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Emmanuel Gheerbrant. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. Proceedings of the National Academy of Sciences of the United States of America, 2009, 106 (26), pp.10717-10721. 10.1073/pnas.0900251106 . mnhn-02264831

HAL Id: mnhn-02264831

<https://mnhn.hal.science/mnhn-02264831>

Submitted on 7 Aug 2019

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Paleocene emergence of elephant relatives and the rapid radiation of African ungulates

Emmanuel Gheerbrant¹

Unité Mixte de Recherche 7207, Centre National de la Recherche Scientifique, Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements, Case 38, Département Histoire de la Terre, Muséum National d'Histoire Naturelle, 8, Rue Buffon, 75005 Paris, France

Edited by Elwyn L. Simons, Duke University Lemur Center, Durham, NC, and approved May 11, 2009 (received for review January 14, 2009)

Elephants are the only living representatives of the Proboscidea, a formerly diverse mammalian order whose history began with the 55-million years (mys) old *Phosphatherium*. Reported here is the discovery from the early late Paleocene of Morocco, ca. 60 mys, of the oldest and most primitive elephant relative, *Eritherium azzouzororum* n.g., n.sp., which is one of the earliest known representatives of modern placental orders. This well supported stem proboscidean is extraordinarily primitive and condylarth-like. It provides the first dental evidence of a resemblance between the proboscideans and African ungulates (paenungulates) on the one hand and the lousinines and early macroscelideans on the other. *Eritherium* illustrates the origin of the elephant order at a previously unknown primitive stage among paenungulates and "ungulates." The primitive morphology of *Eritherium* suggests a recent and rapid paenungulate radiation after the Cretaceous-Tertiary boundary, probably favoured by early endemic African paleoecosystems. At a broader scale, *Eritherium* provides a new old calibration point of the placental tree and supports an explosive placental radiation. The Ouled Abdoun basin, which yields the oldest known African placentals, is a key locality for elucidating phylogeny and early evolution of paenungulates and other related endemic African lineages.

Africa-Morocco | Afrotheria | Paenungulata | Placentalia | Proboscidea

The elephant order (Proboscidea) includes some of the most derived and spectacular extant placental mammals. Today, it is represented by only 3 species. However, the fossil record shows that this diversity is relictual, and that the order has a remarkably rich and long history (1). The early history of the proboscideans is endemic to Africa, where they have their oldest record 55 million years ago (mys) at the beginning of the Eocene, with primitive representatives such as *Phosphatherium* (2). Reported here is the discovery in Morocco of a new, earliest known proboscidean predating *Phosphatherium* by 5 mys. It demonstrates an early history of elephant relatives into the Paleocene and close to the beginning of the placental radiation (3, 4). It provides the first evidence of a transitional stage between modern ungulates, especially African ungulates, and primitive condylarth-like mammals (Louisininae here) from the beginning of the Tertiary.

The proboscidean reported here was discovered in Sidi Chennane quarries of the Ouled Abdoun phosphate basin, Morocco, 10–20 km south of Grand Daoui quarries where *Phosphatherium* occurs, in an overlying Ypresian level (1, 5–7). It comes from the "lower bone bed" horizon of local phosphate "bed IIa" that yielded other mammals, including the earliest hyaenodontids (8) and which lies close to the local Thanetian base above the Danian "bed IIb." Its Thanetian age is indicated by its stratigraphic position and by the associated elasmobranch fauna (SI Appendix, Table S1). The low position of the lower bone bed in Thanetian beds IIa involves the locally undistinguished Selandian age, i.e., an early Late Paleocene age as old as ca. 60 mys. The early Late Paleocene age of the mammal level of Sidi Chennane phosphate quarries makes them the oldest known placental mammal localities from Africa.

Systematic Palaeontology

Placentalia Owen, 1837
Paenungulata Simpson, 1945
Proboscidea Illiger, 1811
Family indet.
Eritherium azzouzororum n.g., n.sp.
(Figs. 1 and 2).

Etymology. *Eritherium* (monotypic genus), from *eri* (g.), early, and *therion* (g.), beast; *azzouzororum*, species dedicated to people from Ouled Azzouz village close to Sidi Chennane, who recovered most of the fossils.

Locality and Age. Morocco, NE Ouled Abdoun basin, Sidi Chennane quarries; phosphate bed IIa, lower bone-bed horizon, early Thanetian (incl. Selandian). Type locality: Quarry A4, N 32° 38' 18.04'', W 06° 42' 57.10''.

Holotype. MNHN [Muséum National d'Histoire Naturelle] PM69: Skull rostrum preserving maxilla with P³⁻⁴ and M¹⁻³ (length of P³-M³ = 27 mm), Fig. 1 A–G.

Hypodigm. There are 15 specimens representing upper and lower jugal dentition and skull part, including the holotype, MHNL PAL 2006.0.18–20 (P³⁻⁴, M¹⁻³), OCP DEK/GE 307 (M₁₋₃), MNHN PM50 (I₂, P₂₋₄, M₁₋₃).

Diagnosis. Most primitive and smallest known proboscidean, along with *Khamsaconus*. Dental and cranial morphology closest to *Phosphatherium*, and to *Khamsaconus* (known only by one tooth). Main proboscidean synapomorphies: I₁ enlarged, larger than I₂, I₁₋₂ with high (styliform), labio-lingually compressed, asymmetric, and procumbent crown; I₃ strongly reduced; C₁ very small; (d)P₁ small and simple; molar hypoconulid labial; coronoid retromolar fossa enlarged. Proboscidean synapomorphies with more ambiguous distribution: Orbit anterior rim bordered by maxillary and with high lateral jugal bony blade; no postcingulum and lingual cingulum on M¹⁻³; P₃₋₄ more or less simplified; molar mesoconid present; molar cristid obliqua labial; postentoconulid on M₁₋₂. The combination of these features is distinct from all other ungulates, including primitive hyracoids.

Differs from *Phosphatherium* by a smaller size (60–70%) and primitive features: Bunodont-lophodont molars, small M₃, full eutherian lower dental formula (retention of I₃ and (d)P₁), maxillary less developed on the orbit and orbit position above P⁴-M¹ level. Other primitive features: Shorter mandibular symphysis; upper premolars with no trace of protoloph and weaker

Author contributions: E.G. designed research, performed research, analyzed data, and wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: gheerbra@mnhn.fr.

This article contains supporting information online at www.pnas.org/cgi/content/full/0900251106/DCSupplemental.

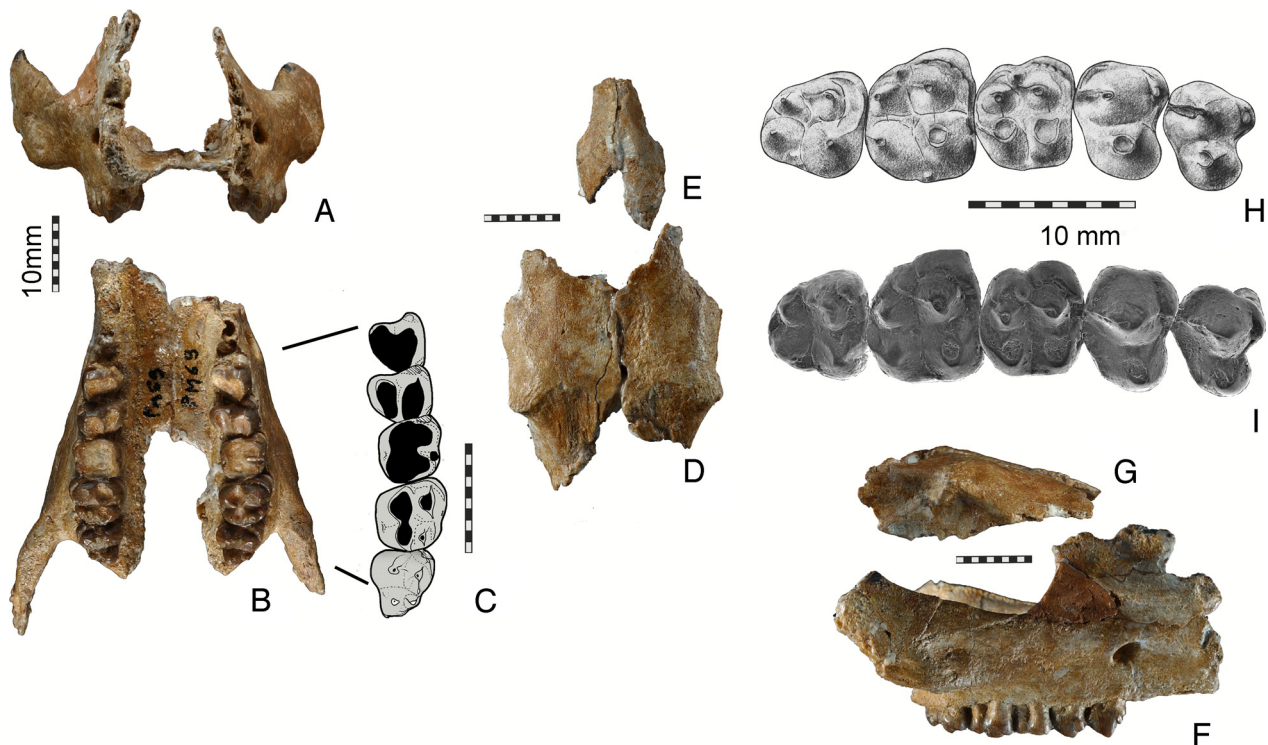


Fig. 1. Skull and upper dentition of *Eritherium azzouzorom* n.g., n.sp. (A–G) Holotype, MNHN PM69. (A and B) Anterior part of skull (rostrum) with maxilla and jugals in mesial and ventral views and showing nasal cavity, zygomatic arches and jugal dentition. (C) Left P_{3-4} , M_{1-3} , occlusal sketch. (D and E) Frontals and nasals in dorsal view, specimen MHNT PAL 2006.0.18–20 (Museum National d’Histoire Naturelle de Toulouse). (F and G) Frontal and rostrum (jugal and right maxillary with P_{3-4} , M_{1-3}) in lateral view (G is reversed for reconstruction). (H and I) Right P_{3-4} , M_{1-3} in occlusal view (H is SEM view of I). (Scale bar, 10 mm.)

metacone; more developed mesostyle and ectocingulum (upper molars); postmetacristid distinct (lower molars); C_1 larger; I_{1-2} less enlarged and slender; M_2^2 less enlarged with respect to M_1^1 ; absence of submaxillary fossa. *Khamsaconus* differs by: Smaller size (50%), large postentoconule, more anterior hypocone with respect to metacone, preprotocrista ending at mesio-lingual basis of paracone, and related reduced paracingulum.

Description. See characters K1–143 in *SI Appendix*. The estimated body mass of *Eritherium azzouzorom*, inferred from allometric relation of tooth size [regression equations from Damuth et al. (9) and Janis (10)], varies between 3 and 8 kg, with a median estimation most comparable to the body weight of the largest extant hyraxes (e.g., *Procavia*, 4–5 kg).

Characters Study and Relationships with Proboscideans

Among ungulate mammals, the dental and cranial morphology of *Eritherium* closely recalls the primitive proboscideans *Khamsaconus* and *Phosphatherium*. There are also some dental resemblances with primitive hyraxes such as *Seggeurius*, with lousinine “condylarths” *Monshyus* and *Microhyus*, and with primitive macroscelideans such as *Chambius*. However, detailed comparative anatomical study (characters K1–143, see *SI Appendix*) and an extended phylogenetic analysis with TNT (11) among lophodont ungulates demonstrate unambiguous relationships with *Phosphatherium* and proboscideans (Fig. 3). This is supported in unweighted parsimony analysis, with strong Bremer and bootstrap indices, and in the “implied weighting” exact analysis.

Several identified proboscidean synapomorphies (see *Diagnosis* and Table 1) support relationships of *Eritherium* to *Phosphatherium* and Proboscidea. Some deserve special comments: C_1 is more reduced than in embrithopods (K6). (d) P_1 (K9) is smaller and simpler than in sirenians and desmostylians; its

reduction fits well the proboscidean evolutionary trend toward its loss, with the remarkable intermediate state of *Phosphatherium* whose (d) P_1 is present in juvenile individuals (specimen OCP DEK/GE 450) but lost in adults. The enlarged I_1 (K3), reduced C_1 (K6) and (d) P_1 (K9), hypoconulid in labial position (K37) and well developed coronoid retromolar fossa (K55) are unambiguous synapomorphies.

Several derived features shared with *Phosphatherium*, that are distinctive among paenungulates, are strikingly reversed in later proboscideans (Table 1). The simplified P_{3-4} (K14–15, K18, K21) shared with *Numidothierium* is distinctive from later proboscideans (Table 1) but also from the inferred generalized paenungulate morphotype. The cladistic analysis suggests indeed that the simplified P_{3-4} is unexpectedly reversed in Proboscidea with respect to the ancestral paenungulate (molarized) morphotype, and that advanced proboscideans secondarily acquired molarized premolars. Alternative hypothesis of convergent molarization of premolars in several paenungulate lineages cannot, however, be excluded, which would emphasize again the primitive pattern of *Eritherium*. Other proboscidean features of *Eritherium* are occasionally known in other paenungulates. Enlarged and procumbent lower incisors (K1–2) are generalized in tethytherians, and some embrithopods share moderately enlarged I_1 (K3). However, I_{1-2} of *Eritherium* is more proboscidean-like in the procumbent, high (styliform), and asymmetric crown (inferred in I_1), and in the larger I_1 (alveolus). Strong reduction of I_3 (K5) occurs in *Ocepeia*, but in a less advanced stage; the *Eritherium* condition foreshadows the loss of this tooth in *Phosphatherium* and more advanced proboscideans. Proboscidean synapomorphies, such as the high lateral jugal bony blade (K125) and the presence of a molar mesoconid (K34), imply convergences with sirenians and hyracoids, respectively. An alternative interpretation of the evolution of the high jugal (zygoma, K125) in our cladistic analysis is that it is a tethytherian feature secondarily lost in the desmostylians. Other derived features shared

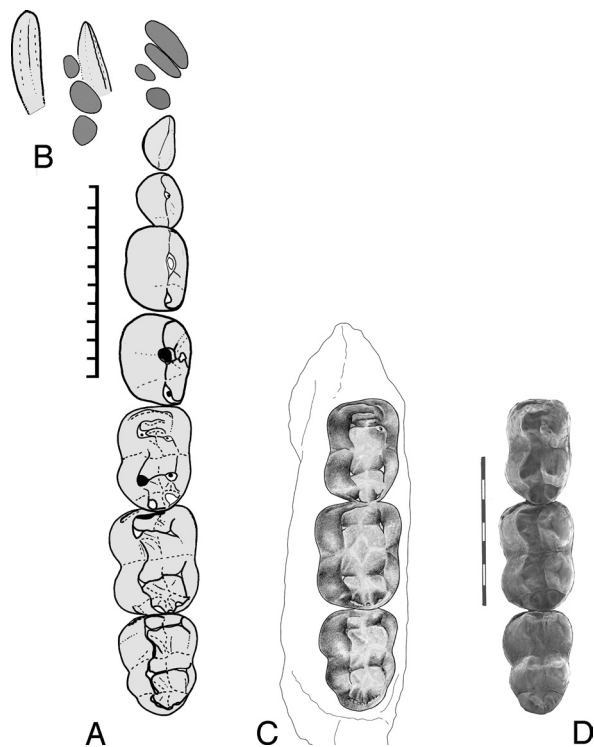


Fig. 2. Lower dentition of *Eritherium azzouzorom* n.g., n.sp. (A) Reconstruction of lower tooth row: M_{3-1} , P_{4-1} and alveoli for C_1 , I_{3-1} in occlusal view, based on specimens OCP DEK/GE 307 (M_{3-1}), MNHN PM28 (P_{4-2} , alveoli of C_1 , I_{3-1}), PM84 [(d) P_1]. (B) Sketch of enlarged and styliform I_2 in occlusal (dorsal) and lingual views, plus alveoli of (d) P_1 , C_1 and I_3 from specimen MNHN PM50. (C and D) Left M_{3-1} , specimen OCP DEK/GE 307, in occlusal view (drawing and SEM photograph). (Scale bar, 10 mm.)

with proboscideans, such as reduced preparacrista (K93) and conules (K95), are known in other paenungulates as either convergences or more inclusive synapomorphies. The maxillary extension and related reduction of jugal on the antorbital rim (K118) is a classic proboscidean synapomorphy. The jugal extends further anteriorly in *Eritherium* than in *Phosphatherium*, but it is still more reduced than in the eutherian condition. The feature is made less significant with regard to *Eritherium* plesiomorph condition and with regard to incipient jugal reduction in hyracoids (12). The P_2 small, simple, and single-rooted (K11–12) in *Eritherium* and *Phosphatherium* also recalls sirenians and desmostylians. P_2 is more simplified in *Eritherium* and *Phosphatherium* (K11) (2) as a unique and unexpectedly derived trait with respect to other early proboscideans. However, our analysis does not support their autapomorphic grouping, implying either convergence or reversals in proboscideans.

Eritherium also shows remarkable shared primitive features with *Phosphatherium* by contrast to later proboscideans, such as the retention of C_1 and of molar centrocrista and mesostyle. Other striking plesiomorphies of *Eritherium* are unknown in *Phosphatherium* and later proboscideans, such as the small size (60–70% of *Phosphatherium*), bunodont incipiently bilophodont molars, small M^3_3 , full eutherian dental formula (retention of I_3 and (d) P_1), orbit above P^4 - M^1 level, and maxillary less developed on the orbit (K118). *Eritherium* shares poorly advanced bilophodonty with *Khamsaconus* (13) and supports its proboscidean relationships (5, 7). However, *Khamsaconus* is distinctive (see *Diagnosis*) with some of the shared differences with *Phosphatherium*, suggesting a more advanced lophodont trend and possible familial distinction. In addition to several recognized primitive tethytherian and paenungulate traits (see *SI Appendix*), *Erith-*

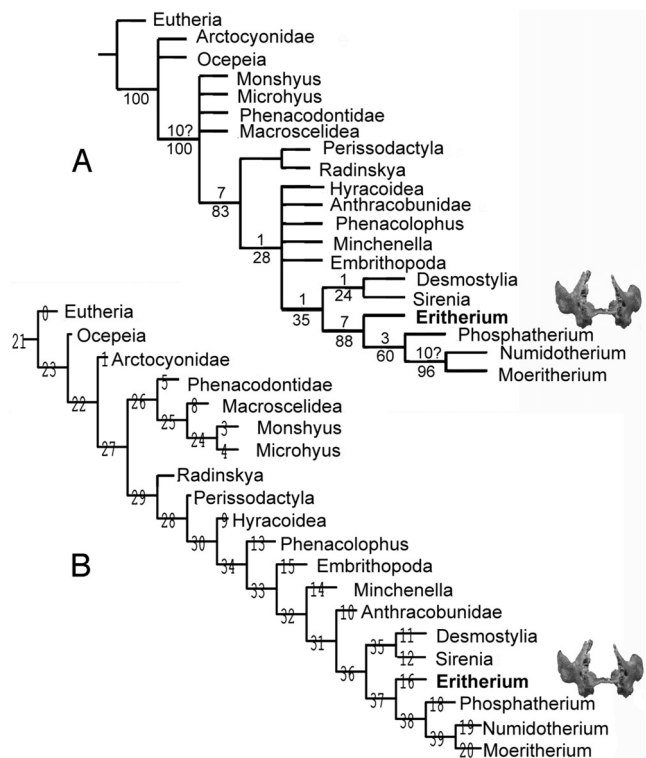


Fig. 3. Relationships of *Eritherium azzouzorom* n.g., n.sp. Cladograms resulting from parsimony analysis with TNT program (11) based on modified matrix for *Phosphatherium* analysis (7) (see *SI Appendix*). With respect to *Phosphatherium* analysis (7), several basal taxa are added to test basal relationships of Paenungulata, and *Khamsaconus*, which TNT “pruned tree” procedure (11) identifies as the most unstable taxon, is excluded from the analysis. (A) Consensus of 14 most parsimonious trees ($L = 455$ steps, $CI = 58.7$; $CI = 41.8$) resulting from exact analysis (nelsen); upper numbers in nodes refer to Bremer indices, lower numbers refer to bootstrap indices. (B) Standard TNT “implied weighting” analysis ($L = 457$ steps, $RI = 58.4$; $CI = 41.6$) with congruent topology to that resulting from *Phosphatherium* study (7), in particular with similar primitive position of Anthracobunia and Embrithopoda within Tethytheria. In both cases the proboscidean (basal) relationship of *Eritherium azzouzorom* n.g., n.sp. is well supported.

erium allows the identification of additional convergences in these groups, such as the large M^3_3 , the submaxillary fossa, and the orbit anterior to P^4 .

Supraordinal Relationships

The TNT unweighted parsimony analysis including *Eritherium* yields a very poorly resolved consensus tree mainly resulting from the unstable position of *Khamsaconus*. Analysis without *Khamsaconus* shows that, besides the robust proboscidean relationships of *Eritherium*, basal relationships among paenungulates remain unstable (7), as illustrated by the basal polytomy in the consensus (Fig. 3A). This polytomy is basically related to our poor fossil knowledge of the ancestral morphotype of several orders such as Embrithopoda, Desmostylia, and Anthracobunia. Our analysis supports a Sirenia–Desmostylia clade sister group of Proboscidea within Tethytheria. The standard TNT “implied weighting” analysis yields a topology (Fig. 3B), which is nearly identical to that of Gheerbrant et al. (7).

Eritherium is remarkably reminiscent of the early Tertiary European lousinines *Microhyus* and *Monshyus* and early macroscelideans *Chambius* and *Herodotius*, in such primitive features as the bunodont incipiently lophodont molars (in addition to the small size, small M^3_3 , and full dental formula). This is the initial report of resemblances between the lousinine “condylarths”

Table 1. Proboscidean synapomorphies of *Eriotherium azzouzorom* n. g., n.sp.

K	RI	State	Homoplasy	Description
3	100	0→1*		I ₁ enlarged and probably high crowned
5	83	0→1	c: <i>Ocepeia</i>	I ₃ strongly reduced
6	77	01→2*		C ₁ very small
9	69	01→2	c: ?	(d)P ₁ small and simple
14,	42,	1→0	r: Paenungulata/Tethytheria, <i>Daouitherium</i> ,	Simplified premolars: P ₃₋₄ : paraconid and
15,	42,	0→1	<i>Moeritherium</i> , and advanced proboscideans	ectocingulid reduced; P ₃ : metaconid reduced
18,	25,	0→1		
21	50	1→0		
34	20	0→1	r: <i>Numidotherium</i> ; c: Hyracoidea	M ₁₋₃ : Mesoconid
35	28	01→2	r: <i>Numidotherium</i> , <i>Daouitherium</i> , <i>Barytherium</i>	M ₁₋₃ : Cristid obliqua labial
37	44	0→2*		M ₁₋₃ : hypoconulid labial
39	33	0→1	r: <i>Numidotherium</i> , <i>Daouitherium</i> , <i>Barytherium</i>	M ₁₋₂ : Postentoconulid
55	62	1→2*		Coronoid retromolar fossa enlarged
86	50	1→0	r: <i>Moeritherium</i>	M ₁₋₃ : No postcingulum
87	63	3→2	r: <i>Moeritherium</i>	M ₁₋₃ : No lingual cingulum
118	83	0→1	c: Embrithopoda	Skull: Orbit mesially bordered by maxillary
125	75	0→1	c: Sirenia	Skull: Jugal high, with ventral process
11–12	33,	1→2	11(1)–12(1): also <i>Desmostylia</i> and <i>Sirenia</i> ; r?:	P ₂ small, simplified and uniradicular
	33	0→1	<i>Numidotherium</i> , <i>Daouitherium</i> , <i>Barytherium</i> , <i>Moeritherium</i>	

Proboscidean synapomorphies of *Eriotherium azzouzorom* n. g., n. sp. K, character number (see description in [SI Appendix](#)). It should be noted that all characters listed are preserved and observed in available material of *Eriotherium*. r and c, reversion and convergence known in taxa compared; RI: Retention Index.

*Nonhomoplastic state.

(Apheliscidae) and the proboscideans. The bunodont incipient lophodont morphotype is derived relative to the eutherian condition, and it is distinct from the perissodactyl pattern. This morphotype is an additional morphological character (14–18) and one of the most remarkable dental characters reported (16, 17) for close relationships of paenungulates, macroscelideans, and lousinines. However, our parsimony analysis does not formally support sister-group relationships of the Macroscelidea plus Louisininae and the Paenungulata by contrast to molecular (19, 20) and recent morphological (14–18, 21) analyses advocating the Afrotheria clade. The recovered topology (Fig. 3) shows a sister-group relationship of Laurasian lophodont ungulates such as perissodactyls to paenungulates, instead of the macroscelideans (and lousinines). Similarly, our analysis does not discriminate clearly Laurasian (e.g., phenacodontids) and African (e.g., *Ocepeia*) “condylarths” as possible early ungulate representatives of molecular laurasiatherian and afrotherian clades. Fossil gaps, and especially for African taxa, most probably explain poorly resolved cladistic basal relationships of the Paenungulata in our tree (Fig. 3). These gaps are illustrated by our poor knowledge of the ancestral morphotype of several key paenungulates orders; for instance, the ancestral relative size of the last molar in paenungulates is challenged by *Eriotherium* (M₃ not enlarged). At lower level in the tree, the morphological and fossil gap is even worse for the phylogenetic analysis of the superordinal clade Afrotheria including Tenrecoidea and Tubulidentata, which are excluded from this study because of the lack of Paleogene data. In this respect, the cladistic study of *Eriotherium* does not help to test the question of the macroscelidean position within Afrotheria. However, *Eriotherium* dental morphology argues for a bunodont-lophodont, i.e., ungulate-like, ancestral morphotype for the Paenungulata, Louisininae, and Macroscelidea, within putative Afrotheria.

Discussion and Implications for the Placental Radiation

Eriotherium, *Phosphatherium*, *Daouitherium*, and *Numidotherium* provide the most complete basal evolutionary sequence known among paenungulate and “ungulate” mammals. Such a remarkable early fossil record for the Proboscidea provides evidence for

(i) the emergence of a modern ungulate order at a previously unreported primitive stage, still close to the generalized early Tertiary condylarth-like grade, and (ii) one of the most spectacular examples of morphological evolution known in Mammalia (1). The discovery of *Eriotherium* especially reveals a major evolutionary leap in proboscidean evolution at the beginning of the Eocene, with the development of the true lophodony and the large body size (22). It shows that Paleocene-Eocene (PE) transition is a key period of evolution in Africa for (at least) Proboscidea, as it is classically in Laurasia for several other placental orders (23). In this instance, Africa matches Laurasia in major early evolutionary events of placentals.

The elephant order, that can now be traced back to early Late Paleocene, ca. 60 mys, is one of the earliest known “modern” placental orders, beside few other Paleocene occurrences such as xenarthrans, lipotyphlans, carnivores, euprimates, and rodents (24, 25). The order Proboscidea is one of the earliest known putative Afrotheria, if not the earliest.

The remarkably poorly derived morphology of *Eriotherium* from the inferred paenungulate ancestral morphotype supports a recent proboscidean origin (i.e., recent before *Eriotherium*, ca. 60 mys) and a rapid paenungulate radiation at the Cretaceous-Tertiary (KT) transition, which is also supported by the latest genomic studies (26–28). Rapid paenungulate radiation and fossil gaps may explain poorly resolved interordinal relationships. Such a rapid paenungulate radiation is most consistent with the “conventional” view of the placental adaptive radiation at the beginning of the Tertiary in relation to major KT events, and it may reflect the adaptive response to favourable early Tertiary African conditions, such as the colonization of local free niches (29). *Eriotherium* provides new and outstanding fossil data for calibrating the placental tree. In this regard, morphological phylogenies (3, 4) that place the Paenungulata and Proboscidea in nested or apical position suppose in light of *Eriotherium* either an old, or more likely, a rapid and basically explosive placental radiation; the latter is supported by the phylogeny of Wibble et al. (4) that refutes known pre-Tertiary crown placentals. Paradoxically, molecular phylogenetic topologies (19, 20) advocating a basal position of Afrotheria do not refute the rapid placental

radiation based on *Eritherium* (a low position of Paenungulata and Proboscidea in the molecular placental tree is not consistent with a significant earlier age versus *Eritherium* of other ordinal divergences). However, a rapid placental and paenungulate radiation at the KT transition obviously does not exclude Cretaceous roots of several basal lineages, especially for stem afrotherians and paenungulates.

Following *Phosphatherium*, the discovery of *Eritherium* confirms the long African endemic history of the Proboscidea. *Eritherium* also provides the most reliable evidence for the African origin of the Paenungulata.

Materials and Methods

Detailed comparative characters study and phylogenetic relationships of *Eritherium* among lophodont ungulates were developed with the program TNT (11), complemented with Winclada and Nona (e.g., matrix construction and character distribution in the trees). Details of the 143 dental and cranial characters studied and of the phylogenetic analysis are provided in *SI Appendix*

dix. Determination and biostratigraphic characterization (by H. Cappetta) of the selachian fauna from the fossiliferous level of *Eritherium* are provided and further commented in *SI Appendix*.

ACKNOWLEDGMENTS. The author thanks F. Escuillie and P. Dalous (Musée d'Histoire Naturelle de Toulouse) for providing material of *Eritherium* for study and/or for Muséum National d'Histoire Naturelle (MNHN) collection; P. Louis and C. Letenneur for drawings; P. Loubry and C. Lemzaouda for photographs; R. Vacant for preparation and casts; H. Cappetta for determination of the associated selachian fauna and for biostratigraphic comments; and useful comments on the manuscript were provided by E.K. Seiffert, P. Tassy, and an anonymous reviewer. The author also thanks the Geological Survey of the OCP mining centre of Khouribga for help with the field work, especially B. Bouya and M. Amaghazaz for logistic support, and our field collaborators O. Selloum and A. Mazzi, which helped to find and locate material of *Eritherium*. M. Bichara and S. Mesloul also helped with the field work. Field work was funded by the Centre National de la Recherche Scientifique (Unité Mixte de Recherche 5143) and MNHN (Bonus Qualite Recherche). This work was supported by the Collaboration Agreement with the Ministère de l'Energie et des Mines, the Office Chérifien des Phosphates (OCP) of Morocco, Universities Cadi Ayyad (Marrakech) and Chouaïb Doukkali (El Jadida).

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