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Early African Fossils Elucidate the Origin of Embrithopod Mammals

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SUMMARY

Modern mammals rapidly evolved in the early Cenozoic in all continental provinces, including in Africa, with one of the first placental branches, the Afrotheria [1, 2]. Afrotherian evolution is at the origin of the major radiation of African ungulate-like mammals, including extant hyrax, elephant, and sea cow orders, which all belong to the Paenungulata. The paenungulate radiation also includes the extinct order Embrithopoda of uncertain interordinal relationships, which is best known for the giant and strangely specialized Oligocene genus *Arsinoitherium*. The Ouled Abdoun basin, Morocco, yielded exceptional Paleocene-Eocene fossils documenting the early paenungulate evolution [3–8]. Here we report two new small Ypresian species, *Stylolophus minor* n.g., n.sp. and *cf. Stylolophus* sp., which are the earliest and most primitive embrithopods. The cladistic analysis relates the Embrithopoda to crown paenungulates as the stem-group of the Tethytheria, which makes crown tethytherians restricted to extant elephant and sea cow orders. The Embrithopoda is therefore an early tethytherian offshoot predating the elephant and sea cow divergence. The resulting phylogeny supports a strictly African early radiation of the paenungulates excluding the Phenacolo-phidae and Anthracobunia. It sustains an at least early Paleocene African origin of the Embrithopoda. The unique tooth pattern of the embrithopods (hyperdilambdodont and pseudolophodont molars) is resolved as evolving early and directly from the dilambdodont (W-shaped labial molar crests) ancestral paenungulate morphotype. The specialized upper molar morphology with two transverse crests is convergent and non-homologous in embrithopods and crown Tethytheria. These convergences for specialized folivorous diet were driven by free herbivorous African niches in the early Paleogene.

RESULTS AND DISCUSSION

Placentals comprise the largest radiation of living mammals, as the result of an evolutionary history dating back to the Cretaceous-Paleogene (K-Pg) transition. Molecular phylogeny identified the first major splitting clades at the base of placentals [1, 2]. Unfortunately, the fossil record of the initial placental radiation remains poor, especially for the key K-Pg period of evolution and for some major continental centers of evolution. This is especially true for the Arabo-African Island, which was the center of radiation of one of the main placental clades, the Afrotheria. The Ouled Abdoun phosphate series, in Morocco, yielded the only known Paleocene and early Eocene fossil remains of stem and early crown paenungulate afrotherians [3–8]. The paenungulates, today represented by orders of hyraxes (Hyracoidea), elephants (Proboscidea), and sea cows (Sirenia), were major components of the African endemic herbivorous megafauna during the Paleogene. The paenungulates also include a remarkable extinct order, the Embrithopoda. Embrithopods are strangely specialized and large, ungulate-like mammals known in the Paleogene of Arabo-Africa and Eurasia. The best known is the rhino-sized *Arsinoitherium zitelli*, discovered in the early Oligocene of the Fayum [9, 10]. It is characterized by a highly specialized dentition with hyperdilambdodont molars [11] and by a pair of huge hollow nasal horns [9].

Embrithopods are enigmatic placentals with uncertain phylogenetic relationships because of their unusual autapomorphic morphology. They are included in the Paenungulata [12], but with debated interordinal relationships. The order initially related to the Hyracoidea [9] is most consensually placed as the sister group to the Proboscidea [13–15], although it is sister group to the Sirenia in some recent works [16]. Here, we report the discovery of the oldest and most primitive known embrithopods from Ypresian Ouled Abdoun phosphate levels. They shed new light on the origin and early history of the Embrithopoda. Their phylogenetic analysis helps to clarify the basal radiation and interordinal phylogeny of the Paenungulata and Tethytheria, as well as the evolution of key embrithopod synapomorphies.

Systematic Paleontology

Placentalia Owen, 1837.

Afrotheria Stanhope et al., 1998.

Paenungulata Simpson, 1945.

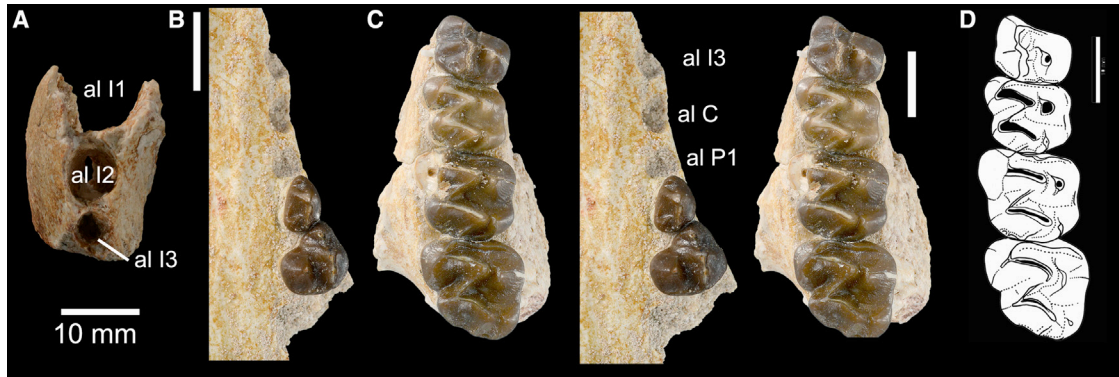


Figure 1. *Styolophus minor* n. g., n. sp.

Specimen OCP DEK/GE 667.

(A) Right premaxillary in occlusal view showing alveoli of I_1^{1-3} .

(B) Anterior part of left maxillary with P_2^{2-3} and alveoli of P_1^1 , C_1^1 , and I_3^3 in occlusal stereophotographic view.

(C) Posterior part of right maxillary with P_4^4 and M_1^{1-3} in occlusal stereophotographic view.

(D) Sketch of occlusal outlines of right P_4^4 and M_1^{1-3} .

Length of M_1^{1-3} series: 40 mm. Scale bar, 10 mm. Photographs by Philippe Loubry (CR2P, MNHN).

Tethytheria McKenna, 1975.

Embrithopoda Andrews, 1906.

Family indet.

***Styolophus minor* n. g., n. sp. Gheerbrant**

LSID urn:lsid:zoobank.org:act:9B31342F-7FBA-44E7-8B46-4C5D5341FBA5.

LSID urn:lsid:zoobank.org:act:B4367769-7BE7-4EBF-A9EA-2E18E409D80E.

Figures 1 and 2.

Holotype

OCP DEK/GE 668, right dentary bearing roots of I_{1-2} , alveolae of I_3 , C_1 , and P_2 , and crown of P_1 , P_{3-4} , and M_{1-3} .

Hypodigm (Figures 1 and 2)

Three specimens documenting upper and lower dentition: holotype; OCP DEK/GE 667, a damaged skull rostrum (maxillary and premaxillary fragments, with cheek teeth); and MNHN.F PM30, fragment of left dentary with broken dP_4 and M_1 and tooth germs of M_2 and P_4 .

Etymology

Generic name from stylos (Greek “pillar”), styles, and lophos (Greek “crest”), lophs, in reference to the upper molar lophs corresponding to the transverse development of the labial crests linking the enlarged parastyle and mesostyle; species name refers to the small size.

Localities and Horizon

Morocco, northeast Ouled Abdoun basin (Grand Daoui and Sidi Chennane quarries), intercalary phosphate beds II/I and possibly phosphate bed I, early Ypresian.

Diagnosis

S. minor shares with the Embrithopoda the hyperdilambdodont morphotypic molar pattern. It differs from all known embrithopods, including *Palaeoamasia*, by its very small size and primitive state of hyperdilambdodonty, with less lingual paracone and metacone and correlatively shorter pseudolophs (preparacrista, premetacrista) and with retention of more developed postparacrista, postmetacrista, and pseudohypocone; cheek

teeth with brachyodont low crown; M_1^{1-2} with one lingual root and with separated paracone and protocone roots; P_2 single-rooted and simple; and P_2^{2-3} double-rooted and simple. Anterior incisors are enlarged (especially their root), and I_1 is partially hypsodont.

Description

See characters 0–208 in [Data S1](#) (detailed description in preparation; E.G., A.S., and L.K., unpublished data). The molar series of *S. minor* (Figures 1 and 2) is about 20% longer than that of *Phosphatherium escuilliei* [17]. We inferred from tooth size [18] a 20–31 kg body mass for *S. minor*.

cf. *Styolophus* sp. indet.

Referred Material (Figures 3 and S1)

MNHN.F PM53, several pieces of a broken skull of the same individual, including a fragment of the snout with anterior part of parietals, right frontal and nasal, left maxillary with cheek teeth, and broken petrosals.

Locality and Horizon

Morocco, northeast Ouled Abdoun Basin (unknown quarry), upper phosphate horizons, probably sillons A–B, middle Ypresian ([Data S1B](#)).

Description

See characters 0–208 in [Data S1](#) (detailed description in preparation; E.G., A.S., and L.K., unpublished data). This species is most closely related to the younger species *S. minor* in dental morphology. It differs most remarkably in its larger size (30%–40% larger in tooth size). It also differs by derived traits of the molars such as longer pseudolophs and smaller postparacrista, postmetacrista, and pseudohypocone. The body mass of *cf. Styolophus* sp. indet. is estimated from tooth size as 60–88 kg, i.e., about 3.6 times heavier than *S. minor*.

Comparisons

The Moroccan Ypresian species *S. minor* and *cf. Styolophus* sp. share several key morphotypic dental features of the order Embrithopoda, such as the hyperdilambdodont pattern

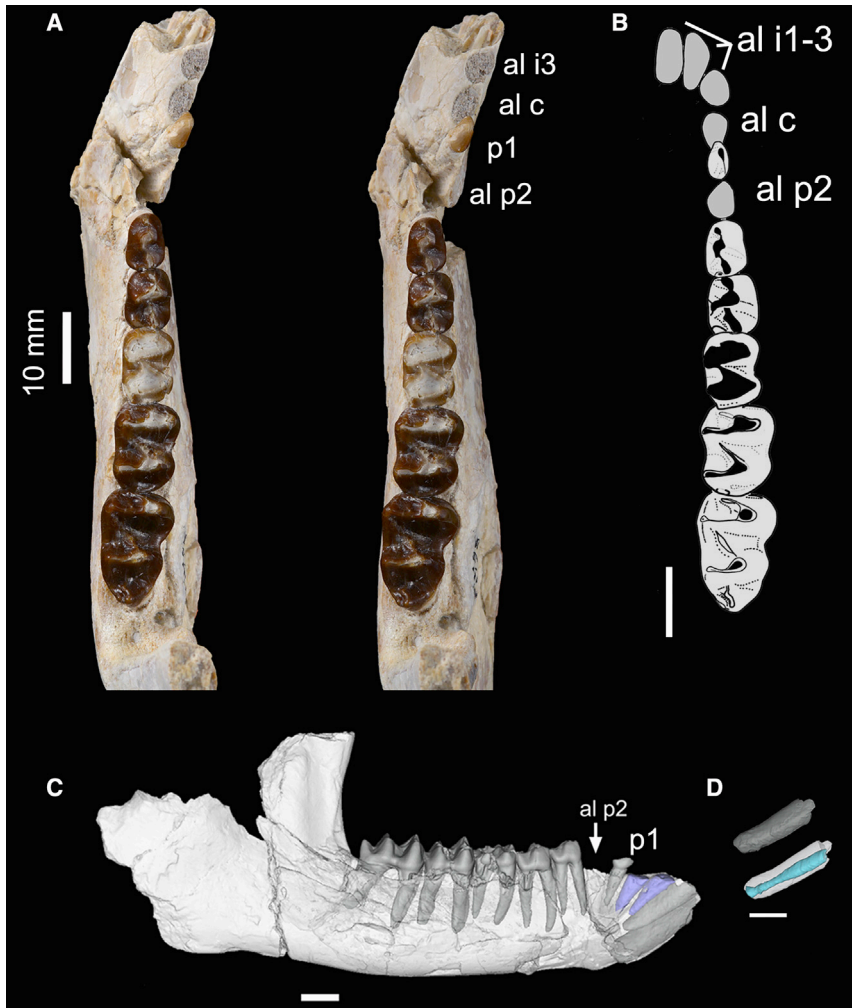


Figure 2. *Stylolophus minor* n. g., n. sp.

Holotype, specimen OCP DEK/GE 668.

(A) Right lower jaw in occlusal stereophotographic views.

(B) Reconstruction of lower tooth row: sketch of occlusal outlines of M_{1-3} , P_{3-4} , and P_1 and of alveoli of I_{1-3} , C_1 , and P_2 .

(C) 3D model reconstructed from computed tomography (CT) scans of the lower jaw OCP DEK/GE 668 (holotype) showing by transparency the large and procumbent roots of I_1 and I_2 in *S. minor*; the view shows the teeth roots of M_{1-3} , P_{3-4} , P_1 , and I_{2-1} and the teeth alveoli of P_2 , C_1 , and I_3 .

(D) Detail of I_1 root (3D model reconstructed from CT scans), showing the widely open pulp canal at the root apex, which indicates that the tooth was still growing in adult stage (partial hypsodonty).

Length of M_{1-3} series: 38.5 mm. Scale bar, 10 mm.

Photographs by Philippe Loubry (MNHN). Drawing by Charlene Letenneur (MNHN).

(enlarged W-shaped ectoloph linked to enlarged styles); presence of two sharp pseudolophs (elongated preparamacrista and premetacrista); hypoconulid cingulid-like and lingually located; M_3 hypoconulid lobe small, compressed laterally and lingually set; cristid obliqua lingual on the trigonid; and reduced entocristid (postfossid opened lingually). Comparisons emphasize the primitive morphology of the two Moroccan species within the Embrithopoda. They differ from all other embrithopods, including Palaeoamasiidae, by their small size and plesiomorphic traits, such as a primitive hyperdilambdodont state with less lingual paracone and metacone and correlatively shorter pseudolophs, and by retention of prominent postparamacrista, postmetacrista, and pseudohypocone (metaconule in Paenungulata [7]). Other primitive features of *Stylolophus* with respect to palaeoamasiids are the lower crown of cheek teeth, M^{1-2} with only one lingual root and with separated paracone and protocone roots, P_2 single rooted and simple, and P^2 double rooted and simple. In addition, the petrosal of *cf. Stylolophus* sp., although damaged, shows a likely separated foramen for the *aquaeductus cochleae*, in contrast to *Arsinoitherium*, in which this foramen and the fenestra cochleae remain undivided as a single perilymphatic foramen [19]. *S. minor* reveals a remarkable mor-

photypic condition of the Embrithopoda in the presence of enlarged anterior incisors with hypertrophied root (Figures 1A and 2C). I_{1-2} are large and procumbent (Figure 2C), and I_1 is partly hypsodont, as shown by its open root in the holotype (adult individual) (Figure 2D).

Enlarged and procumbent anterior lower incisors are most likely representative of the ancestral embrithopod morphotype. However, the anterior dentition remains poorly known in the order, even in *Arsinoitherium*, in which the first incisor is unknown. Andrews [9] reconstructed in *A. zitelli* a quite distinctive homodont

anterior tooth battery with all teeth, from P^1_1 to I^1_1 , of similar size, orientation, and morphology. It displays especially subvertical I_{1-2} , in contrast to *Stylolophus*. However, some specimens of *A. zitelli*, such as MNHN.F LBE 579, display large and procumbent alveoli of I_{1-2} , in a quite similar disposition to the holotype of *S. minor*. If Andrews's reconstruction [9] is correct, it suggests that the small and vertical I_{1-2} is secondary in the order, as are some other remarkable characters of *Arsinoitherium*, such as the orbit posterior and the narrow zygomatic arches.

The dental morphology of the new Moroccan species is clearly closer to that of the Palaeoamasiidae than to the more derived Arsinoitheriidae *Arsinoitherium* and *Namatherium*, which have more specialized hyperdilambdodonty. Arsinoitheriids differ indeed in the absence of a pseudohypocone (fully regressed), P^{3-4} with postcingulum extended posteriorly, and M^3 more offset lingually with respect to M^{1-2} . In addition, *Namatherium* has a lingual cingulum on the upper premolars and a more anterior zygomatic process, and *Arsinoitherium* has molarized premolars with a hypocone.

Our comparative anatomical study unambiguously confirms unique specialized embrithopod features in *Stylolophus*, but also its plesiomorphic morphology within the order.

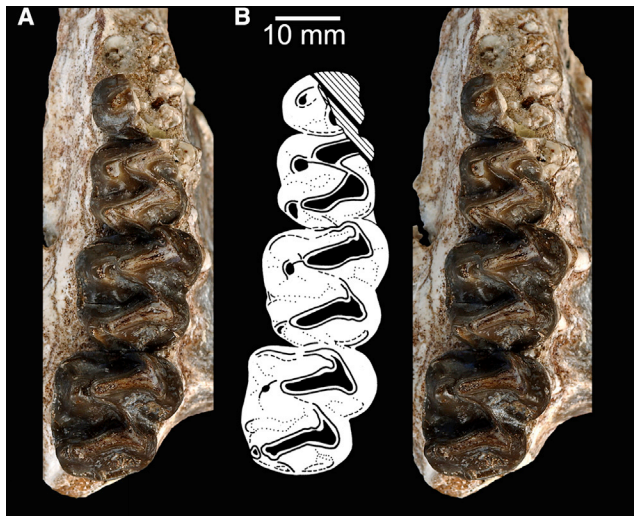


Figure 3. *cf. Stylophus* sp.

Specimen MNHN.F PM53, left maxillary with upper cheek teeth.

(A) P^4 (damaged), M^{1-3} in occlusal stereophotographic view.

(B) Sketch of the occlusal view of P^4 and M^{1-3} .

Length of M^{1-3} series: 55.3 mm. Scale bar, 10 mm. Photographs by Philippe Loubry (MNHN). See also [Figure S1](#).

Phylogenetic Relationships and Character Evolution in Embrithopoda, Tethytheria, and Paenungulata

We investigated the relationships of *S. minor* and *cf. Stylophus* sp. among various lophodont and stem ungulate-like placentals using parsimony analysis with TNT [20] of 209 dental and cranial characters, 68% of which are known in *S. minor* ([Data S1](#)). It unambiguously places *S. minor* and *cf. Stylophus* sp. as the basal-most embrithopods, arranged in sequence with *S. minor* being the first branch ([Figure 4A](#)). *S. minor* and *cf. Stylophus* sp. are therefore the most primitive known embrithopods. Although being very plesiomorphic within the order, their embrithopod relationship is indicated by noticeable specialized traits. The most remarkable is the hyperdilambdodont pattern ([Figures 1 and 3](#)). Other embrithopod molar synapomorphies of *Stylophus* are homoplastic, but they form altogether a suite of characters exclusive to the Embrithopoda: hypoconulid lingual, cristid obliqua very lingual on the trigonid, small and lingually located hypoconulid lobe in M_3 , and talonid widely open lingually. Some embrithopod skull synapomorphies are also identified in *S. minor*, such as the palate concave between the premolars. In addition, *cf. Stylophus* sp. shows a remarkable intranasal rostrum pattern through the development of large paranasal sinuses ([Figure S1](#)), which is reminiscent of the very large hollow air space developed in the nasal horn of *Arsinoitherium*. As a result, *S. minor* shows that the ancestral morphotype of the order Embrithopoda was well established by the earliest Eocene, even in early small plesiomorphic species.

Within the Embrithopoda, the cladistic analysis does not include the new Moroccan species *S. minor* and *cf. Stylophus* sp. in a single generic clade. *cf. Stylophus* sp. most remarkably differs by its larger size, consistently with its slightly higher stratigraphic provenance ([Data S1B](#)). Otherwise, their close morphological affinity argues against a distinct genus for the larger Ouled

Abdoun species that is provisionally referred to an unnamed new species of *Stylophus*. *S. minor* and *cf. Stylophus* sp. are regarded as successive chronospecies of a new Ypresian mammal lineage found in Ouled Abdoun series. The intraordinal relationships of other embrithopods remain poorly solved in our analysis, and especially for the poorly known palaeoamasiids *Hypsamasia* and *Crivadiatherium*, as previously found by Erdal et al. [21]. It should be particularly noted that the node grouping the palaeoamasiids *Hypsamasia* and *Crivadiatherium* with arsinotheriids, to the exclusion of *Palaeoamasia* ([Figures 4A and 4B](#)), relies mostly on character optimizations, and it is poorly supported with low Bremer support.

At higher, interordinal systematic rank, our cladistic analyses (analyses 1–10; [Table S1](#) and [Data S1](#)) recover two topologies within Tethytheria: (1) a clade (Embrithopoda (Proboscidea, Sirenia)) and (2) a clade (Embrithopoda, Proboscidea). The sister-group relationship of the Embrithopoda to both the Sirenia and Proboscidea, i.e., its stem tethytherian position, is found in nearly all our analyses ([Table S1](#) and [Data S1](#)). It is supported by analyses constraining the Afrotheria and Afroinsectiphilia (analyses 7–10), and it is also found in unconstrained analysis (analysis 1) and in analysis with TNT's "implied weighting" option (analysis 2; [Figure 4A](#)). Of note, it is most usually associated with the clade Paenungulatomorpha [7]. The alternative, previously consensual sister-group relationship of the Embrithopoda and the Proboscidea is found marginally in three analyses (analyses 1, 3, and 7), especially with unordered features (analysis 3).

The relationship of *Eritherium* within Tethytheria is noticeably unstable in our analyses, depending on relationships of the Proboscidea with respect to the Sirenia and the Embrithopoda. *Eritherium* is found as a stem proboscidean, as initially established [6], only in cladograms recovering the clade (Proboscidea, Embrithopoda). In other MPTs, it is sister group either to both the Proboscidea and Sirenia (most frequent topology) or to all tethytherians. Consequently, in this study, the *Eritherium* position is unexpectedly unresolved within Tethytheria (polytomy in consensus trees or low Bremer support).

The stem tethytherian position of the Embrithopoda is the best supported phylogenetic hypothesis found here, both in our parsimony analyses and in character transformation within paenungulates. It implies that the crown-group Tethytheria only includes extant orders. It is most consistent with an ancestral dilambdodont tooth morphotype of the paenungulates [7, 8] from which evolved the specialized hyperdilambdodont and pseudolophodont molar pattern of the embrithopods ([Figure 4C](#)). Such a paenungulate ancestral dilambdodont morphotype is supported by our MPTs ([Figure 4A](#)) recovering the clade Paenungulatomorpha, with a stem paenungulate relationship of early dilambdodont genera *Ocepeia* and *Abdounodus* [7], and also by the dilambdodont morphology of early crown paenungulates such as *Eritherium* and *Seggeurius*. Embrithopods' hyperdilambdodont and pseudolophodont molars evolved by enlargement of labial molar structures of the "primary trigon" such as the styles, styler shelf, and ectoloph, at the expense of the lingual structures [11]. The stem tethytherian position of the Embrithopoda found here allows to identify a remarkable opposite early trend of the crown Tethytheria (Sirenia, Proboscidea) to reduce labial molar structural elements (styler shelf and cusps, ectoloph), combined with development of the lingual lophs and true bilophodonty

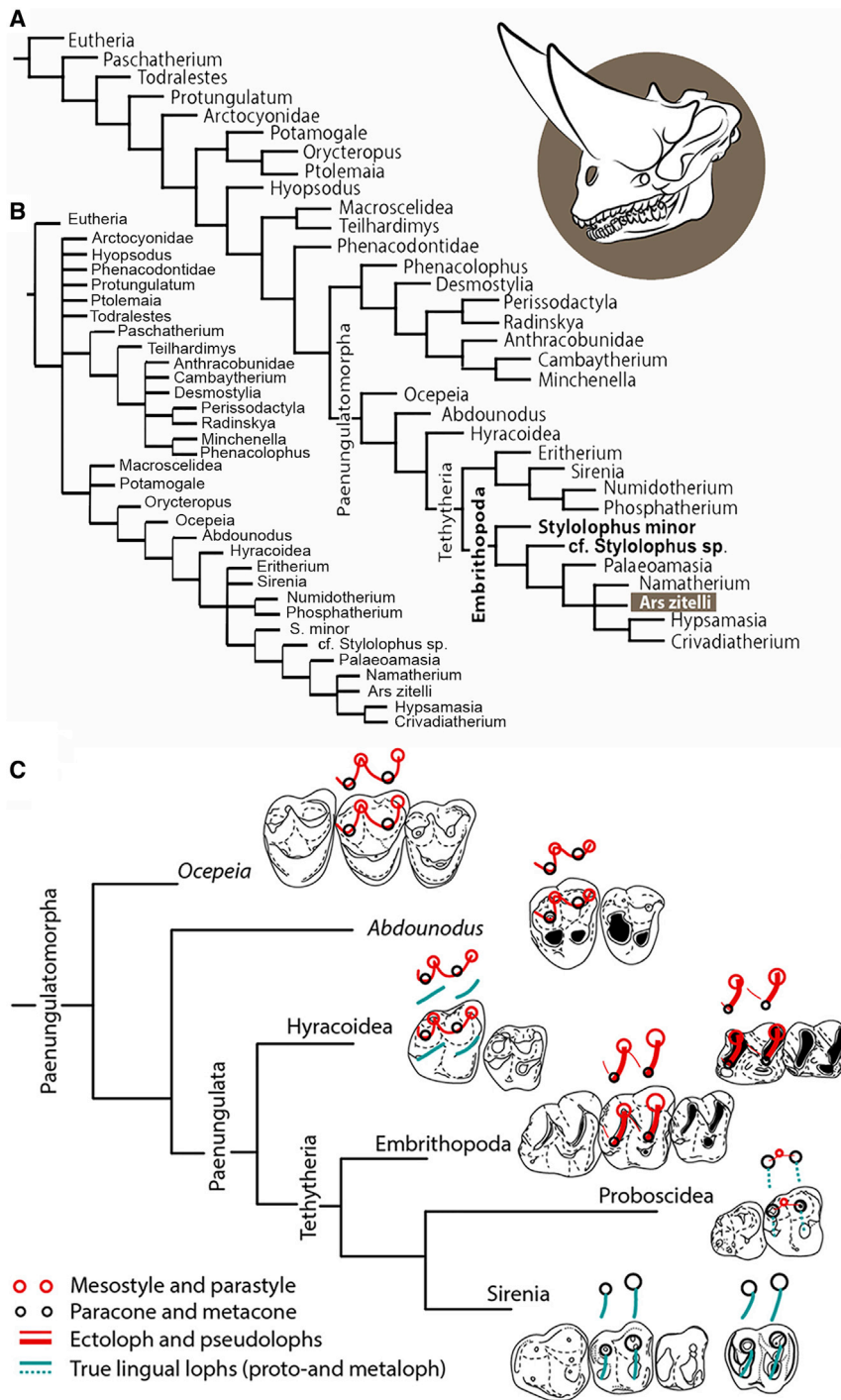


Figure 4. Relationships of *Stylophorus* and the Embrithopoda.

(A) Strict consensus of the two most parsimonious trees (MPTs) resulting from parsimony analysis of *Stylophorus* relationships using TNT with the "implied weighting" option. These trees most noticeably recover the embrithopod relationship of *S. minor* and *cf. Stylophorus* sp. and the stem tethytherian relationships of the Embrithopoda. Crown Tethytheria are indeed restricted in this topology to the extant orders Sirenia (sea cows) and Proboscidea (elephants). It should be noted that the relationship of *Erethium* is unstable in our analyses (Data S1). Its basal position to both the sirenians and proboscideans seen in this tree, instead only to proboscideans [6], is actually poorly supported (e.g., low bootstrap and Bremer indices; see Data S1). The relationship of *Erethium* within crown tethytherians is best considered unresolved in our analyses (see the main text). Besides the well-supported stem embrithopod position of *Stylophorus*, the intraordinal relationship of the embrithopods remains also poorly solved, mostly because of our still poor knowledge of the palaeoamasids. Retention index (RI): 57.9; consistency index (CI): 35.7; tree length (L): 883 steps. Matrix and details of the cladistic analysis, including Bremer index, are provided in Data S1. Drawing of the skull of *Arsinotherium zitelli* by Charlene Letenneur (MNHN).

(B) Strict consensus of 24 MPTs resulting from parsimony analysis of *Stylophorus* relationships using TNT with the clade Afrotheria (extant and fossil taxa) constrained. It should be noted that most of the resulting MPTs (19 trees) support the sister-group relationship of the Embrithopoda to the clade (Sirenia, Proboscidea), i.e., the stem tethytherian position of Embrithopoda. RI: 57.7; CI: 35.6; L: 885 steps. See comments in the main text.

(C) Hypothesis on the origin of the hyperdilambdodont and pseudolophodont molar pattern of the Embrithopoda within the Paenungulatomorpha, based on the interordinal relationships found in this study (Figure 4A). The recovered stem Tethytheria position of the Embrithopoda implies that their autapomorphic hyperdilambdodont pattern originated directly from the paenungulate ancestral dilambdodont morphotype. In this topology, two major and non-homologous lophodont structural trends of upper molars are recognized in the early tethytherian evolution: (1) in the Embrithopoda, there is enlargement of the labial cusps (styles) and crests (ectoloph) forming the hyperdilambdodont and pseudolophodont pattern and a reduction of the lingual structures (protocone and pseudohypocone); and (2) in the crown Tethytheria (Proboscidea and Sirenia), there is a reduction of the labial structures (styles and ectoloph) and a development

of the lingual crests and cusps forming the protoloph and metaloph and the true bilophodont pattern. These two structural trends are mutually exclusive within the Tethytheria. The hyperdilambdodont-pseudolophodont pattern of the Embrithopoda results from the transverse extension of the dilambdodont ectoloph (mostly preparacrista and premetacrista) inherited from the ancestral morphotype of the paenungulatomorphans and paenungulates, which is elucidated especially by *Ocepeia* and *Abdounodus* [7, 8]. Drawings by Charlene Letenneur (MNHN). Occlusal sketches of upper molars (not to scale): *Ocepeia daouiensis* (M¹⁻³), *Abdounodus hamdii* (M¹⁻²), Hyracoidea: *Seggeurius amourensis* (M¹ and M³), Embrithopoda: *Stylophorus minor* (M¹⁻³), *Palaeoamasias kansui* (M²⁻³), Proboscidea: *Erethium azzouzorom* (M²⁻³), Sirenia: *Eotherioides sandersi* (M¹⁻³), and *Protosiren* sp. (M²⁷). Black circles, paracone and metacone; red circles, mesostyle and parastyle; red lines, ectoloph; green line, protoloph and metaloph linking paracone to protocone and metacone to pseudohypocone.

See also Figure S2, Table S1, and Data S1.

(Figure 4C). As a result, *S. minor* helps to elucidate two divergent and non-homologous lophodont specializations at the tethytherian root (Figure 4C), with morphological and functional emphasis of either (1) labial molar crests and cusps in the hyperdilambodont and pseudolophodont pattern of embrithopods or (2) lingual molar crests and cusps in the true lophodont pattern of crown tethytherians (extant elephant and sea cow orders). These two structural trends are mutually exclusive in the Tethytheria; by contrast, the hyraxes order retained both structural trends with the evolution of more or less specialized and combined dilambdodonty (selenodonty) and true bilophodonty in several lineages [22].

Significance of *Stylolophus*

The discovery of the earliest and basal-most embrithopods in the early Eocene of Morocco sheds new light on the basal diversification of the Tethytheria and the early evolution of African ungulate-like mammals. The phylogenetic trees including *Stylolophus* exclude any relationships of the Asian phenacoloiphids to the Embrithopoda, in agreement with enamel microstructure [23]. More generally, they support a strictly African endemic early radiation of the paenungulates and tethytherians, independently from early non-African bilophodont ungulates such as phenacoloiphids, anthracobunids, and desmostylians that are instead related to Laurasian Euungulata and Perissodactyla (Figure 4A), as found in recent studies [24]. They also show that the order Embrithopoda is an extinct stem tethytherian branch that evolved before the divergence of the extant orders Proboscidea and Sirenia (Figure 4A). It supports at least an early Paleocene origin and early evolution of the Embrithopoda, taking into account the age of earliest crown tethytherians [25, 26]. Phylogenetic analysis of *Stylolophus* also elucidates the evolution of major dental specializations in Paenungulata and Tethytheria, including the most specialized one of the Embrithopoda (hyperdilambodonty) that is homologized here with the dilambdodont ancestral morphotype of the paenungulates (Figure 4C) and is shown to correspond to an early lophodont functional convergence with the crown Tethytheria. The repeated lophodont specializations for the folivorous diet within tethytherians and paenungulates was driven by remarkable favorable herbivorous niches of the Island Africa during the Paleogene.

By the onset of the Eocene, embrithopods already had the morphotypic hyperdilambodont dental pattern and specialized skull characters such as a developed nasal sinus system. They display distinctive specializations and are larger with respect to coeval (and sympatric) crown tethytherians from the early Ypresian of Ouled Abdoun basin such as *Phosphatherium*.

Our cladistic analysis supports the Embrithopoda monophyly [21]. The embrithopods distribution in both Arabo-Africa (*Stylolophus*, Arsinoitheriidae) and Eurasia (Palaeoamasiidae) [21, 27] is the most demonstrative mammalian evidence of trans-Tethyan dispersals involving Africa (Figure S2). The basal embrithopod position and early age of *Stylolophus*, as well as the supraordinal relationships to the Afrotheria/Paenungulata, all indicate at least an earliest Paleogene African center of origin for the Embrithopoda. This supports the embrithopod colonization of Eurasia from Africa, most consistently following a—remarkable—early or middle Eocene trans-Tethyan dispersal event.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
 - Institutional abbreviations
 - Phylogenetic analysis
 - Geochemical study
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures, one table, and one data file and can be found with this article online at <https://doi.org/10.1016/j.cub.2018.05.032>.

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AUTHOR CONTRIBUTIONS

E.G. designed and performed research, analyzed data, and wrote the paper. A.S. and L.K. performed research, analyzed data, and wrote the paper. L.K. made the geochemical analysis.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Murphy, W.J., Eizirik, E., O’Brien, S.J., Madsen, O., Scally, M., Douady, C.J., Teeling, E., Ryder, O.A., Stanhope, M.J., de Jong, W.W., and Springer, M.S. (2001). Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294, 2348–2351.
2. Springer, M.S., Murphy, W.J., Eizirik, E., and O’Brien, S.J. (2003). Placental mammal diversification and the Cretaceous-Tertiary boundary. *Proc. Natl. Acad. Sci. USA* 100, 1056–1061.

3. Gheerbrant, E., Sudre, J., and Cappetta, H. (1996). A Palaeocene proboscidean from Morocco. *Nature* 383, 68–71.
4. Gheerbrant, E., Sudre, J., Iarochene, M., and Mourni, A. (2001). First ascertained African “condylarth” mammals (primitive ungulates: cf. *Bulbulodentata* & cf. *Phenacodonta*) from the Earliest Ypresian of the Ouled Abdoun Basin, Morocco. *J. Vertebr. Paleontol.* 21, 107–118.
5. Gheerbrant, E., Sudre, J., Cappetta, H., Iarochene, M., Amaghaz, M., and Bouya, B. (2002). A new large mammal from the Ypresian of Morocco: evidence of a surprising diversity of early proboscideans. *Act. Pal. Pol.* 47, 493–506.
6. Gheerbrant, E. (2009). Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. *Proc. Natl. Acad. Sci. USA* 106, 10717–10721.
7. Gheerbrant, E., Filippo, A., and Schmitt, A. (2016). Convergence of Afrotherian and Laurasiatherian Ungulate-Like Mammals: First Morphological Evidence from the Paleocene of Morocco. *PLoS ONE* 11, e0157556.
8. Gheerbrant, E., Amaghaz, M., Bouya, B., Goussard, F., and Letenneur, C. (2014). *Ocepeia* (Middle Paleocene of Morocco): the oldest skull of an afrotherian mammal. *PLoS ONE* 9, e89739.
9. Andrews, C.W. (1906). A Descriptive Catalogue of the Tertiary Vertebrata of the Fayum, Egypt. British Museum (British Museum (Natural History)), p. 324.
10. Sanders, W.J., Rasmussen, D.T., and Kappelman, J. (2010). Embrithopoda. In *Cenozoic Mammals of Africa*, L. Werdelin, and W.J. Sanders, eds. (University of California Press), pp. 115–122.
11. Court, N. (1992). A unique form of dental bilophodonty and a functional interpretation of peculiarities in the masticatory system of *Arsinoitherium* (Mammalia, Embrithopoda). *Hist. Biol.* 6, 91–111.
12. Simpson, G.G. (1945). The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85, 1–350.
13. Court, N. (1992). The skull of *Arsinoitherium* (Mammalia, Embrithopoda) and the higher order interrelationships of ungulates. *Palaeovertebrata* 22, 1–43.
14. Tassy, P., and Shoshani, J. (1988). The Tethytheria: elephants and their relatives. In *The Phylogeny and Classification of the Tetrapods, Volume 2, Mammals*, and M.J. Benton, eds. (Clarendon Press), pp. 283–315.
15. Fischer, M., and Tassy, P. (1993). The interrelation between Proboscidea - Sirenia - Hyracoidea - Mesaxonia: the morphological evidence. In *Mammal Phylogeny*, F.S. Szalay, M. Novacek, and M. McKenna, eds. (Springer-Verlag), pp. 217–234.
16. Seiffert, E.R. (2007). A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. *BMC Evol. Biol.* 7, 224.
17. Gheerbrant, E., Sudre, J., Tassy, P., Amaghaz, M., Bouya, B., and Iarochene, M. (2005). Nouvelles données sur *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Eocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes. *Geodiversitas* 27, 239–333.
18. Damuth, J.D. (1990). Body Size in Mammalian Paleobiology, J. Damuth and B.J. MacFadden, eds. (Cambridge University Press), pp. 29–253.
19. Court, N. (1990). Periotic anatomy of *Arsinoitherium* (Mammalia, Embrithopoda) and its phylogenetic implications. *J. Vert. Pal.* 10, 170–182.
20. Goloboff, P.A., Farris, J.S., and Nixon, K.C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
21. Erdal, O., Antoine, P.O., and Sen, S. (2016). New material of *Palaeoamasia kansui* (Embrithopoda, Mammalia) from the Eocene of Turkey and a phylogenetic analysis of Embrithopoda at the species level. *Palaeontology* 59, 631–655.
22. Rasmussen, D.T., and Simons, E.L. (1991). The oldest hyracoids (Mammalia: Pliohyracidae): new species of *Sagatherium* and *Thyrohyrax* from the Fayum. *N. Jahrb. Geo. Pal. Abh.* 182, 187–209.
23. von Koenigswald, W. (2012). Unique differentiation of radial enamel in *Arsinoitherium* (Embrithopoda, Tethytheria). *Hist. Biol.* 25, 183–192.
24. Cooper, L.N., Seiffert, E.R., Clementz, M., Madar, S.I., Bajpai, S., Hussain, S.T., and Thewissen, J.G.M. (2014). Anthracobunids from the middle eocene of India and Pakistan are stem perissodactyls. *PLoS ONE* 9, e109232.
25. Yans, J., Amaghaz, M., Bouya, B., Cappetta, H., Iacumin, P., Kocsis, L., Mouflih, M., Selloum, O., Sen, S., Storme, J.-Y., and Gheerbrant, E. (2014). First carbon isotope chemostratigraphy of the Ouled Abdoun phosphate Basin, Morocco; implications for dating and evolution of earliest African placental mammals. *Gondwana Res.* 25, 257–269.
26. Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Yans, J., and Amaghaz, M. (2014). Comprehensive stable isotope investigation of marine biogenic apatite from the late Cretaceous-early Eocene phosphate series of Morocco. *Palaeogeog. Palaeoclimatol. Palaeoecol.* 394, 74–88.
27. Sen, S. (2013). Dispersal of African mammals in Eurasia during the Cenozoic: ways and whys. *Geobios* 46, 159–172.
28. Nixon, K.C. (1999). Winclada (BETA) Version 0.9.9.
29. Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Ulianov, A., Chiaradia, M., and Bardet, N. (2016). Gradual changes in upwelled seawater conditions (redox, pH) from the late Cretaceous through early Paleogene at the northwest coast of Africa: negative Ce anomaly trend recorded in fossil bio-apatite. *Chem. Geol.* 421, 44–54.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
TNT 1.5	Goloboff et al. (2008) [20]	http://www.lillo.org.ar/phylogeny/tnt/
Winclada and NONA	Nixon (1999) [28]	http://www.diversityoflife.org/winclada/

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources, reagents and scripts should be directed to and will be fulfilled by the Lead Contact, Dr. Emmanuel Gheerbrant (emmanuel.gheerbrant@mnhn.fr).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The fossil specimens here identified as *S. minor* and *cf. Stylolophus* sp. come from the phosphate series of the Ouled Abdoun Basin (Morocco), and in particular from the North-Eastern quarries (Grand Daoui and Sidi Chennane quarries). Most of this material was found by local people living close to the phosphate quarries. Specimen OCP DEK/GE 667 of the species *S. minor* was donated to Office Cheriffien des Phosphates (OCP) collections by F. Escuillié; specimen OCP DEK/GE 668, holotype of *S. minor*, was donated to OCP collections by S. Xerri. These specimens are in provisional deposit for study in the MNHN (CR2P laboratory), prior to their final deposit in the Office Cheriffien des Phosphates (specimens registered with OCP acronym). Casts are deposited in MNHN paleontological collections.

The age of *S. minor* and *cf. Stylolophus* sp. material was determined based on the associated selachian fauna and on a geochemical analysis that is detailed in [Data S1B](#) (see also [Method Details](#) below). *S. minor* comes from the Intercalary phosphate Beds II/I [25, 26], and possibly from the phosphate Bed I, and it is dated as early Ypresian, ca. 56 to 54 ma (see [Data S1](#)). Specimen MNHN.F PM53 of *cf. Stylolophus* sp. comes from upper levels of the local phosphate series of middle Ypresian age, probably from the so called “sillons” phosphate levels [25, 26]. The selachians found in the matrix of MNHN.F PM53 and the geochemical analysis support a middle Ypresian age and a stratigraphical correlation with the beginning of the EECO climatic event [25, 26], corresponding to an age of ca. 53–51 ma (see [Data S1](#)).

Study, preparation and casts of the material of *S. minor* and *cf. Stylolophus* sp were all made at the CR2P (MNHN) laboratory.

The new taxonomic actions established herein are registered in ZooBank LSID urn:lsid:zoobank.org:pub:8F4A215C-4A62-4B27-B42E-E17965590A38 .

METHOD DETAILS

Institutional abbreviations

OCP DEK/GE: collections of the Office Cheriffien des Phosphates, Direction des Exploitations, Service Géologique, Khouribga, Morocco; MNHN.F: paleontological collections of the Museum national d’Histoire Naturelle, Paris, France.

Phylogenetic analysis

Comparative character analysis and phylogenetic relationships of *Stylolophus minor* and *cf. Stylolophus* sp. among various lophodont and non lophodont ungulate-like mammals were studied using maximum parsimony analyses with the programs TNT1.5, Winclada, and Nona [20, 28].

Details of the 209 studied dental and cranial characters and of the phylogenetic analysis are provided in [Data S1](#). Our cladistic reference analysis and resulting MPTs, which recover the clade Paenungulatomorpha (stem and crown paenungulates), are based on the implied weighting analysis (Analysis 2, [Data S1](#)). The unweighed analysis (Analysis 1, [Data S1](#)) recovers the Altungulata group clustering the Perissodactyla and Paenungulata, instead the Paenungulatomorpha found in the implied weighting analysis. It is not retained here because it conflicts with molecular phylogenies showing that the lophodont “ungulates” Perissodactyla and Paenungulata are convergent clades that belong respectively to the distinct major supraordinal placental clades Laurasiatheria (Euungulata) and Afrotheria. [Table S1](#) summarizes all our cladistic analyses (see also [Data S1](#)).

Geochemical study

Trace element analyses of the matrix and in some case of the material of *Stylolophus minor* and *cf. Stylolophus* sp. provide valuable data on their stratigraphic provenance in the Ouled Abdoun Basin [29]. The analyses were performed on polished surface of the fossils with Laser Ablation ICP-MS at the Institute of Earth Sciences of University of Lausanne in Switzerland (for details see [29]). To support the stratigraphic origin of the here described fossils, Ce-anomaly was calculated from the obtained rare earth element concentrations: $Ce/Ce^* = 2Ce_N / (La_N + Pr_N)$, where N refers to Post Achaeon Australian Shale normalized values. Then the data were compared with existing database [29]. Further details are provided in [Data S1](#).

DATA AND SOFTWARE AVAILABILITY

All data are provided in the [Supplemental Information](#): [Figures S1](#) and [S2](#) and [Table S1](#) include data related to [Figures 3](#) and [4](#) and [STAR Methods](#). Phylogenetic data and analyses related to [Figure 4](#) and [STAR Methods](#) are available in [Data S1](#). Geochemical and stratigraphical data for the dating of the fossils related to [STAR Methods](#) are available in [Data S1](#).

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Supplemental Information

**Early African Fossils Elucidate
the Origin of Embrithopod Mammals**

Emmanuel Gheerbrant, Arnaud Schmitt, and László Kocsis

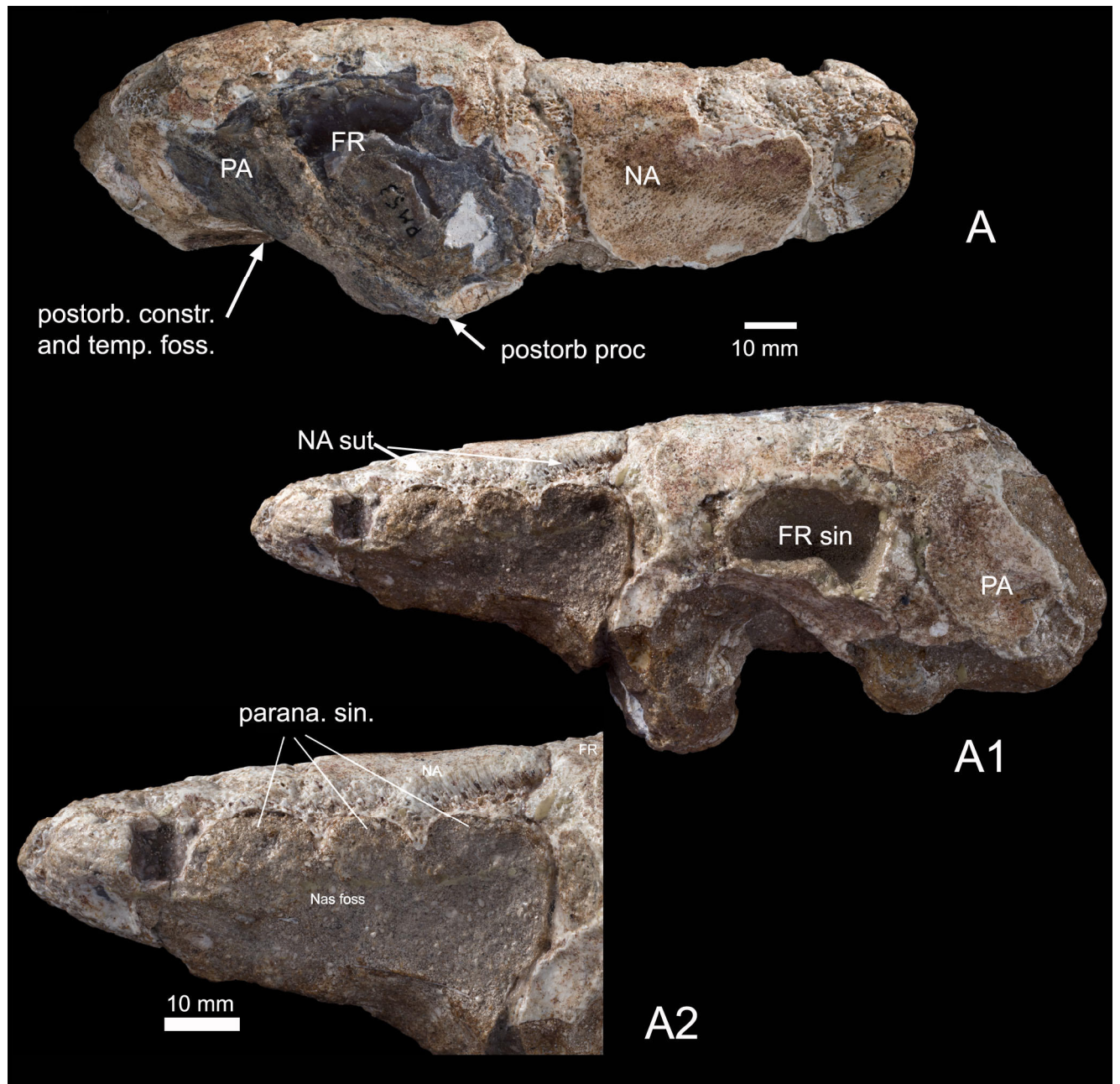


Figure S1: cf. *Styolophus* sp. Specimen MNHN.F PM53, fragment of the rostrum, with the right nasal, the right frontal, the anterior part of the right parietal, and part of the right orbito-temporal fossa. Related to Figure 3.

A. Dorsalview; **B1-2.** Medial view. NA: nasal; FR: frontal; PA: Parietal; OS: orbitosphenoid; cr. orbito.: crista orbitotemporalis; Parana. sin.: paranasal sinuses; FR sin.: frontal sinus; postorb. proc.: postorbital process; postorb. constr.: postorbital constriction; Nas. sut.: nasal suture. Scale-bar = 10 mm. Photographs by Lilian Cazes (CR2P, CNRS/MNHN).

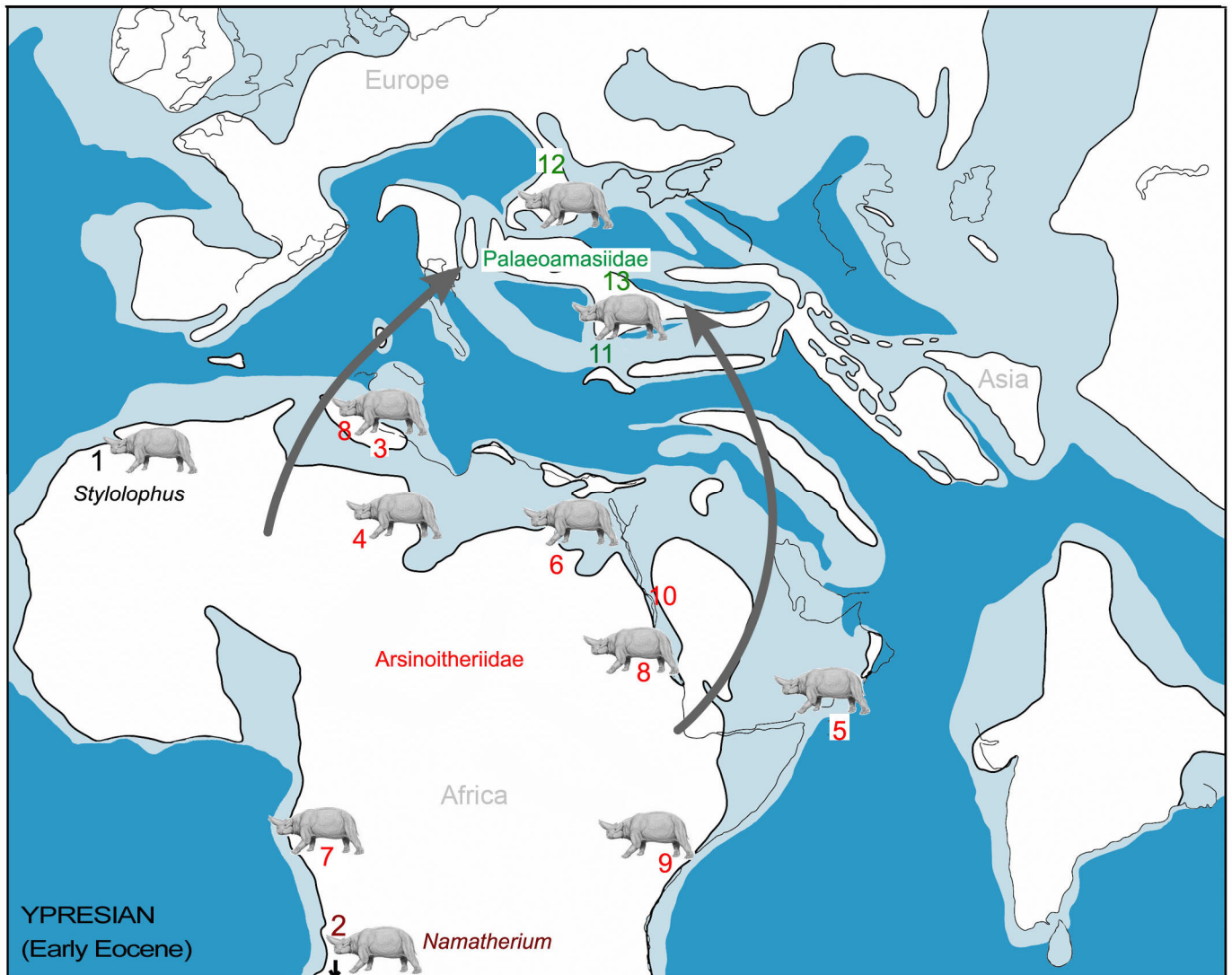


Figure S2: Paleogeographic distribution of the Embrithopoda, and hypothesis of the African origin of the Embrithopoda and Palaeoamasiidae supported by discovery of *Stylolophus*. Related to Figure 4.

1. *Stylolophus minor* n. g., n. sp. and cf. *Stylolophus* sp., Ypresian of the Ouled basin, Morocco; 2. *Namatherium*, Lutetian of Black Crow, Namibia; 3. *Arsinoitherium*, late Eocene of Bir Om Ali, Tunisia; 4. *Arsinoitherium*, late Eocene and early Oligocene of Dur At-Talah, Lybia; 5. *Arsinoitherium*, early Oligocene of Thaytiniti and Taqah, Oman; 6. *Arsinoitherium*, early Oligocene of the Fayum, Egypt; 7. *Arsinoitherium*, early Oligocene of Malembe, Angola; 8. early or late Oligocene of Oued El Grigema, Tunisia; 9. *Arsinoitherium*, late Oligocene of Chilga, Ethiopia; 10. late Oligocene of Harrat Al Ujayfa, Saudi Arabia; 11. *Arsinoitherium*, late Oligocene of Losidok, Kenya; 12. *Palaeoamasias* and *Hypsamasias*, Ypresian?-Lutetian of Anatolia, Turkey; 13. Eocene/Oligocene transition of Boyabat Basin, Turkey (modified from [S1]).

Ana- lysis	Type of analysis and constraint	Trees number	Trees Length	RI; CI	Comments
1.	“Traditional search”, 51 characters ordered	12	876	58.4; 36	Clades: “Altungulata”; Desmostylia sister-group (Perissodactyla, Anthracobunia); Embrithopoda: 1) sister-group to Proboscidea (6 MPTs); 2) sister-group to (Proboscidea + Sirenia) (6 MPTs).
2.	Idem 1 with “Implied Weighting”	2	883	57.8; 35.7	Clades: Paenungulatomorpha; Desmostylia sister- group (Perissodactyla, Anthracobunia); Embrithopoda sister-group to (Proboscidea, Sirenia)
3.	“Traditional search”, <i>no character ordered</i>	4	816	56.6 38.4	Clades: “Altungulata”; Desmostylia sister-group of Perissodactyla + Anthracobunia; Embrithopoda sister-group to Proboscidea
4.	Idem 3 with “Implied Weighting”	1	825	55.9; 37.9	Clade Paenungulatomorpha ; Desmostylia sister- group of Perissodactyla and <i>Radinskya</i> ; Embrithopoda sister-group to (Sirenia, Proboscidea)
5.	Analysis without Desmostylia, “Traditional search”, 51 characters ordered	16	836	61.3; 37.7	Clades: Paenungulatomorpha; Embrithopoda sister-group to (Sirenia, Proboscidea) , with unresolved position of <i>Eritherium</i>
6.	Idem 5 with “Implied Weighting”	2	845	59; 37	Clades: Paenungulatomorpha; Embrithopoda sister-group to (Sirenia, Proboscidea)
7.	Clade Afrotheria constrained (extant and fossil taxa) ; “Traditional search”, 51 characters ordered	24	885	57.7 35.6	Clades: Paenungulatomorpha; polytomy of Tethytheria: 5 MPTs with Embrithopoda and Proboscidea sister-group ; 19 MPTs with Embrithopoda sister-group to (Sirenia, Proboscidea) ; <i>Eritherium</i> stem Tethytheria or sister-group to (Proboscidea, Sirenia)
8.	Clade Afrotheria constrained (extant and fossil taxa); idem 7 with “Implied Weighting”	1	893	57.1; 35.3	Clades: Paenungulatomorpha; Embrithopoda sister-group to (Eritherium (Sirenia, Proboscidea))
9.	Clade Afroinsectiphilia constrained; “Traditional search”, 51 characters ordered	40	888	57.5; 35.5	Clades: Paenungulatomorpha; Embrithopoda sister-group to (Sirenia, Proboscidea) ; <i>Eritherium</i> with unsolved position to (Proboscidea, Sirenia) and Embrithopoda; 19 MPTs recovering Afrotheria (Afroinsectiphilia + Paenungulata)
10.	Clade Afroinsectiphilia constrained; idem 9 with “Implied Weighting”	1	899	56.6;3 5.0	Clades: Paenungulatomorpha; Embrithopoda sister-group to (Eritherium (Sirenia, Proboscidea))

Table S1 – Cladistic analyses performed in this work of the relationships of *Stylolophus*.
Related to Figure 4, STAR Methods and Data S1.

All parsimony analyses were made with the “traditional search” command of TNT. Matrix with 33 taxa, 209 characters, 17 uninformative characters (inactivated for calculation of the indices), 51 additive (ordered) characters.

Supplemental References

- S1. Sen, S. (2013). Dispersal of African mammals in Eurasia during the Cenozoic: Ways and whys. *Geobios* 46, 159-172.
- S2. Gheerbrant, E., Filippo A., and Schmitt, A. (2016). Convergence of Afrotherian and Laurasiatherian Ungulate-Like Mammals: First Morphological Evidence from the Paleocene of Morocco. *PLoS ONE* 11, 1-35. Doi:10.1371/journal.pone.0157556.
- S3. Koenigswald, W.v. (2012). Unique differentiation of radial enamel in *Arsinoitherium* (Embrithopoda, Tethytheria). *Hist. Biol.* 25, 183–192.
<http://dx.doi.org/10.1080/08912963.2012.714658>
- S4. Koenigswald, Wv, Holbrook, L.T., Rose, K.D. (2011) Diversity and evolution of Hunter–Schreger Band configuration in tooth enamel of perissodactyl mammals. *Act. Pal. Pol.* 56,11–32.
- S5. Mao, F.Y., Wang Y.Q., Jin, X. (2016). New records of archaic ungulates from the Lower Eocene of Sanshui Basin, Guangdong, China. *Hist. Biol.* 2016, 28 (6), 787–802. DOI: 10.1080/08912963.2015.1034120
- S6. Rose, D., Holbrook, L. T., Rana, R. S., Kumar, K., Jones, K. E., Ahrens, H.E., Missiaen, P., Sahni, A., and Smith, T. (2014). Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. *Nature Comm.* 5570. doi:10.1038/ncomms6570.
- S7. Tabuce, R., Delmer, C., and Gheerbrant, E. (2007). Evolution of the tooth enamel microstructure in the earliest proboscideans (Mammalia). *Zool. J. Lin. Soc.* 149, 611–628.
- S8. Tabuce, R., Seiffert, E., Gheerbrant, E., Alloing-Séguier, L., and Koenigswald von, W. (2016). Tooth enamel microstructure in Hyracoidea reveals unique enamel types among mammals. *J. Mamm. Evol.* 24, 91–110 (2017). DOI 10.1007/s10914-015-9317-6.
- S9. Pickford, M., Senut, B., Morales, J., Mein, P., and Sanchez, I.M. (2008). Mammalia from the Lutetian of Namibia. *Mem. Geol. Surv. Namibia* 20, 465–514.
- S10. Erdal, O., Antoine, P. O ., and Sen, S. (2016). New material of *Palaeoamasia kansui* (Embrithopoda, Mammalia) from the Eocene of Turkey and a phylogenetic analysis of Embrithopoda at the species level. *Palaeontology* 59, 631–655.
- S11. Court, N. (1992). The skull of *Arsinoitherium* (Mammalia, Embrithopoda) and the higher order interrelationships of ungulates. *Palaeovertebrata* 22, 1-43.
- S12. Cooper, L.N., Seiffert, E.R., Clementz, M., Madar, S.I., Bajpai, S., Hussain, S.T., and Thewissen, J.G.M. (2014). Anthracobunids from the middle Eocene of India and Pakistan are stem perissodactyls. *PLoS ONE* 9:e109232
- S13. Wible, J.R., Rougier, G.W., and Asher, R.J. (2007). Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature* 447, 1003–1006.
- S14. Asher, R.J., Maree, S., Bronner, G., Bennet, N.C., Bloomer, P., Czechowski, P., Meyer, M., and Hofreiter, M. (2010). A phylogenetic estimate for golden moles (Mammalia, Afrotheria, Chrysochloridae). *BMC Evol. Biol.* 10 (69), 1-13. doi:10.1186/1471-2148-10-69.
- S15. Benoit, J., Lehmann, L., Vatter, M., Lebrun, R., Merigeaud, S., Costeur, L., and Tabuce, R. (2015). Comparative Anatomy and Three-Dimensional Geometric-Morphometric Study of the Bony Labyrinth of Bibymalagasia (Mammalia, Afrotheria). *J. Vert. Pal.*, 35(3) DOI: 10.1080/02724634.2014.930043.

- S16. Ravel, A., and Orliac, M. (2015). The inner ear morphology of the 'condylarthran' *Hyopsodus lepidus*. *Hist. Biol.* 27 (8), 957–969. <http://dx.doi.org/10.1080/08912963.2014.9158>
- S17. Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Ulianov, A., Chiaradia, M. and Bardet (2016). Gradual changes in upwelled seawater conditions (redox, pH) from the late Cretaceous through early Paleogene at the northwest coast of Africa: Negative Ce anomaly trend recorded in fossil bio-apatite. *Chemical Geol.* 421, 44-54.