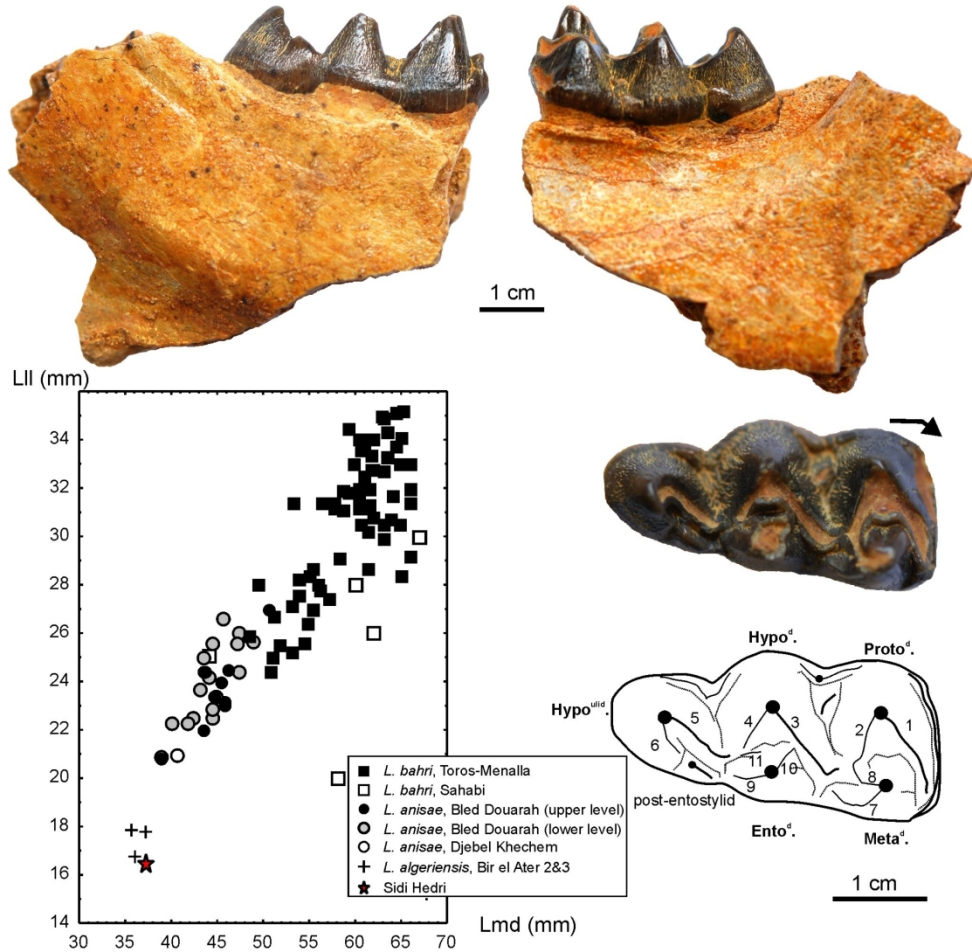
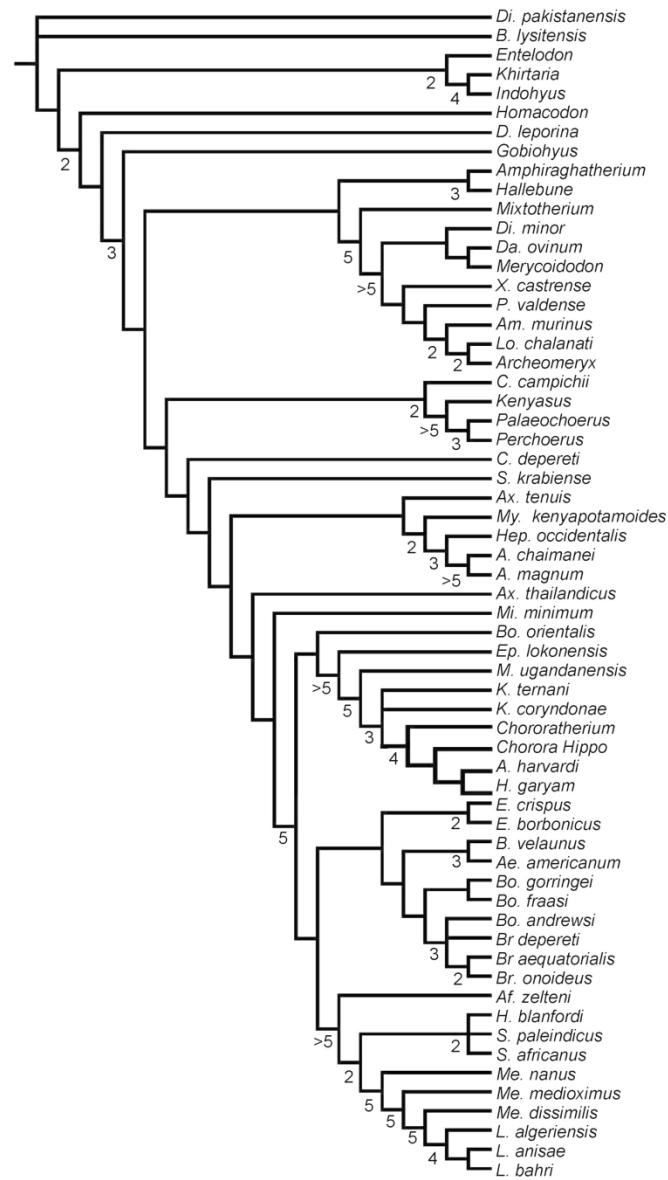


Figure 5. Left m/3 from Sidi Hedri (SHI03) in (A) labial, (B) lingual and, (C) occlusal views with scheme. Comparisons of m/3 dimensions of *Libyosaurus* species by origin. Abbreviations: Protod., protoconid; Metad., metaconid; Hypod., hypoconid; Entod., entoconid; Hypoulid., hypoconulid; 1, preprotocristid; 2, postprotocristid; 3, prehypocristid; 4, posthypocristid; 5, prehypocristulid; 6, posthypocristulid; 7, postectometacristid; 8, postmetacristid; 9, postectoentocristid; 10, preentocristid; 11, postentocristid.

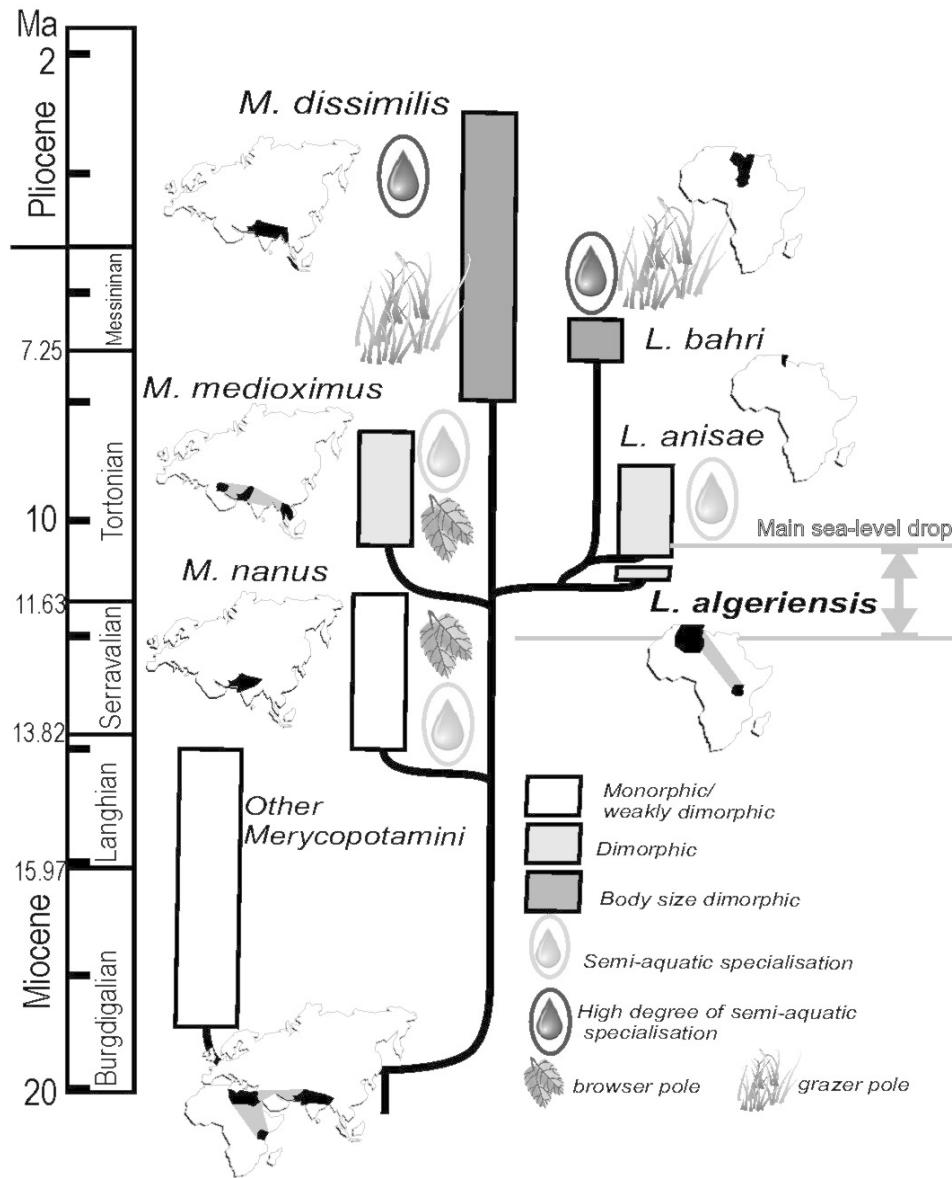
178x179mm (300 x 300 DPI)



Phylogenetic results. Strict consensus tree of 18 equally most parsimonious trees of 1266 steps each (CI=0.30; RI=0.64). Bremer indices (> 1) are indicated at nodes.

165x295mm (300 x 300 DPI)

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Paleobiogeographical scenario for Merycopotamini implied by new phylogeny with paleoecological inferences from Lihoreau et al. (2014). The geochronological time scale is from Hilgen et al. (2012).

91x113mm (300 x 300 DPI)

## Supporting information for Lihoreau *et al.*

### I List of characters for cladistics analysis

From Lihoreau *et al.* (2016), Boisserie *et al.* (2017), and 5 new characters (63, 80, 139, 156, 162)

#### Anterior lower teeth

- |   |   |
|---|---|
| <p><b>1. Number of lower incisors:</b><br/>           0. three<br/>           1. two<br/>           2. one</p> <p><b>2. Lower incisor morphology:</b><br/>           0. not caniniform<br/>           1. at least one caniniform lower incisor</p> <p><b>3. Relative dimensions of lower incisors:</b><br/>           0. all of equal size<br/>           1. one or two more developed</p> <p><b>4. Most developed incisor:</b><br/>           0. I/2<br/>           1. I/3<br/>           2. I/1</p> <p><b>5. Transverse section of lower incisors crowns:</b><br/>           0. strongly irregular<br/>           1. about rounded</p> <p><b>6. Lower incisor cervix morphology:</b><br/>           0. no deep indentation<br/>           1. indented cervix, indentation as long as the root diameter on the cervix<br/>           2. deep indentation longer than the root diameter at cervix</p> <p><b>7. Crown of I/1:</b><br/>           0. straight<br/>           1. spatulate, with convex mesial and distal border</p> <p><b>8. Presence of a median lingual pillar (lingual rib) on lower I/1:</b><br/>           0. yes<br/>           1. no</p> <p><b>9. Lower canine cross section at cervix:</b><br/>           0. subcircular<br/>           1. elliptical</p> | <p><b>10. Cristids on lower canine enamel caps:</b><br/>           0. none<br/>           1. one distal<br/>           2. two, one mesial and one distal<br/>           3. one mesial</p> <p><b>11. Wear on lower canine:</b><br/>           0. distal wear facet contact with canine<br/>           1. mesial wear facet contact with I3/</p> <p><b>12. Groove on labial side of lower canine:</b><br/>           0. no<br/>           1. yes</p> <p><b>13. Groove on lingual side of lower canine:</b><br/>           0. no<br/>           1. yes</p> <p><b>14. Lower canine in male:</b><br/>           0. fang-like<br/>           1. premolariform<br/>           2. incisiform</p> <p><b>15. Crown of lower canine in male:</b><br/>           0. small near premolar size<br/>           1. at least twice the premolar size<br/>           2. prolonged growth to ever-growing</p> <p><b>Lower premolars</b></p> <p><b>16. P/1 roots:</b><br/>           0. one<br/>           1. two</p> <p><b>17. Paraconid on lower premolars:</b><br/>           0. no<br/>           1. yes</p> <p><b>18. Accessory cusp on the preprotocristid of all lower premolars:</b><br/>           0. none<br/>           1. at least one<br/>           2. at least two</p> |
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Lihoreau et al. Supporting information

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- 19. Elongated P/3:**  
0. no (shorter or equal than M/1 length)  
1. yes (longer than M/1 length)
- 20. Three lobed P/3:**  
0. no  
1. yes
- 21. Orientation of postprotocrisid on P/3:**  
0. distal  
1. distolingual  
2. distolabial
- 22. High cingulid on labial face of P/3:**  
0. no  
1. yes
- 23. Endoprotocrisid on P/3:**  
0. no  
1. yes
- 24. Entoconid on P/3:**  
0. never  
1. at least on some specimens
- 25. P/3 hypoconid:**  
0. no  
1. yes
- 26. Preprotocrisid mesiolingually curved on P/3:**  
0. no  
1. yes
- 27. Mesial accessory cusp on preprotocrisid on P/3:**  
0. simple slope  
1. Shoulder like structure on lateral view  
2. adorned with accessory cusp
- 28. Lingual contour at cervix of P/4 in occlusal view:**  
0. convex to straight  
1. concave
- 29. Labial wall on P/3 or P/4:**  
0. convex  
1. concave
- 30. Change in the orientation of the preprotocrisid mesially to the junction of accessory mesiolingual crest on lower premolars:**  
0. no  
1. yes
- 31. Orientation of the endoprotocrisid on P/4:**  
0. absent  
1. separated from postprotocrisid at the protoconid apex and then straight and distolingual  
2. fused with postprotocrisid in part and then curved mesiolingually
- 32. Distolingual cingulid on P/4 in lingual view:**  
0. forming a continuous wall lingually until the distostylid  
1. reaching the level of the distal basin and keeping be shallow until the distostylid  
2. reaching the level of distal basin and then being high when joining the distostylid (distolingual notch of cingulid)
- 33. Presence of a preentocrisid on P/3 and/or on P/4:**  
0. no  
1. yes
- 34. Mesiolingual secondary cristid on P/4 (cristid connecting lingual margin and preprotocrisid):**  
0. no  
1. yes
- 35. Labial cingulid form a V (indentated) on P/4 before to reach the distal cingulid:**  
0. no  
1. yes
- 36. Marked postprotofossid on P/4:**  
0. absent  
1. present
- 37. Postectoprotocrisid on P/4:**  
0. no  
1. yes
- 38. Hypoconid on P/4:**  
0. no  
1. yes (even incipient)
- 39. Ectoprotofossid on P/4:**  
0. absent  
1. frequent
- 40. Postprotocrisid position on P/4 (in regard of a mesiodistal midline):**  
0. median or labial  
1. lingual

Lihoreau et al. Supporting information

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- 41. Endoprotofossid on P/4:**  
0. reaches lingual border  
1. reaches lingual cingulid wall
- 42. Postentocristid on P/4:**  
0. no  
1. short  
2. long, which reaches cingulid distally
- 43. Preprotocristid direction on P/4:**  
0. mesiolingual (but can be moderately curved)  
1. lingual then mesial  
2. mesial then lingual
- 44. Entostylid on P/4:**  
0. no  
1. yes  
2. continuous junction with cingulid without clear apex
- 45. Metaconid on P/4:**  
0. no  
1. yes (indeed an entostylid surrounded by cingulid and not formed by cingulid)
- Lower molars**
- 46. Premetacristid on lower molars:**  
0. strong  
1. reduced or missing
- 47. Paraconid on lower molars, almost on unworn specimens:**  
0. yes  
1. no
- 48. Lower molar trigonid:**  
0. equal in height with talonid  
1. higher than talonid
- 49. Connection between premetacristid and preprotocristid on lower molars:**  
0. yes  
1. no
- 50. Postectoprotocristid on lower molars:**  
0. absent  
1. reduced in the valley to fully developed at least on M/1
- 51. Postprotofossid on lower molars at least on M/3:**  
0. no  
1. yes
- 52. Postmetacristid on M/1-2:**  
0. curving toward postprotocristid forming a transverse bridge with it  
1. orientated straight toward the centre of the tooth  
2. forming a rounded postmetaconulid not preferentially orientated  
3. joins prehypocristid
- 53. Ectoprotofossid on lower molars:**  
0. absent  
1. present
- 54. Ectometafossid on lower molars:**  
0. yes  
1. no
- 55. Endometacristid on lower molars:**  
0. no or slightly expressed much more like an enamel fold  
1. present
- 56. Postectometacristid on lower molars:**  
0. lightly marked to absent  
1. always present and well-marked
- 57. Premetafossid on lower molars:**  
0. present  
1. absent
- 58. Preentocristid:**  
0. absent  
1. present
- 59. Preentocristid connects:**  
0. endohypocristid  
1. prehypocristid toward the cuspid apex  
2. prehypocristid toward its mesial extremity
- 60. Postectoentocristid on lower molars:**  
0. absent  
1. present but more like a keel on cusp  
2. present and well individualized from the cusp
- 61. Ectoentocristid:**  
0. present  
1. absent
- 62. Postentocristid on lower molars:**  
0. absent  
1. present
- 63. Postencristid mesiodistally oriented and**



**comprised between the posthypocristid and the entoconid (=the entoconid fold):**

- 0. no
- 1. yes

**64. Prehypocristid dividing in two mesial arms on lower molars:**

- 0. yes
- 1. no

**65. Prehypocristid inflated (not salient when unworn) ) in transverse valley of lower molars:**

- 0. no
- 1. yes (even to form a conulid)

**66. Prehypocristid reaches:**

- 0. median part of transverse valley
- 1. lingual part of transverse valley
- 2. labial part of the transverse valley

**67. Main arm of prehypocristid connects:**

- 0. trigonid distal walls (junction between cristids from metaconid and protoconid)
- 1. postmetafossid
- 2. lingual margin of transverse valley
- 3. postmetacristid

**68. Posthypocristid joins:**

- 0. nothing or distostylid
- 1. postentocristid
- 2. postectoentocristid

**69. Endohypocristid on lower molars:**

- 0. absent
- 1. present

**70. Posthypofossid on lower molars:**

- 0. absent
- 1. present

**71. Entostylid on lower molars that could sometimes be linked to an entocristid:**

- 0. never
- 1. frequently present

**72. Ectostylid on lower molars:**

- 0. no cingulid
- 1. a shallow and constant cingulid in front of the transverse valley
- 2. frequently developed cingulid in a /some stylid at least on m1

**73. Ectocrystilid on lower molars :**

- 0. no
- 1. yes even if variable

**74. Cingulid surrounding m/3 hypoconulid:**

- 0. no specimen exhibiting such extension
- 1. occasionally bordering the labial wall

**75. Presence of one or many postentostylid on M/3:**

- 0. no
- 1. yes

**76. Ectohypocristulid on M/3:**

- 0. absent
- 1. not complete
- 2. present joining the summit of hypoconulid

**77. Distostylid on M/1-M/2:**

- 0. median
- 1. lingual
- 2. none

**78. Mesial part of loop-like hypoconulid:**

- 0. open
- 1. pinched

**79. Posthypocristulid:**

- 0. complete
- 1. incomplete

**80. Posthypocristulid incomplete due to:**

- 0. a groove separates the cristid in two part
- 1. It lacks a part or totality of the cristid

**81. Entoconulid:**

- 0. no
- 1. yes

Anterior upper teeth

**82. Number of upper incisors:**

- 0. 3
- 1. 2
- 2. none

**83. Central upper incisor:**

- 0. morphologically similar to I2/ and/or I3/ peg-like, morphologically different from others
- 1. morphologically similar to I2/ and/or I3/ peg-like, morphologically different from others
- 2. caniniform

**84. I3/ reduced in size compared to I1/:**

- 0. no
- 1. yes

**85. Upper canine morphology:**

- 0. strong, with circular or elliptic cross section

Lihoreau et al. Supporting information

1. strong and laterally compressed (blade-like)
2. premolariform

**86. Canine size root:**

0. equivalent to slightly longer than the crown
1. at least twice the size of the crown
2. prolonged to continuous growth of root
3. prolonged and continuous growth of crown

**87. Dimorphic upper canine:**

0. no
1. yes

**Upper premolars****88. Diastem C-P1/ ou C-P/:**

0. yes
1. no

**89. Diastem P1/-P2/:**

0. no
1. yes

**90. Number of upper premolar:**

0. 4
1. 5
2. 3

**91. Distolabial crests of upper premolars****(postparacrista):**

0. simple
1. with a maximum of two accessory cusps
2. with more than two accessory cusps at least on one premolar

**92. Number of mesial crests on P1-3/:**

0. one
1. two

**93. Disto-lingual basin in P2/:**

0. yes
1. no

**94. Accessory cusp on disto-lingual cingulum of P3/:**

0. none
1. one cingular style
2. protocone (surrounded by a cingulum)

**95. Metacone on P3/:**

0. no
1. yes

**96. P3/ root pattern:**

0. one mesial root, two distal root not fused

1. one mesial root and fused distal ones

**97. P4/ paracone:**

0. simple with crest
1. complex with fossa
2. very complex with more fossae

**98. Orientation of preparacrista on P4/:**

0. mesial
1. labial

**99. Postprotocrista on P4/:**

0. absent
1. present

**100. Postprotocrista on P4/ joins:**

0. base of paracone
1. distostyle
2. metastyle

**101. Preprotocrista on P4/ joins:**

0. mesiostyle
1. base of the paracone then mesiostyle
2. parastyle

**102. Postectoprotocrista on P4/:**

0. absent
1. present

**103. P4/ protocone:**

0. rounded
1. crescentic

**104. In lingual view protocone of P4/ is:**

0. displaced mesially
1. median

**105. P4/ mesial margin:**

0. concave
1. convexe

**106. Strong development of distostyle on P4/:**

0. no
1. yes

**107. Mesial accessory cusp on P4/ that can be linked to mesiostyle:**

0. no
1. yes

**108. P4/ metacone:**

0. absence
1. presence

**109. P4/ paracone higher than the protocone:**

Lihoreau et al. Supporting information

0. slightly higher than protocone  
1. much higher than protocone

**110. P4/ endoparacrista:**

0. absence  
1. presence

**111. Distal accessory cusp on postprotocrista of P4/ that can be linked to distostyle:**

0. no  
1. yes

**Upper molars****112. Height of lingual cingulum compared to unworn protocone height on upper molars:**

0. one third  
1. half  
2. no cingulum

**113. Mesio-distal ribs development of labial cusps of upper molars:**

0. almost half the molar length  
1. pinched (inferior to one third of molar length)  
2. enlarged (superior to half the molar length)

**114. Postectoprotocrista:**

0. absent  
1. present

**115. Postprotocrista:**

0. present  
1. absent

**116. Protocone and metaconule junction on upper molars:**

0. none  
1. premetacristule with postectoprotocrista  
2. premetacristule with postprotocrista  
3. postprotocrista and lingual part of metaconule

**117. Premetacristule divided in two mesial arms:**

0. no  
1. yes

**118. Ectometacristule on upper molars:**

0. absent  
1. present at least on M1/  
2. not frequent and only on M2/ or M3/

**119. Postmetafossule:**

0. absent

1. present

**120. Secondary cristule labial to metaconule eventually an endometacristule or enamel knob:**

0. no  
1. yes

**121. Distostyle on upper molars:**

0. yes  
1. no

**122. Distostyle position on upper molars levels:**

0. metaconule  
1. metacone

**123. Secondary ectometafossule lingual to ectometacristule:**

0. absent or very light  
1. present mesially at least on M1/ linked to ectometacristule

**124. Paraconule on upper molars:**

0. present  
1. absent

**125. M2/ paraconule when present:**

0. similar in size with protocone  
1. smaller than protocone

**126. Postparacristule extends to connect:**

0. none  
1. base of the paracone  
2. transverse valley

**127. Preparacrista connects the parastyle:**

0. no, separated by a groove  
1. yes, lingually  
2. yes, labially

**128. Endoparacrista on upper molars:**

0. absence  
1. presence

**129. Ectoparafossa on upper molars:**

0. no  
1. yes

**130. Ectocristyle:**

0. frequently present  
1. absent

**131. Premetacrista and postparacrista connect:**

0. no connection  
1. direct connection in a centrocrista

Lihoreau et al. Supporting information

2. connection to mesostyle (via ectocristyle or not)

**132. Endometacrista and endometacristule forming a transverse crest:**

- 0. absence
- 1. presence

**133. Parastyle development:**

- 0. enamel knob
- 1. smaller or equal than mesostyle
- 2. larger than mesostyle

**134. Premetacristule invade labial part of the transverse valley:**

- 0. no
- 1. yes

**135. Position of metaconule on upper molar:**

- 0. labial side of the protocone
- 1. distal side of the protocone

**136. M2/ metaconule:**

- 0. similar in size with protocone
- 1. smaller than protocone

**137. Mesostyle on upper molars:**

- 0. no
- 1. yes

**138. Mesostyle:**

- 0. enamel knob
- 1. half to the size of labial cusp
- 2. larger than labial cusp

**139. Cingulum at the junction between postparacrista and premetacrista forming labial structure on mesostyle:**

- 0. high triangular cingulum
- 1. wing-like cingulum
- 2. low or absent cingulum

**140. Division of the mesostyle on upper molar:**

- 0. no, one style or continuous cristae
- 1. two apices in unworn molars but still connected by cristae
- 2. fully isolated style apices

**141. Metastyle:**

- 0. reduced to enamel knob or absent
- 1. fully developed

**142. Root fusion on upper molars:**

- 0. four roots with occasional fusion close to cervix, the root apices always remaining free

- 1. fully fused lingual roots
- 2. three roots

**143. Lingual cingulum on upper molars:**

- 0. no
- 1. yes
- 2. developed in entostyle

**144. Hypocone on upper molars (at least M2/:**

- 0. yes
- 1. no

**145. Shape of M1/:**

- 0. triangular
- 1. quadrate

**146. Shape of M3/:**

- 0. triangular
- 1. quadrate

**147. M3/ size:**

- 0. Larger than M2/
- 1. equal in size with M2/
- 2. reduced (less than 60%)

**148. Mesiolingual style on upper molar mesial cingulum:**

- 0. no
- 1. yes

**Mandible**

**149. Symphysis morphology in sagittal section, ventral border:**

- 0. convex
- 1. straight to almost straight
- 2. concave

**150. Symphysis morphology in sagittal section, dorsal border:**

- 0. convex
- 1. straight or almost straight
- 2. markedly concave

**151. Diastem C-P/1:**

- 0. absent
- 1. present

**152. Bone fusion at symphysis in adult specimens:**

- 0. no
- 1. yes

**153. Maximal thickness of the symphysis in sagittal section:**

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0. in the middle part  
1. in the rostral part  
2. in the nugal part
- 154. Symphysis extension:**  
0. extends nuchally between C and P/1  
1. extend nuchally between P/1 and P/3  
2. extends nuchally to P/3
- 155. Number and position of main external foramen:**  
0. numerous  
1. only one below the anterior part of the premolar row  
2. two, one below the anterior part and the other below the posterior
- 156. Mandibular notch:**  
0. no  
1. yes, long extension behind coronoid process  
2. yes, short extension below m/3
- 157. Transverse constriction of mandible at C-P/1 diastema:**  
0. no  
1. yes
- 158. Mandibular protuberance at the C/P/1 level:**  
0. no  
1. yes
- 159. P/1-P/2 diastema:**  
0. absent  
1. present
- 160. P/2-P/3 diastema:**  
0. yes  
1. no
- Cranium**
- 161. Opening of internal choanes:**  
0. at M3/  
1. nugal to M3/
- 162. Opening of main palatal foramen:**  
0. at palatine-maxillary junction in front of molars to P3  
1. on maxillary in front of P2-P1  
2. on maxillary cranial to P1
- Enamel microstructure**
- 163. Enamel ornamentation:**
0. no  
1. yes
- 164. Schmelzmuster composed of:**  
0. two layers  
1. three layers  
2. one layer
- 165. Inner radial enamel:**  
0. absent  
1. present
- 166. HSB percent of Schmelzmuster:**  
0. absent  
1. less than 75%  
2. more than 76%
- 167. Outer radial enamel:**  
0. less or equal to 20%  
1. more than 20%
- 168. Hsb zone:**  
0. thin with bands always less than 100µm  
1. large (equal or more than 100µm)
- 169. Regular aspect (constant width):**  
0. yes  
1. no
- 170. HSB variable (SD>20):**  
0. no  
1. yes
- 171. HSB angle with EDJ:**  
0. >70°  
1. <70°
- 172. Orientation of HSB:**  
0. straight  
1. bent
- 173. HSB definition (decussation angle and size of transition zone):**  
0. clear  
1. blurry
- 174. Division of HSB:**  
0. anastomosis  
1. bifurcation  
2. no division
- 175. HSB configuration:**  
0. curved  
1. transverse

Lihoreau et al. Supporting information

**176. Synchronous prism undulation on horizontal section:**

0. no
1. yes but few
2. yes but more or equal to 4

**177. IPM in inner portion:**

0. closed sheath
1. Inter row sheets

**178. IPM in middle portion:**

0. closed sheath
1. Inter row sheets
2. no IPM

**179. IPM in outer portion:**

0. closed sheath
1. no IPM

**180. Prism angle with EDJ:**

0. equal or more than 60°
1. less than 60°
2. tends to diminish in the inner part

**181. Prism diameter:**

0. mean between 3 and 3.9  $\mu\text{m}$
1. small diameter mean below 3  $\mu\text{m}$
2. large diameter mean above or equal to 4

## II List of taxa included in the phylogenetic analysis.

### Abbreviations for repository institutions

AMNH	American Museum of Natural History, New York, USA
ARCCH	Authority for Research and Conservation of Cultural Heritage, Addis Ababa, Ethiopia
CGM	Cairo Geological Museum, Cairo, Egypt
CNRD	Centre National de la Recherche pour le Développement, Ndjamena, Chad
CROZ	Musée Crozatier, Le Puy-en-Velay, France
DMR	Department of Mineral Resources, Bangkok, Thailand
DPC	Division of Fossil Primates, Duke Lemur Center, Durham, NC USA
FSL	Collection de la Faculté de Sciences de Lyon
GSP	Geological Survey of Pakistan, Museum of Natural History in Islamabad, Pakistan
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHM	Natural History Museum, London, UK
NMK	National Museums of Kenya, Nairobi, Kenya
PMH	Peabody Museum, Harvard University, Cambridge, USA
UM	Université de Montpellier, France
UNM	Uganda National Museum, Uganda
UU	Utrecht University, Netherland
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
YU	Department of Geology, Yangon University, Yangon, Myanmar



**HIPPOPOTAMOIDEA** Gray, 1821 sensu Gentry & Hooker (7)**Hippopotamidae** Gray, 1821*Morotochoerus ugandensis* Pickford, 1998

- Temporal and geographical distribution  
Early Miocene; eastern Africa
- Origin of examined material  
- Moroto, Uganda (UNM)
- References: (22-24)

*Kenyapotamus coryndonae* Pickford, 1983

- Temporal and geographical distribution  
Late Miocene; eastern Africa
- Origin of examined material  
- Nakali Formation, Kenya (NMK)  
- Namurungule Formation, Samburu Hills, Kenya (NMK)  
- Ngeringerowa, Ngorora Formation, Kenya (NMK)
- References: (1, 15-18)

*Kenyapotamus ternani* Pickford, 1983

- Temporal and geographical distribution  
middle Miocene; eastern Africa
- Origin of examined material  
- Napudet, Lothidok Formation, Turkana, Kenya (NMK)  
- Kipsaramon, Muruyur Bed, in the Tugen Hills, Kenya (NMK)  
- Fort Ternan Beds, Nyanza rift, Kenya (NMK)  
- Maboko and ngorora Formations, Kenya (NMK)
- References: (77)

*Chororatherium roobii* Boisserie et al. 2017

- Temporal and geographical distribution  
Late Miocene; eastern Africa
- Origin of examined material  
- Chorora Formation, Bechitat, Ethiopia (ARCCH)
- References: (79)

## Hippopotamine from Chorora

- Temporal and geographical distribution  
Late Miocene; eastern Africa
- Origin of examined material  
- Recent bed of Chorora Formation, Teso Tadecho, Odakora North, and Gutosadeent, Ethiopia (ARCCH)
- References: (79)

*Archaeopotamus harvardi* (Coryndon, 1977)

- Temporal and geographical distribution  
Late Miocene; eastern Africa
- Origin of examined material  
- Nawata Formation, Lothagam, Kenya (NMK)
- References: (19-20)

*Hexaprotodon garyam* Boisserie et al., 2005

- Temporal and geographical distribution  
Late Miocene; central Africa
- Origin of examined material  
- Anthracotheriid Unit, Toros-Ménalla, Chad (CNAR)

- References: (21)

**“Anthracotheriidae”** Leidy, 1869

*Siamotherium krabiense* Suteethorn *et al.*, 1988

- Temporal and geographical distribution  
Late middle and late Eocene; southeastern Asia
- Origin of examined material  
- Krabi Basin, Thailand (DMR, cast at UM)
- References: (25-27)

*Heptacodon occidentalis* (Osborn and Wortman, 1894)

- Temporal and geographical distribution  
early Oligocene, North America
- Origin of examined material  
- South Dakota, USA (AMNH)
- References: (28-29)

*Anthracotherium chaimanei* Ducrocq 1999

- Temporal and geographical distribution  
Late Eocene, southeastern Asia
- Origin of examined material  
- Krabi Basin, Thailand (DMR, cast at UM)
- References: (27)

*Anthracotherium magnum* Cuvier, 1822

- Temporal and geographical distribution  
Early late Oligocene, Europe
- Origin of examined material  
- Cadibona, Italy (NHM)  
- Digoïn, France (cast at UM)  
- Moissac, France (cast at UM)  
- Phosphorites du Quercy, France (MNHN, cast at UM)
- References: (30-32)

*Myaingtherium kenyapotamoides* Tsubamoto *et al.* 2011

- Temporal and geographical distribution  
Late middle Eocene, Asia
- Origin of examined material  
- Pondaung formation, Myanmar (YU)
- References: (33)

*Anthracokeryx tenuis* Pilgrim and Cotter, 1916

- Temporal and geographical distribution  
Late middle Eocene, Asia
- Origin of examined material  
- Pondaung formation, Myanmar (AMNH)
- References: (32, 34)

*Anthracokeryx thailandicus* Ducrocq, 1999

- Temporal and geographical distribution  
Late Eocene, southeastern Asia
- Origin of examined material  
- Krabi Basin, Thailand (DMR, cast at UM)
- References: (27, 35)

*Microbunodon minimum* Cuvier, 1822

- Temporal and geographical distribution  
Late Oligocene, Europe
- Origin of examined material  
- La Milloque, France (cast at UM)
- References: (35-36)

*Bothriogenys orientalis* Ducrocq, 1997

- Temporal and geographical distribution  
Late Eocene, southeastern Asia
- Origin of examined material  
- Krabi Basin, Thailand (DMR, cast at UM)
- References: (3, 27)

*Bothriogenys fraasi* (Schmidt, 1913)

- Temporal and geographical distribution  
Early Oligocene, northern Africa
- Origin of examined material  
- Jebel Quatrani fm., Fayum, Egypt (SMNS, NHM)
- References: (3, 37-38)

*Bothriogenys gorringei* (Andrews and Beadnell, 1902)

- Temporal and geographical distribution  
Early Oligocene, northern Africa
- Origin of examined material  
- Jebel Quatrani fm., Fayum, Egypt (AMNH, SMNS, NHM)
- References: (3, 37-38)

*Bothriogenys andrewsi* (Schmidt, 1913)

- Temporal and geographical distribution  
Late Early Oligocene, northern Africa
- Origin of examined material  
- Upper Sequence of the Jebel Qatrani Formation, Fayum Depression, Egypt (SMNS, CGM, DPC)
- References: (3, 37-38, 80)

*Epirigenys lokonensis* Lihoreau et al. 2015

- Temporal and geographical distribution  
late Early/early Late Oligocene, Kenya
- Origin of examined material  
- Lok 13, Lokone sandstone Formation, Turkana, Kenya (NMK)
- References: (78)

*Brachyodus aequatorialis* Mc Innes 1951

- Temporal and geographical distribution  
Early Miocene, Eastern Africa
- Origin of examined material  
- Rusinga, Kenya (NMK)
- References: (38-40)

*Brachyodus onoideus* (Gervais, 1848-52)

- Temporal and geographical distribution  
Early Miocene, Western Europe
- Origin of examined material  
- Chilleur au bois, France (NHM, MNHN, UM)

- References: (40)

*Brachyodus depereti* (Fourteau, 1918)

- Temporal and geographical distribution  
Early Miocene, Northern Africa
- Origin of examined material  
- Moghara, Egypt (cast in NHM)
- References: (40-41)

*Bothriodon velaunus* (Cuvier, 1824)

- Temporal and geographical distribution  
Early Oligocene, Western Europe
- Origin of examined material  
- Ronzon, France (CROZ, NHM, UM2)
- References: (32)

*Aepinacodon americanum* (Leidy, 1856)

- Temporal and geographical distribution  
Late Eocene-early Oligocene, Northern America
- Origin of examined material  
- South Dakota, USA (AMNH)
- References: (29, 32)

*Elomeryx crispus* (Gervais, 1849)

- Temporal and geographical distribution  
Late Eocene-early Oligocene, Europe
- Origin of examined material  
- Detan Dverce, Czech Republic (cast at UM)
- References: (32, 42-43)

*Elomeryx borbonicus* (Geais, 1934)

- Temporal and geographical distribution  
Late Oligocene and early Miocene, Western Europe
- Origin of examined material  
- Saint Henri, France (AMNH, NHM, FSL, UM)
- References: (42-45).

*Afromeryx zelteni* Pickford, 1991

- Temporal and geographical distribution  
Early Miocene, Africa
- Origin of examined material  
- Gebel Zelten, Libya (NHM)  
- Baragoï, Buluk, Ombo, Nabwal Hill (NMK)
- References: (41)

*Sivameryx palaeindicus* (Lydekker, 1877)

- Temporal and geographical distribution  
Early Miocene, Indian subcontinent
- Origin of examined material  
- Sind, Pakistan (PMH, GSP)  
- Kamlial fm. Potwar plateau, Pakistan (PMH, GSP)  
- Bugti, Pakistan (NHM, AMNH)
- References: (46)

*Sivameryx africanus* (Andrews, 1914)

- Temporal and geographical distribution  
Early Miocene, East and North Africa
- Origin of examined material
  - Karungu, Kenya (NMK)
  - Rusinga, Kenya (NMK)
  - Gebel Zelten, Libye (NHM, MNHN)
- References: (41)

*Hemimeryx blanfordi* Lydekker, 1883

- Temporal and geographical distribution  
Late Oligocene-early Miocene, Indian sub-continent
- Origin of examined material
  - Sind, Lower Manchar Formation (NHM, GSP)
  - Potwar plateau, Kamli Formation, Pakistan (GSP)
  - Bugti, Chitarwata Formation Pakistan (NHM, UM)
- References: (46)

*Merycopotamus nanus* Falconer, 1868

- Temporal and geographical distribution  
Middle Miocene; Indian subcontinent
- Origin of examined material
  - Potwar plateau, Chinji formation, Pakistan (HPM, NHM, AMNH)
- References: (47)

*Merycopotamus medioximus* Lihoreau et al. 2004

- Temporal and geographical distribution  
Late Miocene; Indian subcontinent, Thailand, Iraq.
- Origin of examined material
  - Pakistan (AMNH, GSP, UU)
- References: (47) Ajouter Lihoreau et al. 2004

*Merycopotamus dissimilis* (Falconer and Cautley, 1837)

- Temporal and geographical distribution  
Late Miocene-Pliocene; Indian subcontinent
- Origin of examined material
  - Pakistan, India, Myanmar, Nepal, Indonesia (AMNH, PMH, GSP, NHM)
- References: (47)

*Libycosaurus algeriensis* Ducrocq et al., 2001

- Temporal and geographical distribution  
Late Miocene; central and northern Africa
- Origin of examined material
  - Nementcha formation, Bir el Ater 2 and 3, Algeria (UO2) and Sidi Hedri, Tunisia (ONM)
- References: (81, 82)

*Libycosaurus anisae* (Black, 1972)

- Temporal and geographical distribution  
Late Miocene; northern Africa
- Origin of examined material
  - Beglia formation, Bled Douarah and Djebel Kechrem el Artsouma (ONM)
- References: (41, 48-50)

*Libycosaurus bahri* Lihoreau et al. 2014

- Temporal and geographical distribution  
Late Miocene; central and northern Africa

- Origin of examined material
  - Anthracotheriid Unit, Toros-Ménalla (CNAR)
- References: (38, 41, 50-52)

**SUOIDEA** Gray, 1821**Palaeochoeridae** Matthew, 1924*Palaeochoerus quercyi* (Filhol, 1882) (= *Doliochoerus quercyi*)

- Temporal and geographical distribution
  - Late Oligocene; western Europe
- Origin of examined material
  - Pech Desse, Quercy, France (UM)
  - Pech de Fraysse, Quercy, France (UM)
- References: (53-54)

**Tayassuidae** Palmer, 18971*Perchoerus probus* Leidy, 1869

- Temporal and geographical distribution
  - Late Eocene-Early Miocene – North America
- References: (55-56)

**Suidae** Gray, 1821*Kenyasus rusingensis* Pickford 1986

- Temporal and geographical distribution
  - Early Miocene - Africa
- Origin of examined material
  - Rusinga, Kenya (NMK)
- References: (55-56)

**RUMINANTIA****Lophiomerycidae** Janis, 1987*Lophiomeryx chalaniati* Pomel, 1854

- Temporal and geographical distribution
  - Oligocene; Europe
- Origin of examined material
  - Garouillas, France (UM)
- References: (57)

**Archeomerycidae** Simpson, 1945*Archeomeryx optatus* Matthew and Granger, 1925

- Temporal and geographical distribution
  - Middle Late Eocene; Mongolia and China
- Origin of examined material
  - Ula Usu, China (cast UM)
- References: (58)

**DICHOBUONOIDEA** Gill, 1872**Diacodexiidae** Gazin, 1955*Diacodexis pakistanensis* Thewissen et al. 1983

- Temporal and geographical distribution
  - Early or Middle Eocene; Pakistan
- Origin of examined material
  - Barbora banda, Pakistan (casts UM)
- References: (59)

*Bunophorus grangeri* Sinclair, 1914

- Temporal and geographical distribution  
Early Eocene; North America
- Origin of examined material
  - Big Horn basin, Wyoming, USA (casts UM)
- References: (60)

**Dichobunidae** Turner, 1849*Dichobune leporina* Cuvier, 1822

- Temporal and geographical distribution  
Late Eocene; Europe
- Origin of examined material
  - Escamps, Rosières and Aubrelong, France (UM)
- References: (60-61)

**Homacodontidae** Marsh, 1874*Homacodon vagans* Marsh, 1872

- Temporal and geographical distribution  
Early-middle Eocene; North America
- Origin of examined material
  - Cast of specimens from the Twin Buttes, USA (UM)
- References: (60)

**Helohyidae** Marsh, 1877*Gobiohyus orientalis* Matthew and Granger, 1925

- Temporal and geographical distribution  
Middle Eocene; central and southern Asia
- Origin of examined material
  - Irdin Manha, Ulan Shireh, Mongolia (AMNH)
- References: *The attribution of G. orientalis to the Helohyidae follows (62-63) and (64). It is recognized that (65), notably, proposed a different interpretation, excluding Asian forms from the Helohyidae.*

**Raoellidae** Sahni et al., 1981*Khirtharia* spp corresponds to the three following species :*Khirtharia dayi* Pilgrim, 1940

- Temporal and geographical distribution  
Late Eocene; Indian subcontinent
- Origin of examined material
  - Chorlakki, Pakistan (casts UM)
- References: (66)

*Khirtharia inflata* (Ranga Rao, 1972)

- Temporal and geographical distribution  
Late Eocene; Indian subcontinent
- Origin of examined material
  - Subattu formation, India (casts UM)
- References: (67)

*Khirtharia aurea* Thewissen *et al.* 2001

- Temporal and geographical distribution  
Middle Eocene; Indian subcontinent
- Origin of examined material
  - Chorgali formation, Pakistan (casts UM)
- References: (68-69)

*Indohyus indirae* Ranga Rao, 1971

- Temporal and geographical distribution



- Late Eocene; Indian subcontinent  
 • References: (67)

### Other early cetartiodactyl families

#### **Cebochoeridae** Lydekker, 1883

##### *Cebochoerus campichii* Pictet 1855-57

- Temporal and geographical distribution  
Middle Eocene; Western Europe
- Origin of examined material  
- Robiac, France (UM)
- References: (61, 70)

#### **Choeropotamidae** Owen, 1845

##### *Choeropotamus depereti* Stehlin 1908

- Temporal and geographical distribution  
Middle Eocene; Europe
- Origin of examined material  
- Euzet, France (UM)
- References: (61, 70-71)

##### *Hallebune krumbiegeli* Erfurt and Sudre, 1995

- Temporal and geographical distribution  
Middle Eocene; Europe
- Origin of examined material  
- Geiseltal, Germany (cast UM)
- References: (61, 70-71)

*Amphirhagatherium* spp corresponds to the two following species :

##### *Amphirhagatherium neumarkensis* Erfurt and Haubold 1989

- Temporal and geographical distribution  
Middle-Late Eocene; Europe
- Origin of examined material  
- Geiseltal, Germany (Cast UM)
- References: (61, 70-71)

##### *Amphirhagatherium weigelti* (Heller, 1934)

- Temporal and geographical distribution  
Middle-Late Eocene; Europe
- Origin of examined material  
- Geiseltal, Germany (Cast UM)
- References: (61, 70-71)

#### **Mixtotheriidae** Pearson, 1927

*Mixtotherium* spp. corresponds to the following species:

##### *Mixtotherium gresslyi* Rutimeyer, 1891

- Temporal and geographical distribution  
Middle-Late Eocene; Europe
- Origin of examined material  
- Egerkingen, Switzerland and La Defense, France (casts UM)
- References: (70)

##### *Mixtotherium lavergnensis* (Sudre, 1977)

- Temporal and geographical distribution  
Middle-Late Eocene; Europe
- Origin of examined material  
- Lavergne, France and Eclepens-gare, Switzerland
- References: (72)

**Amphimerycidae** Pearson, 1927*Amphimeryx murinus* (Cuvier, 1822)

- Temporal and geographical distribution  
Late Eocene; Europe
- Origin of examined material
  - Escamps, Rosières 2 and St Néboule, France (casts UM)
- References: (61, 70, 72)

**Anoplotheriidae** Bonaparte, 1850*Diplobune minor* (Filhol, 1877)

- Temporal and geographical distribution  
Late Eocene-early Oligocene; Europe
- Origin of examined material
  - Itardies, France (UM)
- References: (73)

*Dacrytherium ovinum* Owen, 1857

- Temporal and geographical distribution  
Late Eocene; Europe
- Origin of examined material
  - Fons and Euzet, France (UM)
- References: (70, 72)

**Xiphodontidae** Flower, 1884*Xiphodon castrensis* Kowalesky, 1873

- Temporal and geographical distribution  
Late Eocene; Europe
- Origin of examined material
  - Robiac and Le Bretou, France (UM)
- References: (70, 72)

**Cainotheriidae** Camp and Van der Hoof, 1940*Paroxacron valdense* (Stehlin, 1906)

- Temporal and geographical distribution  
Late Eocene-Early Oligocene; Europe
- Origin of examined material
  - Escamps, France (UM)
- References: (70, 72)

**Entelodontidae** Lydekker, 1883*Entelodon* spp corresponds to the two following species :*Entelodon deguilhemi* Repelin, 1919

- Temporal and geographical distribution  
Early Oligocene; Europe
- Origin of examined material
  - Villebramar and Quercy, France (cast UM2)
- References: (74)

*Entelodon magnum* (Aymard, 1846)

- Temporal and geographical distribution  
Early Oligocene; Europe
- Origin of examined material
  - Ronzon and Quercy, France
- References: (74)

**Merycoidodontidae** Lydekker, 1883*Merycoidodon* sp

- Temporal and geographical distribution  
Oligocene; North America
- Origin of examined material  
- Big Badland, South Dakota, USA (UM2)
- References: (75)

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## III Matrix of 181 characters and 61 taxa

6	<i>Diacodexis pakistanensis</i>	0	0	0	-	0	0	0	?	1	2
7	1	0	0	1	0	0	1	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	-	0	0	0	1
10	0	1	1	0	0	0	0	1	0	0	0
11	-	0	0	1	0	1	0	0	0	0	0
12	0	1	0	0	0	1	0	0	0	-	0
13	0	0	1	1	?	1	1	0	0	0	1
14	0	?	0	0	1	1	2	0	0	0	1
15	0	0	1	0	0	0	0	0	0	3	0
16	0	0	0	1	0	0	1	1	0	1	0
17	1	1	0	0	0	1	0	-	2	-	0
18	0	1	0	0	1	0	1	0	0	0	1
19	?	1	?	0	0	1	0	?	0	2	1
20	-	-	-	-	-	-	-	-	-	0	0
21	0	0	1	?	?	?	?	?	?	?	?
22	?	?	?	?	?	?	1	0	0	0	0
23	?	0	?	0	0	0	0	0	0	2	0
24	0	0	0	0	0	0	-	0	2	0	0
25	0	1	1	0	0	0	0	1	0	0	1
26	-	0	0	1	0	0	1	0	0	0	0
27	0	1	0	0	0	0	0	0	0	-	0
28	?	?	?	?	?	?	?	?	?	?	?
29	?	?	?	?	?	?	?	?	?	?	?
30	?	?	?	?	?	?	?	?	?	?	?
31	?	?	?	?	?	?	?	?	?	?	?
32	?	?	?	?	?	?	?	?	?	?	?
33	?	?	?	?	?	?	?	?	?	?	?
34	0	0	1	0	0	0	0	1	0	0	1
35	0	0	0	0	0	1	0	0	0	0	1
36	0	2	0	0	0	0	0	0	?	?	0
37	?	?	?	?	?	?	?	?	0	0	?
38	0	0	0	0	1	1	0	0	0	1	1
39	0	0	0	0	0	0	0	1	0	3	0
40	0	0	0	0	0	0	0	0	1	0	0
41	1	0	2	0	0	0	0	-	2	-	0
42	1	0	1	0	2	0	?	?	?	?	?
43	?	?	?	?	?	?	?	?	?	?	?
44	?	?	?	?	?	?	?	?	?	?	?
45	?	?	?	?	?	?	?	?	?	?	?
46	0	0	1	0	0	0	0	1	0	0	1
47	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0
49	-	0	0	0	0	1	0	0	0	0	1
50	0	2	0	0	0	0	0	0	0	-	0
51	?	?	?	?	?	?	1	0	0	0	?
52	?	0	0	0	0	-	0	0	0	1	0
53	0	0	0	0	0	0	0	0	1	0	0
54	0	0	0	0	0	0	1	0	1	0	0
55	1	0	2	0	0	1	0	0	-	0	0
56	0	0	1	0	2	0	0	0	2	-	?
57	2	2	0	?	1	0	0	?	0	0	1
58	0	0	1	1	0	0	1	0	?	?	0
59	?	?	?	?	?	?	?	?	?	?	?
60	?	?	?	?	?	?	?	?	?	?	?
61	<i>Dichobune leporina</i>	0	0	0	-	0	0	?	?	1	2
62	?	0	0	1	0	0	1	0	0	0	0
63	0	0	0	0	2	0	0	0	0	0	0
64	0	0	0	1	0	0	0	0	0	0	0
65	0	1	0	0	0	0	0	0	0	0	0
66	-	0	0	0	0	1	0	0	0	0	1
67	0	2	0	0	0	0	0	0	0	-	0
68	?	?	?	?	?	?	1	0	0	0	?
69	?	0	0	0	0	-	0	0	0	1	1
70	0	0	0	0	0	0	0	0	1	0	0
71	0	0	0	0	0	0	1	0	1	0	0
72	1	0	2	0	0	1	0	0	-	0	0
73	0	0	1	0	2	0	0	0	2	-	?
74	2	2	0	?	1	0	0	?	0	0	1
75	0	0	1	1	0	0	1	0	?	?	0
76	?	?	?	?	?	?	?	?	?	?	?
77	?	0	2	0	0	-	0	0	?	1	0
78	<i>Cebochoerus campichii</i>	0	0	0	-	0	0	0	?	1	0
79	?	0	0	2	0	1	0	0	0	0	0

Lihoreau et al. Supporting information

1												
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3												
4		0	0	1	0	0	0	0	0	0	0	0
5		0	0	0	1	0	0	0	0	0	1	0
6		1	0	0	0	1	0	1	0	0	0	0
7		-	1	0	0	0	1	0	0	0	0	1
8		0	2	0	0	0	2	0	0	0	-	0
9		?	?	2	0	0	0	1	0	0	0	2
10		0	0	1	0	1	1	0	0	0	0	1
11		0	0	0	0	0	0	2	0	0	2	0
12		1	0	0	0	0	0	1	0	1	0	0
13		1	0	2	0	1	0	0	-	2	-	0
14		0	1	1	1	1	0	1	0	0	1	2
15		?	2	0	0	1	1	0	0	0	0	2
16		0	0	0	0	0	0	0	0	0	0	0
17		0	0	1	0	0	0	0	0	0	0	0
18		0	0	1	0	1	1	0	0	0	1	0
19		0	0	0	0	0	0	2	0	0	0	0
20		1	0	0	0	0	0	1	0	1	0	0
21		1	0	2	0	1	0	0	-	2	-	0
22		0	1	1	1	1	0	1	0	0	1	2
23		?	2	0	0	1	1	0	0	0	0	2
24		0	0	0	0	0	0	0	0	0	0	0
25		0	0	1	0	0	0	0	0	0	0	0
26		0	0	1	0	0	0	0	0	0	0	0
27		0	0	1	0	0	0	0	0	0	0	0
28		0	0	0	0	0	1	0	0	0	0	0
29		0	0	0	0	0	0	1	0	0	0	0
30		0	0	0	0	0	0	0	0	0	0	0
31		1	0	0	0	0	1	0	0	0	0	0
32		-	0	0	0	0	0	0	0	0	0	0
33		1	2	0	0	1	0	0	0	-	0	?
34		?	?	0	?	?	?	?	?	?	?	?
35		0	?	0	0	1	1	0	0	1	0	1
36		0	1	0	0	0	0	1	0	0	2	0
37		1	1	0	0	0	0	1	1	0	0	1
38		2	0	1	0	1	0	1	1	0	0	?
39		1	1	1	1	1	0	0	0	1	0	1
40		0	1	0	0	1	1	?	?	1	0	1
41		1	1	1	1	0	0	0	0	1	0	0
42		0	1	0	0	1	1	?	?	1	0	1
43		1	1	1	1	0	0	0	0	1	0	0
44		0	1	0	0	1	1	?	?	1	0	1
45		1	1	1	1	0	0	0	0	1	0	0
46		0	0	2	0	0	0	0	0	1	0	0
47		0	0	0	1	?	0	?	0	0	1	?
48		0	0	0	0	0	-	0	0	0	0	1
49		0	0	0	0	0	1	0	0	0	2	1
50		0	0	0	0	0	0	0	0	0	1	0
51		0	0	0	0	0	0	0	0	0	0	0
52		0	0	0	0	0	0	0	0	0	0	0
53		0	0	0	0	0	0	0	0	0	0	0
54		0	0	0	0	0	0	0	0	0	0	0
55		0	0	0	0	0	0	0	0	0	0	0
56		1	0	1	0	0	0	0	1	1	0	1
57		0	1	0	0	0	1	0	0	0	1	0
58		0	0	0	0	0	0	0	0	0	0	0
59		0	0	0	0	0	0	0	0	0	0	0
60		0	0	0	0	0	0	0	0	0	0	0

*Gobiohyus orientalis*

*Choeropotamus depereti*

*Siamotherium krabiense*

*Anthracokeryx tenuis*

## Lihoreau et al. Supporting information

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4		0	0	0	0	0	2	0	0	0	-	0	0
5		0	0	1	?	?	0	1	0	0	0	1	0
6		0	?	1	0	?	?	?	?	1	0	?	?
7		?	0	0	0	0	0	0	1	0	1	1	1
8		0	0	0	1	0	0	1	1	1	0	1	0
9		2	0	2	0	1	0	1	1	2	0	0	?
10		?	1	1	1	0	0	0	?	1	0	2	1
11		?	?	?	?	?	?	?	?	?	?	?	?
12		?	?	?	?	?	?	?	?	?	?	?	?
13		<i>Anthracokeryx thailandicus</i>	?	?	?	?	?	?	?	?	?	?	?
14		?	?	?	?	?	0	0	0	0	0	0	0
15		0	0	0	0	0	0	0	0	1	1	0	0
16		0	1	0	0	0	0	0	0	0	0	0	0
17		1	0	0	0	0	0	0	0	1	1	0	1
18		2	1	0	0	0	1	0	0	0	0	0	0
19		0	1	0	0	0	2	0	0	0	-	0	?
20		?	?	?	?	?	?	?	?	?	?	?	0
21		0	?	1	0	1	0	0	0	1	0	0	0
22		0	0	0	0	0	?	0	0	0	2	1	?
23		0	0	0	1	0	0	1	2	1	0	1	0
24		2	0	1	0	1	0	1	1	0	0	1	0
25		1	1	1	1	0	0	0	0	1	0	2	1
26		2	?	1	0	1	1	0	0	1	?	?	?
27		?	?	?	?	?	?	?	?	?	?	?	?
28		?	?	?	?	?	?	?	?	?	?	?	?
29		<i>Microbunodon minimum</i>	0	0	0	-	0	0	0	0	0	1	1
30		?	?	?	?	?	?	?	?	?	?	?	?
31		1	0	0	0	0	0	0	0	1	0	1	0
32		0	0	0	0	0	0	0	0	1	1	0	0
33		0	0	0	0	0	0	0	1	0	1	0	0
34		1	0	0	0	0	0	0	0	1	1	0	1
35		2	1	1	0	0	1	0	0	0	0	0	0
36		0	1	0	0	0	2	0	0	0	-	0	0
37		0	0	1	3	1	1	0	0	0	0	1	0
38		0	?	1	1	1	0	0	0	1	0	1	0
39		0	0	0	0	0	0	1	0	0	2	0	0
40		0	0	0	1	0	0	1	2	1	0	1	0
41		2	0	1	0	1	0	1	1	0	0	1	0
42		1	1	1	1	0	0	0	1	1	1	2	1
43		2	1	1	0	1	1	0	0	1	0	0	2
44		1	0	1	0	0	0	0	0	0	0	0	0
45		0	0	0	0	0	0	0	0	0	0	0	0
46		?	0	?	1	1	1	0	0	0	0	1	1
47		0	0	0	0	0	0	1	0	1	1	0	0
48		0	0	0	1	1	0	1	1	1	0	1	0
49		2	0	2	0	1	0	1	2	0	0	1	?
50		2	1	1	1	0	1	0	?	0	1	2	1
51		1	1	0	0	0	1	?	0	1	?	?	?
52		?	?	?	?	?	?	?	?	?	?	?	?
53		<i>Anthracotherium chaimanei</i>	?	?	?	?	?	?	?	?	?	?	?
54		?	?	?	?	?	?	?	?	?	?	?	?
55		0	0	0	0	0	0	0	0	1	0	0	1
56		0	1	0	1	0	0	1	0	0	0	0	0
57		1	0	0	1	1	0	0	0	1	1	0	1
58		0	1	0	1	0	0	1	0	0	1	1	1
59		1	0	0	0	1	1	0	0	0	-	1	?
60		?	?	0	1	1	0	1	0	0	0	1	1
		0	?	1	1	1	1	0	1	1	0	0	0
		?	0	0	0	0	0	0	1	0	1	1	1

Lihoreau et al. Supporting information

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	0	1	0	1	1	0	1	2	1	0	1	0
	2	0	1	0	1	0	1	1	0	0	1	0
	2	1	1	1	0	1	?	?	?	?	?	?
	?	?	?	?	?	?	1	0	1	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
<i>Anthracotherium magnum</i>	0	0	0	0	1	0	0	1	0	0	0	0
	0	0	0	0	1	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	1	0	0	1
	0	1	0	1	0	0	1	0	0	0	0	0
	1	0	0	1	1	0	0	0	1	1	0	1
	0	2	0	1	0	0	1	0	0	?	1	1
	0	0	0	0	1	2	0	0	0	-	1	0
	0	0	0	1	?	1	1	0	0	0	1	1
	0	1	1	1	1	1	1	1	?	0	0	0
	0	0	0	0	0	0	0	1	0	1	1	1
	0	1	0	?	1	0	1	2	1	0	1	0
	2	0	2	0	1	0	1	1	0	0	1	0
	2	1	1	1	0	1	0	0	0	1	0	1
	2	0	0	0	1	1	0	?	1	0	0	2
	0	0	0	0	0	0	0	0	1	2	0	0
	0	0	0	0	0	0	0	0	1	2	0	0
<i>Myaingtherium kenyaotamoides</i>	?	?	?	?	?	1	1	0	0	0	?	0
	?	?	?	?	?	1	1	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	?	0
	0	0	1	0	1	0	0	0	0	0	0	0
	0	1	0	0	1	1	0	0	0	0	1	1
	1	0	1	0	0	0	1	0	0	0	0	1
	0	0	0	0	0	1	2	0	0	0	-	1
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	1	0	1	0	0	1	1	0	0
	0	0	0	0	0	0	?	2	1	0	1	1
	1	0	0	0	0	0	0	1	1	0	0	1
	1	1	0	0	0	1	0	1	0	2	-	0
	1	2	1	1	1	0	1	?	?	1	0	?
	2	?	?	1	0	0	1	?	?	1	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
<i>Bothriogenys orientalis</i>	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	0	0	0	0	0	2	0
	1	0	0	1	2	1	1	1	1	1	0	1
	0	1	0	0	0	0	0	0	0	1	0	0
	1	0	0	0	0	0	1	0	1	1	0	1
	1	1	0	1	0	1	0	0	0	1	0	1
	0	2	1	0	0	1	1	0	0	-	0	?
	?	?	?	?	?	0	0	0	0	?	0	0
	0	?	1	1	1	0	0	0	1	1	0	1
	0	0	0	0	0	0	0	1	0	1	1	1
	0	?	0	0	0	0	1	1	1	0	1	0
	2	0	1	0	1	0	1	1	0	0	0	0
	1	1	1	1	1	0	0	1	0	1	0	0
	1	?	?	?	?	1	1	1	0	1	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
<i>Bothriogenys fraasi</i>	?	?	?	?	?	?	?	?	?	?	?	?
	0	?	?	?	?	0	0	0	0	0	2	0
	1	0	0	1	1	1	0	1	2	1	?	1
	0	1	0	0	0	0	0	0	0	1	0	1
	1	0	0	0	0	0	0	0	1	1	0	1
	1	1	0	1	0	1	0	0	0	1	1	0
	0	1	1	1	0	0	1	0	0	-	0	?
	?	?	2	0	?	0	0	0	0	1	0	0
	0	?	1	1	1	0	1	0	1	0	0	0
	0	0	0	0	?	0	0	1	0	1	1	1
	0	0	0	1	0	0	1	2	1	0	1	0
	2	0	2	0	1	0	1	1	2	0	1	?
	1	1	1	1	0	0	1	2	1	0	2	0
	1	?	1	0	1	0	1	0	1	?	?	?

## Lihoreau et al. Supporting information

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4		?	?	?	?	?	?	?	?	?	?	?
5		?	?	?	?	?	?	?	?	?	?	?
6		<i>Bothriogenys gorringei</i>	?	0	0	?	0	0	1	1	1	2
7		0	0	1	0	0	0	0	0	0	0	0
8		1	0	0	1	2	1	1	2	1	0	1
9		0	1	0	0	0	0	?	0	0	1	0
10		1	0	0	0	0	0	0	1	?	0	1
11		2	2	0	0	0	1	0	0	0	?	0
12		1	1	1	1	0	0	1	0	0	-	0
13		0	0	?	?	?	?	?	?	?	?	?
14		?	?	1	1	1	0	1	0	1	0	0
15		0	0	0	0	0	1	1	1	0	?	1
16		0	0	0	1	0	0	1	1	1	0	1
17		2	0	2	0	1	0	1	1	0	0	1
18		1	1	1	1	0	0	0	2	1	0	2
19		2	1	1	0	1	0	1	0	1	1	1
20		0	0	0	0	1	1	0	2	?	?	?
21		?	?	?	?	?	?	?	?	?	?	?
22		?	?	1	1	1	0	0	1	1	0	0
23		0	0	0	0	0	0	1	?	?	?	0
24		0	?	0	1	0	0	?	?	?	1	0
25		2	?	2	?	1	0	1	2	0	1	?
26		1	1	1	?	?	?	?	?	?	?	?
27		?	?	?	?	?	?	?	1	?	?	?
28		?	?	?	?	?	?	?	?	?	?	?
29		?	?	?	?	?	?	?	?	?	?	?
30		<i>Brachyodus aequatorialis</i>	1	1	1	1	0	?	1	?	1	?
31		0	?	?	1	0	0	0	0	0	1	0
32		1	0	0	1	1	1	0	2	1	1	?
33		0	1	0	0	0	0	0	0	2	0	1
34		1	0	1	0	0	0	1	0	1	1	1
35		1	2	0	0	0	0	0	?	2	0	0
36		0	1	1	1	0	1	1	0	-	0	1
37		2	1	2	0	0	0	0	?	?	0	0
38		0	?	1	1	1	0	1	0	1	0	0
39		0	0	0	0	1	0	1	1	0	0	1
40		0	0	0	1	0	0	1	2	1	0	0
41		2	0	2	0	1	0	1	1	2	0	0
42		1	1	1	1	1	0	0	1	1	2	0
43		1	1	1	0	0	1	1	1	?	?	?
44		?	?	?	?	?	?	?	?	?	?	?
45		<i>Brachyodus onoideus</i>	1	1	1	1	0	0	1	1	1	2
46		0	0	0	1	0	0	0	0	0	0	0
47		1	0	0	1	1	0	1	0	2	1	0
48		0	1	0	0	0	0	0	0	2	0	1
49		1	0	1	0	0	0	0	1	0	1	1
50		1	2	1	0	0	1	0	1	1	2	0
51		0	0	1	1	0	0	1	0	-	0	1
52		2	1	2	0	0	0	0	0	1	0	0
53		0	?	1	1	1	0	1	0	1	0	0
54		0	0	0	0	1	0	1	1	0	0	0
55		0	0	0	1	0	0	1	1	1	0	0
56		0	0	0	1	0	0	1	2	1	0	1
57		2	0	2	0	1	0	1	1	2	0	0
58		1	1	1	1	?	0	0	1	1	2	0
59		1	1	1	0	0	1	1	2	1	2	0
60		0	0	0	0	1	1	0	0	1	2	1
61		0	1	0								
62		<i>Brachyodus depereti</i>	2	1	1	1	0	?	-	-	?	?
63		?	?	?	1	0	0	0	0	0	0	0



Lihoreau et al. Supporting information

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	1	0	0	1	1	0	0	0	2	1	1	0
	0	1	0	0	0	0	0	0	0	2	0	1
	1	0	1	0	0	0	0	1	0	1	1	1
	2	2	0	0	0	1	0	1	1	2	0	0
	0	0	1	1	0	0	1	0	0	-	0	?
	?	?	?	?	?	?	0	0	?	?	?	?
	0	?	1	1	1	1	0	0	1	0	0	0
	0	0	0	0	0	0	1	0	0	0	0	0
	?	0	0	1	0	0	1	2	1	0	1	0
	2	0	2	0	1	0	1	1	2	0	1	?
	1	1	?	1	?	0	0	1	1	1	?	0
	?	?	1	0	0	1	?	?	1	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
<i>Bothriodon velaunum</i>	0	0	0	1	0	0	0	0	0	0	1	2
	0	0	0	1	0	0	0	0	0	0	0	0
	0	0	0	1	2	1	0	0	1	0	0	0
	0	1	0	0	0	0	0	0	0	1	0	1
	1	0	0	0	0	0	0	0	1	1	0	1
	2	2	0	0	0	1	0	0	1	2	0	0
	0	1	?	0	0	0	1	1	0	-	0	0
	0	0	2	0	0	0	1	0	0	0	1	0
	0	?	1	1	1	1	0	0	1	0	1	0
	0	0	0	0	0	0	1	1	0	0	1	1
	0	0	0	0	0	0	0	2	2	0	1	1
	2	0	1	0	1	0	1	2	2	1	0	0
	1	1	1	1	0	0	0	?	1	1	2	1
	1	1	1	0	1	0	0	0	1	1	1	1
	0	0	0	0	1	1	0	0	1	0	0	1
	0	1	0	0	1	0	0	0	1	0	0	1
<i>Aepinacodon americanum</i>	0	?	?	1	0	?	0	?	?	?	?	?
	?	?	0	0	1	0	0	0	0	0	0	0
	1	0	0	1	1	1	0	0	1	2	0	0
	1	1	0	0	1	0	0	0	2	1	0	1
	1	0	1	0	0	0	0	1	1	1	0	1
	2	2	0	0	0	1	0	1	1	2	0	0
	0	1	1	?	?	?	1	?	?	?	?	0
	0	0	2	0	0	0	1	0	0	0	1	0
	0	?	1	1	1	0	0	0	1	1	1	0
	0	0	0	0	0	0	1	1	0	0	0	0
	0	0	0	0	0	0	0	2	2	0	1	1
	2	0	1	0	1	0	1	1	2	1	?	?
	1	1	1	1	0	0	0	?	1	1	2	1
	1	?	0	0	1	0	0	0	1	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
<i>Elomeryx crispus</i>	0	0	0	1	0	0	0	1	0	1	2	0
	0	0	1	0	0	0	?	0	0	1	0	0
	0	0	1	?	1	0	0	1	1	1	1	0
	1	0	0	0	0	0	0	1	0	0	0	1
	0	0	0	0	0	0	0	1	1	1	0	0
	2	0	0	0	1	0	1	1	2	1	0	0
	1	1	1	0	0	1	?	0	-	?	0	0
	0	1	1	1	0	0	0	0	0	0	0	0
	?	1	1	1	1	0	0	1	0	0	0	0
	0	0	0	0	0	0	1	1	0	1	1	1
	0	0	1	0	0	1	2	2	0	1	1	2
	0	2	0	1	0	1	1	0	0	1	0	1
	1	1	1	0	0	1	0	1	0	1	?	1
	?	1	?	1	1	1	0	1	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?
<i>Elomeryx borbonicus</i>	0	0	0	1	0	0	0	0	1	0	1	2
	0	0	0	1	0	0	0	1	0	0	1	0
	1	0	0	1	2	1	0	0	1	1	1	1
	0	1	0	1	0	0	1	1	0	1	0	1
	1	0	0	0	0	0	0	1	?	1	1	1
	2	2	0	0	0	1	0	1	1	2	0	0

## Lihoreau et al. Supporting information

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4		0	2	1	1	1	0	1	1	0	-	0	0
5		0	0	1	1	1	0	0	0	0	0	0	0
6		0	?	1	1	1	?	0	0	1	0	0	0
7		0	0	0	0	0	0	1	?	0	1	0	0
8		1	0	0	1	0	0	1	2	2	0	1	1
9		2	0	1	0	1	0	1	1	1	1	1	0
10		2	1	1	1	0	0	2	0	1	0	2	1
11		1	2	1	0	1	1	1	0	1	1	1	2
12		0	0	0	0	1	1	0	0	1	1	1	1
13		1	1	0	0								
14	<i>Afromeryx zelteni</i>	?	?	?	?	?	?	?	?	?	1	?	?
15		?	?	0	1	0	0	1	0	0	1	0	0
16		0	0	1	2	1	0	0	1	1	?	0	1
17		1	0	0	0	1	1	0	2	1	0	1	1
18		0	1	0	0	0	0	0	1	1	0	1	2
19		2	0	0	0	1	0	0	0	0	0	0	0
20		1	1	?	1	0	1	1	1	1	0	0	?
21		0	?	1	1	0	0	0	1	1	0	0	0
22		?	1	1	1	1	0	0	1	0	0	0	0
23		0	0	0	0	0	1	1	0	0	0	0	0
24		0	0	1	0	1	-	-	2	0	1	1	2
25		0	2	0	1	0	1	1	1	0	1	0	2
26		1	1	1	0	0	1	0	1	0	2	1	2
27		0	1	0	0	1	1	1	1	0	0	1	1
28		0	0	0	0	1	1	1	1	0	0	1	1
29		0	0	0	1	0	0	1	1	0	0	0	0
30		1	1	?	?	?	?	?	?	?	?	?	?
31		0	1	1	1	1	?	0	0	1	0	0	0
32		0	0	0	0	0	0	1	1	0	0	0	0
33		0	0	0	1	0	0	1	1	2	0	1	1
34		2	0	1	0	1	0	1	1	1	0	1	0
35		2	1	1	1	0	0	?	?	1	0	2	0
36		2	?	1	1	0	1	?	?	1	?	?	?
37		?	?	?	?	?	?	?	?	?	?	?	?
38	<i>Sivameryx palaeindicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
39		?	?	?	?	?	1	0	1	0	0	1	0
40		1	0	0	1	2	1	0	0	2	1	0	0
41		0	1	0	1	0	1	1	1	2	1	0	0
42		1	0	?	0	0	0	0	0	1	1	0	1
43		2	2	0	0	0	1	0	1	2	0	0	0
44		0	1	1	1	0	0	1	1	0	-	0	?
45		?	?	0	?	?	?	?	?	1	?	?	0
46		0	?	1	1	1	?	?	?	1	?	1	?
47		?	0	0	?	?	0	1	1	0	0	0	0
48		1	0	0	1	0	0	1	2	2	0	1	1
49		2	0	1	0	1	0	1	1	?	0	1	?
50		2	1	1	1	0	0	2	1	1	0	2	0
51		2	0	1	1	0	1	?	?	1	2	1	0
52		-	-	-	-	-	-	-	-	-	1	1	2
53		1	1	0									
54	<i>Hemimeryx blanfordi</i>	?	?	?	?	?	?	?	?	?	?	1	2
55		?	?	0	?	?	1	0	1	0	0	1	0
56		1	0	0	1	2	1	0	0	2	1	0	0
57		0	1	0	1	0	1	0	0	0	2	1	0
58		1	0	0	0	0	0	0	0	?	1	0	1
59		2	2	?	0	0	1	0	1	2	0	0	0
60		0	2	1	0	0	0	1	1	0	-	0	?
		?	?	?	?	?	?	?	?	?	?	?	?
		?	?	1	1	0	-	0	0	1	0	0	0
		0	0	0	0	0	0	1	1	?	0	0	0

Lihoreau et al. Supporting information

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4		0	0	0	1	0	1	-	-	2	0	1	1
5		2	0	1	0	1	0	1	1	2	0	1	1
6		2	1	1	1	0	0	2	1	1	0	2	0
7		2	1	0	1	0	1	?	?	1	2	1	0
8		-	-	-	-	-	-	-	-	-	1	1	2
9		1	1	0									
10		1	1	0									
11		0	1	0	0	0	-	0	?	?	?	1	1
12		0	0	0	1	1	1	0	1	0	0	1	0
13		0	0	0	1	2	1	0	0	2	1	0	0
14		0	1	0	1	0	1	0	0	2	1	0	1
15		1	0	1	0	0	0	0	1	0	1	1	1
16		2	1	?	0	0	1	0	1	2	0	0	0
17		0	1	1	1	?	0	1	1	0	-	0	0
18		0	0	0	1	?	0	0	0	1	1	0	0
19		0	1	1	1	1	1	0	0	1	0	1	0
20		0	0	0	0	0	0	1	0	0	0	0	0
21		0	0	0	1	0	1	-	-	2	0	1	1
22		2	0	1	0	1	0	1	1	1	0	1	1
23		2	1	1	1	0	0	?	0	1	0	0	1
24		2	2	1	0	0	1	1	1	1	0	0	1
25		1	1	1	1	1	1	1	2	1	1	1	1
26		1	?	2									
27		0	?	?	0	0	-	?	?	?	?	1	1
28		0	?	?	0	2	1	0	1	0	0	1	0
29		0	0	0	1	1	1	0	0	1	0	1	0
30		0	0	0	0	0	0	1	0	0	0	0	0
31		?	0	0	1	0	1	-	-	2	0	1	1
32		2	0	1	0	1	0	1	1	1	1	1	1
33		1	1	1	1	0	0	2	0	1	1	0	1
34		0	2	1	0	0	1	1	1	1	1	1	1
35		1	1	1	1	1	1	1	2	1	1	1	2
36		1	1	1	1	1	1	1	2	1	1	1	2
37		0	0	0	0	0	0	1	0	0	0	0	2
38		0	0	0	1	0	1	-	-	2	0	1	1
39		2	0	1	0	1	0	1	1	1	2	1	1
40		2	1	1	1	0	0	2	0	1	1	0	1
41		2	0	1	0	1	0	1	1	1	1	1	1
42		2	1	1	1	0	0	2	0	1	1	0	1
43		2	2	0	0	0	1	1	2	1	?	?	?
44		?	?	?	?	?	?	?	?	?	?	?	?
45		?	?	?	?	?	?	?	?	?	?	?	?
46		?	?	?	?	?	?	?	?	?	?	?	?
47		0	0	0	1	2	1	0	0	2	1	0	0
48		0	1	0	1	0	1	1	2	2	1	0	1
49		1	0	1	0	0	0	0	1	0	1	1	1
50		2	2	0	1	?	1	0	1	2	0	0	0
51		0	2	1	1	1	0	1	1	1	0	0	?
52		?	?	0	2	?	?	?	?	?	?	?	?
53		?	?	?	?	?	?	?	?	?	?	?	?
54		?	?	?	?	?	0	1	0	0	0	0	2
55		0	0	0	1	0	1	-	-	2	0	1	1
56		2	0	1	0	1	0	1	1	2	1	1	1
57		1	1	1	1	0	0	?	?	?	?	?	?
58		?	2	?	?	?	1	?	?	1	1	1	1
59													
60													

## Lihoreau et al. Supporting information

1													
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4		1	1	1	1	1	1	1	2	1	1	1	2
5		1	1	0									
6		<i>Libycosaurus anisae</i>	?	0	1	2	1	0	0	0	?	1	1
7		0	1	0	0	2	1	0	2	0	0	1	0
8		0	0	0	1	2	1	0	0	2	1	0	0
9		0	1	0	1	0	1	1	2	1	1	0	1
10		1	0	1	0	0	0	0	1	0	1	1	1
11		2	1	0	1	1	1	0	1	2	0	0	0
12		0	2	1	1	1	0	1	1	1	0	0	?
13		?	?	0	2	0	?	0	1	2	1	0	0
14		0	?	1	1	1	1	0	0	1	1	1	0
15		0	0	0	0	0	0	1	0	0	0	0	2
16		0	0	0	1	0	1	-	-	2	0	1	1
17		2	0	1	0	1	0	1	1	2	1	1	1
18		?	1	1	1	0	0	?	0	1	0	2	0
19		2	0	1	0	0	1	1	2	1	?	?	?
20		?	?	?	?	?	?	?	?	?	?	?	?
21		<i>Libycosaurus bahri</i>	2	0	1	2	1	0	0	1	1	1	0
22		1	0	0	2	1	0	2	0	0	1	0	0
23		0	0	1	2	1	0	0	2	1	0	0	0
24		1	0	1	0	1	1	2	1	1	0	1	1
25		0	1	0	0	0	0	1	0	1	1	1	2
26		1	0	1	1	1	0	1	2	0	0	0	0
27		2	1	1	1	0	1	1	1	1	0	0	0
28		1	0	2	?	0	0	1	2	1	0	0	0
29		1	1	1	1	1	0	0	1	0	1	0	0
30		0	0	0	0	0	1	0	0	0	0	2	0
31		0	0	1	0	1	-	-	2	0	1	1	2
32		0	1	0	1	0	1	1	2	1	1	1	1
33		0	1	0	?	?	?	?	?	?	?	?	?
34		0	1	0	1	1	1	0	0	1	1	0	1
35		1	2	?	1	0	?	1	0	0	-	0	?
36		?	?	?	?	?	?	?	?	?	?	?	?
37		?	?	1	1	1	1	0	0	1	1	0	1
38		1	0	0	0	1	1	0	1	0	?	1	1
39		0	1	0	0	1	0	1	2	0	0	1	0
40		2	0	1	0	1	0	1	1	0	0	0	?
41		1	1	1	1	0	0	0	0	?	?	?	?
42		?	?	?	?	?	?	?	?	?	?	?	?
43		0	0	0	0	1	1	0	2	1	1	0	1
44		1	1	1	1	1	1	0	0	1	1	0	1
45		?	?	?	?	?	?	?	?	?	?	?	?
46		?	?	?	?	?	?	?	?	?	?	?	?
47		?	?	?	?	?	?	?	?	?	?	?	?
48		?	?	?	?	?	?	?	?	?	?	?	?
49		?	?	?	?	?	?	?	?	?	?	?	?
50		?	?	?	?	?	?	?	?	?	?	?	?
51		?	?	?	?	?	?	?	?	?	?	?	?
52		?	?	?	?	?	?	?	?	?	?	?	?
53		?	?	?	?	?	?	?	?	?	?	?	?
54		?	?	?	?	?	?	?	?	?	?	?	?
55		<i>Kenyapotamus coryndonae</i>	?	0	?	?	?	1	2	0	1	1	?
56		0	0	1	0	2	?	0	?	0	0	2	1
57													
58													
59													
60													

Lihoreau et al. Supporting information

1													
2													
3													
4		?	1	1	1	0	1	1	-	1	2	1	0
5		1	1	?	1	1	0	0	?	0	?	?	0
6		1	0	0	?	1	?	1	0	1	?	0	1
7		2	1	0	1	0	1	1	0	0	0	0	1
8		1	2	1	1	1	2	0	0	0	-	0	?
9		?	?	?	?	?	?	?	?	1	0	?	1
10		0	1	1	0	1	1	0	0	1	1	0	1
11		1	0	0	1	1	1	2	?	0	2	0	?
12		1	0	0	?	1	0	1	1	0	1	1	0
13		?	0	0	0	1	0	1	0	2	0	0	0
14		2	1	1	1	1	0	?	?	?	1	?	2
15		?	1	0	0	?	?	?	?	1	2	0	2
16		0	1	0	1	1	1	0	0	1	2	1	1
17		0	1	?	?								
18		0	1	?	?								
19		?	?	?	?								
20		1	0	0	?	1	?	?	0	1	?	0	1
21		2	1	0	1	0	1	1	0	0	0	0	1
22		1	?	1	?	1	2	0	0	0	-	0	?
23		?	?	?	?	?	?	?	?	?	0	?	1
24		0	?	2	0	1	1	0	0	1	1	0	1
25		?	0	0	1	1	1	2	1	0	2	0	1
26		1	0	0	?	1	0	1	1	0	1	1	0
27		?	0	0	?	1	0	1	0	?	?	0	0
28		2	1	1	1	1	0	0	1	1	1	0	2
29		0	?	0	0	1	0	?	?	1	?	?	?
30		?	?	?	?	?	?	?	?	?	?	?	?
31		?	?	?	?	?	?	?	?	?	?	?	?
32		?	?	?	?	?	?	?	?	?	?	?	?
33		?	?	?	?	?	?	?	?	?	?	?	?
34		?	?	?	?	?	?	?	?	?	?	?	?
35		?	?	?	?	?	?	?	?	?	?	?	?
36		?	?	?	?	?	?	?	?	?	?	?	?
37		?	?	?	?	?	?	?	?	?	?	?	?
38		?	?	?	?	?	?	?	?	?	?	?	?
39		?	?	?	?	?	?	?	?	?	?	?	?
40		?	?	?	?	?	?	?	?	?	?	?	?
41		?	?	?	?	?	?	?	?	?	?	?	?
42		?	?	?	?	?	?	?	?	?	?	?	?
43		?	?	?	?	?	?	?	?	?	?	?	?
44		?	?	?	?	?	?	?	?	?	?	?	?
45		?	?	?	?	?	?	?	?	?	?	?	?
46		?	?	?	?	?	?	?	?	?	?	?	?
47		?	?	?	?	?	?	?	?	?	?	?	?
48		?	?	?	?	?	?	?	?	?	?	?	?
49		?	?	?	?	?	?	?	?	?	?	?	?
50		?	?	?	?	?	?	?	?	?	?	?	?
51		?	?	?	?	?	?	?	?	?	?	?	?
52		?	?	?	?	?	?	?	?	?	?	?	?
53		?	?	?	?	?	?	?	?	?	?	?	?
54		?	?	?	?	?	?	?	?	?	?	?	?
55		?	?	?	?	?	?	?	?	?	?	?	?
56		?	?	?	?	?	?	?	?	?	?	?	?
57		?	?	?	?	?	?	?	?	?	?	?	?
58		?	?	?	?	?	?	?	?	?	?	?	?
59		?	?	?	?	?	?	?	?	?	?	?	?
60		?	?	?	?	?	?	?	?	?	?	?	?

## Lihoreau et al. Supporting information

1												
2												
3												
4	1	2	1	1	1	2	0	0	0	-	0	0
5	0	0	0	3	1	0	1	0	?	0	0	2
6	0	1	2	0	1	1	0	0	1	1	0	1
7	1	0	0	1	1	0	2	0	0	2	0	0
8	1	0	0	?	0	?	-	-	0	?	1	0
9	?	0	0	0	1	0	1	0	2	0	0	0
10	2	1	1	1	1	0	0	1	1	1	0	2
11	0	0	0	0	1	?	1	2	1	?	?	?
12	?	?	?	?	?	?	?	?	?	?	?	?
13	?	?	?	?	?	?	?	?	?	?	?	?
14	<i>Hexaprotodon garyam</i>		0	0	1	2	1	2	0	1	1	?
15	0	0	1	0	2	0	0	0	0	0	2	1
16	?	1	1	1	0	1	1	-	1	2	1	0
17	1	1	0	1	1	0	0	?	0	?	?	1
18	1	0	1	1	1	3	1	1	1	0	0	1
19	?	0	1	?	0	1	1	0	3	0	?	1
20	1	2	1	1	1	2	0	0	0	-	0	0
21	0	0	0	3	1	0	?	0	?	0	0	2
22	0	1	2	0	1	1	0	0	1	1	0	1
23	1	0	0	1	1	0	2	0	0	2	0	0
24	1	0	0	?	?	0	-	-	0	?	1	0
25	?	0	0	0	1	0	1	0	2	0	0	0
26	2	1	1	1	1	0	?	1	1	1	0	2
27	0	0	0	0	1	?	1	?	1	1	1	1
28	1	1	1	1	1	1	1	2	1	2	1	2
29	1	1	1	1	1	1	1	2	1	2	1	2
30	<i>Palaeochoerus quercyi</i>		0	0	1	?	0	1	0	0	1	3
31	0	1	1	0	2	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	-	0	-	0	0
33	0	0	0	1	0	0	1	1	0	0	1	1
34	1	0	0	1	1	0	0	0	0	1	1	0
35	-	1	0	0	0	1	1	0	1	0	0	0
36	0	1	0	0	0	0	0	0	0	0	0	0
37	?	1	0	0	2	1	?	?	?	?	?	1
38	0	1	0	0	0	0	-	0	0	1	0	0
39	0	1	0	0	0	0	0	0	0	0	0	0
40	1	1	0	0	0	2	2	0	1	0	0	0
41	-	1	1	1	0	1	0	0	1	0	1	0
42	0	1	0	0	1	0	0	0	0	0	0	0
43	1	1	0	2	?	0	1	0	0	0	?	0
44	0	?	1	0	1	1	0	0	1	0	1	0
45	0	1	0	0	0	2	2	0	1	0	0	1
46	1	0	0	0	1	0	1	0	0	1	0	1
47	0	1	0	0	1	0	0	-	2	-	0	1
48	0	1	1	1	0	0	1	0	0	1	?	1
49	?	2	0	0	0	1	0	?	0	1	1	2
50	0	0	0	0	0	0	0	0	1	0	0	1
51	0	0	0	0	0	0	0	?	0	0	0	0
52	1	1	0	0	?	0	?	0	0	1	3	0
53	<i>Perchoerus probus</i>		0	1	?	0	?	0	0	1	3	0
54	1	1	0	2	0	0	0	0	0	?	0	0
55	?	0	?	?	0	0	-	0	?	0	0	0
56	0	0	1	0	0	0	?	?	?	?	1	1
57	0	0	1	1	0	0	0	0	1	0	0	-
58	?	1	?	0	1	0	0	1	0	1	0	0
59	1	0	0	?	0	0	0	?	?	0	0	?
60	?	0	2	?	?	1	0	0	0	?	0	0
61	?	0	0	0	-	0	0	0	0	1	0	0
62	1	0	0	0	2	2	0	1	0	0	1	0

Lihoreau et al. Supporting information

1													
2													
3													
4		0	0	?	0	0	1	0	0	0	0	1	1
5		0	0	0	1	0	0	-	2	-	0	?	0
6		1	1	1	1	0	1	0	1	1	?	?	2
7		2	?	0	1	1	?	0	0	?	?	?	?
8		?	?	?	?	?	?	?	?	?	?	?	?
9		?	?	?	?	?	?	?	?	?	?	?	?
9	<i>Amphimeryx murinus</i>		0	0	1	1	0	0	0	0	1	1	0
10		?	0	0	2	0	0	1	0	1	1	2	0
11		0	0	1	0	0	1	0	0	0	-	0	0
12		0	0	0	1	0	0	-	0	0	0	1	1
13		1	0	1	0	0	3	0	1	0	0	1	1
14		2	0	1	1	0	1	0	1	3	1	0	0
15		0	0	0	0	0	0	1	1	1	1	0	0
16		?	?	2	?	?	?	1	0	0	0	?	2
17		1	0	0	0	1	2	2	0	1	1	1	0
18		0	0	0	0	0	2	1	0	0	2	0	0
19		0	0	1	-	-	0	0	2	2	0	1	1
20		2	0	1	1	1	0	1	1	2	0	0	2
21		0	1	1	1	1	0	1	0	0	0	0	1
22		2	0	1	0	1	0	0	0	2	1	0	0
23		-	-	-	-	-	-	-	-	-	0	0	0
24		0	0	2	?	?	?	?	?	?	?	?	?
25	<i>Khirtaria</i> spp.		?	?	?	?	?	?	?	?	?	?	?
26		?	?	?	?	?	0	0	0	0	0	0	0
27		0	0	0	0	0	0	0	1	0	0	0	0
28		1	0	1	0	0	1	0	0	0	0	1	1
29		1	0	0	1	-	0	1	1	1	1	1	0
30		0	0	1	0	1	0	2	0	0	1	0	0
31		0	0	0	0	1	?	0	1	0	?	?	?
32		?	?	?	?	?	?	?	?	?	?	?	?
33		?	?	?	?	?	?	?	?	?	?	?	?
34	<i>Mixtotherium</i> spp.		?	?	?	?	?	?	?	?	1	2	0
35		0	0	0	1	0	1	0	1	1	2	0	?
36		1	1	0	0	0	0	0	1	-	?	0	0
37		0	0	1	0	0	0	0	0	0	1	0	0
38		1	0	0	0	0	1	1	0	0	1	0	-
39		1	0	1	0	1	0	0	0	1	0	1	0
40		2	0	0	0	0	1	0	1	0	0	?	?
41		?	0	1	?	1	0	0	0	0	?	2	1
42		0	1	1	1	1	0	0	1	0	0	0	0
43		1	0	0	0	0	1	0	0	2	0	0	0
44		0	1	-	0	0	1	0	2	0	0	0	2
45		0	2	0	1	1	1	1	0	0	1	2	2
46		1	1	1	1	0	?	?	1	?	?	?	?
47		?	?	?	1	1	?	?	0	1	1	1	0
48		0	0	0	0	0	?	?	?	?	?	?	?
49		1	0	1	0	0	0	0	1	0	1	1	0
50		-	2	0	0	0	1	0	1	1	0	0	0
51		0	1	0	0	0	0	1	1	0	-	0	?
52		?	?	?	?	?	?	0	0	1	0	1	0
53		1	1	1	1	1	1	2	0	1	0	1	0
54		0	0	0	0	0	2	1	0	0	0	0	0
55		0	0	1	-	0	0	0	2	2	0	0	1
56		2	0	1	1	1	0	1	1	0	0	0	2
57		2	1	1	1	1	1	?	?	?	?	?	?
58		?	0	?	?	0	1	?	0	0	1	1	1
59													
60													

## Lihoreau et al. Supporting information

1													
2													
3													
4		1	0	0	0	1	0	0	?	1	1	0	0
5		0	1	2									
6		<i>Dacrytherium ovinum</i>	0	0	?	?	?	0	0	?	?	1	2
7		1	0	0	2	0	0	0	0	1	0	0	0
8		0	0	1	1	1	0	0	0	2	2	1	0
9		0	1	0	1	0	0	0	1	0	0	1	0
10		1	1	1	0	0	0	0	0	0	0	1	0
11		-	1	1	0	0	1	0	1	2	0	0	0
12		1	0	0	0	0	0	1	0	0	-	0	0
13		?	?	2	0	?	1	0	0	0	0	0	2
14		0	1	1	1	0	-	2	0	1	0	1	1
15		0	0	0	0	1	0	1	0	0	0	0	0
16		0	0	1	-	0	0	1	0	2	0	1	1
17		2	0	2	1	1	0	1	1	0	0	1	2
18		0	1	1	1	0	0	1	0	0	0	?	1
19		1	?	?	?	?	?	?	?	?	?	?	?
20		?	?	?	?	?	?	?	?	?	?	?	?
21		<i>Diplobune minor</i>	0	0	1	0	0	0	0	1	1	2	1
22		0	0	1	0	0	0	0	1	1	0	0	0
23		1	1	1	1	0	0	0	2	0	1	0	0
24		0	0	1	0	0	0	0	0	0	1	1	0
25		0	1	0	0	0	0	1	0	1	1	0	-
26		1	1	0	0	1	1	1	2	2	0	0	0
27		0	0	0	0	0	1	0	0	-	0	0	2
28		1	2	0	0	1	0	0	0	0	1	2	0
29		1	1	1	1	2	2	0	1	0	1	0	0
30		0	0	0	0	2	1	0	0	0	0	0	0
31		0	1	-	0	0	1	0	2	0	0	1	2
32		0	1	1	0	0	1	0	0	0	1	2	0
33		0	0	0	0	0	0	0	0	0	0	1	0
34		0	0	0	0	?	0	1	-	?	?	1	?
35		?	?	?	?	?	?	0	0	0	0	1	2
36		1	0	1	1	1	1	2	0	1	0	1	0
37		0	0	1	0	0	2	1	0	1	0	0	0
38		0	0	1	-	0	0	0	0	2	0	0	1
39		2	0	1	1	0	1	1	1	1	1	1	2
40		0	1	1	1	2	0	1	0	0	0	1	1
41		1	0	0	0	0	0	0	?	0	2	1	0
42		-	-	-	-	-	-	-	-	-	0	0	0
43		0	0	2									
44		<i>Entelodon spp.</i>	0	0	0	1	?	0	0	1	0	0	0
45		0	0	0	0	1	1	0	0	1	0	0	0
46		0	0	0	0	0	0	0	0	0	0	0	0
47		0	0	1	0	0	-	0	0	0	0	1	0
48		1	1	0	0	1	0	1	1	0	1	1	0
49		0	0	1	0	1	0	0	0	0	1	0	0
50		0	0	0	0	0	0	-	1	0	0	0	0
51		0	0	?	?	1	1	0	0	0	1	2	0
52		1	0	0	1	0	-	0	0	0	1	0	0
53		0	0	0	0	1	2	0	1	0	-	0	0
54		0	0	0	0	0	1	0	0	1	0	1	0
55		0	0	0	0	1	0	-	2	-	0	1	1
56		0	1	0	2	0	0	2	0	0	2	1	1
57		2	0	0	0	0	0	0	1	1	1	1	1
58		1	0	0	0	0	0	2	1	?	0	0	0
59		0	2										
60		<i>Indohyus indirae</i>	?	?	?	?	?	?	?	?	?	?	?
		?	?	?	?	?	0	0	?	?	?	?	?



Lihoreau et al. Supporting information

1												
2												
3												
4	?	?	?	?	0	0	0	1	0	0	0	0
5	0	0	1	0	0	0	0	0	0	0	1	1
6	1	0	0	0	0	0	1	0	1	1	1	0
7	0	0	0	0	1	0	2	0	0	1	0	0
8	?	?	?	?	?	?	?	0	0	?	0	0
9	1	0	0	0	-	-	0	0	0	0	0	0
10	0	1	1	0	0	2	0	0	2	0	1	0
11	1	0	0	1	1	0	-	2	-	0	2	1
12	1	?	1	0	0	?	?	?	?	?	?	?
13	?	?	?	?	?	1	0	?	?	?	?	?
14	?	?	?	?	?	?	?	?	?	?	?	?
15	<i>Merycoiodon</i> sp.	?	?	?	?	?	?	?	?	0	1	0
16	0	0	0	1	0	0	0	0	0	2	0	1
17	1	1	1	1	0	0	0	1	0	0	1	0
18	1	0	1	0	0	1	1	0	0	1	0	1
19	0	1	0	0	-	0	0	0	0	1	1	2
20	2	1	0	0	1	0	1	3	2	0	0	1
21	2	0	0	?	0	1	?	?	?	?	0	0
22	0	0	1	?	0	0	0	0	1	0	0	0
23	0	0	1	1	2	2	0	1	0	0	0	0
24	0	1	0	0	2	0	0	0	2	0	0	0
25	0	2	-	0	1	-	-	2	0	0	1	2
26	0	1	1	0	0	1	1	0	0	1	?	2
27	1	1	1	0	0	1	?	0	?	?	1	2
28	0	0	0	0	1	1	0	0	?	?	?	?
29	?	?	?	?	?	?	?	?	?	?	?	?
30	<i>Amphiragatherium</i> spp.	?	?	?	?	?	?	?	?	?	1	?
31	?	?	?	2	0	0	1	0	1	1	0	0
32	0	1	1	0	0	0	0	0	0	2	1	0
33	1	1	0	1	1	0	0	0	0	0	0	0
34	1	0	0	0	0	0	0	1	0	1	1	1
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36	1	2	0	0	0	2	0	0	0	-	0	?
37	?	?	?	?	?	?	?	0	1	0	1	2
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40	1	0	0	0	0	0	1	1	1	0	?	1
41	?	0	0	0	1	0	1	0	0	0	0	2
42	1	1	1	1	0	0	0	0	?	?	0	2
43	2	1	0	0	1	?	?	?	1	?	?	?
44	?	?	?	?	?	?	?	?	?	?	?	?
45	?	?	?	?	?	?	?	?	?	?	?	?
46	<i>Hallebune krumbiegeli</i>	?	?	?	?	?	?	?	?	?	?	?
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54	0	1	?	0	0	1	2	1	0	3	0	0
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58	?	?	?	0	1	1	?	?	0	?	?	?
59	?	?	?	?	?	?	?	?	?	?	?	?
60	?	?	?	?	?	?	?	?	?	?	?	?
	<i>Archaeomeryx optatus</i>	0	0	0	-	?	0	?	?	?	1	?
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## Lihoreau et al. Supporting information

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<i>Lophiomyx chalaniati</i>			0	0	1	2	0	0	1	?	1	?
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## Supplementary References

- 1 Boisserie J-R, Lihoreau F, Orliac M, Fisher RE, Weston EM, et al. (2010) Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). *Zool J Linn Soc* 158: 325–366.
- 2 Alloing-Séguier L *et al.* (2014) Enamel microstructure evolution in anthracotheres (Mammalia, Cetartiodactyla) and new insights on hippopotamoid phylogeny. *Zool J Linn Soc* 171: 668–695.
- 3 Ducrocq S (1997) The anthracotheriid genus *Bothriogenys* (Mammalia, artiodactyla) in Africa and Asia during the Paleogene: phylogenetical and paleobiogeographical relationships. *Stuttgarter Beiträge zur Naturkunde* 250: 1-44.
- 4 Damuth J (1990) in *Body size in Mammalian Paleobiology: estimation and biological implications*, eds Damuth J, McFadden (Cambridge University press, Cambridge), pp. 229-253.
- 5 Hershkovitz P (1971) Basic crown patterns and cusp homologies of mammalian teeth. In: Dahlberg AA, editor editors. *Dental morphology and evolution*. Chicago: The University of Chicago Press. pp. 95–150.
- 6 Butler PM (1978) Molar cusp nomenclature and homology. In: Butler PM, Joysey KA, editors. *Development, Function and Evolution of Teeth*. London: Academic Press. pp. 439–453.
- 7 Gentry AW, Hooker JJ (1988) The phylogeny of the Artiodactyla. In: Benton MJ, editor editors. *The phylogeny and classification of the Tetrapods, Volume 2 : Mammals*. Oxford: Clarendon Press. pp. 235–272.
- 8 Made J van der (1996) Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time. *Contributions to Tertiary and Quaternary Geology* 33: 3–254.
- 9 Tassy P (1996) Dental homologies and nomenclature in the Proboscidea. In: Shoshani J, Tassy P, editors. *The Proboscidea Evolution and Palaeoecology of Elephants and their Relatives*. Oxford: Oxford University Press. pp. 21–25.
10. Van Valen L (1966) Deltatheridia, a new order of mammals. *Bulletin of the American Museum of Natural History* 132: 1–128.
- 11 Hünermann KA (1968) Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän = Pont) Rheinhessens (Südwestdeutschland). *Mémoires suisses de Paléontologie* 86: 1–96.
- 12 Orliac M (2006) *Eurolistriodon tenarezensis*, sp. nov., from Montréal-du-Gers (France): implications for the systematics of the European Listriodontinae (Suidae, Mammalia). *J Vertebr Paleontol* 26: 967–980.
- 13 Orliac M (2007) Le rôle des Listriodontinae dans la différenciation des Suidae (Mammalia) ; paléoanatomie, systématique, phylogénie. Unpublished dissertation, Paris: Université Pierre et Marie Curie - Paris VI. pp. 702.
- 14 Smith JB, Dodson P (2003) A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *J Vertebr Paleontol* 23: 1–12.

Lihoreau et al. Supporting information

- 15 Pickford M (1983) On the origins of Hippopotamidae together with descriptions of two species, a new genus and a new subfamily from the Miocene of Kenya. *Geobios* 16:193-217.
- 16 Nakaya H, Pickford M, Nakano Y, Ishida H (1984) The late Miocene large mammal fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *Afr Study Monogr* suppl 2:87-131.
- 17 Nakaya H, Pickford M, Yasui K, Nakano Y (1987) Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *Afr Study Monogr* suppl 5:47-98.
- 18 Tsujikawa H (2005) The updated late Miocene large mammal fauna from Samburu Hills, northern Kenya. *Afr Study Monogr* suppl 32:1-50.
- 19 Coryndon SC (1977) The taxonomy and nomenclature of the Hippopotamidae (Mammalia, Artiodactyla) and a description of two new fossil species. *Proc Koninkl Nederland Acad Wetenschap* 80:61-88.
- 20 Weston EM (2003) in *Lothagam. The dawn of humanity in eastern Africa*, eds Harris JM, Leakey MG (Columbia University Press, New York), pp 380-410.
- 21 Boisserie J-R, Likius A, Vignaud P, Brunet M (2005) A new late Miocene hippopotamid from Toros-Menalla, Chad. *J Vertebr Paleontol* 25:665-673.
- 22 Pickford M (1998) A new genus of Tayassuidae (Mammalia) from the Middle Miocene of Uganda and Kenya. *Ann Paléontol* 84:275-285.
- 23 Pickford M, Sawada Y, Tayama R, Matsuda Y, Itaya T, Hyodo H, Senut B (2006) Refinement of the age of the Middle Miocene Fort Ternan Beds, Western Kenya, and its implications for Old World biochronology. *C R Geosciences* 338:545-555.
- 24 Orliac M, Boisserie J-R, Lihoreau F, MacLatchy L (2010) Early Miocene hippopotamids (Cetartiodactyla) constrain the phylogenetic and spatiotemporal settings of hippopotamid origin. *Proc Natl Acad Sci USA* 107: 11871-11876.
- 25 Suteethorn V, Buffetaut E, Helmcke-Ingavat R, Jaeger J-J, Jongkanjanasoontorn Y (1988) Oldest known Tertiary mammals from south east Asia: middle Eocene primate and anthracotheres from Thailand. *N Jb Geol Pal Mh* 9:563-570.
- 26 Ducrocq S (1994) Les anthracothères paléogènes de Thaïlande : paléogéographie et phylogénie. *C R Acad Sci* 318:549-554.
- 27 Ducrocq S (1999) The late Eocene Anthracotheriidae (Mammalia, Artiodactyla) from Thailand. *Palaeontogr Abt A* 252:93-140.
- 28 Scott WB (1940) in *The Mammalian fauna of the White River Oligocene*, eds Scott WB, Jepsen GL (Transaction of the American Philosophical Society, Philadelphia), pp. 363-746.
- 29 Macdonald JR (1956) The North American anthracotheres. *J Paleontol* 30: 615-645.
- 30 Cuvier G (1822) *Recherches sur les ossements fossiles* (Edmond d'Ocagne éditeur, Paris).
- 31 Leymerie A (1851) Mémoire sur un nouveau type pyrénéen parallèle à la craie proprement dite. *Mém Acad Sci Toulouse* 4:388-394.

- 32 Lihoreau F, Ducrocq S (2007) in *The Evolution of Artiodactyls*, eds Prothero DR, Foss SE (The Johns Hopkins University Press, Baltimore), pp 89-105.
- 33 Tsubamoto T *et al.* (2011) A new anthracotheriid artiodactyl from the Eocene Pondaung Formation of Myanmar. *Vertebrata Palasiatica* 49: 85-113.
- 34 Pilgrim GE (1928) The Artiodactyla from the Eocene of Burma. *Memoir of the Geological Survey of India Paleontologia Indica* 13: 1-44.
- 35 Lihoreau F, Blondel C, Barry J, Brunet M (2004) A new species of the genus *Microbunodon* (Mammalia, Artiodactyla) from the Miocene of Pakistan: phylogenetic relationships and palaeobiogeography. *Zool Scr* 33:97-115.
- 36 Brunet M (1968) Découverte d'un crâne d'Anthracotheriidae, *Microbunodon minimum* (Cuvier), à la Milloque (Lot et Garonne). *C R Acad Sci* 267:835-838.
- 37 Schmidt M (1913) Ueber Paarhufer der fluviomarinen Schichten des Fajum. *Geol Paläont Abh* 11:155-263.
- 38 Black CA (1978) In *Evolution of African Mammals*, eds Maglio VJ, Cooke HBS (Harvard University Press, Cambridge), pp. 423–434.
- 39 MacInnes DG (1951) Miocene Anthracotheriidae from East Africa. *Fossil Mammals of Africa* 4: 1-24.
- 40 Dineur H (1981) Le genre *Brachyodus*, anthracotheriidae (Artiodactyla, Mammalia) du Miocène inférieur d'Europe et d'Afrique. Unpublished PhD thesis, Université Paris 6. pp. 180.
- 41 Pickford M (1991) in *The Geology of Libya vol. 4*, eds Salem MJ, Hammuda OS, Eliagoubi BA (Elsevier, Amsterdam,), pp 1483–1490.
- 42 Hellmund M (1991) Revision der Europäischen species der Gattung *Elomeryx* Marsh 1894 (Anthracotheriidae, Artiodactyla, Mammalia)-Odontologische Untersuchungen. *Palaeontogr Abt A* 220:1-101.
- 43 Lihoreau F *et al.* (2009) First complete skulls of *Elomeryx crispus* (gervais, 1849) and of *Protaceratherium albigense* (Roman, 1912) from a new Oligocene locality near Moissac (sw France). *J Vertebr Paleontol* 29(1): 242–253.
- 44 Geais G (1934) Le *Brachyodus borbonicus* des argiles de St. Henri (près Marseille). *Trav Lab Géol. Fac Sci Lyon, Mém.* 21:1-54.
- 45 Kostopoulos DS, Koufos GD, Christanis K (2012) On some anthracotheriid (Artiodactyla, Mammalia) remains from northern Greece: comments on the palaeozoogeography and phylogeny of *Elomeryx*. *Swiss J Palaeontol* 131(2): 303-315.
- 46 Pickford M (1987) Révision des suiformes (Artiodactyla, Mammalia) de Bugti (Pakistan). *Ann Paléontol* 73 : 289-350.
- 47 Lihoreau F *et al.* M (2007) Anatomical revision of the genus *Merycopotamus* (Artiodactyla ; Anthracotheriidae) : its significance on late Miocene mammal dispersions in Asia. *Palaeontology* 50:503–524.

- 1  
2  
3  
4 48 Black CC (1972) A new species of *Merycopotamus* (Artiodactyla: Anthracotheriidae) from the late  
5 Miocene of Tunisia. *Notes du service de géologie de Tunisie* 37: 5-39.
- 6  
7 49 Pickford M (2006) Sexual and individual morphometric variation in *Libycosaurus* (Mammalia,  
8 Anthracotheriidae) from the Maghreb and Libya. *Geobios* 39:267–310.
- 9  
10 50 Lihoreau F, et al. (2014) Description and palaeobiology of a new species of *Libycosaurus*  
11 (Cetartiodactyla, Anthracotheriidae) from the Late Miocene of Toros-Menalla, northern Chad. *Journal of*  
12 *Systematic Palaeontology* 12 (7) 761-798
- 13  
14 51 Pickford M (2008) *Libycosaurus petrocchii* Bonarelli, 1947, and *Libycosaurus anisae* (37, 1972)  
15 (Anthracotheriidae, Mammalia): nomenclatural and geochronological implications. *Ann Paléont* 94:39–55.
- 16  
17 52 Lihoreau F, et al. (2006) Evidence for Late Miocene Chado-Libyan bioprovince: a new possible  
18 dispersal ability for early Chadian Hominids. *Proc Natl Acad Sci USA* 103:8763–8767.
- 19  
20 53 Ginsburg L (1974) Les Tayassuidés des Phosphorites du Quercy. *Palaeovertebrata* 6:55-85.
- 21  
22 54 Hellmund M (1992) Schweineartige (Suina, Artiodactyla, Mammalia) aus oligo-miozänen  
23 Fundstellen Deutschlands, der Schweiz und Frankreichs II. Revision von *Palaeochoerus* Pomel, 1847 und  
24 *Propalaeochoerus* Stehlin, 1899 (Tayassuidae). *Stuttgarter Beitr Naturkde B* 189:1-75.
- 25  
26 55 Orliac MJ, Antoine P-O, Ducrocq S (2010) Phylogenetic relationships of the Suidae (Mammalia,  
27 Cetartiodactyla): new insights on the relationships within Suoidea. *Zool Scr* 39: 315–330.
- 28  
29 56 Harris JM, Liu L-P (2007) in *The Evolution of Artiodactyls*, eds Prothero DR, Foss SE (The Johns  
30 Hopkins University Press, Baltimore), pp 130-150.
- 31  
32 57 Brunet M, Sudre J (1987) Evolution et systématique du genre *Lophiomeryx* Pomel 1853  
33 (Mammalia, artiodactyla). *Münchner Geowiss Abh* 10:225-241.
- 34  
35 58 Colbert EH (1941) The osteology and relationships of *Archaeomeryx* an ancestral ruminant.  
36 *American Museum Novitates* 1135: 1-24.
- 37  
38 59 Thewissen JGM, Russell DE, Gingerich PD, Hussain ST (1983) A new dichobunid artiodactyl  
39 (mammalia) from the Eocene of North-West Pakistan. *Proceedings of the Koninklijk Nederlandse*  
40 *Akademie van Wetenschappen* 86(2):153-180.
- 41  
42 60 Theodor JM, Erfurt J, Métails G (2007) in *The Evolution of Artiodactyls*, eds Prothero DR, Foss SE  
43 (The Johns Hopkins University Press, Baltimore), pp 32-58.
- 44  
45 61 Sudre J (1978) Les Artiodactyles de l'Éocène moyen et supérieur d'Europe occidentale  
46 (Systématique et évolution). *Mém Trav. Instit. Montpellier Ecole Pratique des Hautes Etudes* 7:1-229.
- 47  
48 62. Coombs WP, Jr, Coombs MC (1977) The origin of anthracotheres. *N Jb geol Pal Mh* 10:584-599.
- 49  
50 63. Coombs MC, Coombs WP, Jr (1977) Dentition of *Gobiohyus* and a reevaluation of the Helohyidae  
51 (Artiodactyla). *J Mamm* 58:291-308.
- 52  
53 64. Ducrocq S, Chaimanee Y, Suteethorn V, Jaeger J-J (1997) First discovery of Helohyidae  
54 (Artiodactyla, Mammalia) in the Late Eocene of Thailand: a possible transitional form for  
55 Anthracotheriidae. *C R Acad Sci* 325:367-372.
- 56  
57  
58  
59  
60

65. Foss SE (2007) in *The evolution of artiodactyls*, eds Prothero DR, Foss SE (The Johns Hopkins University Press, Baltimore), pp 85-88.
66. Thewissen JGM, Gingerich PD, Russell DE (1987) Artiodactyla and Perissodactyla (mammalia) from the Early-Middle Eocene Kuldana Formation of Kohat (Pakistan). *Cont Mus Paleont* 27:247-274.
67. Kumar K, Sahni A (1985) Eocene mammals from the upper Subathu group, Kashmir Himalaya, India. *J Vertebr Paleontol* 5:153-168.
68. Thewissen JGM, Williams EM, Hussain ST (2001) Eocene Mammal Faunas from Northern Indo-Pakistan. *J Vertebr Paleontol* 10: 347-366
69. Orliac MJ, Ducrocq S (2012) Eocene raoellids (Mammalia, Cetartiodactyla) outside the Indian Subcontinent: palaeogeographical implications. *Geol Mag* 149:80–92.
70. Erfurt J, Métalis G (2007) in *The Evolution of Artiodactyls*, eds Prothero DR, Foss SE (The Johns Hopkins University Press, Baltimore), pp 59-84.
71. Hooker JJ, Thomas KM (2001) A new species of *Amphirhagatherium* (Choeropotamidae, Artiodactyla, Mammalia) from the late Eocene Headon hill formation of southern England and phylogeny of endemic european anthracotherioids. *Palaeontology* 44: 827-853.
72. Hooker JJ, Weidmann M (2000) The Eocene mammal faunas of Mormont, Switzerland. *Mémoires suisses de Paléontologie* 120:1-141.
73. Sudre J (1974) D'importants restes de *Diplobune minor* (Filhol) à Itardies (Quercy). *Palaeovertebrata* 6(1-2) : 47-54
74. Brunet M (1975). Les grands mammifères chefs de file de l'immigration oligocène et le problème de la limite Eocène-Oligocène en Europe. Unpublished Doctoral dissertation, Université de Poitiers. pp. 542
75. Stevens MS, Stevens JB (2007) in *The evolution of artiodactyls*, eds Prothero DR, Foss SE (The Johns Hopkins University Press, Baltimore), pp 157-168.
76. Geisler JH, Theodor JM, Uhen, MD, Foss SE (2007) in *The Evolution of Artiodactyls*, eds Prothero DR, Foss SE (The Johns Hopkins University Press, Baltimore), pp 19–31.
77. Boisserie, J.-R., Kiarie, C., Lihoreau, F. & Nengo, I. (2017). Middle Miocene *Kenyapotamus* (Cetartiodactyla, Hippopotamidae) from Napudet, Turkana Basin, Kenya. *Journal of Vertebrate Paleontology*, 37(1), e1272055.
78. Lihoreau, F., Boisserie, J.-R., Manthi, F. K. & Ducrocq, S. (2015). Hippos stem from the longest sequence of terrestrial cetartiodactyl evolution in Africa. *Nature Communications*, 6, 6264.
79. Boisserie, J. R., Suwa, G., Asfaw, B., Lihoreau, F., Bernor, R. L., Kato, S., & Beyene, Y. (2017). Basal hippopotamines from the upper Miocene of Chorora, Ethiopia. *Journal of Vertebrate Paleontology*, 37(3), e1297718.
80. Sileem, A. H., Sallam, H. M., Hewaidy, A. A., Gunnell, G. F., & Miller, E. R. (2015). Anthracotheres (Mammalia, Artiodactyla) from the upper-most horizon of the Jebel Qatrani Formation, latest early Oligocene, Fayum Depression, Egypt. *Egyptian Journal of Paleontology*, 15, 1-11.



Lihoreau et al. Supporting information

81 Ducrocq, S., Coiffait, B., Coiffait, P. E., Mahboubi, M., & Jaeger, J. J. (2001). The Miocene  
8 Anthracotheriidae (Artiodactyla, Mammalia) from the Nementcha, eastern Algeria. *Neues Jahrbuch für*  
9 *Geologie und Palaontologie-Monatshefte*, (3), 145-156.

82 Lihoreau, F., Hautier, L., & Mahboubi, M. (2014). The new Algerian locality of Bir el Ater 3: validity  
10 of *Libycosaurus algeriensis* (Mammalia, Hippopotamoidea) and the age of the Nementcha Formation.  
11 *Palaeovertebrata*, 39, e1.

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