

A proboscidean from the late Oligocene of Eritrea, a “missing link” between early Elephantiformes and Elephantimorpha, and biogeographic implications

Jeheskel Shoshani^{*,†}, Robert C. Walter[§], Michael Abraha[¶], Seife Berhe[¶], Pascal Tassy^{**}, William J. Sanders^{††}, Gary H. Marchant[‡], Yosief Libsekal^{‡‡}, Tesfalidet Ghirmai^{¶¶}, and Dietmar Zinner^{‡‡§§}

*Department of Biology, University of Asmara, P.O. Box 1220, Asmara, Eritrea; [†]Elephant Research Foundation, 106 East Hickory Grove Road, Bloomfield Hills, MI 48304; [§]Department of Earth and Environment, Franklin and Marshall College, Lancaster, PA 17604-3003; [¶]Eritrean Geological Survey, Department of Mines, Ministry of Mines and Energy, P.O. Box 272, Asmara, Eritrea; ^{¶¶}Global Resources, P.O. Box 4588, Asmara, Eritrea; ^{**}USM203/Unité Mixte de Recherche 5143 Centre National de la Recherche Scientifique Paléobiodiversité, CP 38, Muséum National d'Histoire Naturelle, 57 Rue Cuvier, 75231 Paris Cedex 05, France; ^{††}Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109; ^{‡‡}Department of Archeology, National Museum of Eritrea, P.O. Box 1220, Asmara, Eritrea; and ^{§§}Department of Cognitive Ethology, Deutsches Primatenzentrum, Kellnerweg 4, D-37077 Göttingen, Germany

Edited by David B. Wake, University of California, Berkeley, CA, and approved September 9, 2006 (received for review May 5, 2006)

We report on a late Oligocene proboscidean species from Eritrea, dated to 26.8 ± 1.5 Mya. This “missing link” between early elephantiformes and Elephantimorpha is the oldest known non-gomphotheres proboscidean to probably display horizontal tooth displacement, typical of elephants [Elephantimorpha consists of Mammutida (mastodons) and Elephantida, and Elephantida includes gomphotheres, stegodons, and elephants]. Together with the newly discovered late Oligocene gomphotheres from Chilga, Ethiopia, the Eritrean taxon points to the importance of East Africa as a major area for the knowledge of the early evolution of Elephantimorpha before the faunal exchange between Eurasia and Africa.

evolution | NE Africa | palaeontology | horizontal tooth displacement

Proboscideans have been a part of the Afro-Arabian landscape since at least the early Eocene, ~55 Mya (1). Paleogene proboscidean fossils have been recovered from northern Africa (Algeria, Egypt, Libya, Mali, Morocco, Sudan, and Tunisia), western Africa (Senegal), central Africa (Angola) (1–6), eastern Africa (Ethiopia) (7, 8), and the Arabian Peninsula (Oman) (9). Aside from a small, isolated tusk fragment from Baluchistan, Pakistan, dated to the late Oligocene and showing ivory structural pattern consistent with attribution to gomphotheres, stegodons, or elephants (10), the fossil record of definitive Paleogene proboscideans and the evidence for the major early radiations of proboscideans (moeritheres, numidotheres, and palaeomastodonts) appear to be best documented in Afro-Arabia. The fossil site of Dogali (Eritrea, Fig. 1) described here and the Chilga site in Ethiopia (7, 8) are in close proximity and are the only known late Oligocene mammal sites from the whole of Africa. The paleobiogeographical implications of these sites in the context of proboscidean evolution in Africa and across the Arabian Peninsula are discussed below.

The initial radiation of Elephantimorpha that replaced the archaic Elephantiformes proboscideans and deinotheres was centered in Africa and was primarily a basal Neogene event [Elephantiformes includes Phiomidae, Palaeomastodontidae, and Elephantimorpha; Elephantimorpha consists of Mammutida (mastodons) and Elephantida (gomphotheres, stegodons, and elephants) (11)]. Although the earliest gomphotheres is from the late Oligocene, ~27 Mya (7, 8), the oldest known mammutid dates to the early Miocene, 22 Mya (12), and the subsequent diversification of these groups occurred during the early Miocene, ~22–20 Mya. Early to early-middle Miocene African sites dated to 22–16 Mya and yielding mammutid and gomphotheres fossils are known from northern Africa (Kabylie, Algeria; Moghara and Siwa, Egypt; and Gebel Zelten, Libya), eastern Africa (Buluk, Legetet, Karungu, Loperot, Meswa

Bridge, Mfwangano, Muruorot, Mwiti, Rusinga, and Songhor, Kenya), and Namibia (12–15). Before the discovery of fossil proboscideans at Chilga, Ethiopia, and now from Dogali, there was an absence of evidence from the time period between the earlier (moeritheres and numidotheres) and later radiation (Mammutida and Elephantida) of proboscideans. In addition, the phylogenetic connections of elephantimorphs to more archaic taxa were uncertain and subject to considerable debate (2, 8, 16–17). The fossil from Dogali (Figs. 2 and 3) is therefore well suited temporally as well as morphologically to bridge the gap of lack of evidence (acting as a “missing link”); and it helps us to better understand the biogeographical inferences of early proboscidean radiation between Africa and Arabia. Furthermore, the new data from Dogali enable us to test competing hypotheses about the relationship among elephantimorphs, phiomids, and palaeomastodonts. The two prevailing hypotheses tested are (i) *Phiomia*, family Phiomidae, is a precursor of Elephantida (Gomphotherioidea and Elephantoida), and *Palaeomastodon*, family Palaeomastodontidae, is a precursor of Mammutida (mastodontids), that is, Elephantimorpha is paraphyletic, and (ii) *Phiomia* and *Palaeomastodon* are a sequence of sister taxa to Elephantimorpha (Mammutida and Elephantida) (18–20).

Systematic Paleontology. Class Mammalia Linnaeus, 1758.

Order Proboscidea Illiger, 1811.

Nonranked category Elephantida Tassy and Shoshani, 1997.

Family *incertae sedis*.

Eritreum melakeghebrekristosi gen. et sp. nov.

Holotype. National Museum of Eritrea (NME) field number DOG87.1, left mandibular ramus with m2 and m3, right mandibular ramus with m2 and partial first lophid of m3, portions of mandibular symphysis (in two parts) with remnants of tusk alveoli (Figs. 2 and 3).

Etymology. *Eritreum* from the name of the new nation of Eritrea in the Horn of Africa, and *melakeghebrekristosi* in honor of the farmer, Melake Ghebrekristos, who found the specimen and realized its importance.

Author contributions: J.S. performed research; J.S., R.C.W., M.A., S.B., P.T., W.J.S., G.H.M., Y.L., T.G., and D.Z. analyzed data; and J.S., R.C.W., S.B., P.T., and W.J.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS direct submission.

[†]To whom correspondence may be addressed. E-mail: dzinner@gwdg.de or jshosh@sun.science.wayne.edu.

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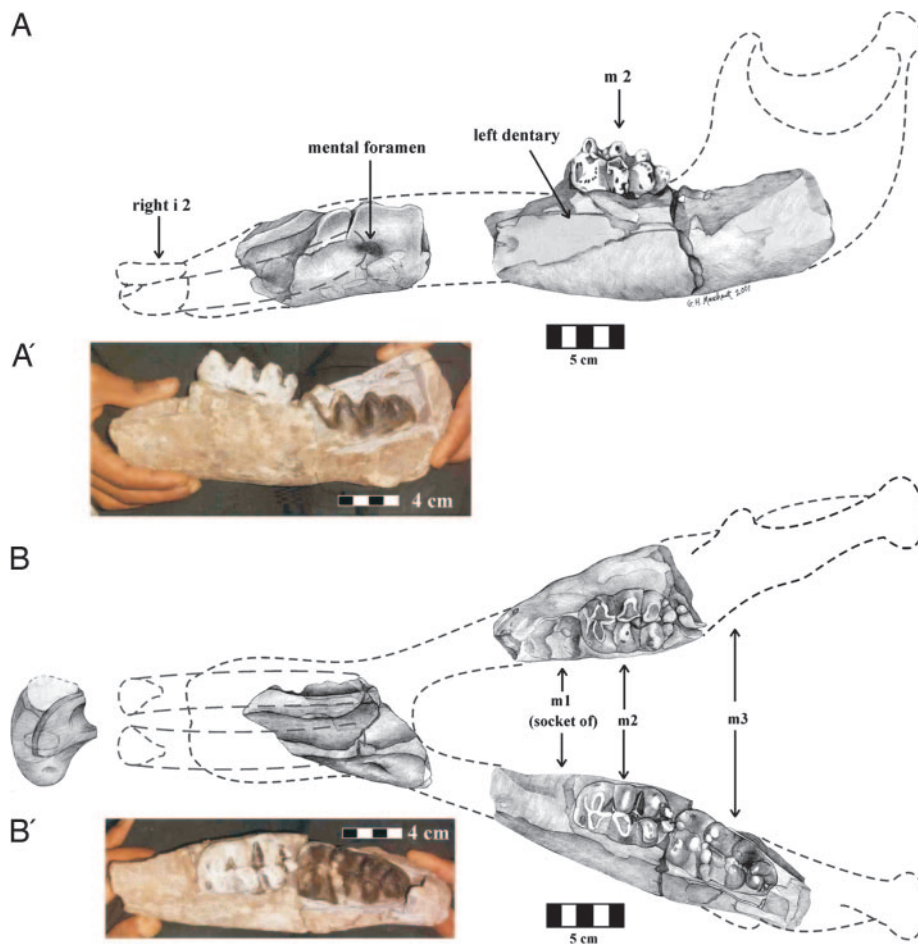


Fig. 2. Reconstruction of the lower jaw of *E. melakeghebrekristosi* gen. et sp. nov. from Dogali, Eritrea. (A) Lateral view of dentary. (A') Lingual view of left m2 (in occlusion) and m3 (in crypt or alveolus). (B) Occlusal view of reconstructed lower jaw. (B') Occlusal view of left m2 and m3. Note that the lower left third molar was originally in the alveolus, and only the dorsal surfaces of two ridges were exposed. We removed most of the bone to expose the tooth, but left it in the crypt. (Artwork by G.H.M.)

in Elephantida. The pyriform section of alveolus of incisor measures 3.5 cm dorsoventrally and 2.3 cm at its widest point. Based on these remains, we conservatively reconstruct this mandible to be ≈ 50 cm long, 30 cm wide, and 20 cm high, bearing tusks ≈ 20 cm long and, perhaps, to have slanted gently downwards anteriorly (Fig. 2).

The right and left m2 each have three complete lophids and a thick postcingulid. Each half-lophid has two conelets; the conelet closer to the median sulcus (adaxial conelet or mesoconelet) is smaller than the conelet that is farther from the midline (abaxial conelet). The postcingulid is constructed of two bulbous conelets, with the one on the pretrite side being larger than the one on the posttrite side and connected to the third lophid. In occlusal view, the enamel wear figures exhibit the cloverleaf trefoil pattern typical of advanced gomphotheres (Fig. 3) without cement on the crown. All three interlophids are blocked by anterior and posterior accessory central conules.

Posterior to the right m2 is a partial first lophid of m3. On the left side, the m3 was in the crypt or socket and was covered with bone and matrix. This tooth germ was excavated and left in the alveolus (Fig. 2, Table 1). The third left molar resembles the second molars just described, except that it is larger and has four complete lophids, with ecto- and entoflexus for each interlophid. The fourth lophid is made of two bulbous cones; the pretrite is slightly larger than the posttrite and is entirely disconnected from the third lophid. No postcingulum is observed posterior to

the fourth lophid, but only an inflated rugosity of the enamel, so that this m3 displays an intermediate condition between *Phiomia* (three lophids and a small postcingulid) and gomphotheres (those with four lophids and a postcingulid). The enamel inflation, rather than being a true postcingulid, at the posterior end of m3 in *Eritreum* is morphologically more derived than the condition in the early mammutid *Eozygodon*, in which there is a very thin enamel inflation on the posterior face of the fourth lophid in m3, despite the fact that the molars of *Eritreum* are much smaller.

The lophids do not exhibit mammutid traits, such as zygodont or “yoke”-shaped lophids (23), nor do they have zygodont crests on their posttrite sides. The anterolingual cingulid is reduced, unlike *Palaeomastodon* and *Phiomia*, and similar to the condition in mammutids and gomphotheres, an elephantimorph trait (20).

Discussion. Overall, the teeth of *E. melakeghebrekristosi* occupy an intermediate morphology between early elephantiform taxa (*Palaeomastodon* and *Phiomia*) and elephantimorph taxa, including mammutids and gomphotheres (incorporating *Gomphotherium*, family Gomphotheriidae, superfamily Gomphotherioidea). The teeth are larger than m2 and m3 of most palaeomastodonts and smaller than all mammutids and gomphotheres, even all diminutive “pygmy” gomphotheres from Ghaba, Oman, Gebel Zelten, Libya, and Siwa, Egypt (Fig. 4). *Eritreum* resembles advanced *Gomphotherium* (e.g., *G. angustidens*) in having a trefoil pattern on molars

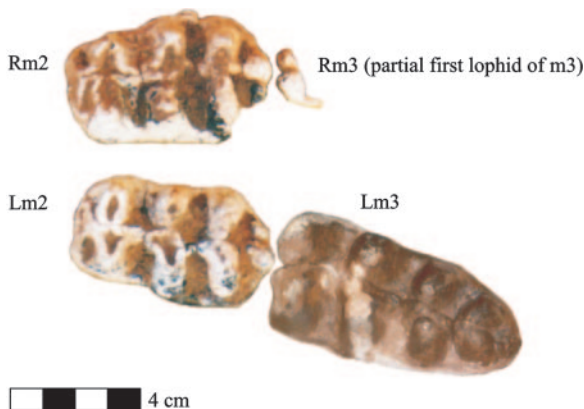


Fig. 3. Occlusal view of dentition of *E. melakeghebrekristosi* gen. et sp. nov. (composite of different photographs).

(trefoil wear patterns are present in a rudimentary manner in *Phiomia* and *Palaeomastodon*) and in lacking “zygodont crests.” The lower third molar of *Eritreum* lacks a postcingulid, unlike m3 in early gomphotheres. The reduced anterolingual cingulid in *Eritreum* is a derived feature shared with mammutids, gomphotheres, and elephantids.

Based on data from *G. angustidens* (24), the individual age, and the evolutionary stage of the Dogali specimen, the first lower molars would have been *in situ* when the animal died. These teeth (m1s) on both sides may have fallen out during burial. In the Dogali specimen, when the first and the second lower molars would have been simultaneously in occlusion, the third lower molar (m3) would be far at the posterior end of the lower jaw and inside the growing

Table 1. Data (in mm) on lower cheek teeth of *E. melakeghebrekristosi* gen. et sp. nov. from Dogali, Eritrea

Feature	m2 (Right)	m2 (Left)	m3 (Left)
No. of lophids	x3x*	x3x*	4x†
Total length	64.4	63.6	82.0
Width at lophid 1	35.4‡	34.0	38.0
Width at lophid 2	40.6	37.5	39.5
Width at lophid 3	40.4	39.5	39.0§
Width at heel/lophid 4	20.0	19.0	28.0§
Crown height at lophid 1	24.0¶	23.4	29.0
Crown height at lophid 2	25.0	25.0	28.5
Crown height at lophid 3	25.5	25.5	22.5
Crown height at heel/lophid 4	~15+	~23	20.0
Enamel thickness on lophid 1	3.0	3.0	—
Enamel thickness on lophid 2	3.0	3.0	—
Enamel thickness on lophid 3	—	—	—
Enamel thickness on heel/lophid 4	—	—	3.5**

*The heel contains two posterior cingular cusps; the pretrite cusp (conelet) is larger than the posttrite cone.

†The lower left third molar was originally in the crypt (socket or alveolus), and only the dorsal surfaces of two ridges were exposed. We removed most of the bone to expose the tooth but left it in the crypt.

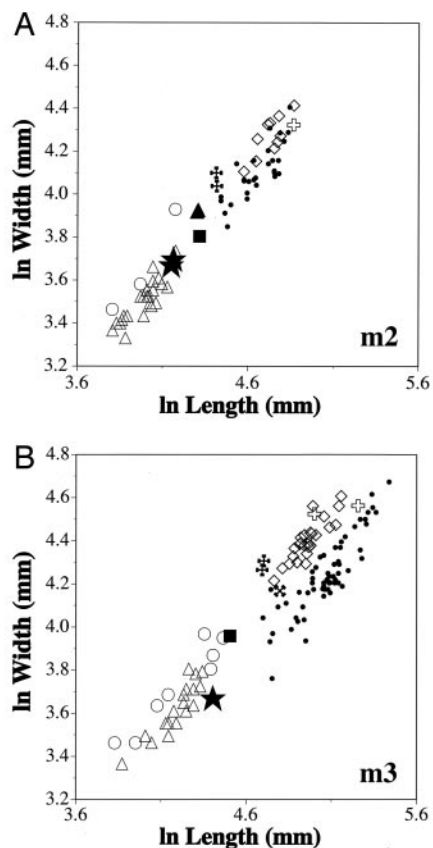
‡Widths were measured at the base (the widest point) of the crown.

§Measurement is approximate because bone obstructed full exposure of the tooth (see †).

¶Heights were measured at the posttrite (the highest point) of the crown.

||Enamel thickness was measured on the pretrite side only on ridges 1 and 2; ridge 3 is not worn enough to expose the enamel thickness.

**This enamel thickness was measured at the base of ridge 4, and it may be greater than if it had been measured on the pretrite side. The last, fourth, ridge was partly broken during preparation and then glued back in place, allowing us to measure the enamel thickness, which would otherwise not be possible because the tooth had not been exposed.



★, *Eritreum melakeghebrekristosi* ●, Miocene African and Eurasian *Gomphotherium* spp.
○, Fayum *Palaeomastodon* ◇, *Zygolophodon turicensis* and *Z. gobiensis*
△, Fayum *Phiomia* ◻, *Z. metachinjensis*
■, Chilga *Phiomia* ✱, *Z. aegyptensis*
▲, Chilga cf. *Gomphotherium*

Fig. 4. Bivariate plots of natural log-transformed m2 and m3 length versus width in *E. melakeghebrekristosi* gen. et sp. nov. and other fossil elephantiform proboscideans. Comparative dimensions are from Sanders *et al.* (8). (A) m2. (B) m3. The Dogali molars fall well outside the range of all known species of *Gomphotherium* and are within the upper size limit for Fayum palaeomastodonts. A complete list of specimens and data used to construct these plots can be obtained from W.J.S. Families of genera included in this figure are *Palaeomastodon*, family Palaeomastodontidae; *Phiomia*, family Phiomiidae; *Eozygodon* and *Zygolophodon*, family Mammutidae; *Gomphotherium*, family Gomphotheriidae.

bone, and we conjecture that there would have physically been no space for this tooth to erupt and be in the same horizontal level of occlusion as m1 and m2. Fig. 2A' depicts the m3 still in the crypt (socket), and the dorsal tips of its anterior unworn cusps are ≈ 1 cm below the occlusal surface of the worn cusps of m2. In addition, the roots in m3 have not yet developed, whereas they are well developed in the m2. We hypothesize that at a later stage of development, when the roots of m3 would have grown, the tooth would move upwards and forwards to be at the same horizontal level of occlusion of m2 (m1 would probably have fallen out by that time). From these anatomical features and the conjectured timing of dental eruption, we conclude that the mandible of *E. melakeghebrekristosi* may have exhibited horizontal tooth displacement (similar to slow movement on a conveyor belt), a trait of Elephantimorpha, including the living elephants (19, 20). Conversely, in primitive Elephantiformes such as *Palaeomastodon* and *Phiomia*, with complete dentition (p2-m3), when the state of wear is comparable to that seen on Dogali m2s, the m3 would have been entirely

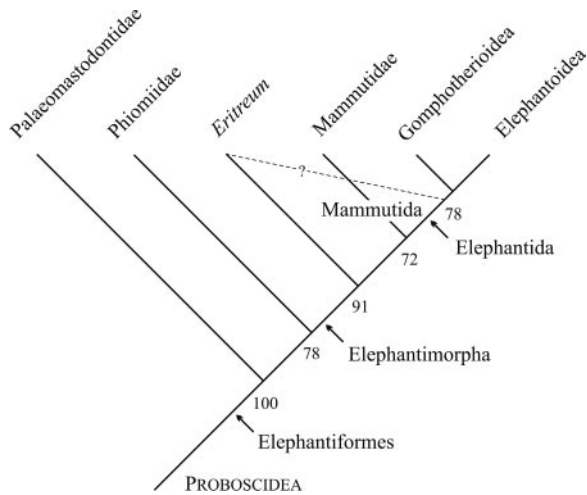


Fig. 5. Cladogram depicting *E. melakeghebrekristosi* gen. et sp. nov. as the earliest offshoot of Elephantimorpha (results based on edited and augmented character matrix of Shoshani (19); no. of taxa = 40; no. of characters = 125; Tree Length = 238; Consistency Index = 0.69, Retention Index = 0.88). Note, however, that an equally parsimonious solution is when *Eritreum* is the earliest offshoot of Elephantida. Bootstrap or branch support values are given for the major clades. Synapomorphies for Elephantimorpha and Elephantida and an explanation for why we favor *Eritreum* as the earliest offshoot of Elephantimorpha over *Eritreum* as a member of Elephantida, are given in the text.

erupted and in occlusion. In mammutids, the sequence of eruption of m1, m2, and m3 is intermediate between Elephantiformes (*Palaeomastodon* and *Phiomia*) and Elephantida. Additional specimens of *Eritreum* or closely related taxa may help in evaluating whether the alternative hypothesis that *Eritreum* is a member of Elephantida is better supported than that *Eritreum* is a member of Elephantimorpha (Fig. 5).

In comparing data used to identify dental ages for extant African elephants and for fossil gomphotheres (24–26), we estimate that the Dogali individual was a subadult, close to the age of 26 at death. Using data from Andrews (2) and Roth (27), we extrapolate the shoulder height to have been ≈ 130 cm and the body mass ≈ 484 kg (Fig. 6). Extrapolation of the shoulder height of *Eritreum* was based on data for *Palaeomastodon parvus* from Andrews (2) on these

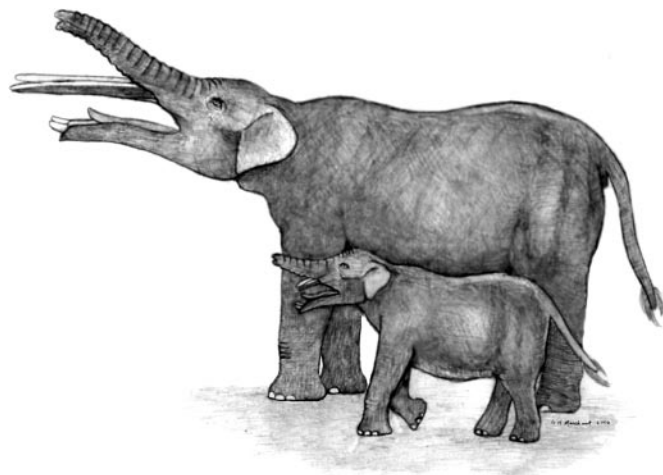


Fig. 6. Restoration of *Gomphotherium angustidens* [the larger individual, ≈ 200 cm tall at the shoulder, after Osborn (16) and Tassy (34)] and *Eritreum melakeghebrekristosi* gen. et sp. nov. (≈ 130 cm tall at the shoulder, based on data presented here). (Artwork by G.H.M.)

Table 2. A partial, nonranked classification of Proboscidea with emphasis on families discussed in this paper and the taxon from Dogali, Eritrea (modified after ref. 11)

Proboscidea Illiger, 1811
Elephantiformes Tassy, 1988
Family Palaeomastodontidae Andrews, 1906*
Family Phiomiidae Kalandadze and Rautian, 1992*
Elephantimorpha Tassy and Shoshani, 1997
Family <i>incertae sedis</i>
<i>Eritreum melakeghebrekristosi</i> gen. et sp. nov.*
Mammutida Tassy and Shoshani, 1997*
Family Mammutidae Hay, 1922*
Elephantida Tassy and Shoshani, 1997
Superfamily Gomphotherioidea Maglio, 1973 (in part)*
Family Gomphotheriidae Hay, 1922*
Superfamily Elephantoidae Gray, 1821
Family Stegodontidae Osborn, 1918*
Family Elephantidae Gray, 1821

Arrangements of taxa correspond to the branching pattern in Fig. 5. The nonranking applies to ranks or categories above the Superfamily level following Recommendation 29a and Article 36a of the International Commission of Zoological Nomenclature (11, 33), see text for details.

*Extinct taxon.

skeletal elements: length of m2 (4.5 cm), length of mandibular fragment (36 cm), length of humerus (45.2 cm), and length of incomplete ulna (38 cm). The reconstructed jaw of *E. melakeghebrekristosi* (Fig. 2) was reduced to the same scale as *P. parvus* by using the size of m2 as the measurement criterion for both animals. The humerus and the ulna were then fit to the scaled *P. parvus* with the calculated shoulder height of $127 \text{ cm} \pm 5 \text{ cm}$. Using these extrapolations, we estimate the shoulder height of *E. melakeghebrekristosi* to have been between 122 and 132 cm. By using Roth's (27) 12 equations to calculate the body mass of *Eritreum* from the extrapolated shoulder height, a range from 309.47 to 434.39 kg (average of 371.51 kg) was obtained. Benedict's (28) data on body mass of living elephants indicate that elephants with the same shoulder height have different weights, with variation of 20–40%. Thus, if we add 74 kg (20% of 372 kg) or 149 kg (40% of 372 kg) to 372 kg, we obtain a range of 446–521 kg (average 484 kg) for the estimated body mass of *E. melakeghebrekristosi*. It is noted, however, that *Eritreum* was not a fully grown individual (≈ 26 years old), and it probably would have achieved a larger size.

Results of character analysis [taxon $n = 40$; character $n = 125$; run in PAUP (29) and MacClade (30)] are depicted in Fig. 5. *E. melakeghebrekristosi* can be equally placed as the earliest offshoot of Elephantimorpha or of Elephantida (additional data and descriptions are available in Appendices A–D, which are published as supporting information on the PNAS web site). Both clades of Elephantida and Elephantimorpha have bootstrap values $>70\%$, which is indicative of reasonably good branch support (31). There are two good characters in support of *Eritreum* to join Elephantimorpha and only one good character in support of *Eritreum* to join Elephantida. In addition, the bootstrap value for Elephantimorpha with *Eritreum* is higher (91%) compared with the bootstrap value for Elephantida (78%). For these reasons, we favored the alternative that *Eritreum* is a member of the clade Elephantimorpha rather than of Elephantida.

The synapomorphies that *Eritreum* shares with Elephantimorpha include hypothesized horizontal tooth displacement (character 67 in Appendices B and C; this is a good character with consistency index, CI = 1.0, see Appendix D) and reduced cingulum on the anterolingual side of lower molars (character 46; CI = 1.0). The hypothesized horizontal tooth displacement of *Eritreum* would put this genus within the Elephantimorpha clade. A good synapomorphy that *Eritreum* shares with Elephan-

tida is the reduced angular process of dentary (character 96, CI = 1.0). Two other characters that might be used as possible synapomorphies for Elephantida, *Eritreum* included, are the complete and well delineated cloverleaf trefoil pattern on the pretrite side of the lower molars and lack of zygodont posttrite crest (characters 55 and 66, respectively); these characters are weak for this clade (details in *Appendix A*). Additional synapomorphies for these and other nodes in Fig. 5 are found in Shoshani (19) and Tassy (20) and in *Appendix D*.

The cladistic position of *Eritreum* in Fig. 5 is intermediate between *Phiomia* and *Palaeomastodon* on one hand, and between *Mammutida* and *Elephantida* on the other. The morphological (especially the horizontal tooth displacement) and temporal (late Oligocene) characters of *Eritreum* are well suited to fill this missing link gap, a hypothesis that was predicted ≈ 84 years ago (32).

Taxa depicted in Fig. 5 and Table 2 within the order Proboscidea and above the superfamily category level (Elephantiformes, Elephantimorpha, Mammutida, and Elephantida) are not assigned formal ranks or categories (following the International Code of Zoological Nomenclature (33), ICZN, see below), because to give them ranks would imply that we are certain of their phylogenetic position (11). For the same reason we did not assign a family rank to *E. melakeghebrekristosi*. Following the ICZN (Recommendation 29a and Article 36a), taxonomists have to abide by the rules for the Family Group, but it is not required to follow any rules for ranks above the Family Group; a Family Group includes categories of Superfamily, Family, Subfamily, Genus, and Tribe.

The hypothesis that *Phiomia* is the sister taxon to Elephantida and *Palaeomastodon* is the sister taxon to Mammutida (18) increases the tree length by 10 steps. Employing the parsimony principle, this hypothesis is rejected in favor of the more recent

hypothesis (19, 20) that *Phiomia* and *Palaeomastodon* are a sequence of sister taxa to Elephantimorpha as depicted in Fig. 5 and Table 2.

When viewed in a paleobiogeographical context, *E. melakeghebrekristosi* provides additional evidence that East Africa preserves major, previously unknown aspects of proboscidean differentiation during the transition from Paleogene to Neogene (late Oligocene to early Miocene), preceding the arrival of proboscidean immigrants from Eurasia (7). The proximity of Dogali, Eritrea, and Chilga, Ethiopia (only 200–250 km apart) (7,8) in this region lends credence to this hypothesis. Data presented here provide additional evidence for an African contribution to major events in proboscidean evolution and that East Africa in particular was an important Afro-Arabian setting of proboscidean evolution during the basal radiation of Elephantiformes (7, 8, 10, 17).

We appreciate help received from the Government of Eritrea. We extend special gratitude to Margarita Lopez-Martinez (Geology Department, Centro de Investigación Científica y de Educación Superior de Ensenada, B.C., México) for assistance in the $^{40}\text{Ar}/^{39}\text{Ar}$ dating on the DG-2 basalt sample. Credit for Fig. 1 is given to the Cartography Section (Department of Mines, Ministry of Mines and Energy, Asmara); for Figs. 2, 3, and 5 to G.H.M.; and for Fig. 4 to Bonnie Miljour (Museum of Paleontology, University of Michigan). Support for participation in this project comes from a Scott Turner Award, Department of Geological Sciences, University of Michigan (W.J.S.). The family of Ato Melake Ghebrekristos, Habtom Kahsay, Andrew Kitchen, Derek Wildman, Nicole Dehli, and Sandra Shoshani helped us in various aspects of this project. Cyrille Delmer and Emmanuel Gheerbrant (both from Muséum National d'Histoire Naturelle, Paris, France), Daryl P. Domning (Howard University, Washington, DC), and an anonymous reviewer made constructive comments on an earlier version of this paper.

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