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

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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 azzouzorum 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 louisinines 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 paleocoenocystems. 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.

Systematic Palaeontology

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

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

Locality and Age. Morocco, NE Ouled Abdou 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 [Museum 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, M1–2), OCP DEK/GE 307 (M1–3), MNHN PM50 (I2, P2–4, M1–3).

Diagnosis. Most primitive and smallest known proboscidean, along with Khamascanus. Dental and cranial morphology closest to Phosphatherium, and to Khamascanus (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)P3 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.

Differ from Phosphatherium by a smaller size (60–70%) and primitive features: Bunodont-lophodont molars, small M1–3, full eutharian lower dental formula (retention of I3 and (d)P3), maxillary less developed on the orbit and orbit position above P3-M1 level. Other primitive features: Shorter mandibular symphysis; upper premolars with no trace of protoloph and weaker plications.

Author contributions: E.G. designed research, performed research, analyzed data, and wrote the paper.
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Among ungulate mammals, the dental and cranial morphology of *Eritherium* closely recalls the primitive proboscideans *Kham saconus* and *Phosphatherium*. There are also some dental resemblances with primitive hyraxes such as *Seggewius*, with louisienne “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: C1 is more reduced than in embrithopods (K6), (d)P1 (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)P1 is present in juvenile individuals (specimen OCP DEK/GE 450) but lost in adults. The enlarged I1 (K3), reduced C1 (K6) and (d)P1 (K9), hypococonulid 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 P3–4 (K14–15, K18, K21) shared with *Numido therium* is distinctive from later proboscideans (Table 1) but also from the inferred generalized paenungulate morphotype. The cladistic analysis suggests indeed that the simplified P3–4 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 I1 (K3). However, I1–2 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 I1 (K3). However, I1–2 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 I1 (K3).
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 P2 allows the identification of additional convergences in these groups, such as the large M3, the submaxillary fossa, and the orbit anterior to P4.

**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. 34). This polytomy is basically related to our poor fossil knowledge of the ancestral morphotype of several orders such as Embrithopoda, Desmostylia, and Anthracocinina. 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 louisinines *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 M3, and full dental formula). This is the initial report of resemblances between the louisinine “condylarths”
Eritherium azzouzorum (Apheliscidae) and the proboscides. The bunodont incipient lophodont morphology is derived relative to the eutherian condition, and it is distinct from the perissodactyl pattern. This morphology is an additional morphological characteristic (14–18) and one of the most remarkable dental characters reported (16, 17) for close relationships of paenungulates, macroscelidians, and lousiniines. 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 superordinal clade Afrotheria including Tenrecoidea and Tufodi (1). The discovery of Eritherium especially reveals a major evolutionary leap in proboscidean evolution at the beginning of the Eocene, with the development of the true lophodonty 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 myr, 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 Eritherium from the inferred paenungulate ancestral morphotype supports a recent proboscidean origin (i.e., recent before Eritherium, ca. 60 myr) 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). Eritherium 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 Eritherium either an old, or more likely, a rapid and basically explosive placental radiation; the latter is supported by the phylogeny of Wible et al. (4) that refutes known pre-Tertiary crown placentals. Para-adoxically, molecular phylogenetic topologies (19, 20) advocating a basal position of Afrotheria do not refute the rapid placental

Table 1. Proboscidean synapomorphies of Eritherium azzouzorum n. g., n. sp.*

<table>
<thead>
<tr>
<th>K</th>
<th>RI</th>
<th>State</th>
<th>Homoplasy</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>100</td>
<td>0→1*</td>
<td>c: Ocepeia</td>
<td>1, enlarged and probably high crowned</td>
</tr>
<tr>
<td>5</td>
<td>83</td>
<td>0→1</td>
<td>c: ?</td>
<td>1, strongly reduced</td>
</tr>
<tr>
<td>6</td>
<td>77</td>
<td>0→2*</td>
<td>c: ?</td>
<td>C, very small</td>
</tr>
<tr>
<td>9</td>
<td>69</td>
<td>0→2</td>
<td>c: ?</td>
<td>(d)P, small and simple</td>
</tr>
<tr>
<td>14,</td>
<td>42,</td>
<td>1→0</td>
<td>r: Paenungulata/Tethytheria, Daouitherium, Moeritherium, and advanced proboscideans</td>
<td>Simplified premolars: P2–4: paraconid and ectocingulid reduced; P5: metaconid reduced</td>
</tr>
<tr>
<td>15,</td>
<td>42,</td>
<td>0→1</td>
<td>Moeritherium</td>
<td></td>
</tr>
<tr>
<td>18,</td>
<td>25,</td>
<td>0→1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>50</td>
<td>0→1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>50</td>
<td>0→1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>23,</td>
<td>50,</td>
<td>0→1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>34</td>
<td>20</td>
<td>0→1</td>
<td>r: Numidotherium; c: Hyracoidea</td>
<td>M1–3: Mesocinion</td>
</tr>
<tr>
<td>35</td>
<td>28</td>
<td>0→1</td>
<td>r: Numidotherium, Daouitherium, Barytherium</td>
<td>M1–3: Cristid obliqua labial</td>
</tr>
<tr>
<td>37</td>
<td>44</td>
<td>0→2*</td>
<td>r: Moeritherium, Daouitherium, Barytherium</td>
<td>M1–3: hypoconulid labial</td>
</tr>
<tr>
<td>39</td>
<td>33</td>
<td>0→1</td>
<td>r: Moeritherium, Daouitherium, Barytherium</td>
<td>M1–2: Postentocingulid</td>
</tr>
<tr>
<td>55</td>
<td>62</td>
<td>1→2*</td>
<td>r: Numidotherium, Daouitherium, Barytherium</td>
<td>Coronoid retromolar fossa enlarged</td>
</tr>
<tr>
<td>65</td>
<td>50</td>
<td>1→0</td>
<td>r: Moeritherium</td>
<td>M1–3: No postcingulium</td>
</tr>
<tr>
<td>67</td>
<td>63</td>
<td>3→2</td>
<td>r: Moeritherium</td>
<td>M1–3: No lingual cingulum</td>
</tr>
<tr>
<td>118</td>
<td>83</td>
<td>0→1</td>
<td>c: Embrithopoda</td>
<td>Skull: Orbit mesially bordered by maxillary</td>
</tr>
<tr>
<td>125</td>
<td>75</td>
<td>0→1</td>
<td>c: Sirenia</td>
<td>Skull: Jugal high, with ventral process</td>
</tr>
<tr>
<td>11–12</td>
<td>33,</td>
<td>1→2</td>
<td>11(1)–12(1); also Desmostyliia and Sirenia; r?: Simplified premolars: P2–4: paraconid and ectocingulid reduced; P5: metaconid reduced</td>
<td></td>
</tr>
<tr>
<td>33</td>
<td>0→1</td>
<td>Numidotherium, Daouitherium, Barytherium, Moeritherium</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Proboscidean synapomorphies of Eritherium azzouzorum 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 Eritherium. r and c, reversion and convergence known in taxa compared; RI: Retention Index. *Nonhomoplastic state.

(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 Eritherium reveals a major evolutionary leap in proboscidean evolution at the beginning of the Eocene, with the development of the true lophodonty 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.
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.

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