FIFTEEN

Proboscidea

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Proboscideans are represented in modern Africa by the savanna and forest elephants *Loxodonta africana* and *L. cyclotis*, whose sub-Saharan distribution is increasingly fragmented and threatened (Kingdon, 1997). These species and the Asian elephant *Elephas maximus* constitute the last remnants of a once-flourishing order that enjoyed its maximum diversity in the Miocene (Shoshani and Tassy, 1996; Todd, 2006). More advanced species are easily recognized as proboscideans by their large, projecting tusks, enormous, pneumatized crania with retracted nasal apertures, massive bodies and graviportal postcranial adaptations, but archaic forms are identifiable to the order only by more subtle features (Mahboubi et al., 1986; Gheerbrant et al., 2002, 2005). Together with the extinct embrithopods and desmostylians, as well as sirenians and hyraxes, proboscideans belong to a larger grandorder, the Paenungulata (Simpson, 1945). In turn, paenungulates, elephant shrews, tenrecs, chrysochlorids, and aardvarks are placed in the superordinal clade Afrotheria (Asher et al., 2003; Tabuce et al., 2008; Asher and Seiffert, this volume, chap. 46), primarily based on the results of molecular analyses (e.g., Springer et al., 1997, 2003; Stanhope et al., 1998; Murphy et al., 2001; Scally et al., 2001) and more tenuously on morphological criteria (Asher et al., 2003; Sánchez-Villagra et al., 2007; Seiffert, 2007; Tabuce et al., 2007b; Asher and Lehmann, 2008).

The molecular data have been interpreted as suggesting Cretaceous origins for Afrotheria and an early Paleocene divergence of Proboscidea (e.g., Eizirik et al., 2001; Springer et al., 2003). Such ancient divergence estimates, however, seem overly reliant on assumptions of molecular rate homogeneity and are discordant with the paleontological evidence (Allard et al., 1999). In fact, the oldest unequivocal fossil evidence of proboscideans, from North Africa, dates only to the latest Paleocene (Gheerbrant et al., 2002, 2003; Gheerbrant, 2009). Subsequent to this first appearance, Proboscidea remained an endemic Afro-Arabian order until the late Oligocene (Antoine et al., 2003), and nearly all of its important phylogenetic events and adaptive radiations appear to have initiated in this part of the Old World.

Since the last major review of African Proboscidea (Coppens and Beden, 1978, Harris, 1978, and Coppens et al., 1978 in Maglio and Cooke, 1978), a wealth of novel comparative morphological and phylogenetic studies (e.g., Tassy, 1981, 1982, 1988, 1990; Court, 1994a, 1994b; Shoshani, 1996; Pickford, 2001; Sanders, 2004; Gheerbrant et al., 2005) have established a more reliable systematic context of proboscidean relationships, and intensified fieldwork has greatly expanded the number of proboscidean taxa known from the continent (table 15.1). In addition, improvements in radiometric dating and magnetostratigraphy (Feibel, 1999; Ludwig and Renne, 2000) have refined temporal calibration of African Cenozoic geological sequences. As a result, it is now possible to construct a far more informed and comprehensive classification of the order (table 15.1) and more precise synopses of African proboscidean chronostratigraphy and geographic distribution (tables 15.2–15.6). Along with similar progress in paleoecology, biogeography, climatology, and tectonics, these advances facilitate an increasingly accurate recounting of the interplay between changes in the physical landscape and environment, faunal composition, and African proboscidean evolution covering a span of 55 million years.

Proboscideans are one of the oldest surviving and most speciose mammalian groups to have inhabited Africa. The present account documents their evolutionary history, from small, condylarth-like phosphatheres through a series of adaptive diversifications and extinctions to the elephants, the largest and ecologically most dominant extant terrestrial megaherbivores (Eltringham, 1992; Shoshani and Tassy, 1996). Among the advances covered are the identification of a new, late Paleogene cohort of basal taxa (phosphatheres, daouitheres, numidotheres) that has led to a revised definition of Proboscidea and altered conceptions of its ancestral condition; unequivocal recognition of barytheres, deinotheres, and moeritheres as proboscideans; new information about the early fossil records of moeritheres, deinotheres, mammutids, and gomphotheres that phylogenetically connects them with more archaic proboscidean taxa; and isotopic support for adaptive hypotheses about the evolutionary transformation of the craniodental apparatus in elephants. Based on this account, it is clear that the broad sweep of proboscidean evolution is essentially an African story, and that proboscideans epitomize African Mammalia.

TABLE 15.1

Classification and temporal distribution of Afro-Arabian proboscideans

Starred taxa (*) are those identified since the last major review of African Proboscidea (in Maglio and Cooke, 1978).

Abbreviations: e, early; l, late; m, middle; E, Eocene; M, Miocene; O, Oligocene; P, Pliocene, Pal, Paleocene Pl, Pleistocene; R, Recent.

?Order Proboscidea Illiger, 1811	
Family	?Phosphatheriidae Gheerbrant, Sudre, Tassy, Amaghzaz, Bouya, and Iarochène, 2005
Genus	*Khamsaconus* Jaeger, Sigé, and Vianey-Liaud, 1993*
	Khamsaconus bulbosus Jaeger et al., 1993* eE
Order Proboscidea Illiger, 1811	
Suborder	"Plesielephantiformes" Shoshani et al., 2001a*
Family	incertae sedis Gheerbrant, 2009
Genus	*Eritherium* Gheerbrant, 2009*
	E. azzouzorum Gheerbrant, 2009* lPal
Family	Phosphatheriidae Gheerbrant, Sudre, Tassy, Amaghzaz, Bouya, and Iarochène, 2005*
Genus	*Phosphatherium* Gheerbrant, Sudre, and Cappetta, 1996*
	P. escuilliei Gheerbrant et al., 1996* eE
Family	incertae sedis
	Gen. et sp. indet., probably nov. O'Leary, Roberts, Bouare, Sissoko, and Tapanila, 2006* eE
Family	incertae sedis, probably nov. Gheerbrant et al., 2005*
Genus	*Daouitherium* Gheerbrant and Sudre in Gheerbrant et al., 2002*
	D. rebouli Gheerbrant and Sudre in Gheerbrant et al., 2002* eE
Superfamily Barytherioidea Andrews, 1906	
Family	Numidotheriidae Shoshani and Tassy, 1992*
Genus	*Numidotherium* Jaeger in Mahboubi et al., 1986*
	N. koholense Jaeger in Mahboubi et al., 1986* eE
	N. savagei Court, 1995* (= *Arcanotherium savagei* (Delmer, 2009)* lE or eO
Family	Barytheriidae Andrews, 1906
Genus	*Barytherium* Andrews, 1901b
	Barytherium sp. indet. (Birket Qarun, Fayum), probably nov.* lE
	B. grave (Andrews, 1901a) lE
Suborder	incertae sedis
Superfamily Moeritherioidea Andrews, 1906	
Family	Moeritheriidae Andrews, 1906
Genus	*Moeritherium* Andrews, 1901d
	Moeritherium sp. indet. (Birket Qarun, Fayum), probably nov.* lE
	M. chehbeurameuri Delmer, Mahboubi, Tabuce, and Tassy, 2006* lE
	M. lyonsi Andrews, 1901d lE
	M. trigodon Andrews, 1904b eO
Suborder	incertae sedis
Superfamily Deinotherioidea Bonaparte, 1845	
Family	Deinotheriidae Bonaparte, 1845
Subfamily	Chilgatheriinae Sanders, Kappelman, and Rasmussen, 2004*
Genus	*Chilgatherium* Sanders et al., 2004*
	C. harrisi Sanders et al., 2004* lO
Subfamily	Deinotheriinae Bonaparte, 1845
Genus	*Prodeinotherium* Éhik, 1930
	Prodeinotherium sp. indet. Rasmussen and Gutiérrez, 2009* lO
	P. hobleyi (Andrews, 1911) e–mM
Genus	*Deinotherium* Kaup, 1829
	D. bozasi Arambourg, 1934a lM–ePl
Suborder	Elephantiformes Tassy, 1988
Family	Palaeomastodontidae Andrews, 1906
Genus	*Palaeomastodon* Andrews, 1901d
	P. beadnelli Andrews, 1901d eO
	P. sp. nov. A Sanders et al., 2004* lO
	P. sp. nov. B Sanders et al., 2004* lO
Genus	*Phiomia* Andrews and Beadnell, 1902
	P. serridens Andrews and Beadnell, 1902 eO
	P. major Sanders et al., 2004* lO
Superfamily Elephantoidea Gray, 1821	
Family	Mammutidae Hay, 1922
Genus	*Losodokodon* Rasmussen and Gutiérrez, 2009*
	L. lodosokius Rasmussen and Gutiérrez, 2009* lO

Genus . . . . *Eozygodon* Tassy and Pickford, 1983*
E. morotoensis (Pickford and Tassy, 1980)* eM
Genus . . . . *Zygolophodon* Vacek, 1877
Z. aegyptensis Sanders and Miller, 2002* eM
Z. turicensis (Schinz, 1824) mM–?lP
Family . . . . incertae sedis
Genus . . . . incertae sedis
cf. *Gomphotherium* sp. nov. Sanders et al., 2004* lO
Genus. . . . . *Eritreum* Shoshani et al., 2007*
E. melakeghebrekristosi Shoshani et al., 2007* lO
Family . . . . Gomphotheriidae Hay, 1922
Subfamily. . . . . Gomphotheriinae Hay, 1922
Genus . . . . *Gomphotherium* Burmeister, 1837
Gomphotherium sp. (Mwiti) Tassy, 1979b* eM
G. angustidens libycum (Fourtau, 1918) e–mM
G. pygmaeus (Depéret, 1897) mM
Gomphotherium sp. indet. (“pygmy”) e–mM
Subfamily. . . . . Amebelodontinae Barbour, 1927
Genus . . . . *Progomphotherium* Pickford, 2003*
P. maraisi Pickford, 2003* eM
Genus . . . . *Archaeobelodon* Tassy, 1984*
cf. *Archaeobelodon* sp. Tassy, 1984* eM
A. filholi (Frick, 1933) e–mM
Genus . . . . *Afromastodon* Pickford, 2003*
A. coppensi Pickford, 2003* mM
Genus . . . . *Protanancus* Arambourg, 1945
P. macinnesi Arambourg, 1945 mM
Genus . . . . *Amebelodon* Barbour, 1927
A. cyrenaicus Gaziry, 1987b* lM or eP
Genus . . . . *Platybelodon* Borissiak, 1928
Platybelodon sp. Maglio, 1969a eM
Subfamily. . . . . Choerolophodontinae Gaziry, 1976
Genus . . . . *Afrochoerodon* Pickford, 2001*
A. kisumuensis (MacInnes, 1942) e–mM
Genus . . . . *Choerolophodon* Schlesinger, 1917
C. zaltaniensis Gaziry, 1987a* mM
C. ngorora (Maglio, 1974) m–lM
Subfamily. . . . . Tetralophodontinae Van der Maarel, 1932
Genus . . . . *Tetralophodon* Falconer, 1857
Tetralophodon sp. nov. Tsujikawa, 2005a* lM
Gen. et sp. indet. (tetralophodont form) Tassy, 1986* lM
Subfamily. . . . . Anancinae Hay, 1922
Genus . . . . *Anancus* Aymard, 1855
A. kenyensis (MacInnes, 1942) lM–eP
A. sp. nov. Sanders, in press* e–mP
A. capensis Sanders, 2007* lM or eP
A. petrocchii Coppens, 1965 lM or eP
A. osiris Arambourg, 1945 ?eP, lP
Family . . . . Stegodontidae Osborn, 1918
Genus . . . . *Stegodon* Falconer and Cautley, 1847
S. kaisensis Hopwood, 1939 lM–lP
Family . . . . Elephantidae Gray, 1821
Subfamily. . . . . Stegotetrabelodontinae Aguirre, 1969
Genus . . . . *Stegotetrabelodon* Petrocchi, 1941
S. syrticus Petrocchi, 1941 lM or eP
S. orbus Maglio, 1970a lM–eP
Subfamily . . . . Elephantinae Gray, 1821
Genus . . . . *Primelephas* Maglio, 1970a
P. korotorensis (Coppens, 1965) lM–eP
Genus . . . . *Stegodibelodon* Coppens, 1972
S. schneideri Coppens, 1972 ?eP
Genus . . . . *Loxodonta* Cuvier, 1825 (anonymous emendation, 1827)
L. adaurora Maglio, 1970a lM–lP
L. cookei Sanders, 2007* lM or eP
L. exoptata (Dietrich, 1941) eP–lP
L. atlantica (Pomel, 1879) ?lP–mPl
L. africana (Blumenbach, 1797) mPl–R
L. cyclotis (Matschie, 1900) R
Genus . . . . *Mammuthus* Brookes, 1828
M. subplanifrons (Osborn, 1928) ?lM–eP
M. africanavus (Arambourg, 1952) mP–lP
M. meridionalis (Nesti, 1825) ePl
Genus . . . . *Elephas* Linnaeus, 1758
E. ekorensis Maglio, 1970a eP–lP
E. recki Dietrich, 1915 eP–mPl
E. iolensis Pomel, 1895 mPl

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London (formerly the British Museum [Natural History]); CGM, Cairo Geological Museum; DOG, field number, Dogali, Eritrea; DPC, Duke University Primate Center; EP, Tanzanian National Museums (Eyasi Plateau); KBA, Kanam, Kenya; KI, Uganda Museum, Kampala (Kisegi-Nyabusosi); KK, field designation, Kakesio, Tanzania; KNM, National Museums of Kenya: -AT, Aterir; -BC, Chemeron; -KP, Kanapoi; -LT, Lothagam; -ME, Meswa Bridge; -MI, Mwiti; -MP, Mpesida Beds; -NK, Lemudong'o; -RU, Rusinga, Kenya; -TH, Tugen Hills; L followed by a number series (e.g., L 124-1), Ethiopian National Museums (Middle Awash); NAP, Napak, Uganda; NK, Uganda Museum, Kampala (Nkondo-Kaiso area, Nyawiega); PQ-L followed by a number series (e.g., SAM-PQ-L 2562), Langebaanweg; SAM, Iziko South African Museum; UM, University of Michigan Museum of Paleontology; WM, Tanzanian National Museums (Wembere-Manonga).

DENTAL ABBREVIATIONS

C or c, upper or lower canine; DI, upper deciduous incisor; di, lower deciduous incisor; DP or dp, deciduous premolar (e.g., DP3 is the upper third deciduous premolar and dp3 is the lower third deciduous premolar); ET, enamel thickness; H, height; HI, hypsodonty index, H × 100/W; I or i, incisor (e.g., I2 is the upper second incisor and i2 is the lower second incisor); L, length; l., left; LF, lamellar frequency, number of loph(id)s or plates per 100 mm; M or m, molar (e.g., M1 is the upper first molar, and m1 is the lower first molar); P or p, premolar (e.g., P3 is the upper third premolar, and p3 is lower third premolar); r., right; W, width; x, as in x3x, denotes a tooth comprised of three lophs with an anterior and posterior cingulum; +, indicates a missing portion of a tooth, and that the original dimension was greater.

DENTAL DEFINITIONS

ABAXIAL CONELET The outer, main cone in each half-loph(id) (Tassy, 1996a)

ACCESSORY CENTRAL CONULES Enamel-covered pillars situated at the anterior and/or posterior faces of the loph(id)s or plates, or in the transverse valleys, partially blocking them centrally (Tobien, 1973b)

ADAXIAL CONELET(S) The inner, or meso-, conelet(s) in each half-loph(id) (Tassy, 1996a)

ANANCOIDY Alternation of paired half-loph(id)s, in which lingual half-loph(id)s are anterior to buccal half-loph(id)s (Tobien, 1973b)

CHEVRONING The arrangement of half-loph(id)s to occlusally form an anteriorly pointing V, or chevron (Tobien, 1975)

CHOERODONTY Occurrence of accessory tubercles within transverse valleys (Osborn, 1942)

CRESCENTOIDS Enamel crests running from the apices of abaxial conelets of pretrite half-loph(id)s to the bottom of transverse valleys, and ending near the middle axis of the crown (Tobien, 1975)

INTERMEDIATE MOLARS DP4/dp4, M1/m1, and M2/m2

POSTTRITE Refers to the less worn half of each loph(id), which is lingual in lower and buccal in upper molars (Vacek, 1877)

PRETRITE Refers to the more worn half of each loph(id), which is buccal in lower and lingual in upper molars (Vacek, 1877)

PTYCHODONTY Plication or infolding of enamel borders with grooving of the sides of the molars (Osborn, 1942)

TREFOIL A tripartite enamel wear figure of a half-loph(id) formed by the conelets and associated anterior and posterior accessory central conules

ZYGODONT CRESTS Enamel crests running from the apices of the abaxial conelets of the posttrite half-loph(id)s to the bottom of the transverse valleys, and ending near the middle axis of the crown (Tobien, 1975).

Systematic Paleontology

?Order PROBOSCIDEA Illiger, 1811
Family ?PHOSPHATHERIIDAE Gheerbrant, Sudre, Tassy, Amaghzaz, Bouya, and Iarochène, 2005
Genus *KHAMSACONUS* Jaeger, Sigé, and Vianey-Liaud in Sudre et al., 1993
KHAMSACONUS BULBOSUS Jaeger, Sigé, and Vianey-Liaud in Sudre et al., 1993
Figures 15.1A and 15.1B

Age and Occurrence Early Eocene, northern Africa (table 15.2).

Diagnosis Gheerbrant et al. (1998). Smallest known tethythere and possible proboscidean, with DP4 especially similar to DP4 in *Phosphatherium escuilliei* in its incipient bilophodont structure, absence of conules, and presence of a large postentoconule, but much smaller and of more primitive construction, including a lower, more bunodont crown, poorly advanced lophodonty, larger postentoconule, and more differentiated preparacrista.

Description Sudre et al. (1993); Gheerbrant et al. (1998). Only a diminutive DP4 (L = 4.66 mm; W = 3.78 mm; figures 15.1A, 15.1B) is known for this species. This tooth is molariform with inflated, blunt cusps, and a distinct buccal cingulum. The protoloph and metaloph are incipient and separated by a distinct interloph, which is continuous with a deeply notched entoflexus. The protocone and hypocone are subequal in size. The postentoconule is large, bulbous, and located behind the hypocone and metacone. A well-developed distocrista links the postentoconule and postmetacrista, and a sizable preparacrista is connected to the parastyle.

Remarks There is a strong resemblance between DP4 in *Khamsaconus* and *Phosphatherium* (Gheerbrant et al., 1998), particularly in the absence of conules, occlusal outline, development of an incipient protoloph and metaloph, absence of a lingual cingulum, and reduced postprotocrista. The presence of a distocrista is a proboscidean feature. Although cladistic analysis suggests a close affinity between it and *Phosphatherium* (Gheerbrant et al., 2005), *Khamsaconus* is very primitive and too poorly known for definite referral to Proboscidea, and the spatial arrangement of its enamel types lacks the synapomorphic condition of the earliest definitive proboscideans (Tabuce et al., 2007a).

Order PROBOSCIDEA Illiger, 1811
Suborder "PLESIELEPHANTIFORMES" Shoshani, Shoshani, and Tassy, 2001a

"Plesielephantiform" proboscideans derive from the early Paleogene of a geographically isolated Afro-Arabia (Coryndon and Savage, 1973; Maglio, 1978; Holroyd and Maas, 1994; Rögl, 1998; Harzhauser et al., 2002). This proposed suborder includes primitive proboscideans that have bilophodont molars, such as phosphatheres and barytherioids (Shoshani et al., 2001a), and if valid should also incorporate daouitheres,

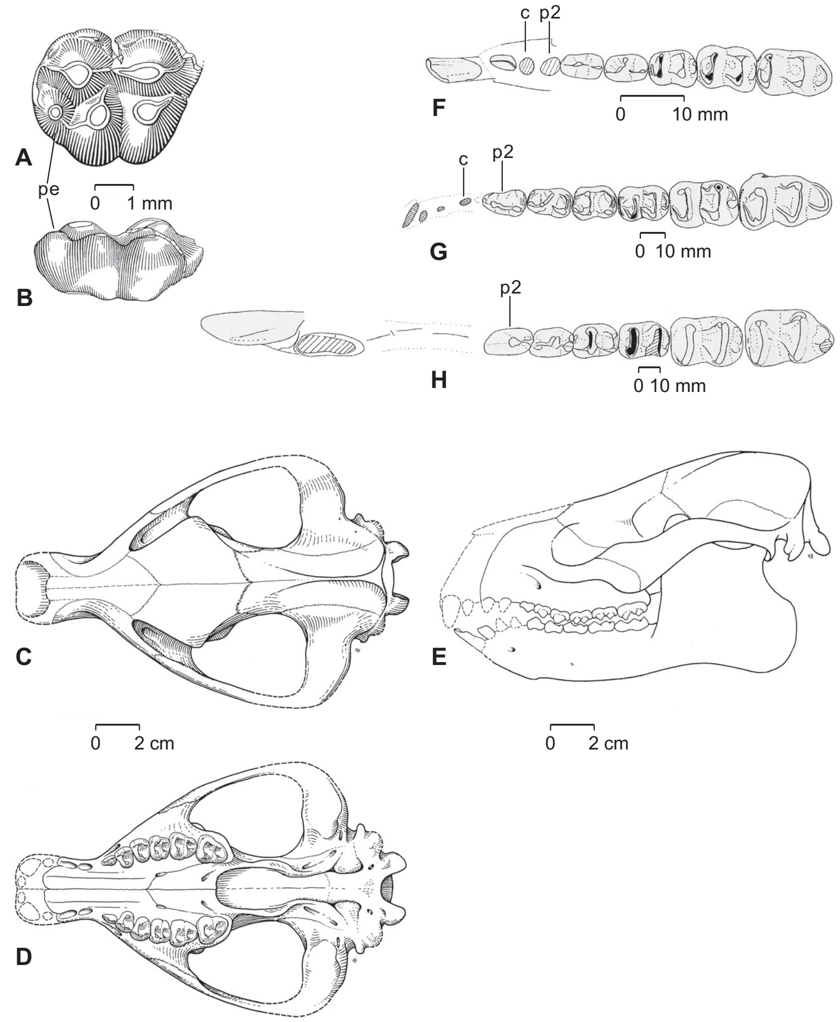

FIGURE 15.1 Aspects of ?proboscidean and "plesielephantiform" craniodental morphology. A) Right DP4, *Khamsaconus bulbosus*, occlusal view (Sudre et al., 1993: figure 2); anterior is to the left. B) Right DP4, *K. bulbosus*, lingual view. C) Cranial reconstruction, *Phosphatherium escuilliei*, dorsal view (Gheerbrant et al., 2005: figure 8A). D) Cranial reconstruction, *P. escuilliei*, ventral view (Gheerbrant et al., 2005: figure 8B). E) Skull reconstruction, *P. escuilliei*, lateral view (Gheerbrant et al., 2005: figure 8C). F) Reconstruction, left lower tooth series, *P. escuilliei*, occlusal view (Gheerbrant et al., 2005: figure 14). G) Reconstruction, right lower tooth series, *Daouitherium rebouli*, occlusal view (Gheerbrant et al., 2005: figure 27). H) Reconstruction, left lower tooth series, *Numidotherium koholense*, occlusal view (Gheerbrant et al., 2005: figure 27). A, B, copyright © Elsevier B. V. C-H, copyright permission, © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris.

ABBREVIATIONS: c, lower canine; p2, second lower premolar; pe, postentoconule.

which share gnathic and dental features with these taxa (Gheerbrant et al., 2002). Deinotheres, however, should not be included in "Plesielephantiformes," as they appear to be more closely related to Elephantiformes (Gheerbrant et al., 2005).

The primitive lophodont taxa included in "Plesielephantiformes" do not constitute a monophyletic clade, but rather consist of a sequential suite of stem groups at the base of more advanced proboscidean groups (Gheerbrant et al., 2005). However, the bilophodont molars of "Plesielephantiformes" (Shoshani et al., 2001a) indicate a lophodont ancestry for the Proboscidea (Gheerbrant et al., 2005). These taxa are notably distinguished from Elephantiformes and deinotheres by inferred absence of a trunk and lesser development of tusks. Furthermore, despite remarkable similarity between barythere and deinotheriine molars (Harris, 1978), the dental morphology of the earliest deinotheres indicates descent from a bunolophodont ancestor (Sanders et al., 2004) and independent acquisition of lophodonty.

Family PHOSPHATHERIIDAE Gheerbrant et al., 2005

This early Eocene African family is comprised of some of the oldest and most primitive recognizable proboscideans. Comprised of only one or two species (depending on the status of *Khamsaconus*), Phosphatheriidae is nonetheless among the best-known early representatives of the modern orders of ungulates, documented by good skull and dental material. The discovery of phosphatheres and relegation of South Asian anthracobunids, once thought to be archaic proboscideans (Wells and Gingerich, 1983; West, 1983, 1984; Gingerich et al., 1990; Kumar, 1991; Shoshani et al., 1996), to the phylogenetic fringes of Tethytheria (Gheerbrant et al., 2005; Tabuce

TABLE 15.2
Major occurrences and ages of Afro-Arabian "Plesielephantiformes" and moeritheres
? = Attribution or occurrence uncertain; alt. Alternatively.

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
?PROBOSCIDEA, EARLY EOCENE ?PHOSPHATHERIIDAE, EARLY EOCENE				
Khamsaconus bulbosus	N'Tagourt2, Ouarzazate Basin, Morocco (type)	Ait Ouarithane or Jbel Ta'louit Fm.	Early Eocene (early Ypresian, ca. 55 Ma)	Sudre et al., 1993
FAMILY INDET., LATE PALEOCENE				
Eritherium azzouzorum	NE Ouled Abdoun Basin, Morocco (type)	phosphate beds II	late Paleocene	Gheerbrant, 2009
PHOSPHATHERIIDAE, EARLY EOCENE				
Phosphatherium escuilliei	Grand Daoui Quarries, Ouled Abdoun Basin, Morocco (type)	"Intercalaire couches II-I"	Early Eocene (early Ypresian, ca. 55 Ma)	Gheerbrant et al., 1996, 1998, 2003, 2005; Gheerbrant, 1998
FAMILY INDET., EARLY EOCENE				
Gen. et sp. indet., probably nov.	Tamaguélelt, Mali	Phosphate beds, Tamaguélelt Formation	Early Eocene (Ypresian)	Patterson and Longbottom, 1989; Moody and Sutcliffe, 1993; O'Leary et al., 2006
FAMILY INDET., PROBABLY NOV., EARLY EOCENE				
Daouitherium rebouli	Grand Daoui Quarries, Ouled Abdoun Basin, Morocco (type)	"Intercalaire couches II-I"	Early Eocene (early Ypresian, ca. 55 Ma)	Gheerbrant et al., 2002
NUMIDOTHERIIDAE, EARLY EOCENE–LATE EOCENE OR EARLY OLIGOCENE				
Numidotherium koholense	El Kohol, Algeria (type)	El Kohol Fm.	Early Eocene (late Ypresian)	Mahboubi et al., 1984, 1986
Numidotherium savagei (= "*Barytherium* small species") (= "*Arcanotherium savagei*")	Dor el Talha (Dur at Talhah), Libya (type)	Evaporite Unit	Latest Eocene or early Oligocene	Arambourg and Magnier, 1961; Savage, 1969, 1971; Wight, 1980; Court, 1995; Shoshani et al., 1996; Le Blanc, 2000; Delmer, 2009
BARYTHERIIDAE, LATE EOCENE–EARLY OLIGOCENE				
Barytherium sp. indet.	Fayum, Egypt	Birket Qarun Fm.	Late Eocene, ~37 Ma, early Priabonian	Seiffert, 2006
Barytherium grave	Fayum, Egypt (type)	Qasr el Sagha Fm.	Late Eocene	Andrews, 1901a, 1901b, 1904b, 1906; Simons, 1968; Harris, 1978
	Dor el Talha (Dur at Talhah), Libya	Idam Unit	Early Oligocene	Arambourg and Magnier, 1961; Savage, 1969, 1971; Wight, 1980; Shoshani et al., 1996
?*Barytherium* sp. indet. ("cf. Barytherioidea")	Thaytiniti, Oman	Shizar Mb., Ashawq Fm.	Late Eocene, 33.7–33.3 Ma	Thomas et al., 1989, 1999; Seiffert, 2006

Taxon	Occurrence (Site, Locality)	Stratigraphic Unit	Age	Key References
MOERITHERIIDAE, LATE EOCENE–EARLY OLIGOCENE				
Moeritherium sp. indet.	Fayum, Egypt	Birket Qarun Fm.	Late Eocene, ~37 Ma, early Priabonian	Seiffert, 2006
Moeritherium chehbeurameuri	Bir el Ater, Algeria (type)	Sandy, fluvio-deltaic member	Late Eocene, ?Priabonian	Delmer et al., 2006
	?Kenchella, Algeria		Late Eocene, ?Priabonian	Pickford and Tassy, 1980; Delmer et al., 2006
Moeritherium lyonsi (including "*M. gracile*," "*M. ancestrale*," "*M. pharaonensis*," and "*M. latidens*")	Fayum, Egypt (type)	Qasr el Sagha Fm.	Late Eocene	Andrews, 1901a, 1901b, 1902, 1906; Matsumoto, 1923; Petronievics, 1923; Osborn, 1936; Deraniyagala, 1955; Coppens and Beden, 1978; Holroyd et al., 1996
	Dor el Talha (Dur at Talhah), Libya	Evaporite Unit	Latest Eocene or early Oligocene	Savage, 1971; Wight, 1980; Le Blanc, 2000
Moeritherium trigodon (including "*M. andrewsi*" and "*M. trigonodon*")	Fayum, Egypt (type)	Gebel el Qatrani Fm.	Early Oligocene, ca. 33–30 Ma	Andrews, 1904a, 1906; Schlosser, 1911; Matsumoto, 1923; Osborn, 1936; Coppens and Beden, 1978; Seiffert, 2006
	Dor el Talha (Dur at Talhah), Libya	Idam Unit	Early Oligocene	Savage, 1971; Wight, 1980; Le Blanc, 2000

et al., 2007b) have returned the focus on proboscidean origins to Africa.

Genus *PHOSPHATHERIUM* Gheerbrant, Sudre, and Cappetta, 1996

PHOSPHATHERIUM ESCUILLEI Gheerbrant, Sudre, and Cappetta, 1996

Figures 15.1C–15.1F, 15.2A, and 15.2B

Age and Occurrence Early Eocene, northern Africa (table 15.2).

Diagnosis Modified from Gheerbrant et al. (2005). Differs from *Khamsaconus* by larger size, smaller postentoconule in DP4, lower bunodonty, enamel type development (Tabuce et al., 2007), and more developed lophodonty. Distinct from other proboscideans in numerous primitive features of the skull and dentition, including: face twice as long as the braincase; long nasals located anteriorly on the cranium; very weakly pneumatized cranial bones; presence of hypoglossal foramen; strong postorbital constriction; low braincase; narrow mandibular corpus; short, unfused mandibular symphysis; dental formula; and small tooth size (figures 15.1C–15.1E, 15.2A, 15.2B). Substantially smaller than *Daouitherium*, with single-rooted p2, simpler lower premolars, lesser size difference between the molars, lower mandibular condyle, and narrower mandibular corpus.

Description Gheerbrant et al. (1998, 2005). The cranium is relatively long (L = 170 mm; W = 100–120 mm, H = 63 mm) and condylarth-like, with an elongated face, narrow snout, long, high maxillae (suggesting long nasals), and a large, unretracted nasal fossa (figures 15.1C–15.1E). The basicranium is moderately elevated above the level of the palate. Infraorbital foramina are large and slightly above the P2–P3 boundary. The development of the infraorbital fossa and foramen and high position of the maxilla suggest a mobile snout and upper lip. The orbit opens above P4, and exhibits a lacrimal foramen. The zygomatics extend broadly above P2–M2 and flare widely laterally. Strongly compressed bilaterally, the braincase has a small cerebral cavity, and is ornamented by salient sagittal and nuchal crests. The glenoid fossa is vast and supported by a very robust basis of the squamosal; these are probably proboscidean synapomorphies. There is a small but broad postglenoid process.

The dentary is brevirostrine, with the symphysis extending to p3, and coronoid process moderately high above a low condyle. Mandibular foramina are small, and positioned below c and p4–m1. The angular processes protrude behind the articular condyles as wide blades. Estimated length of the mandible is 110–115 mm.

The dental composition of *Phosphatherium* is very primitive, particularly in the inferred retention of P1 and c (or p1); the preferred dental formula is I3/2-C1/1-P4/3-M3/3 (figure 15.1F), and the most reasonable alternative is I3/2-C1/0-P4/4-M3/3 (Gheerbrant et al., 2005). The lower incisors are i1–2. Molars are bilophodont, with sharp, continuous loph(id)s. Molar size increases posteriorly through the series, most markedly between M1–M2 and m1–m2. In upper molars, the protoloph is wider than the

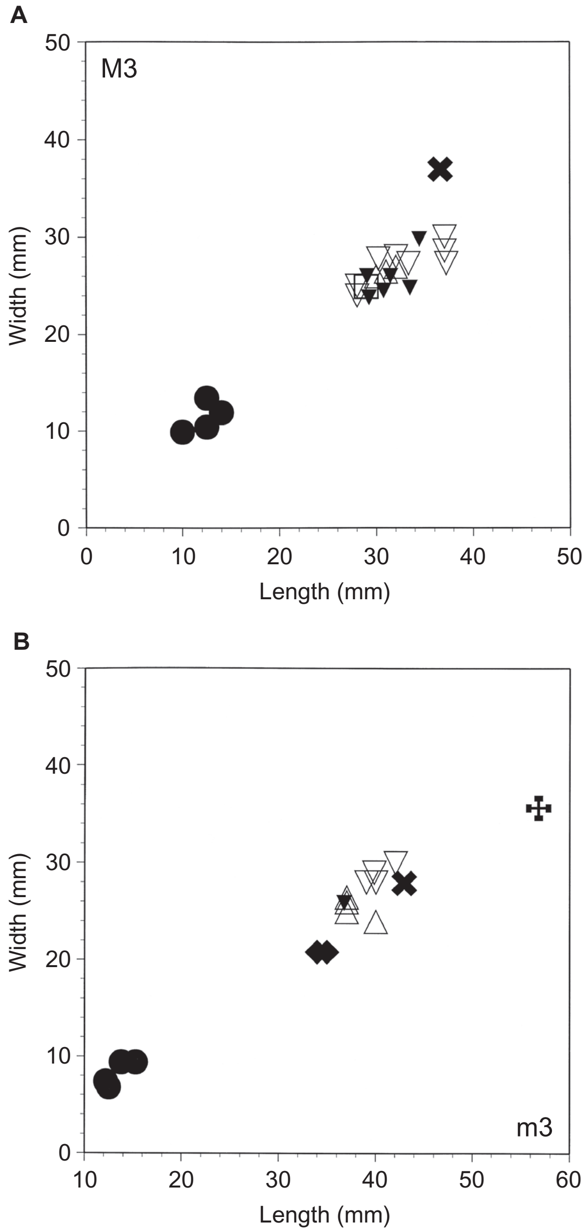

FIGURE 15.2 Bivariate plots of M3 (A) and m3 (B) crown length versus width in phosphatheres, daouitheres, numidotheres, and moeritheres. Comparative dimensions supplementing original measurements are from Andrews (1906), Matsumoto (1923), Tobien (1971), Mahboubi et al. (1986), Court (1995), Gheerbrant et al. (2002, 2005), and Delmer et al. (2006). Symbols: closed circle, *Phosphatherium escuilliei*; closed diamond, *Daouitherium rebouli*; X, *Numidotherium koholense*; cross, *Numidotherium savagei*; open square, *Moeritherium chehbeurameuri*; open inverted triangle, *M. lyonsi*; open triangle, *M. trigodon*.

metaloph. Lower molars have an elongate occlusal outline, with independent distocingulids. In m1–2, the distocingulid bears a hypoconulid and a variable entoconulid. In m3, the hypoconulid contributes to a pronounced third, distal lobe, but there is no distinct postentoconulid.

The lower central incisor is typically enlarged. Its crown is not very large, but the root is hypertrophied. The i2 is smaller than i1 and spatulate (figure 15.1F). Both are slightly procumbent. The p3 and p4 are similar: simple elongate teeth, each with a high, sharp, transversely compressed protoconid, cristiform talonid, and a long mesiodistal crest linking the trigonid to the talonid. The p4 is slightly larger and more molariform than p3. Length of p2–m3 is about 50 mm (Gheerbrant et al., 2005).

In the upper tooth row, P1 is separated from P2 by a short diastema. P2 is a small, simple, two-rooted tooth. It is elongated and sharp. Similar in size and morphology, P3 and P4 are molariform and three-rooted. Each has a well-developed protocone. Three buccal cusps are apparent: a large paracone, parastyle, and small metacone. A low, continuous protoloph links the protocone to the paracone. C and P1 were evidently medium- to large-sized teeth.

Remarks Except for *Eritherium* and possibly for *Khamsaconus*, *Phosphatherium* is the most primitive and smallest known proboscidean, with an estimated body mass of 10–15 kg (Gheerbrant et al., 1996; Gheerbrant, 1998). Despite its archaic morphology, *Phosphatherium* exhibits a number of proboscidean synapomorphies, including a well-developed zygomatic process of the maxillary contributing significantly to the lower border of the orbit and to the zygomatic arch, large pars mastoidea in the periotic, labial position of the hypoconulid, true lophodonty, enlarged i1, loss of i3 and p1 or c, and frontal contact with the squamosal (Gheerbrant et al., 1998, 2005). Coeval with *Khamsaconus*, *Daouitherium*, and an unnamed taxon from Mali, *Phosphatherium* belongs to the oldest radiation of the order. The existence of such diversity in North Africa at the base of the Eocene suggests that the origin of Proboscidea is even older and likely African (Gheerbrant et al., 1996). In fact, the recent discovery of the very diminutive *Eritherium azzouzorum* from the Ouled Abdoun basin, Morocco, dated to the late Paleocene (Gheerbrant, 2009), appears to confirm the deeper antiquity of proboscideans in Africa. The age and morphology of *Phosphatherium*, along with evidence from other early Eocene proboscideans, favor a true lophodont ancestral morphotype for Proboscidea (Gheerbrant et al., 1996, 1998).

Family INCERTAE SEDIS

GEN. ET SP. INDET., PROBABLY NOV. O'Leary, Roberts, Bouare, Sissoko, and Tapanila, 2006

Age and Occurrence Early Eocene, northern Africa (table 15.2).

Diagnosis O'Leary et al. (2006). Intermediate in size between *Phosphatherium* and *Daouitherium*.

Description O'Leary et al. (2006). Known only from a toothless dentary from Mali which preserves alveoli for p3–m3, the base of the ramus, and part of the symphysis. The ramus is rooted lateral to m3 and may have been posteriorly inclined. The corpus is robust with a thick symphysis that is strongly angled medially and extends posteriorly as far as the mesial edge of p4. Posteriorly, the corpus widens lateral to the alveoli for m2–3. Alveoli suggest that the teeth were double rooted. Three mandibular foramina are present, approximately along a horizontal line above midheight of the corpus.

Remarks The posterior expansion of the corpus is typical of basal proboscideans, and the position of the ramus resembles the condition in *Phosphatherium*, *Daouitherium*, and *Numidotherium koholense* (O'Leary et al., 2006). Although this specimen was originally placed in Numidotheriidae (O'Leary et al., 2006), its overall morphology more closely resembles that of phosphatheres and daouitheres.

Family INCERTAE SEDIS
Genus *DAOUITHERIUM* Gheerbrant and Sudre in Gheerbrant et al., 2002
DAOUITHERIUM REBOULI Gheerbrant and Sudre in Gheerbrant et al., 2002

Figures 15.1F, 15.1G, and 15.2B

Age and Occurrence Early Eocene, northern Africa (table 15.2).

Diagnosis Modified from Gheerbrant et al. (2002). Primitive proboscidean with bilophodont molars similar to those in other "plesielephantiforms." Differs from *Phosphatherium* and more closely resembles barytherioids in its larger tooth size (figure 15.2B), more molarized premolars, deeper mandibular corpus, and higher mandibular ramus. Distinguished from barytherioids by retention of four teeth anterior to p2 and its more primitive anterior dentition lacking a diastema in the dentary. The large hypoconids in p2 and p3, and extension of enamel onto the buccal side of anterior roots in its premolars, are probably autapomorphic.

Description Gheerbrant et al. (2002). No cranium is known for this species. The dentary is large (L ≥ 240 mm) and robust with a tall ramus (H ≥ 120 mm), and the height of the condyle above the tooth row (at least 50 mm) suggests that the basicranium was elevated well above the level of the palate. Although the symphysis is missing, crowding of anterior teeth indicates that the mandible was brevirostrine.

The lower dental formula is not known with certainty but may be I3-C1-P3-M3 (alternatively, I3-C0-P4-M3 or I2-C1-P4-M3), possibly preserving one lower incisor more than *Phosphatherium* (figures 15.1F, 15.G). The alveoli for the anterior dentition show that the first two incisors were upright and that i1 was larger than i2. Alveoli for i3 and the canine are diminutive. The p2 is a simple, cutting tooth with a triangular occlusal outline and similar in size to p3–4. The p3 is submolariform with a well-developed, basined talonid, and like p4 has a paraconid and metaconid. The p4 is molariform and nearly bilophodont, though the hypolophid is small.

Molar size increases from m1–3, especially between m1 and m2 (figure 15.1G). The hypolophid is wider than the protolophid. The occlusal outline is elongated. The first and second molars have well-developed distal cingulids; in m2 it bears a small hypoconulid behind the hypoconid, and in m3 this is extended to form a third, distal lobe. Length of p2–m3 = 140 mm.

The only upper tooth preserved for *Daouitherium* is a P3 or P4 with a submolariform morphology similar to that in *Phosphatherium*, but with a less distinct metacone.

Remarks *Daouitherium rebouli* is the oldest known large-bodied (tapir-sized) mammal from Africa and appears to have been sympatric with *Phosphatherium escuilliei*. Although its dental formula obviates descent from *Phosphatherium*, *Daouitherium* is in most other morphological aspects more derived than that taxon in the direction of the barytherioids (Gheerbrant et al., 2002, 2005). Its stratigraphic association with *Phosphatherium* was unexpected, but nevertheless strengthens the case for an old African origin and basal radiation of Proboscidea (Gheerbrant et al., 2002).

Superfamily BARYTHERIOIDEA Andrews, 1906

Numidotherium and *Barytherium* constitute this superfamily, which is united by similarities in craniodental and postcranial morphology. Shared postcranial features such as limb proportions and orientation of articular facets suggest similar postures, unaffected by significant differences in size and weight. *Barytherium* evolved to elephantine size, and even the more lightly built numidotheriids were larger than *Phosphatherium* and *Daouitherium*. Barytherioids contrast with phosphatheriids and daouitheres especially in the more derived configuration of their skulls and reduction in number of teeth, and occur later in geological time (table 15.2).

Family NUMIDOTHERIIDAE Shoshani and Tassy, 1992
Genus *NUMIDOTHERIUM* Jaeger in Mahboubi et al., 1986
NUMIDOTHERIUM KOHOLENSE Jaeger in Mahboubi et al., 1986

Figures 15.1H, 15.2A, 15.2B, 15.3A–15.3C

Age and Occurrence Early Eocene, northern Africa (table 15.2).

Diagnosis Based in part on Mahboubi et al. (1986). Smallest of the barytherioids (shoulder height about 1 m), with an elevated, moderately pneumatized cranium that broadens at the level of the frontal and has an anteriorly placed nasal opening. Resembles other "plesielephantiforms" in the bilophodonty of its molars, and *Barytherium* in particular in the relatively large size of its head. I1-3 and C are retained (the latter reduced), and the lower dentition anterior to p2 includes only two incisors (figure 15.1H). Tooth size greater than in *Phosphatherium* and *Daouitherium* (figures 15.2A, 15.2B).

Description Mahboubi et al. (1984, 1986); Court (1994a). The cranium is characterized by the great height of the glenoid and occipital condyles above the palatal plane, the vertical disposition of the basicranium (strongly angled relative to the palate), an extensive submaxillary fossa, projecting zygomatic apophyses, and upwardly sweeping, laterally flared zygomatic arches (figures 15.3A, 15.3B). Bounded posteriorly by postorbital apophyses of the frontal, the orbits are situated above P3–4 and are continuous with capacious temporal fossae. The nasal fossa is much higher than broad; the premaxillary is short and high, contributing to a narrow snout; and the infraorbital foramen is positioned low on the cranium, above P2. The nuchal planum is angled forward and bordered superiorly by a crest, but there is no sagittal crest.

The dentary has a massive, tall ramus that dominates the relatively slender corpus (figure 15.3C). The body of the dentary decreases markedly in height anterior to p2. There is a mandibular foramen low on the corpus, below p2–3, and a long diastema separates the cheek teeth from the incisors. The symphysis is extended posteriorly to p4.

The adult dental formula is I3/2-C1/0-P3/3-M3/3, with all teeth in occlusion simultaneously. The cheek teeth are preceded by three deciduous premolars in each jaw quadrant. In the upper dentition, I2 is the largest incisor and caninelike, with a high crown (about 45 mm) covered with thin enamel. A sizable diastema separates the incisors from the premolars. The P2 has a triangular outline, with a low protocone and single main outer cusp. The P3 is wider than long, with a feeble anterior transverse loph, and no hypocone; P4 is similar in morphology but larger. Upper molars are bilophodont, very tapirlike, and become progressively larger from M1 to M3. They are wider anteriorly than posteriorly. The two main buccal cusps in each possess a postparacrista and postmetacrista, respectively.

The most salient feature of the lower dentition is the tusklike, semiprocumbent central incisor (crown length about 35 mm; figures 15.1H, 15.3C). This and the smaller lateral

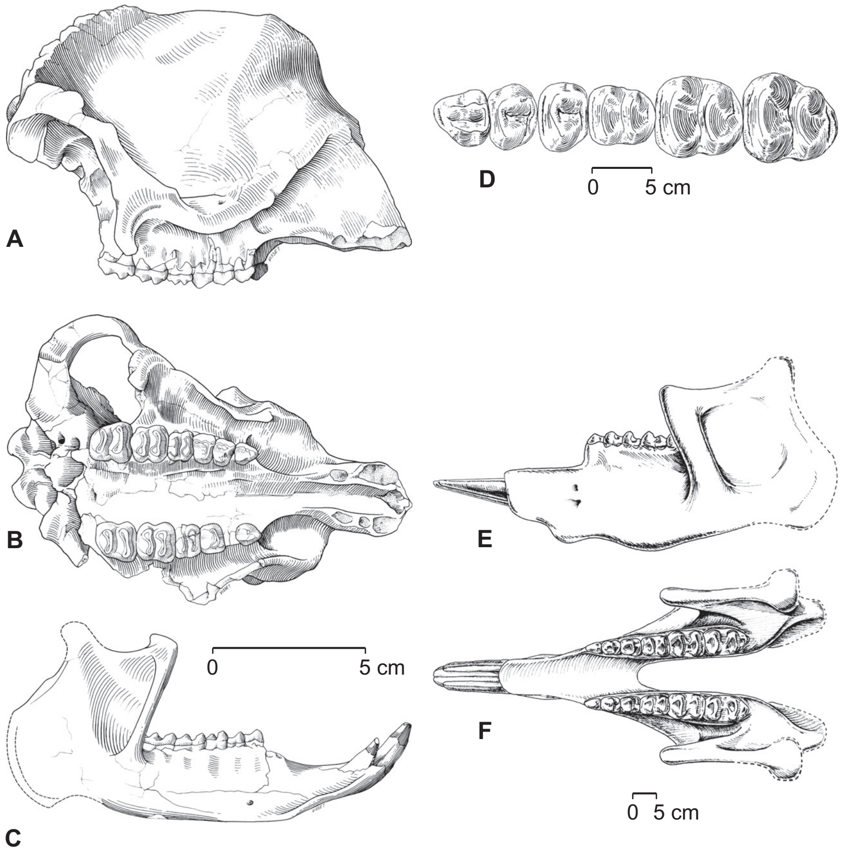

FIGURE 15.3 Aspects of barytherioid cranial, mandibular, and dental morphology. A) Cranium, *Numidotherium koholense*, lateral view (from Mahboubi et al., 1986:26, figure 4). B) Cranium, *N. koholense*, ventral view (Mahboubi et al., 1986:29, figure 7). C) Mandible, *Numidotherium koholense*, lateral view (Mahboubi et al., 1986:30, figure 8). D) Left P2–M3, *Barytherium grave*, occlusal view (Delmer, 2005). E) Mandibular reconstruction, *B. grave*, lateral view (Delmer, 2005). F) Mandibular reconstruction, *B. grave*, dorsal view (Delmer, 2005). A-C, with permission of E. Schweizerbart'sche Verlagsbuchhandlung OHG. D-F, courtesy of C. Delmer.

incisor are spatulate. The lateral incisor bears numerous distolabial serrations. The premolars are moerithere-like, longer than broad, with a prominent median cusp located anteriorly, and much lower hypoconids located posteriorly, on the buccal side of the talonids. Masticatory wear on the root of p2 suggests ventrolateral movement of the dentary, consistent with a behavior such as stripping leaves from slender branches (Court, 1993). The lower molars are rectangular in occlusal shape, with two main lophids and strong distocingulids closely appressed to the posterior lophid, except in m3, where there is a prominent posterior shelf or talonid. These molars increase in length from m1 to m3, especially between m1 and m2.

Postcranials are well represented and exhibit proportions and morphology typical of graviportal animals with plantigrade manus and pes. Nevertheless, to Court (1994a) the configuration of joint complexes suggested an ambulatory or semisprawling mode of locomotion, rather than a parasagittal recruitment of limbs. The humerus is equal in length (L = 300 mm) to the forearm bones and is robust in construction, with a strong deltoid ridge, deep olecranon fossa, broad epicondyles, and a superiorly oriented head. It primitively retains an entepicondylar foramen. The radius and ulna are distally fused in a pronated position. The ulnar olecranon process is very low and posteriorly projecting, permitting full extension of the forelimb. A fragmentary pelvic bone shows the acetabulum to be oriented downward. The ilium is broad. The femur is straight and much longer (405 mm) than the tibia (260 mm). Its head is globular, directed upward, and has a deep fovea. The neck is short and flattened, the greater trochanter is low and massive, and there is a third trochanter. The astragalus and calcaneum anticipate the morphology of these elements in the palaeomastodonts: the astragalus has a prominent medial process, the ectal facet is larger than the sustentacular facet, and the neck is short and narrow; in the calcaneum, the tuber calcanei is massive and connected to the rest of the element by a flattened neck.

Remarks *Numidotherium koholense* encompasses the most extensive early proboscidean fossil collection (Mahboubi et al., 1986; Court, 1994a). It was one of the largest terrestrial mammals of its time, initiating an impressive size increase among proboscideans. Nonetheless, it is much smaller than *Barytherium grave*, from which it also differs in having only two roots on its lower cheek teeth, and a nonbilophodont p4 (Mahboubi et al., 1986). In addition, in *B. grave* the proportions of the ectal and sustentacular facets are reversed, there is no entepicondylar foramen or fovea capitis femoris, the distal femoral condyles are more symmetrical, and the scapular coracoid process is more prominent (Andrews, 1906; Mahboubi et al., 1986; Court, 1994a).

The proboscidean status of *N. koholense* is marked by the strong development of I2 and i1, the elevation of the cranial glenoid and external auditory meatus, the structure of the astragalus, the anterior position of the orbit, and the absence of a condylian foramen (Mahboubi et al., 1984). Its position within Proboscidea vis-à-vis *Moeritherium* has been debated (e.g., Tassy and Shoshani, 1988; Tassy, 1996c), but it appears to belong to a more primitive radiation (Court, 1992, 1994a, 1994b; Gheerbrant et al., 2005). The presence of a subdivided perilymphatic foramen in the periotics of *N. koholense* and *Prorastomus sirenoides* (Court, 1990; Court and Jaeger, 1991), the most primitive known sirenian, shows that its absence in later sirenians and proboscideans is a convergence, rather than a synapomorphy (Court, 1994b).

NUMIDOTHERIUM SAVAGEI Court, 1995
Figure 15.2B

Partial Synonymy *Barytherium* sp., Harris, 1978; *Barytherium* sp., Wight, 1980; *Barytherium* sp. nov., Shoshani et al., 1989; small *Barytherium*, Shoshani et al., 1996.

Age and Occurrence Late Eocene or early Oligocene, northern Africa (table 15.2).

Diagnosis Based on Court (1995); Delmer (2005). Resembles *Numidotherium koholense* but was larger (1.0–1.5 m shoulder height and approximately 200 kg; Shoshani et al., 1996), with bigger teeth (figure 15.2B). In addition, the ramus is rooted more anteriorly on the dentary, the metaconid is better developed in the premolars, the ulna is more robust with a broader distal epiphysis, and the carpus is wider anteriorly than in *N. koholense*. The scapular supraglenoid tubercle is smaller than in *Barytherium grave* and lacks the medially deflected coracoid process of *N. koholense*.

Description Based in part on Court (1995). The dentary is fragmentary but corresponds closely with the morphology in *N. koholense*, except for the position of the ramus. It is less robust overall than the dentary of *Barytherium*.

The lower dental formula is inferred to be I2-C0-P3-M3, all in occlusion at the same time in adults. The central incisors are large, spatulate teeth (H = 52 mm; mesiodistal W = 31 mm; labiolingual W = 27 mm) with mammillons ornamenting the distolabial margins of the crown. Except for the worn apex, the crown is covered in enamel. The p2 is triangular in occlusal outline, with a high protoconid and accompanying metaconid, and a much lower talonid hosting a buccally placed hypoconid. The p3 is more rectangular with a more equal-sized protoconid and metaconid. In the p4, there is greater separation between the protoconid and metaconid, which form a true lophid connected by a transverse ridge. The molars are bilophodont, with the protolophid higher than the hypolophid, and well-developed distocristids. In m3, the distocristid is transformed into a large hypoconulid lobe. A prominent cristid descends anteromedially into the transverse valley from the hypoconid, in each molar.

M1–3 are bilophodont, each with prominent mesial and lingual cingulae and a weak entoflexus. The M3 has a strong distocrista, with a distinct paraconule and metaconule. M1–2 exhibit well-defined postparacrista, -protocrista, and -hypocrista.

Postcranially, *N. savagei* shares traits characteristic of *N. koholense*, including an ulnar styloid process, probable possession of a free os centrale in the carpus, flangelike development of a femoral third trochanter, and asymmetry of the femoral distal condyles.

Remarks This species was originally placed in *Barytherium* (Savage, 1969; Harris, 1978; Shoshani et al., 1989; Shoshani et al., 1996), which seemed reasonable prior to the discovery and full appreciation of the distinctness of *Numidotherium koholense,* and given the abundance of barytheres at the site (Savage, 1971). Morphological contrasts between *N. savagei* and *N. koholense* may be accounted for by an increase in body size but alternatively could mark intergeneric distinctions (Delmer, 2005, 2009). This is supported by the observation that *N. savagei* shares an arrangement of patterns of enamel types (“Schmelzmuster”) with elephantoids but not with *N. koholense* (Tabuce et al., 2007b). Finds associated with *N. savagei* include aquatic plants, fish, turtles, crocodiles, sirenians, and cetaceans (Shoshani et al., 1996), indicating an amphibious habitus for the species.

Family BARYTHERIIDAE Andrews, 1906
Genus *BARYTHERIUM* Andrews, 1901
BARYTHERIUM GRAVE (Andrews, 1901)
Figures 15.2, 15.3D–15.3F

Partial Synonymy *Bradytherium grave*, Andrews, 1901; *Barytherium grave*, Andrews, 1901.

Age and Occurrence Late Eocene–early Oligocene, northern Africa (table 15.2).

Diagnosis Based in part on Harris (1978); Court (1995); Shoshani et al. (1996). Very large-bodied animal (shoulder height approximately 2–3 m; body mass about 3–4 metric tons) with graviportal postcranial adaptations. Characterized by a massive dentary bearing a large, projecting central incisor, and a cranium with anteriorly located orbits, weakly retracted nares, and extensive pneumatization. Differs from *Numidotherium* in body size, the absence of an entepicondylar foramen on the humerus, more massive supraglenoid tubercle on the scapula, and radius not fused distally with the ulna. Teeth larger than other “plesielephantiforms” (compare figures 15.2 and 15.6).

Description Based in part on Andrews (1906); Harris (1978); Shoshani et al. (1996). Cranial remains of this species are fragmentary, but preserve enough structure to show that the zygomatics are robust and flaring; the orbits are set anterior to the premolars, and that the external auditory meatus sits at a level slightly higher than that of the orbit. There is a long diastema between P2 and the incisors. The cranium is elevated in a manner similar to that in *Numidotherium*, with the basicranium strongly angled relative to the palate.

The mandible is deep, with a fused, spoutlike symphysis extending posteriorly to p4 or m1 (figures 15.3E, 15.3F). The ramus is high and is rooted on the corpus at the level of m2. An extensive diastema separates the cheek teeth from the incisors. There are multiple mandibular foramina, the largest of which is located below p2 and above a sizable ventral tuberosity.

The dental formula is I2/2-C0/0-P3/3-M3/3, with all teeth simultaneously in occlusion in adults. The molars are bilophodont with strong distal cingulae(ids), except for m3, which has a prominent posterior heel (figures 15.3D, 15.3F). Cheek tooth occlusal morphology is very similar to that in *Numidotherium*. Incisors project from the lower jaw in a hippolike manner (figures 15.3E, 15.3F), with the central incisor dominant and shearing against the upper lateral incisor. The upper incisors are vertically inserted into their alveoli; the lateral incisor is chisel edged and much larger than I1, and it has enamel restricted to its mesial cutting face. In contrast to deinotheres, the cheek teeth of barytheres were not bifunctional, and served primarily in a simple shearing action (Harris, 1978), probably of leafy matter in a manner similar to that of numidotheres (see Court, 1993).

The most salient features of the postcranial skeleton of *Barytherium* include an enlarged, hooklike scapular coracoid process; sustentacular facet larger than the ectal facet in the astragalus, which exhibits a well-developed medial tubercle; massive humerus greatly expanded distally, longer than the forearm, and with a deep olecranon fossa; radius with an extensive articulation for the humerus and fixed (but not fused) on the ulna in a pronated position; long, anteroposteriorly flattened femur with a third trochanter; and carpal-metacarpal configuration suggesting plantigrade disposition of the manus. An incomplete calcaneum from Fayum, Egypt (UM 13973), has a large fibular facet facing obliquely upward and laterally, a prominent ventral tuberosity below the fibular facet, a transversely compressed neck, and it differs from the calcaneum of *Numidotherium* by its considerably more expanded tuber calcis.

Remarks Barytheres have had a complicated taxonomic history, in part due to their enigmatic morphology that has been more fully comprehended systematically only with the relatively recent discoveries of *Numidotherium* and *Phosphatherium*. First discovered in the Qasr el Sagha Formation, Fayum, Egypt, they were initially placed in a subdivision of Amblypoda, the Barypoda (later Barytheria; Andrews, 1904b), but soon thereafter were transferred to the Proboscidea (Andrews, 1906). Although eventually barytheres were placed in their own suborder within Proboscidea (Simpson, 1945), they have occasionally been excluded from the order (Osborn, 1936, 1942; Deraniyagala, 1955; Harris, 1978). More rigorous reassessment of barytheres, aided by an expanded fossil sample from Dor el Talha, Libya, has demonstrated unequivocally the proboscidean status of *Barytherium* (Tassy, 1982, 1985, 1996c). Features supporting this interpretation include pneumatization of the cranium, elevated nasal opening, hypertrophy of I2, and development of the medial astragalar tuberosity (Shoshani et al., 1996). Based on near identity of posterior molar morphology, barytheres and deinotheriines were regarded as closely affiliated (Harris, 1978), but new discoveries, including those of numidotheres (Mahboubi et al., 1984) and archaic deinotheres (Sanders et al., 2004), suggest a more distant relationship.

The size and slight retraction of the nares imply that *Barytherium* possessed an enlarged proboscis (but probably not a trunk). Recovery of fossil material from near-shore marine settings, and the forward position of the orbit are evidence of at least a semi-aquatic mode of life. The feet and anterior dentition of this odd proboscidean resemble those of hippos, further indicating that it may have occupied a similar, amphibious ecological niche. Stable isotopic analyses support this interpretation and indicate that they browsed on freshwater plants (Liu et al., 2008).

Suborder INCERTAE SEDIS
Superfamily MOERITHERIOIDEA Andrews, 1906
Family MOERITHERIIDAE Andrews, 1906
Figures 15.4A and 15.4B

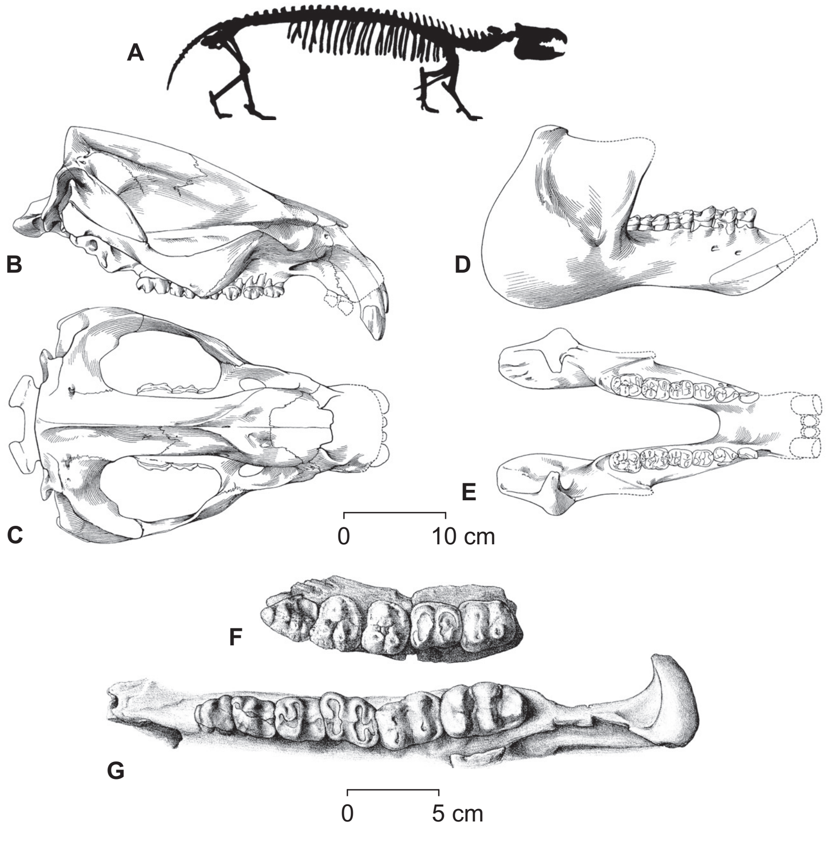

FIGURE 15.4 Aspects of moerithere skeletal and dental morphology. A) Silhouette, moerithere skeletal reconstruction, lateral view (Tobien, 1971: figure 7). B) Cranial reconstruction, *Moeritherium trigodon*, lateral view (Osborn, 1936: figure 42A). C) Cranial reconstruction, *M. trigodon*, dorsal view (Osborn, 1936: figure 42A1). D) Mandibular reconstruction, *M. trigodon*, lateral view (Osborn, 1936: figure 42B). E) Mandibular reconstruction, *M. trigodon*, dorsal view (Osborn, 1936: figure 42B1). F) Right P2–M2, occlusal view (Andrews, 1906: plate X, figure 2). G) Left dentary with p2–m3, occlusal view (Andrews, 1906: plate X, figure 1). A, © 2010 The Society of Vertebrate Paleontology. Reprinted and distributed with permission of the Society of Vertebrate Paleontology. B-E, courtesy of The American Museum of Natural History.

Moeritheres from late Eocene–early Oligocene localities in the Fayum, Egypt, were the first proboscideans with non-elephant-like morphology to be discovered (Andrews, 1901a, 1901b, 1901c, 1901d). Their unusual anatomy has hindered efforts to interpret their intraordinal relationships. Similar in size to a large pig (0.5–0.7 m tall at the shoulders), moeritheres were short-legged with an elongate body (figure 15.4A), with very short-faced, low crania (figure 15.4B; Coppens and Beden, 1978). To Andrews (1906), this unusual morphology indicated that moeritheres were familially distinct from the rest of Proboscidea, though he did note the structural antecendants of more advanced elephantiforms in their dentitions, particularly the enlarged second incisors (Andrews, 1901b).

Subsequently, morphological similarities to sirenians were emphasized, and the inclusion of moeritheres in the Proboscidea was debated (Osborn, 1909, 1921, 1936; Schlosser, 1911; Matsumoto, 1923; Deraniyagala, 1955, Tobien, 1971, Savage, 1976). The systematic uncertainties of moeritheres were acknowledged by Coppens and Beden (1978:333), who could not decide whether moeritheres should be attributed to "Proboscidea, Sirenia, or Desmostylia *incertae sedis*." It was only with the description of a new moerithere cranium from Dor el Talha, Libya, and cladistic treatment of the genus that these strange mammals were more firmly recognized as true proboscideans (Tassy, 1979b, 1981). Their proboscidean synapomorphies include hypertrophied I2s, raised external auditory openings, laterally flared zygomatic arches, an enlarged scapular coracoid process, pronated position of the radius, and a well-developed astragalar medial tubercle (Shoshani et al., 1996).

Found in marine and deltaic sediments along what was once the shoreline of the Tethys Sea (Shoshani et al., 1996; Delmer et al., 2006), moeritheres probably had an amphibious mode of life (Andrews, 1906; Matsumoto, 1923; Coppens and Beden, 1978), with feeding habits similar to those of sirenians or hippos (Osborn, 1909, 1936). Along with barytheres, isotopic analyses also indicate that moeritheres were at least semi-aquatic and consumed freshwater plants (Liu et al., 2008). They are represented by a lone genus, *Moeritherium*, exclusive to the late Paleogene of Africa (table 15.2; Shoshani et al., 1996). Although the genera *Anthracobune* and *Lamhidania* from the middle Eocene of South Asia were proposed to belong in Moeritheriidae (West, 1983, 1984), this hypothesis was overturned, and these taxa were reassigned to their own family, Anthracobunidae (Wells and Gingerich, 1983; Shoshani et al., 1996).

Moeritheres have long been considered to represent the ancestral stock of Proboscidea, due to their possession of primitive features such as elongate, low crania with anteriorly placed external nares and a sagittal crest (Matsumoto, 1923; Tassy and Shoshani, 1988; Shoshani et al., 1996; Tassy, 1996c). However, the discovery of phosphatheriids, daouitheres (Gheerbrant et al., 1996, 2002) and a new, primitive moerithere species with near-lophodont cheek teeth (Delmer et al., 2006), as well as further systematic study (Gheerbrant et al., 2005), reveal a more derived phylogenetic position for *Moeritherium*, with bunolophodonty of the cheek teeth of advanced species shared with elephantiforms.

Genus *MOERITHERIUM* Andrews, 1901
Figures 15.4B–15.4G

Moeritherium includes odd-shaped, semiaquatic species with anatomical convergences on sirenians, desmostylians (Tassy, 1981), and hippos (Osborn, 1936). Species from Fayum, Egypt, and Dor el Talhah, Libya, are especially close morphologically (Andrews, 1906; Matsumoto, 1923; Tassy, 1981). The cranium is remarkable, with its tubular, elongated cerebral cavity, long sagittal crest, and very forward position of the orbits (figures 15.4B, 15.4C). The latter are confluent with capacious temporal fossae and are not bounded posteriorly by postorbital processes. Pneumatization is weak. The auditory meatus is located higher on the cranium than the level of the orbit, but the basicranium is not very elevated or strongly angled relative to the palatal plane. Zygomatic arches are massive. The anterior, low placement of the nasal aperature indicates absence of a trunk (Osborn, 1936). Upper incisors and canines are vertically implanted in their alveoli.

The mandibles are brevirostrine and massively built (figure 15.4D), with lateral broadening of the corpus beginning at the level of p2 and increasing posteriorly. Symphyses are short, fused, and extended back to p3–p4 (figure 15.4E). The anterior border of the ramus is inclined anteriad, and rises at the level of m2–m3. The lower incisors are procumbent.

The moerithere dental formula is I3/2-C1/0-P3/3-M3/3. The permanent teeth were in occlusion simultaneously, and although the second upper and lower incisors are enlarged, they were not evergrowing. First incisors are reduced but evidently were functional, and I3 and the canine are also much reduced. Large diastemata are present between the anterior dentition and premolars. The P2 has an elongated, triangular occlusal outline and consists of an outer row of cusps with a narrow posterolingual shelf. P3 is more square in shape and has an anterior transverse loph and posterior buccal cusp; P4 is morphologically similar but slightly smaller. Upper and lower molars are tetrabunodont and bunolophodont or sublophodont (Osborn, 1936), with buccal and lingual half-loph(id)s separated by a median sulcus (figures 15.4F, 15.4G). There may be substantial postmetaloph ornamentation; M1–M2 metalophs exhibit an association of a convolute (*sensu* Gräf, 1957) and a distocrista, while only the latter is present in M3. Tooth size increases gradually from M1 to M3.

The p2 is small and narrow, with a raised anterior cusp and strong talonid exhibiting a median longitudinal crest. By comparison, the p3 and p4 are broader, with an anterior transverse lophid and a low, more extensive talonid. Lower premolars each have a protostylid (*sensu* Tassy, 1982) on the buccal side of the protolophid. The first and second lower molars have substantial distocingulids, and the m3 has a nascent third lophid (figure 15.4G).

In moeritheres, the postcranium is decidedly not graviportal. The femoral and humeral heads face medially and posteriorly, respectively, rather than upward. Limbs are short, relative to the length of the body (Coppens and Beden, 1978). There are at least 19 thoracic vertebrae, 4 lumbars, 3 fused sacrals, and a short tail (Andrews, 1906). The scapula bears a strong, hooked coracoid process, with supraspinous and infraspinous fossae of similar size; the humerus lacks an epicondylar crest; the radius appears to have been habitually pronated; the femur lacks a third trochanter and bears an enlarged lesser trochanter, which extends posteriorly; and the astragalus has a well-developed medial tubercle (Shoshani et al., 1996). The innominate resembles the pelvis of early sirenians, expecially in its expanded ischium and narrow ilium (Andrews, 1906). The olecranon process of the ulna is high and not reflected posteriorly, indicating a habitually flexed posture of the forearm on the humerus. Humeral length is documented as 240–260 mm, and femoral length as approximately 270 mm (Andrews, 1906).

MOERITHERIUM CHEHBEURAMEURI Delmer, Mahboubi, Tabuce and Tassy, 2006
Figure 15.2B

Partial Synonymy *Mastodon turicensis*, Gaudry, 1891; *Moeritherium trigodon*, Schlesinger, 1912.

Age and Occurrence Late Eocene, northern Africa (table 15.2).

Diagnosis Delmer et al. (2006). Small moerithere (figure 15.2B) with nearly lophodont dentition.

Description Delmer et al. (2006). This species is known from isolated teeth. I2 is diminutive, triangular in cross section, and has a complete covering of enamel and a linguodistally oriented wear facet. Molars are bilophodont and have thin, occasionally rugose enamel. P3 is very wide and lacks a buccal cingulum. The upper molars are nearly lophodont, with the main cusps only separated by a small groove in the center of each loph. They have a strong lingual cingulum, and incipient metaconule and postprotocrista. M1 is substantially smaller than M2. The p3 is poorly molarized and has a narrow protolophid, with the metaconid very small and not separable from the protoconid, and is slightly smaller than p4, which has a strongly developed metaconid. The m1 is rectangular in occlusal view, with no trace of a buccal cingulum. In occlusal view, p4 is longer than wide, with a small paraconid that is distinct from the protolophid.

Remarks The Bir el Ater, Algeria moerithere specimens assigned to *M. chehbeurameuri* are among the oldest yet recovered, with new, undescribed moerithere fossils from the Fayumian Birket Qarun Fm. probably slightly more ancient (table 15.2; Seiffert, 2006).

MOERITHERIUM LYONSI Andrews, 1901

Partial Synonymy *Moeritherium lyonsi*, Andrews, 1901a, 1901b, 1901c, 1901d; *M. gracile*, Andrews, 1902, 1906; *M. gracile*, Matsumoto, 1923; *M. ancestrale*, Petronievics, 1923; *M. pharoahensis*, Deraniyagala, 1955; *M. latidens*, Deraniyagala, 1955; *Moeritherium* cf. *lyonsi*, Tassy, 1981.

Age and Occurrence Late Eocene, northern Africa (table 15.2).

Diagnosis *Moeritherium lyonsi* (and *M. trigodon*) differ from *M. chehbeurameuri* in the more pronounced bunolophodonty of their cheek teeth. *Moeritherium gracile* is synonymized with *M. lyonsi* as a smaller morph of the same species, possibly due to sexual dimorphism (Coppens and Beden, 1978). Crania vary in length from 314 to 370 mm (Andrews, 1906; Tassy, 1981). *Moeritherium lyonsi* has been described as having relatively broader lower molars than *M. trigodon* (Osborn, 1936), but this may not be the case consistently. *Moeritherium lyonsi* is diagnosed by having simple upper molars with no accessory conules, and lower molars each with a low crescentoid blocking the transverse valley between the first and second lophids, and a talonid composed of a stout, centrally located cusp (Tobien, 1978).

MOERITHERIUM TRIGODON Andrews, 1904
Figures 15.2A and 15.2B

Partial Synonymy *Moeritherium trigonodon*, Andrews, 1906; *M. andrewsi,* Schlosser, 1911; *M. andrewsi*, Matsumoto, 1923.

Age and Occurrence Early Oligocene, northern Africa (table 15.2).

Diagnosis *M. andrewsi* is synonymized with *M. trigodon* as a larger morph of the same species, possibly due to sexual dimorphism (Coppens and Beden, 1978). The dental size variation within and between *M. lyonsi* and *M. trigodon* appears insubstantial (figures 15.2A, 15.2B) and could readily fit within the range of variation of other proboscidean species. In contrast, these species may be separable by differences in cranial size, as crania of the latter exceed 380 mm in length (Matsumoto, 1923), reaching an estimated measurement of 440 mm in the massively built skull of AMNH 13430. According to Tobien (1978), in *M. trigodon* M1 and M2 have a posterior fovea behind the second loph, there are zygodont crests on the posterior slope of the first loph in M2 and M3, and the posttrite half-lophs are more crestlike than in *M. lyonsi*. In addition, in *M. trigodon* the lower molars have more conelets in each half-lophid (Tobien, 1978).

Remarks Moeritheres are among the most unusual proboscideans, due to their specialized adaptations to a semi-aquatic life. Dental morphology in *M. chehbeurameuri* suggests derivation from a true lophodont taxon, though this remains to be confirmed in the moerithere tooth sample from the older Birket Qarun localities. Skull morphology in *M. lyonsi* and *M. trigodon* also points to an ancestry rooted in "Plesielephantiformes"; their crania are elongated versions of *Phosphatherium* crania. While the skeletal anatomy of these moeritheres appears too apomorphic to provide direct ancestry to elephantiforms, the bunolophodonty and occlusal organization of their molars anticipate the development of palaeomastodont cheek teeth. It has also been argued that deinothere cheek teeth were evolutionarily transformed from a moerithere-like bunolophodonty (Sanders et al., 2004), but there are no skulls available of the earliest deinotheres to further assess the degree of their relationship to moeritheres.

Suborder INCERTAE SEDIS
Superfamily DEINOTHERIOIDEA Bonaparte, 1845
Family DEINOTHERIIDAE Bonaparte, 1845
Figure 15.5

Deinotheres were specialized browsing proboscideans characterized by low-crowned, bilophodont cheek teeth (but trilophodont deciduous fourth premolars and first molars) and retention of only lower tusks (figure 15.5). Although Mio-Pliocene deinotheres were first documented from Africa in the early 1900s (Andrews, 1911; Haug, 1911), more ancient confamilials eluded search until their recovery in a late Oligocene mammalian fossil assemblage from Chilga, Ethiopia nearly a century later (Kappelman et al., 2003).

The presence of the small, primitive *Chilgatherium* in this assemblage (Sanders et al., 2004) points to an African origin for deinotheres. The larger *Prodeinotherium hobleyi* is characteristic of early Miocene assemblages of eastern Africa (Harris, 1978), but representatives of the genus thereafter migrated to Eurasia, where it is represented in European MN4 sites by *P. bavaricum* (Tassy, 1989) and in the early Miocene of South Asia by *P. pentapotamiae* (Forster Cooper, 1922). During the mid- to late Miocene, *Prodeinotherium* species were replaced by larger, more progressive species of *Deinotherium* (Harris, 1978; Sanders, 2003). *Deinotherium indicum* became extinct in South Asia around 7 Ma (Barry and Flynn, 1989), and *D. giganteum* (as well as *D. gigantissimum*, if it is a separate species from *D. giganteum*) died out in Europe by the end

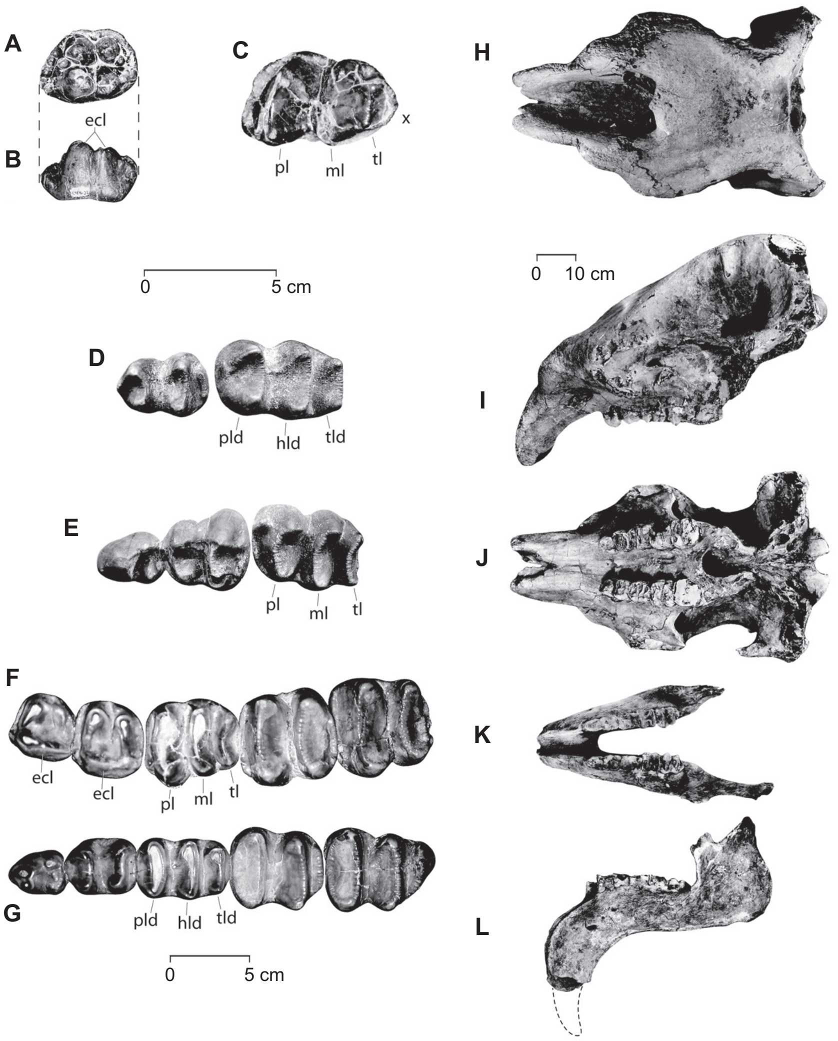

FIGURE 15.5 Aspects of deinotherioid cranial, mandibular, and dental morphology. Anterior is to the left in all specimens. A–E to same scale. A) Occlusal view, right P3, CH9-22, *Chilgatherium harrisi*. B) Buccal view, right P3, CH9-22, *C. harrisi*. C) Occlusal view, M3, CH35-1, *C. harrisi*. D) Occlusal view, dp3–4, NAP I 152′99, *Prodeinotherium hobleyi*. E) Occlusal view, DP2–4, NAP I 152′99, *P. hobleyi*. F) Occlusal view, P3–M3, M15713, *P. hobleyi*. G) Occlusal view, p3–m3, M15713, *P. hobleyi*. H) Dorsal view, cranium M26665, *P. hobleyi*. I) Right lateral view, cranium M26665, *P. hobleyi* (reversed). J) Ventral view, cranium M26665, *P. hobleyi*. K) Occlusal view, mandible with right and left p3–m3 6412:10, *P. hobleyi*. L) Right lateral view, mandible 6412:10, *P. hobleyi* (reversed), lower tusk reconstructed. H-L, courtesy of John Harris.

ABBREVIATIONS: ecl, ectoloph; hld, hypolophid; ml, metaloph; pl, protoloph; pld, protolophid; tl, tritoloph; tld, tritolophid; x, anterior or posterior cingulum(id).

of the Miocene (G. Markov, pers. comm.), but *D. bozasi* persisted in Africa until about 1 Ma (Beden, 1985; Behrensmeyer et al., 1995).

Despite having barythere-like posterior molars, deinotheres appear to be more closely related to elephantiforms than to “plesielephantiforms,” based on features such as hypolophid higher than the protolophid, presence of a hypocone in P3 and P4, and a suite of postcranial synapomorphies, including an enlarged ectal facet and reduced fibular facet in the astragalus (Harris, 1976; Tassy, 1996c; Gheerbrant et al., 2005). Harris's (1978) hypothesis that advanced, lophodont deinotheres derived from a moerithere-like bunolophodont ancestor is supported by the new finds from Chilga, Ethiopia (Sanders et al., 2004). In this revised phylogenetic scheme, deinothere lophodonty is secondarily derived in comparison with the condition of cheek teeth in “Plesielephantiformes” (Gheerbrant et al., 2005).

Subfamily CHILGATHERIINAE Sanders, Kappelman and Rasmussen, 2004

Figures 15.6A and 15.6B

These are diminutive deinotheres, with teeth smaller than in *Prodeinotherium* and *Deinotherium* (figures 15.6A, 15.6B). This monogeneric, monospecific subfamily also differs from deinotheriines in the following features: P3 with bunodont cusps that are more independent in occlusal distribution and that crowd the talonid basin and with a weakly formed ectoloph; m2 with poor expression of cristids; m2, m3, and M3 with at least incipient development of tritoloph(id)s. They are

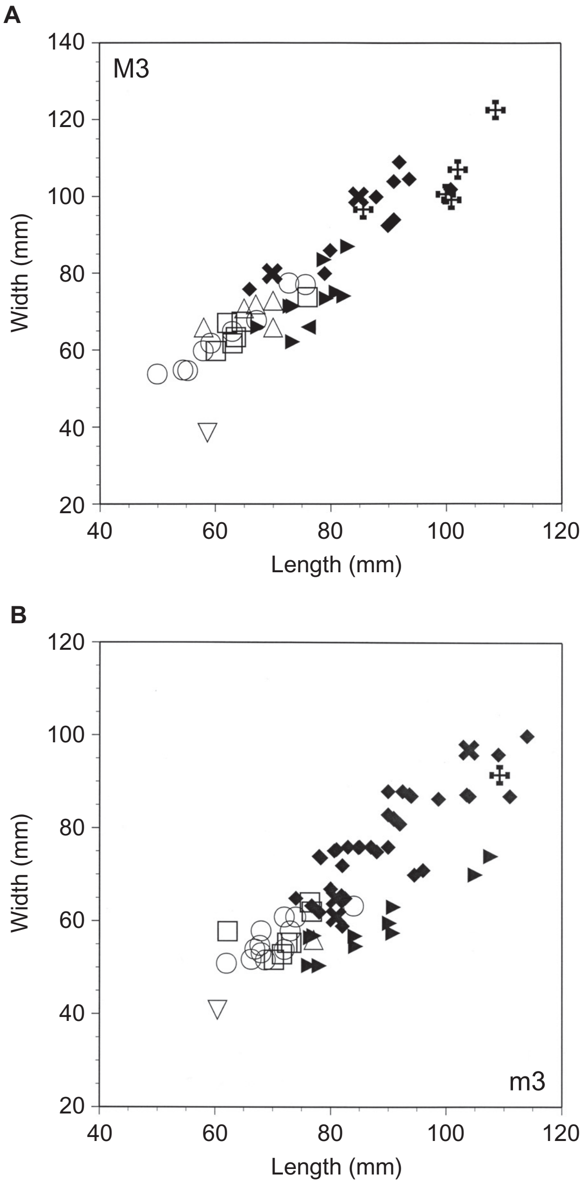

FIGURE 15.6 Bivariate plots of M3 (A) and m3 (B) crown length versus width in deinotheres and barytheres. Comparative dimensions supplementing original measurements are from Bachmann (1875), Weinsheimer (1883), Roger (1886), Andrews (1911), Forster Cooper (1922), Palmer (1924), Éhik (1930), MacInnes (1942), Gräf (1957), Sahni and Tripathi (1957), Symeonidis (1970), Harris (1973, 1977a, 1983, 1987a), Gaziry (1976), Tobien (1988), Tsoukala and Melentis (1994), Huttunen (2000), Sach and Heizmann (2001), Sanders (2003), Sanders et al. (2004), and Delmer (2005).

SYMBOLS: inverted open triangle, *Chilgatherium harrisi*; open circle, *Prodeinotherium hobleyi*; open square, *P. bavaricum* (including "*P. hungaricum*"); open triangle, *P. pentapotamiae*; cross, *Deinotherium bozasi*; closed diamond, *D. giganteum* (including "*D. levius*"); X, D. *indicum;* right-facing closed triangle, *Barytherium grave*; Q, left-facing closed triangle, *Barytherium* sp. indet. (Birket Qarun Fm., Fayum, Egypt).

distinguished from *Phosphatherium, Daouitherium, Numidotherium*, and *Barytherium* (all with bilophodont molars) by development of the m2 distocristid into a third lophid; by development of a postentoconulid in m3; by greater expression of lingual cusps (tetradonty) in P3 (shared with other deinotheres); and by the bunodont (P3) and bunolophodont condition of cheek teeth (Sanders et al., 2004).

Genus *CHILGATHERIUM* Sanders, Kappelman, and Rasmussen, 2004
CHILGATHERIUM HARRISI Sanders, Kappelman, and Rasmussen, 2004
Figures 15.5A–15.5C

Partial Synonymy Deinotheriidae gen. et sp. nov., Kappelman et al., 2003.

Age and Occurrence Late Oligocene, eastern Africa (table 15.3).

Diagnosis As for the subfamily.

Description Sanders et al. (2004). Known only by a small dental sample. In occlusal view, the P3 resembles those in deinotheriines, with an anterior projection on its buccal side, but the cusps are singularly inflated and transversely separated (figure 15.5A). The paracone and metacone abut to form a weak ectoloph, without mammillons (figure 15.5B). The M3 has buccolingually continuous lophs but retains individual cusps at the corners of these lophs. Its tritoloph is low, formed of a transverse row of apical digitations or mammillons, and is closely appressed to the metaloph (figure 15.5C). The metaloph and tritoloph enclose a small basin, as in some posterior molars of *Moeritherium* (Tobien, 1978). A low, arced cingulum is located distal to the tritoloph (figure 15.5C).

The m2 has a more substantial tritolophid, with no distocingulid posterior to it. In m3, the tritolophid is weakly expressed, and its outer cusps are only tenuously connected transversely by several mammillons. The main lophids in both m2 and m3 form transversely continuous crests anchored by individual cusps. Cristids are weakly developed in these teeth.

Remarks Cheek tooth morphology of *Chilgatherium* provides support for Harris's (1969, 1975, 1978) prescient hypothesis that the tritoloph of m1 developed by hypertrophy of the distocingulid, and that the tritoloph of M1 evolved via exaggeration of postmetaloph ornamentation.

Recovery of *Chilgatherium* from Chilga, Ethiopia fills part of the substantial temporal gap between early Miocene deinotheres and early Oligocene moeritheres, and extends the geological age of deinotheres about five million years farther back in time than was previously known. The similarly dated Erageleit Beds at Lothidok, Kenya (Boschetto et al., 1992; Leakey et al., 1995) have not yielded chilgatheres among its mammalian assemblage. The Chilga specimens also clarify the phylogenetic position of deinotheres as part of a separate, later proboscidean radiation from the initial diversification of "plesielephantiforms."

Subfamily DEINOTHERIINAE Bonaparte, 1845
Figures 15.5D–15.5J and 15.5L

Large herbivorous, graviportal proboscideans. Dental formulae 0.0.3/1.0.3 for deciduous teeth and 0.0.2.3/1.0.2.3 for the permanent dentition; second deciduous premolars and third premolars with well-developed external crests; deciduous fourth premolars and first molars trilophodont (figures 15.5D–15.5G); remainder of the cheek teeth bilophodont. Horizontal tooth replacement not developed so that all permanent teeth may be erupted at the same time (figure 15.5J). Mandibular symphysis and lower tusks curved downward so that the tusk tips are vertically or near vertically aligned (figure 15.5L). Skull low with deep rostral trough, retracted external nares, low orbit, inclined occiput, high occipital condyles, elongate paroccipital processes, and diploë (figures 15.5H, 15.5I).

TABLE 15.3
Major occurrences and ages of Afro-Arabian deinotheres
? = Attribution or occurrence uncertain; alt. Alternatively

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
DEINOTHERIIDAE, LATE–OLIGOCENE–EARLY PLEISTOCENE CHILGATHERIINAE, LATE OLIGOCENE				
Chilgatherium harrisi	Chilga, Ethiopia (type)	Chilga Fm.	Late Oligocene, 28–27 Ma	Kappelman et al., 2003; Sanders et al., 2004
DEINOTHERIINAE, EARLY MIOCENE–EARLY PLEISTOCENE				
Prodeinotherium hobleyi	Adi Ugri, Eritrea		Early Miocene	Vialli, 1966; Harris, 1978
	Sbeitla, Tunisia		Early Miocene	Vialli, 1966; Harris, 1978
	Tébessa, Algeria		Early Miocene	Brives, 1919; Vialli, 1966; Harris, 1978
	Moroto II, Uganda		>20.6 Ma (alt. ca. 17.5 Ma)	Bishop and Whyte, 1962; Bishop, 1967; Gebo et al., 1997; Pickford et al., 2003
	Arrisdrift, Namibia	Arrisdrift Gravel Fm.	ca. 20–19 Ma	Anonymous, 1976; Harris, 1977a
	Napak, Uganda		ca. 20.0 Ma	Bishop, 1964; Pickford, 2003; MacLatchy et al., 2006
	Koru, Kenya	Koru Fm.	19.5 Ma	Bishop, 1967; Harris, 1978; Pickford, 1986a
	Bukwa, Uganda		ca. 19.5–19.1 Ma (alt. 23.0 Ma)	Walker, 1969; Harris, 1978; Pickford, 1981; Drake et al., 1988; MacLatchy et al., 2006
	Samburu Hills, Kenya	Nachola Fm.	19.2–15.0 Ma	Pickford et al., 1987
	Wadi Moghara, Egypt	Moghara Fm.	18–17 Ma	Osborn, 1936; Harris, 1978; Miller, 1996, 1999
	Kalodirr, Kenya	Tiati Grits	18.0–16.0 Ma (alt. 17.7–16.6 Ma)	Drake et al., 1988
	Lothidok, Kenya	Moruorot Mb.	17.9–17.5 Ma	Bishop, 1967; Madden, 1972; Pickford, 1981; Tassy, 1986; Boschetto et al., 1992
	Karangu, Kenya (type)	Karangu Fm.	17.8 Ma (alt. 22.5 Ma)	Andrews, 1911; Bishop, 1967; Pickford, 1981; Tassy, 1986; Drake et al., 1988
	Rusinga, Kenya	Wayondo, Hiwegi, and Kulu Fms.	Slightly >17.8 Ma; 17.8 Ma; slightly <17.8 Ma	MacInnes 1942; Bishop, 1967; Harris, 1969, 1973; Pickford, 1981, 1986a; Tassy, 1986
	Mfwangano, Kenya	Hiwegi Fm.	17.8 Ma	Bishop, 1967; Pickford, 1986a; Drake et al., 1988
	Arongo Uyoma (Chianda), Kenya		Early Miocene, cf. Hiwegi and Kulu Fms.	Pickford, 1986a
	Buluk (West Stephanie), Kenya		>17.3 Ma (alt. 16–15 Ma)	Harris and Watkins, 1974; Pickford, 1981; McDougall and Watkins, 1985; Tassy, 1986

TABLE 15.3 (CONTINUED)

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
P. hobleyi continued	Mwiti, Kenya		ca. 17 Ma	Savage and Williamson, 1978; Tassy, 1986; Drake et al., 1988
	Loperot, Kenya		Early Miocene, ca. 17 Ma	Bishop, 1967; Savage and Williamson, 1978; Pickford, 1981; Leakey and Leakey, 1986; Tassy, 1986
	As Sarrar, Saudi Arabia	Dam Fm.	Early middle Miocene, ca. 17–15 Ma (alt. ca. 19–17 Ma)	Thomas et al., 1982; Whybrow and Clements, 1999
	Gebel Zelten, Libya	Qaret Jahanneam Mb., Marada Fm.	ca. 16.5 Ma	Savage and White, 1965; Savage, 1967; Harris, 1973; Sanders, 2008a
	Maboko, Kenya	Maboko Fm.	ca. 16 Ma (alt. slightly >14.7 Ma)	MacInnes, 1942; Bishop, 1967; Tassy, 1986; Feibel and Brown, 1991
	Majiwa, Kenya	Maboko Fm.	ca. 16 Ma (alt. slightly >14.7 Ma)	Andrews et al., 1981
	Muruyur, Tugen Hills, Kenya	Mururyur Beds	15.5 Ma (alt. 14.3–13.2 Ma)	Bishop, 1972; Harris, 1978
	Beni Mellal, Morocco		Middle Miocene, ca. 14 Ma	Lavocat, 1961; Remy, 1976
	Ft. Ternan, Kenya	Ft. Ternan Beds	14.0–13.9 Ma	Shipman et al., 1981; Cerling et al., 1997
	Ombo, Kenya		Middle Miocene	Bishop, 1967; Tassy, 1986
	?Sinda Area, Lower Semliki, Democratic Republic of Congo	Upper Mb., Sinda Beds	?Middle Miocene	Hooijer, 1963; Makinouchi et al., 1992; Yasui et al., 1992
	Alengerr, Kenya	Alengerr Beds	ca. 14.0–12.5 Ma	Bishop et al., 1971; Bishop, 1972; Harris, 1978
	Gebel Cherichera, Tunisia	Beglia Fm.	ca. 13-11 Ma	Harris, 1978
	Ngorora, Tugen Hills, Kenya	Ngorora Fm.	Within 13.0–8.5 Ma interval	Bishop et al., 1971; Hill et al., 1985; 1986; Hill, 2002
Prodeinotherium sp. indet.	Lothidok, Kenya	Eragaleit Beds	Late Oligocene, 27.5–24.0 Ma	Boschetto et al., 1992; Rasmussen and Gutiérrez, 2009
Deinotherium bozasi	Ngorora, Tugen Hills, Kenya	Ngorora Fm.	Within 13.0–8.5 Ma interval	Harris, 1983; Hill, 2002
	Nakali, Kenya	Nakali Fm.	9.9–9.8 Ma	Harris, 1978; Nakatsukasa et al., 2007
	Samburu Hills, Kenya	Lower, Upper Mbs., Namurungule Fm.	ca. 9.5 Ma	Nakaya et al., 1984; Sawada et al., 1998; Tsujikawa, 2005b
	Lothagam, Kenya	Lower and Upper Mbs., Nawata Fm.; Apak and Kaiyumung Mbs., Nachukui Fm.	At least 7.4–5.0 Ma; 6.5–5.0; ca. 3.5–3.0 Ma	McDougall and Feibel, 2003; Harris, 2003
	Middle Awash, Ethiopia	Adu Asa Fm., Kuseralee Mb., Sagantole Fm.	ca. 6.3–5.6 Ma; ca. 5.6–5.2 Ma	Kalb et al., 1982; Renne et al., 1999; WoldeGabriel et al., 2001; Haile-Selassie et al., 2004

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
D. bozasi continued	Tugen Hills, Kenya	Lukeino and Chemeron Fms.	6.2–5.6 Ma; 5.6–1.6 Ma	Bishop et al., 1971; Harris, 1977b; Hill et al., 1985, 1986; Deino et al., 2002; Hill, 2002
	Kanam East, West, Central, Kendu Bay, Kenya	Kanam Fm.	Late Miocene to early Pliocene	Kent, 1942; MacInnes, 1942; Pickford, 1986a; Ditchfield et al., 1999
	Bala, Homa Peninsula, Kenya	Kanam Fm.	Late Miocene to early Pliocene	Pickford, 1986a
	Wadi Natrun, Egypt		Late Miocene or early Pliocene	Bernor and Pavlakis, 1987
	Manonga Valley, Tanzania	Tinde Mb., Wembere-Manonga Fm.	ca. 5.0–4.5 Ma	Harrison and Baker, 1997; Sanders, 1997
	As Duma, Gona Western Margin, Ethiopia		4.5–4.3 Ma	Semaw et al., 2005
	Aramis, Middle Awash, Ethiopia	Aramis Mb., Sagantole Fm.	4.4 Ma	WoldeGabriel et al., 2001
	Kanapoi, Kenya	Kanapoi Fm.	4.2–4.1 Ma	Feibel 2003; Harris et al., 2003
	Omo, Ethiopia (type)	Mursi, Usno, and Shungura Fms.	>4.15 Ma; 3.6–2.7 Ma; 3.6–1.16 Ma	Arambourg, 1934a, 1934b; Arambourg et al., 1969; Beden, 1975, 1976; Brown et al., 1985; Feibel et al., 1989; Alemseged, 2003
	West Turkana, Kenya	Kataboi, Lomekwi, Lokalalei, Kalochoro, Kaitio, and Natoo Mbs., Nachukui Fm.	4.1–1.3 Ma	Harris et al., 1988a, 1988b; Brugal et al., 2003
	East Turkana (Ileret, Allia Bay, Koobi Fora), Kenya	Koobi Fora Fm.	4.1–1.3 Ma	Harris, 1983; Brown, 1994; Behrensmeyer et al., 1997
	Ekora, Kenya		ca. 4.0–3.75 Ma (slightly younger than 4.0 Ma)	Patterson et al., 1970; Behrensmeyer, 1976
	Karonga, Uraha, Malawi	Chiwondo Beds	ca. 4.0–3.0 Ma	Bromage et al., 1995
	Laetoli, Tanzania	Upper Unit, Laetolil Beds; ?Upper Ndolanya Beds	3.8–3.5 Ma; ?~2.7–2.6 Ma	Drake and Curtis, 1987; Harris, 1987a; Sanders, 2005
	Hadar, Ethiopia	Sidi Hakoma, Denen Dora, Kada Hadar Mbs., Hadar Fm.	3.4–2.9 Ma	Taieb et al., 1976; White et al., 1984; Bonnefille et al., 2004
	Praia de Morrungusu, Mozambique		Late Pliocene or early Pleistocene	Harris, 1977a
	Olduvai Gorge, Tanzania	Beds I and II	~1.87–1.6 Ma (alt. 2.10–1.75 Ma)	Osborn, 1936; Leakey, 1965; Hay, 1976; Tamrat et al., 1995
	Chesowanja, Kenya		>1.42 Ma	Bishop et al., 1971; Hooker and Miller, 1979; Beden, 1985
	Marsabit Road, Kenya		Early Pleistocene	Gentry and Gentry, 1969; Harris, 1978
	Kanjera, Kenya	Kanjera Fm.	1.1–1.0 Ma	Behrensmeyer et al., 1995

Genus *PRODEINOTHERIUM* Éhik, 1930

Figures 15.5I, 15.5L, 15.6A, and 15.6B

Small deinotheriines (figure 15.6A, 15.6B). Dental formulas as for the family; second–third molars with well-defined postmetaloph-posthypolophid ornamentation. Skull rostrum turned down parallel to the mandibular symphysis (figures 15.5I, 15.5L); rostral trough and external nares narrow; preorbital swelling close to top of orbit; external nares more anteriorly sited than in *Deinotherium* and nasal bones with anterior median projection; skull roof relatively longer and wider than in *Deinotherium*; occiput more vertically inclined; occipital condyles sited more ventrally than in *Deinotherium*; paroccipital processes shorter. Postcranial skeleton graviportally adapted; scapula with well-developed spine and stout acromion and metacromion; tarsals and carpals narrow but not dolichopodous.

PRODEINOTHERIUM HOBLEYI (Andrews, 1911)

Figures 15.5I, 15.5K, and 15.5L

Partial Synonymy *Deinotherium hobleyi*, Andrews, 1911; *D. cuvieri*, Brives, 1919; *D. bavaricum*, Gräf, 1957; *Deinotherium* sp., Vialli, 1966; *D. cuvieri*, Savage, 1967; *Prodeinotherium hobleyi*, Harris, 1973.

Age and Occurrence Early–middle Miocene, eastern and northern Africa (table 15.3).

Diagnosis Andrews (1911). Differs from *Prodeinotherium bavaricum* by having a more distinct anterointernal cusp in p3, a proportionately less elongate p4, and a more distinct outer tubercle in the talonid of m3.

Description Harris (1973, 1978). Crania are long and low, pneumatized, and have retracted nasal openings suggesting development of a proboscis. The nasals contact the frontal. Although the basicranium is not strongly angled upward, the occipital condyles and external auditory meatus on each side are much higher than the palatal plane (figure 15.5I). Skull length reaches 940 mm.

Mandibles have a broad, elongate, and strongly downcurved symphysis that extends posteriorly to p3 (figure 15.5K). The corpus appears relatively slender, and the ramus anteroposteriorly broad but not high, with a modestly sized coronoid process (figure 15.5L).

The i2s are oval in cross section and lack enamel; conversely, di2s are covered in enamel. These tusks are usually nearly vertical. Wear facets may be present near their tips, indicating their importance for food acquisition (but likely not for digging).

Abundant postcrania of *P. hobleyi* have been recovered from Gebel Zelten, Libya. These are readily distinguishable from those of elephantoids, but exhibit similar graviportal adaptations, such as the upward alignment of the femoral head and greater length of the femur than the tibia. Height of the spinous processes of the anterior thoracic vertebrae, projection of paroccipital processes, and elevation of the occipital condyles suggest that these deinotheres had greater capacity for rotation of the head about the condyles than did elephantoids. The astragalus is relatively narrower than in gomphotheres, but has larger, more vertically oriented articulations for the fibula and tibial malleolus, and an unusual, posteromedially projecting tubercle.

Remarks The oldest African deinotheriines are documented from late Oligocene- early Miocene sites in Kenya and Uganda (table 15.3). *Prodeinotherium hobleyi* is a common element of early Miocene assemblages of eastern Africa (table 15.3), but thereafter declines in relative abundance. The only known crania are from Gebel Zelten in Libya (Harris, 1973), but even partial deinotheriine molars are unmistakable by virtue of their size, smoothness, and characteristic loph(id) shape. *Prodeinotherium hobleyi* teeth of middle Miocene age (e.g., Maboko, Gebel Zelten) are slightly larger than those from the early Miocene (e.g., Rusinga). Most African deinotheriine teeth can be readily allocated to *P. hobleyi* or *D. bozasi* on an overall size basis, although some teeth or tooth fragments from late Miocene horizons appear to be of intermediate size, as might be expected in an ancestor-descendant relationship. Other recognized congeners include the type species from Europe, *Prodeinotherium bavaricum* (von Meyer, 1831), the South Asian species *P. pentapotamiae* (Falconer, 1868), and possibly *P. sinense* from China (Qiu et al., 2007).

Genus *DEINOTHERIUM* Kaup, 1829

Figures 15.6A and 15.6B

Large deinotheres (figures 15.6A, 15.6B). Dental formulae as for the family; tendency for the development of subsidiary styles on P3–4 and for simplification of the postmetaloph ornamentation of second and third molars, compared to *Prodeinotherium*. Rostral trough and external nares wide; preorbital swelling sited anteriorly on the rostrum; skull roof short and narrow at the temporal fossae; occiput slopes gently posteriorly; occipital condyles elevated above the level of the external auditory meatus; and paroccipital processes very elongate. Postcranial skeleton with supposed cursorial modifications to graviportal structure; scapular spine reduced with no acromion or metacromion; carpals and tarsals narrow with dolichopodous metapodials exhibiting functional tetradactyly (Harris, 1978).

DEINOTHERIUM BOZASI Arambourg, 1934

Partial Synonymy *Deinotherium giganteum*, Joleaud, 1928; *D. hopwoodi*, Osborn, 1936; *D. giganteum* var. *bozasi*, Dietrich, 1942.

Age and Occurrence Late Miocene–early Pleistocene, eastern and southern Africa (table 15.3).

Diagnosis Species of *Deinotherium* with teeth of similar size to *D. giganteum* but not found outside Africa. Skull rostrum turned steeply down comparable to that of *Prodeinotherium hobleyi* and in contrast to that of *D. giganteum*. External nares and rostral trough narrower than *D. giganteum*; preorbital swelling reduced and located just in advance of P3; occiput steeply inclined; nasal bones with slight anterior median projection. Mandibular symphysis flexed at right angles.

Description Harris (1976, 1978, 1983). The cranium of *D. bozasi* is relatively higher than in *Prodeinotherium*, with a shorter, narrower roof and more projecting paroccipital processes; cranial length is greater, exceeding 1,100 mm; and the external nares are more posteriorly retracted, suggesting the presence of a longer proboscis. Despite these differences, overall morphological affinity of the cranium of *D. bozasi* is closer to that of *P. hobleyi* than with Eurasian *Deinotherium*.

The mandibular symphysis is relatively shorter than in *P. hobleyi*, but more abruptly flexed downward, and lower tusks are slightly curved posteriorly under the symphysis.

In the astragalus, the posteromedial process is reduced and the tibial facet is flatter, relative to the condition in *Prodeinotherium*. Also, the scapular spine is reduced, and there is no metacromion or acromion. Reconstruction of manus configuration suggests that it was more digitigrade than in *Prodeinotherium*.

Remarks The first specimen of *D. bozasi* to be figured was an isolated upper molar from the Omo, Ethiopia, that Haug (1911) wrongly identified as a lower. Joleaud (1928) attributed the specimen to *Deinotherium giganteum*. Arambourg (1934a, 1934b) mentioned this tooth and described the lectotype mandible when creating the species *D. bozasi*. Subsequently, Haug's (1911) specimen was identified as the holotype of *D. bozasi* (Arambourg, 1947:249), but it was never accessioned into the collections of the Museum National d'Histoire Naturelle, and its current whereabouts are unknown (P. Tassy, pers. comm.).

Similar-aged species of *Deinotherium* are also known from Europe (type species *D. giganteum* Kaup, 1829, possibly including *D. gigantissimum* Stefanescu, 1892) and South Asia (*D. indicum* Falconer, 1845), but thus far only *Prodeinotherium* has been identified in Asia (Qiu et al., 2007). *Deinotherium bozasi* was the last surviving deinothere species and is only represented by small numbers of specimens. Most records are based on teeth or tooth fragments, but crania are known from the younger part of the Koobi Fora Formation (Harris, 1976) and from Hadar. The species has been recovered from as far south as Malawi (Bromage et al. 1995) and Mozambique (Harris, 1977a), but remains from North Africa have so far proved elusive (but see Remy, 1976). As with *Prodeinotherium hobleyi* teeth, there seems to be a temporal size gradient in *D. bozasi* teeth, those from Kanapoi being smaller than those from younger horizons in the Lake Turkana Basin (Harris et al., 2003). The last occurrences of *D. bozasi* appear to have been in Omo Shungura Member K (Beden, 1985) and at Kanjera (Behrensmeyer et al., 1995).

The low-crowned, lophodont teeth of deinotheres are superficially similar to those of tapirs. The lophs have beveled cutting edges that are maintained, though at different angles, throughout the life of the individual for processing the food prior to digestion (Harris 1975). There is an overall increase in size from the earliest representatives of *Prodeinotherium* to the latest representatives of *Deinotherium,* but deinotheriine teeth remain essentially unchanged in morphology from the early Miocene to the early Pleistocene. The conservative nature of their low-crowned lophodont teeth suggests that deinotheriines were well adapted to a browsing diet. Stable isotope analysis confirms that deinotheriines maintained a C_3 diet from their earliest record until their extinction in the early Pleistocene, thereby contrasting with the anancine gomphotheres and elephantids that transitioned to a C_4 diet during the late Miocene (Cerling et al. 2005).

Tobien (1962) noted that the manus and pes of *Deinotherium giganteum* were narrower than those of contemporary elephantoids, and suggested that this feature was a cursorial adaptation. However, this seems less likely in the face of Christiansen's (2004) interpretation that *Deinotherium* was appreciably larger than extant elephants, approaching the size of *Mammuthus trogontherii*, and that the largest individuals of *D. giganteum* would have reached 20,000 kg. Even though their conservative brachyodont teeth suggest that that deinotheriines had a more nutritious diet and greater digestive efficiency than extant elephants, they would have required a substantial amount of daily fodder. Craniodental features, including modest sized lower tusks and a probably short proboscis, suggest that deinotheres were acquiring this forage in jungle and densely vegetated gallery forest habitats (Harris, 1978). This may explain why *D. bozasi* is not found in the more arid northern and southern portions of the continent and why the species became extinct as equatorial habitats became more open and drier. It may also explain why only small numbers of deinotheres are encountered at fossiliferous localities after the early Miocene.

Suborder ELEPHANTIFORMES Tassy, 1988

Elephantiformes consists of palaeomastodonts and elephantoids (mammutids, gomphotheres, stegodonts, and elephants). These elephant-like taxa became the dominant proboscideans in Afro-Arabia during the late Paleogene-Neogene, supplanting numidotheres, barytheres, and moeritheres. United by elongation of the face, posterior shift of the orbits and retraction of the nasal opening (signaling the development of a trunk), and elongation of the mandibular symphysis (Tassy, 1994b), the group is also characterized by trends for increase in body size, expansion of cranial diploë, and impressive enlargement and projection of tusks. Despite their remarkable morphology, and in contrast to their striking diversity and nearly worldwide dispersal during the Miocene (Shoshani and Tassy, 1996; Todd, 2006), Elephantiformes survives today only as Asian and African elephants, the last of the proboscideans.

Family PALAEOMASTODONTIDAE Andrews, 1906

Palaeomastodonts of the Afro-Arabian Oligocene (table 15.4) represent the first comprehensive appearance of elephant-like morphology among proboscideans. Of considerable dimensions, ranging in size from slightly larger than moeritheres to the magnitude of modern Asian elephants (Andrews, 1906; Christiansen, 2004), their postcranial skeletons are correspondingly graviportal (Andrews, 1906).

Palaeomastodont skulls are primitive, with small, low braincases, sagittal crests, and modest pneumatization (Andrews, 1906, 1908). More advanced features shared with elephantoids include short nasals, retraction of the nasal aperature, and backward shift of the orbits to a position above the molars, consistent with the presence of at least a small trunk. Occipital condyles project markedly posteriorly and are strongly convex dorsoventrally, suggesting that the head was capable of moving over a wide vertical arc (Andrews, 1906).

The palaeomastodont dental formula is I1/1-C0/0-P3/2-M3/3, preceded in each jaw quadrant by three deciduous premolars and a "milk" tusk (Andrews, 1906, 1908). Adult teeth were in occlusion simultaneously. Their molars are bunolophodont and very brachyodont, and basically three-lophed.

Palaeomastodont dentaries are conjoined anteriorly by an elongated, nearly straight symphysis which projects beyond the rostrum. Their i2s form moderate-sized, procumbent tusks closely appressed to one another in the midline, and their I2s are oriented down and slightly laterally. The former have a flattened, pyriform shape in cross section; the latter have a lateral enamel band and are more rounded and wider dorsally than ventrally. There are extensive diastemas between the tusks and the anteriormost premolars. Their low-crowned teeth and existence in well-watered forested and woodland conditions (Wight, 1980; Bown et al., 1982; Olson and Rasmussen, 1986; Pickford, 1987b; Bown and Kraus, 1988; Gagnon, 1997; Jacobs et al., 2005) suggest that palaeomastodonts were browsers.

Palaeomastodont taxonomy has remained unstable since their initial discovery in the early 1900s (Moustafa, 1974a,

TABLE 15.4

Major occurrences and ages of Afro-Arabian palaeomastodonts

? = Attribution or occurrence uncertain; alt. Alternatively.

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
PALAEOMASTODONTIDAE, ?LATEST EOCENE–LATE OLIGOCENE				
Palaeomastodon beadnelli (including *"P. parvus"* and *"P. intermedius"*)	Fayum, Egypt (type)	Gebel el Qatrani Fm.	Early Oligocene, ca. 33–30 Ma	Andrews, 1901b, 1905, 1906; Matsumoto, 1922, 1924; Simons, 1968; Seiffert, 2006
Palaeomastodon sp. nov. A	Chilga, Ethiopia	Chilga Fm.	Late Oligocene, 28–27 Ma	Kappelman et al., 2003; Sanders et al., 2004
Palaeomastodon sp. nov. B	Chilga, Ethiopia	Chilga Fm.	Late Oligocene, 28–27 Ma	Kappelman et al., 2003; Sanders et al., 2004
Palaeomastodon sp. indet.	Zella, Libya		?Early Oligocene	Arambourg and Magnier, 1961; Savage, 1971
Phiomia serridens (including "*Ph. minor,*" "*Ph. wintoni,*" and "*Ph. osborni*")	Fayum, Egypt (type)	Gebel el Qatrani Fm.	Early Oligocene, ca. 33–30 ma	Andrews and Beadnell, 1902; Andrews, 1904a, 1905, 1906; Matsumoto, 1922, 1924; Simons, 1968; Seiffert, 2006
	Zella, Libya		?Early Oligocene	Arambourg and Magnier, 1961; Savage, 1971
(*"Ph. minor"* and *"Ph. wintoni")*	Dor el Talha (Dur at Talhah), Libya	Idam Unit	Early Oligocene	Savage, 1971; Wight, 1980; LeBlanc, 2000
("*Ph. osborni*")	Gebel Bon Gobrine, Tunisia		?Early Oligocene (alt. late Oligocene)	Arambourg and Burollet, 1962
Phiomia major	Chilga, Ethiopia (type)	Chilga Fm.	Late Oligocene, 28–27 Ma	Kappelman et al., 2003; Sanders et al., 2004
Phiomia sp. indet.	Dor el Talha (Dur at Talhah), Libya	Evaporite Unit	Latest Eocene or early Oligocene	Savage, 1971; Wight, 1980; LeBlanc, 2000
	?Malembe, Angola		Early Oligocene	Pickford, 1986a, 1987a
	Taqah, Oman	Shizar Mb., Ashawq Fm.	Early Oligocene, 31.5–31.0 Ma	Thomas et al., 1999; Whybrow and Clements, 1999; Seiffert, 2006

1974b; El-Khashab, 1979). Known predominantly from the Fayum, Egypt, palaeomastodonts have alternatively been placed largely or completely in a single genus, *Palaeomastodon* (e.g., Andrews, 1906; Lehmann, 1950; Coppens et al., 1978), separated among a number of species in two genera, *Palaeomastodon* and *Phiomia* (e.g., Schlosser, 1905, 1911; Matsumoto, 1922, 1924; Osborn, 1936; Tobien, 1971, 1978; Moustafa, 1974b; El-Khashab, 1979), and have been further divided at even higher taxonomic levels (Moustafa, 1974b; Kalandadze and Rautian, 1992; McKenna and Bell, 1997; Shoshani and Tassy, 2005).

A number of hypotheses have also been proposed about the phylogenetic relationships of palaeomastodonts. In the most prominent of these, *Palaeomastodon* was considered ancestral to mammutids, and *Phiomia* ancestral to gomphotheriid elephantoids (Matsumoto, 1924; Tobien, 1971, 1978), while others posited a special ancestor-descendant relationship between *Phiomia* and amebelodonts (Osborn, 1919, 1936; Borissiak, 1929; Tobien, 1973a). Most recent, parsimony-based treatments of proboscidean phylogeny have rejected these ideas and recognized *Phiomia* and elephantoids, including mammutids, as sister taxa, and ranked *Palaeomastodon* as their immediate outgroup (Tassy, 1994b, 1996c; Shoshani, 1996).

Genus *PALAEOMASTODON* Andrews, 1901

PALAEOMASTODON BEADNELLI Andrews, 1901

Figures 15.7A, 15.7B, 15.8A, and 15.8B

Partial Synonymy Palaeomastodon parvus, Andrews, 1905; *P. barroisi* (in part), Pontier, 1907; *P. intermedius*, Matsumoto, 1922; *Palaeomastodon* (in part), Lehmann, 1950; *Palaeomastodon (Palaeomastodon) beadnelli*, Coppens et al., 1978.

Age and Occurrence Early Oligocene, northern Africa (table 15.4).

Diagnosis Based in part on Andrews (1901c, 1901d); Matsumoto (1922, 1924); Moustafa (1974b); El-Khashab (1979); Sanders et al. (2004). Distinguished from *Phiomia* by greater length of premolar series, relative to molar row; shorter symphysis (figures 15.8A, 15.8B); wider palate; less complete development of third loph(id)s; absence or less prominent appearance of accessory central conules; more lophodont molar crowns, and tendency for chisel-like wear on loph(id) faces. Molars smaller than those of *Palaeomastodon* sp. nov. A and B (figure 15.7A). Along with *Phiomia serridens*, discernible from moeritheres by anterior projection of i2s, larger size of cheek teeth, and loss of I1, I3, C, i1, and p2, and from nearly all elephantoids by smaller tooth size (figures 15.7A, 15.17B).

Description The skull of *Palaeomastodon beadnelli* is imperfectly known, but similar to that of *Phiomia serridens* (see figure 15.8), except for differences in palatal and symphyseal proportions (Andrews, 1906, 1908; Moustafa, 1974b; El-Khashab, 1979).

Molars wear like lophodont teeth, producing sharp ridges apically, and accessory conules are low and crescentoid-like where present (Matsumoto, 1924). Zygodont crests may be prominent on the posttrite outer conelets of half-loph(id)s. Third loph(id)s of molars may be poorly formed, with posttrite last half-loph(id)s composed of only a diminutive conelet that is considerably smaller than its pretrite counterpart, yielding loph(id) formulae of 2 1/2. Loph(id) formulae for P2-4 and p3-4 are 1, 1 1/2, and 1, 2, respectively.

Palaeomastodont postcranial remains are uncommon, and do not differ significantly in structure between *Palaeomastodon* and *Phiomia* (Andrews, 1906, 1908). Recovered elements are elephant-like, and appear to have been adapted for graviportal support of heavy bodies (Andrews, 1906). For example, the femur is pillar-like with an upwardly facing head; the head of the humerus also faces primarily upward; the humerus has a large and deep olecranon fossa to help stabilize the ulna in extension; and the greatly expanded olecranon process of the ulna is posteriorly reflected and low, permitting its vertical extension on the humerus.

PALAEOMASTODON SP. NOV. A Sanders, Kappelman and Rasmussen, 2004

Figure 15.7A

Partial Synonymy aff. *Palaeomastodon* sp. nov. A, Kappelman et al., 2003.

Age and Occurrence Late Oligocene, eastern Africa (table 15.4).

Description Molars are morphologically identical to those of *P. beadnelli* (figure 15.8F), except for their larger size (figure 15.7A).

PALAEOMASTODON SP. NOV. B Sanders, Kappelman and Rasmussen, 2004

Figures 15.7A and 15.8G

Partial Synonymy Mammutid, Sanders and Kappelman, 2001; aff. *Palaeomastodon* sp. nov. B, Kappelman et al., 2003.

Age and Occurrence Late Oligocene, eastern Africa (table 15.4).

Description Similar to *P. beadnelli* in the weak development of the posttrite side of the tritoloph in M3, yielding a loph formula of 2 1/2, but much larger in crown dimensions (figure 15.7A). The M3 is unique among palaeomastodonts in its rectangular occlusal outline, the pronounced development of its posterior crescentoid, zygodont crests, and cingulae, and its strong enamel rugosity (figure 15.8G; Sanders et al., 2004).

Genus *PHIOMIA* Andrews and Beadnell, 1902

PHIOMIA SERRIDENS Andrews and Beadnell, 1902

Figures 15.8A–15.8E

Partial Synonymy *Palaeomastodon minor*, Andrews, 1904a; *Palaeomastodon wintoni*, Andrews, 1905; *Palaeomastodon minus*, Andrews, 1905; *Palaeomastodon barroisi* (in part), Pontier, 1907; *Phiomia osborni*, Matsumoto, 1922; *Phiomia* (*minus*) *minor*, Matsumoto, 1922; *Phiomia wintoni*, Matsumoto, 1922; *Palaeomastodon* (in part), Lehmann, 1950; *Palaeomastodon* (*Phiomia*) *serridens*, Coppens et al., 1978.

Age and Occurrence Early Oligocene, northern Africa (table 15.4).

Diagnosis Matsumoto (1922, 1924). Similar in size range to *P. beadnelli*, but with a greater tendency for complete molar trilophodonty, more bunolophodont wear, stronger development of central accessory conules, and inferred greater length of the mandibular symphysis (figures 15.8A, 15.8B).

Description The most common palaeomastodont craniodental remains from the Fayum are those of *Phiomia wintoni* (Andrews, 1906), synonymized here under *Phiomia serridens*. These include well preserved mandibles and the most complete cranium known of a palaeomastodont (figure 15.8C, 15.8E), with dimensions of L = 700 mm, and W = 447 mm, proportionally similar to dimensions of a large cranium of *P. beadnelli* (BMNH 8464), with L = 635 mm and W = 420 mm (Andrews, 1906, 1908). Zygomatics are stout and flare laterally widely; the basicranium is not raised much above the level of the palate; skull height is low; and pneumatization is modest. The palate is relatively long, due to persistence of complete premolar-molar series in adults. The associated mandible has a length of 470 mm, including a slightly downturned symphysis that extends for 140 mm (Andrews, 1908). Mandibles of palaeomastodont species differ primarily in symphyseal size, inferred to be longer in *Phiomia serridens* because of the closer approximation of the posterior rim of the symphysis to its anteriormost premolar (see figures 15.8A, 15.8B, 15.8D; Matsumoto, 1922, 1924).

PHIOMIA MAJOR Sanders, Kappelman and Rasmussen, 2004

Figures 15.7A, 15.7B, 15.9A, and 15.10A

Age and Occurrence Late Oligocene, eastern Africa (table 15.4).

Diagnosis Sanders et al. (2004). Largest species of *Phiomia*, with molar size range surpassing that of Fayum palaeomastodonts (figures 15.7A, 15.7B); symphysis and incisors much longer than in other palaeomastodonts; distinguished from *Palaeomastodon* by absence of posttrite cristae, stronger development of accessory central conules, presence of a central conelet in the posterior loph of P4, and full molar trilophodonty.

Description Cheek teeth morphologically similar to those of *Phiomia serridens*. Upper tusks curve downward and outward; of flattened pyriform shape proximally, higher than wide, becoming more rounded toward the tip, with enamel along their outer face, and long for a palaeomastodont (450 mm, compared with a range of 197–250 mm for Fayum *Phiomia serridens*; Sanders et al., 2004). Lower tusks straighter, with a flattened, pyriform shape in cross section, becoming rounder

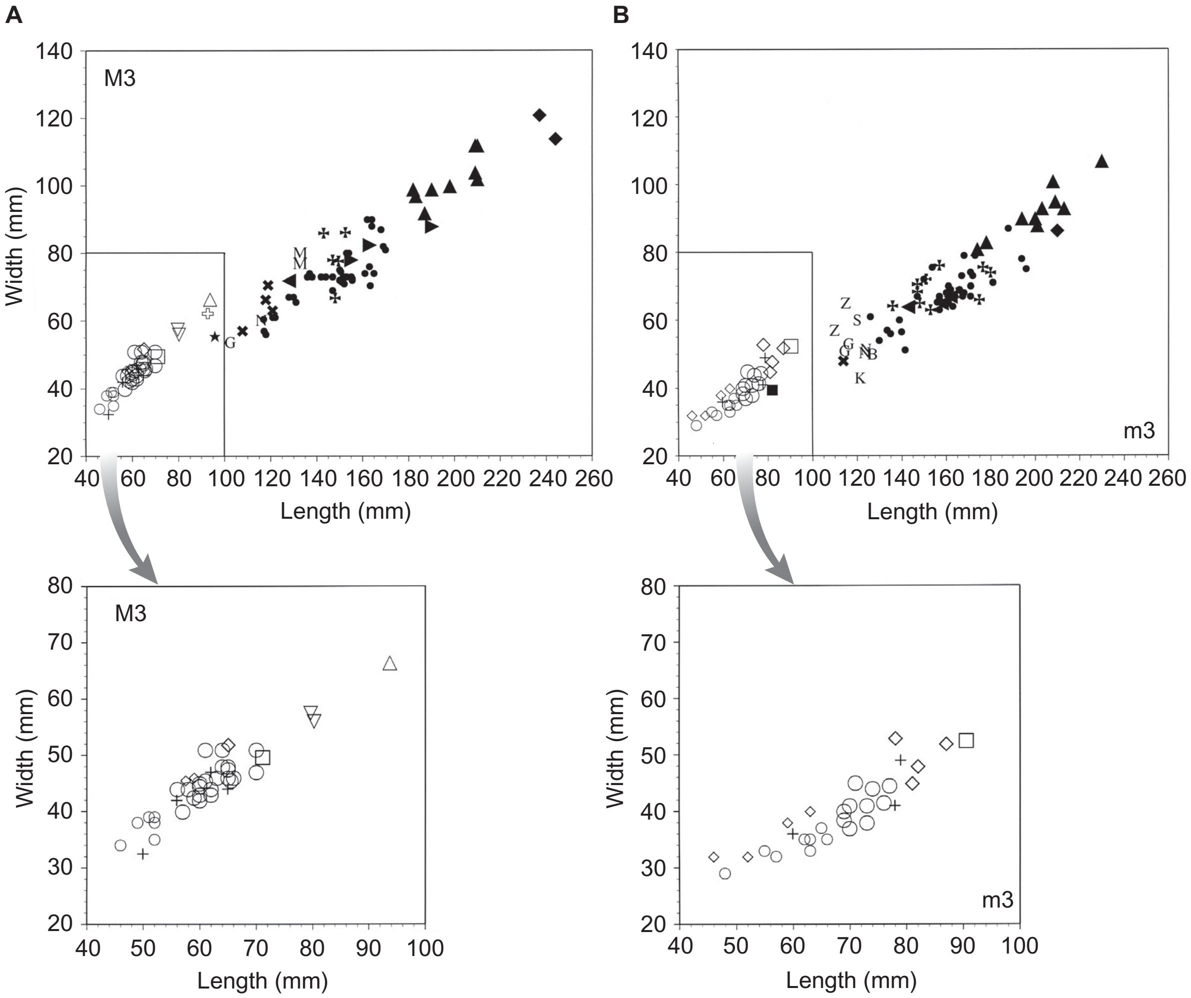

FIGURE 15.7 Bivariate plots of M3 and m3 crown length versus width in palaeomastodonts and Afro-Arabian and selected Eurasian gomphotheriids. A) M3 (palaeomastodont M3 data points detailed in lower plot); B) m3 (palaeomastodont m3 data points detailed in lower plot). Comparative dimensions supplementing original measurements are from Andrews (1906), Fourtau (1918), Forster Cooper (1922), Matsumoto (1924), Lehmann (1950), Bergounioux and Crouzel (1959), Arambourg (1961), Hamilton (1973), Gaziry (1976, 1987a), Tassy (1983b, 1985, 1986), Gentry (1987), Roger et al. (1994), Göhlich (1998), Sanders and Miller (2002), Pickford (2003, 2004, 2005a), Sanders (2003), and Sanders et al. (2004).

SYMBOLS: small open diamond, *Palaeomastodon wintoni* (female); large open diamond, *Palaeomastodon wintoni* (male); inverted open triangle, *Palaeomastodon* sp. nov. A (Chilga, Ethiopia); open triangle, *Palaeomastodon* sp. nov. B (Chilga, Ethiopia); small open circle, *Phiomia serridens* (female); large open circle, *Phiomia serridens* (male); open square, *Phiomia major*; +, Fayum palaeomastodont gen. et sp. indet. (Lehmann, 1950); open cross, *Hemimastodon*; star, cf. *Gomphotherium* sp. nov., Gebel Zelten, Libya; closed square, *Eritreum melakeghebrekristosi*; left-facing closed triangle, *Gomphotherium cooperi*; closed triangle, *G. sylvaticum*; M, *Gomphotherium* sp. (Mwiti-type); closed circle, *G. angustidens* (Europe, including *G. "subtapiroideum"*); cross, *G. angustidens libycum* (Wadi Moghara, Gebel Zelten, Ad Dabtiyah, Gebel Cherichera); right-facing closed triangle, *G. browni*; B, *Gomphotherium pygmaeus*, Bosluis Pan, South Africa; G, "pygmy" gomphothere, Ghaba, Oman; K, *Gomphotherium pygmaeus* (type), Kabylie, Algeria; N, *Gomphotherium pygmaeus*, Ngenyin, Tugen Hills, Kenya; S, "pygmy" gomphothere, Siwa, Egypt; Z, "pygmy" gomphothere, Gebel Zelten, Libya; closed diamond, *Tetralophodon* sp. nov.; X, ?*Tetralophodon* sp. nov. (Chorora).

toward the tip, longitudinally torqued, set close to one another about the midline, and also much longer than those in Fayum *Phiomia serridens* (460 mm compared to maximum of 250 mm; Sanders et al., 2004). Symphysis very long (382 mm, compared with a range of 137–275 mm for Fayum *Phiomia serridens*; Sanders et al., 2004), with a shallow midline channel running its length.

Remarks Differences in molar occlusal morphology and wear patterns in particular support division of palaeomastodonts into two genera. Further sorting of palaeomastodonts within each genus has been based largely on cheek tooth size (Matsumoto, 1922, 1924), resulting in recognition of as many as eight sympatric species in the Fayum (Simons, 1968), though it is difficult to imagine how so many large, morphologically similar species could coexist ecologically. Morphometric differences in the Fayum palaeomastodont dental sample can be accommodated within two genera composed of one sexually dimorphic species each (see Schlosser, 1905, 1911); molar dimensions of *P. beadnelli* and *Ph. serridens* are bimodal and do not exceed the ranges of other, presumably dimorphic proboscidean species (figures 15.7A, 15.7B).

New fossil evidence appears to contradict parsimony-based phylogenies that place *Palaeomastodon* as the sister taxon to a clade of *Phiomia* + elephantoids. Rather, traits in the M3 of "*Palaeomastodon* sp. nov. B," from the late Oligocene of Chilga, Ethiopia, suggest a closer relationship between *Palaeomastodon*

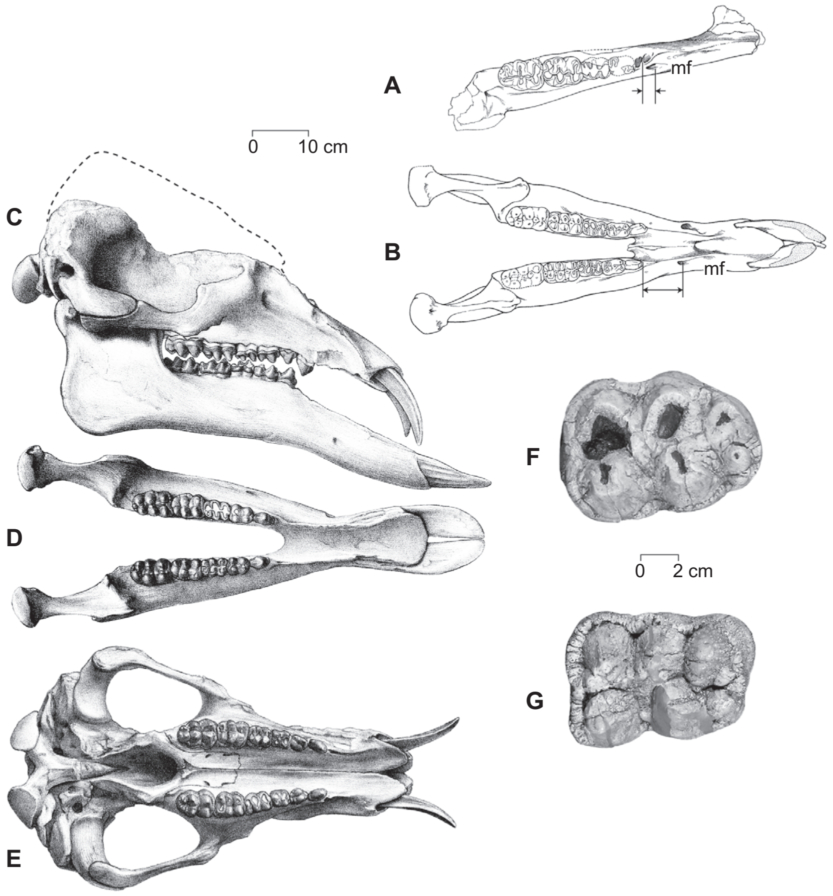

FIGURE 15.8 Aspects of palaeomastodont skull morphology. Anterior is to the right. A) Occlusal view, left dentary (reversed), C10014, *Palaeomastodon beadnelli* (type; Osborn, 1936: plate 90B). B) Occlusal view, mandible, AMNH 13468, *Phiomia serridens* ("*Ph. osborni*" [type]; Osborn, 1936: figure 90A). Arrows indicate greater distance between p3 alveolus and main mandibular foramen than in *P. beadnelli* (consistent with inferred longer symphysis). C) Right lateral view, reconstruction of skull of *Phiomia serridens* (Andrews, 1908: plate 31, figure 1). D) Occlusal view, reconstruction of mandible of *Phiomia serridens* (Andrews, 1908: plate 31, figure 2). E) Ventral view, reconstruction of cranium of *Phiomia serridens* (reversed; Andrews, 1908: plate 31, figure 3). F) Occlusal view, right M3, CH35-V-23, *Palaeomastodon* sp. nov. A. G) Occlusal view, reconstructed cast of right M3, CH14-11, *Palaeomastodon* sp. nov. B. A, B courtesy of the American Museum of Natural History.

and Mammutidae (Sanders et al., 2004). Even more compelling as a link between these taxa is the recent identification of diminutive molars (figures 15.9A, 15.10A) with distinct mammutid features, from the Eragaleit beds at Lothidok, Kenya, placed in the new species *Losodokodon losodokius* (Gutiérrez and Rasmussen, 2007; Rasmussen and Gutiérrez, 2009), dated to the latest Oligocene, ca. 27.5–24.0 Ma (Boschetto et al., 1992). This suggests that the phylogenetic split between mammutids and gomphotheres traces back at least to the beginning of the Oligocene. If so, Elephantiformes will require major systematic revision.

Superfamily ELEPHANTOIDEA Gray, 1821

This very diverse superfamily is composed of mammutids, gomphotheriids, stegodonts, and elephants (and possibly the controversial, primitive South Asian species *Hemimastodon crepusculi*) (Tassy, 1988). Elephantoidea has alternatively been used to refer to a more restricted grouping of tetralophodonts, stegodonts, and elephants (Shoshani and Tassy, 2005), but this usage destabilizes the communicative property of the superfamily as it was originally defined.

Elephantoidea has been circumscribed by a set of traits that includes lengthening of tusks and "conveyor belt" functional succession of cheek teeth (Tassy, 1994b). Some of these features likely related to increased emphases on the trunk for manipulation of objects, on the incisors for social display and interaction, and on delayed ontogenetic development of teeth, in association with increases in body size, life span, behavioral complexity, and dietary flexibility. It is possible, however, that horizontal succession of cheek teeth evolved in parallel among elephantoids, as this mechanism had apparently not yet appeared in the earliest mammutids or gomphotheriids.

Family MAMMUTIDAE Hay, 1922

This family is comprised of elephantoids whose fossil record extends to the terminal Oligocene. By that time, divergence in occlusal morphology between mammutids and gomphotheriids was already marked, suggesting a prior time of divergence. Mammutids first occurred in Africa, emigrated into Europe by the end of the early Miocene, and by the middle Miocene had spread throughout Eurasia and into the New World (Tassy, 1986;

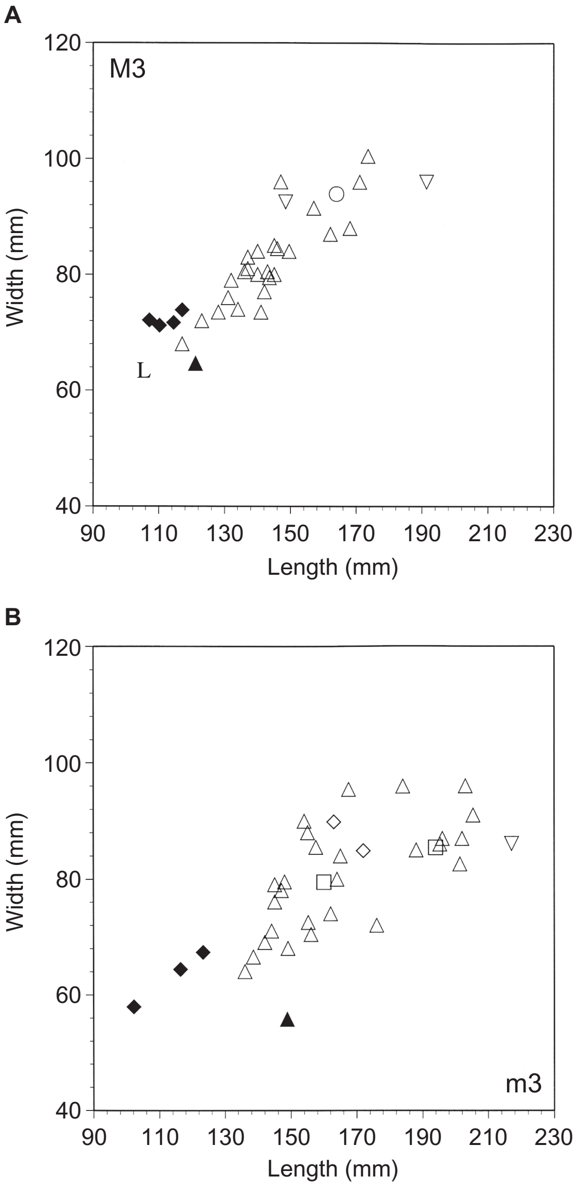

FIGURE 15.9 Bivariate plots of M3 (A) and m3 (B) crown length versus width in African and selected Eurasian mammutids. Comparative dimensions supplementing original measurements are from Osborn (1936), Tassy (1977a, 1983a, 1985), Göhlich (1998), Sanders and Miller (2002), and M. Gutiérrez (pers. comm.).

Symbols: L, *Losodokodon losodokius,* Eragaleit Beds, Lothidok, Kenya; closed diamond, *Eozygodon morotoensis*; closed triangle, *Zygolophodon aegyptensis*; open triangle, *Z. turicensis*; open diamond, *Z. atavus*; inverted open triangle, *Z. metachinjiensis*; open square, *Z. gobiensis*; open circle, *Z. gromovae*.

Mazo, 1996; Saunders, 1996; Tobien, 1996). Nevertheless, despite their initial success, mammutids were progressively marginalized in African faunas throughout the Miocene in comparison with and perhaps as the result of the increasing diversity and importance of gomphotheriids (Coppens et al., 1978; Tobien, 1996).

Mammutid molars are nonbunodont and distinguished by mesoconelets markedly lower than principal, outer conelets (zygolophodonty), mesiodistal narrowing of half-loph(id) pairs apically to form relatively compressed transverse crests, lack of accessory conules in interloph(id)s, and presence of posttrite zygodont crests. Pretrite crescentoids may also extend low into interloph(id)s. These features likely functioned in vertical shearing (Tobien, 1996), and would have been effective for mastication of leafy vegetation.

Genus *EOZYGODON* Tassy and Pickford, 1983
EOZYGODON MOROTOENSIS (Pickford and Tassy, 1980)
Figures 15.9A, 15.9B, and 15.10B–15.10G

Partial Synonymy Mastodont nov. gen. Bishop, 1967; *Zygolophodon* aff. *turicensis* Tassy, 1979a; *Zygolophodon morotoensis* Pickford and Tassy, 1980; *Eozygodon morotoensis* Tassy and Pickford, 1983.

Age and Occurrence Early Miocene, eastern and southern Africa (table 15.5).

Diagnosis Large-bodied mammutid with relatively diminutive teeth (figures 15.9A, 15.B); third molars and I2 smaller than those of most confamilials. Upper molars relatively wide (figures 15.9A, 15.10E, 15.10F). Tusks *Phiomia*-like, dissimilar to those in other mammutids. Loph(id) apices and zygodont crests of unworn molars finely crenulated. Pretrite crescentoids weak or absent.

Description Cranium short, wide, moderately high; basicranium set well above the level of the palate; occipital condyles high and project far posterior to the occiput; rostrum relatively short; palate deep; nasal aperture broad; orbit above M1–M2; infraorbital foramen above P4; large nuchal fossa; upper tusks oriented downward and slightly laterally; upper tooth rows most divergent at M2 (Pickford 2003). Upper tusks short (KNM-ME 7543, L = 510 mm), strongly curved (figure 15.10B) and ovoid to pyriform in cross section, higher than wide (-ME 7543, proximal H = 64.5 mm, W = 51.0 mm), with enamel band ventrolaterally. Lower tusks straighter than uppers (figures 15.10B–15.10D), pyriform in cross section, with distinct dorsomedial longitudinal sulcus, higher than wide and slightly flattened (KNM-ME 19, proximal H = 58.2 mm, W = 36.1 mm). Cheek teeth simultaneously in wear. P4 bilophodont, occlusally square in shape. Molars occlusally rectangular, trilophodont (except m3, which has a diminutive fourth lophid; figure 15.10G), strongly zygolophodont, with broad, open transverse valleys between loph(id)s, and without cementum; posttrite zygodont crests narrow but sharp; median sulci deep; upper cheek tooth crowns surrounded by moderately prominent beaded cingular ribbons (Pickford and Tassy, 1980; Tassy and Pickford, 1983; Pickford, 2003).

Postcrania: astragalus high, with prominent medial tubercle and extensive facet for the tibial malleolus; phalanges high and narrow. Femoral length >1,000 mm, suggesting an animal comparable to the American mastodon in body size (Tassy and Pickford, 1983; see Christiansen, 2004).

Remarks The best represented mammutid in the African fossil record is *Eozygodon morotoensis* (Pickford and Tassy, 1980; Tassy and Pickford, 1983; Tassy, 1986; Pickford, 2003). Documented from several early Miocene sites (table 15.5), *Eozygodon* is the oldest recorded elephantoid in that epoch (Tassy, 1986, 1996b). The reported presence of this species at Wadi Moghara, based on an edentulous dentary (Pickford, 2003), cannot be confirmed. Absence or poor development of fourth loph(id)s in M3/m3, small tooth size (figures 15.9A, 15.9B), strong upper molar cingulae, *Phiomia*-like tusks, and a suite of postcranial features identify this species as the most primitive of the family (Tassy and Pickford, 1983; Tassy, 1986). Molars from Meswa Bridge, Kenya are more primitive than those of Moroto, Uganda in having stronger cingulae, and weaker expression of zygodont

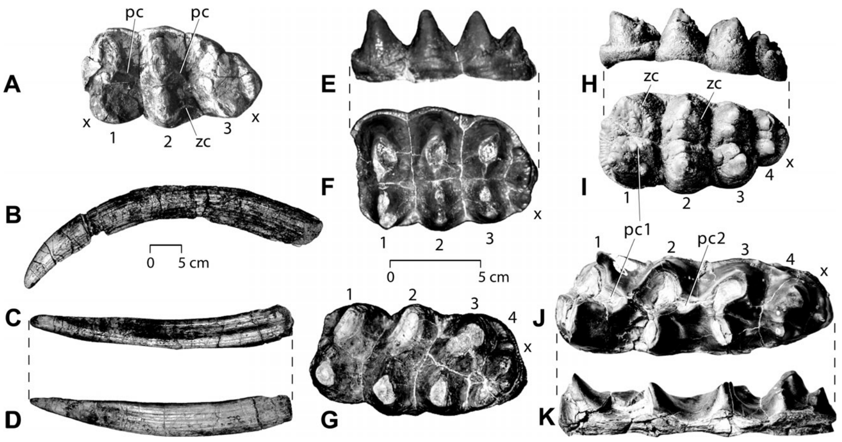

FIGURE 15.10 Aspects of mammutid dental morphology. Anterior is to the left in all specimens. A) Occlusal view, right M3, KNM-LS 18244, *Losodokodon losodokius* (courtesy of M. Gutiérrez). B) Lateral view, right I2, KNM-ME 7543, *Eozygodon morotoensis*. C) Medial view, right i2, KNM-ME 7543, *E. morotoensis*. D) Lateral view, right i2, KNM-ME 7543, *E. morotoensis*. E) Lateral view, right M3, KNM-ME 7545, *E. morotoensis*. F) Occlusal view, right M3, KNM-ME 7545, *E. morotoensis*. G) Occlusal view, right m3, KNM-ME 7547, *E. morotoensis*. H) Medial view, left M3, DPC 12598, *Zygolophodon aegyptensis*. I) Occlusal view, left M3, DPC 12598, *Zygolophodon aegyptensis*. J) Occlusal view, right m3, DPC 9009, *Z. aegyptensis* (type). K) Medial view, right m3, DPC 9009, *Z. aegyptensis* (type).

ABBREVIATIONS: pc, posterior crescentoid; x, anterior or posterior cingulum(id); zc, zygodont crest; 1, 2, 3, . . . , first, second, third, . . . loph(id).

crests and crescentoids. Paleoecological inference suggests that *E. morotoensis* was an inhabitant of dry, dense forests with open areas nearby (Tassy and Pickford, 1983).

Genus *ZYGOLOPHODON* Vacek, 1877

ZYGOLOPHODON AEGYPTENSIS Sanders and Miller, 2002

Figures 15.9A, 15.9B, and 15.10H–K

Age and Occurrence Early Miocene, northern Africa (table 15.5).

Diagnosis Anthony and Friant (1940); Tobien (1975, 1996); Tassy (1977a, 1985); Tassy and Pickford (1983); Sanders and Miller (2002). Mammutid with small molars; third molars narrower than those of confamilials (figures 15.9A, 15.9B). Distinguished from *Eozygodon* by stronger development of pretrite crescentoids, and greater expression of fourth loph(id)s in M3/m3 (figures 15.10H–15.10K), from other congeners by mesiodistally wider interlophids in m3 and anterior convexity of m3 lophids three and four, and from *Mammut* by wider median sulci, absence or trace only of cementum, stronger expression of pretrite crescentoids and cingulae(ids), smaller size, and less mediodistally attenuated loph(id) apices.

Description Only known from dentition. Unworn half-loph(id)s are formed of large outer conelets and smaller, lower mesoconelets; half-lophs are divided by deep, narrow median longitudinal sulci. Lower third molar with four lophids and low postcingulid, and prominent pretrite crescentoids. Upper third molars of putative males are substantially wider and have broader fourth lophs and blunter crests, crescentoids, and loph apices, than M3 of putative females. Loph(id)s are teat shaped in lateral outline (figure 15.10H).

ZYGOLOPHODON TURICENSIS (Schinz, 1824)

Diagnosis Tassy (1985). Molars larger, with more pronounced anterior and posterior pretrite crescentoids than in *Z. aegyptensis*. The lower third molar may exhibit a fifth lophid.

Description Pickford (2007). Two M2s from the Tugen Hills, Kenya are very large for *Z. turicensis* but otherwise resemble the molars of the robust morph of this species. They are trilophodont, with apically anteroposteriorly compressed lophs, and with salient pretrite anterior and posterior crescentoids. The posttrite cusps display zygodont crests. Transverse valleys are broad. A low cingulum runs along the lingual margin of the crown in each of these M2s.

Remarks The sparse remains of *Zygolophodon aegyptensis* unequivocally mark the presence of the genus in Africa. Until recently, the occurrence of *Zygolophodon* in Africa had been hinted at only by a paltry sample of broken teeth, including molar fragments from Gebel Cherichera, Tunisia (Tassy, 1985; Thomas and Petter, 1986), and Gebel Zelten. Of less reliable affinity is a d2 referred to ?*Zygolophodon* cf. *turicensis* from the late Miocene site of Menacer (ex-Marceau), Algeria (Thomas and Petter, 1986; see also Arambourg, 1959), alternatively considered a gomphothere tooth, as is a DP4 from Rusinga, which was originally attributed to *Zygolophodon* (Pickford and Tassy, 1980; Tassy, 1986). A presumed zygolophodont tooth from Khenchella, Tunisia (Gaudry, 1891), may be a moerithere molar (Pickford and Tassy, 1980). More confidence can be given a broken m3 from Daberas Mine, Namibia, which exhibits features typical of *Zygolophodon* and is the first evidence of the genus in southern Africa (Pickford, 2005b), and the M2s from the Tugen Hills, Kenya attributed to *Z. turicensis* (Pickford, 2007). In addition, a fragmentary mammutid P4 from the Moruorot Mb. at Lothidok, Kenya, recently placed in *Eozygodon* (Tassy, 1986; Tobien, 1996; Pickford, 2003), should be returned to its original assignment in *Zygolophodon* (Madden, 1980). Together, this modest sample indicates a pan-African distribution of the genus by the start of the middle Miocene.

Zygolophodon aegyptensis particularly resembles *Z. gromovae* from the middle Miocene of Ulan Tologoj, western Mongolian People's Republic (Dubrovo, 1974). Its presence in North Africa helps document the rich interconnections that existed between Afro-Arabia and Eurasia during the early Miocene. Geological

TABLE 15.5

Major occurrences and ages of Afro-Arabian mammutids and gomphotheriids

? = Attribution or occurrence uncertain; alt. alternatively.

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
		MAMMUTIDAE, LATE OLIGOCENE–?LATE MIOCENE		
Losodokodon losodokius	Lothidok, Kenya	Eragaleit Beds	Late Oligocene, 27.5–24.0 Ma	Boschetto et al., 1992; Gutiérrez and Rasmussen, 2007; Rasmussen and Gutiérrez, 2009
Eozygodon morotoensis	Meswa Bridge, Kenya	Muhoroni Agglomerate	23.5–19.6 Ma (probably 23.0–22.0 Ma)	Bishop et al., 1969; Pickford and Tassy, 1980; Pickford and Andrews, 1981; Tassy and Pickford, 1983; Tassy, 1986
	Elisabethfeld, Namibia		ca. 21 Ma	Pickford, 2003
	Moroto I (type) and II, Uganda		>20.6 Ma (alt. ca. 17.5 Ma)	Pickford and Tassy, 1980; Tassy and Pickford, 1983; Pickford et al., 1986; Gebo et al., 1997; Pickford, 2003, 2007; Pickford et al., 2003; Pickford and Mein, 2006
	Auchas, Namibia	Arrisdrift Gravel Fm.	ca. 20–19 Ma	Pickford, 2003
Zygolophodon aegyptensis	Wadi Moghara, Egypt (type)	Moghara Fm.	ca. 18–17 Ma	Miller, 1996, 1999; Sanders and Miller, 2002
Zygolophodon turicensis	Tugen Hills, Kenya	Mb. A, Ngorora Fm.	ca. 13 Ma	Pickford, 2007
Zygolophodon sp. indet.	Lothidok 4, Kenya	Moruorot Mb.	17.9–17.5 Ma	Tassy, 1986; Boschetto et al., 1992; Tobien, 1996; Pickford, 2003
	?Rusinga, Kenya	Hiwegi Fm.	17.8 Ma	Pickford and Tassy, 1980; Pickford, 1981, 1986b; Drake et al., 1988
	Daberas Mine, Namibia		early or middle Miocene, ca. 17–14 Ma	Pickford and Senut, 2000; Pickford, 2005a
	Gebel Zelten, Libya	Qaret Jahanneam Mb., Marada Fm.	ca. 16.5 Ma	Savage and Hamilton, 1973; Sanders, 2008a
	Gebel Cherichera, Tunisia	Beglia Fm.	ca. 13–11 Ma (alt. ?early Miocene)	Errington de la Croix, 1887; Robinson, 1974; Robinson and Black, 1974; Tassy, 1985; Thomas and Petter, 1986
	?Menacer (ex-Marceau), Algeria		?Late Miocene	Arambourg, 1959; Thomas and Petter, 1986; Pickford, 2007

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
FAMILY INCERTAE SEDIS, LATE OLIGOCENE				
cf. *Gomphotherium* sp.	Chilga, Ethiopia	Chilga Fm.	28–27 Ma	Kappelman et al., 2003; Sanders et al., 2004
	?Gebel Zelten, Libya	?Marada Fm.	?Late Oligocene or basal early Miocene	Pickford, 2003; Sanders, 2008a
Eritreum melakeghebrekristosi	Dogali, Eritrea	Dogali Fm.	26.8 Ma	Shoshani et al., 2001b, 2006
GOMPHOTHERIIDAE, EARLY MIOCENE–LATE PLIOCENE				
GOMPHOTHERIINAE, EARLY MIOCENE–MIDDLE MIOCENE				
"*GOMPHOTHERIUM ANNECTENS* GROUP," EARLY MIOCENE				
Gomphotherium sp.	Songhor, Kenya		Early Miocene, 19.5 Ma	Bishop et al., 1969; Pickford and Andrews, 1981; Pickford, 1986b
	Mfwangano, Kenya	Hiwegi Fm.	17.8 Ma	Drake et al., 1988
	Mwiti, Kenya	Mwiti 5	ca. 17 Ma	Drake et al., 1988
"*GOMPHOTHERIUM ANGUSTIDENS* GROUP," EARLY–LATE MIOCENE				
Gomphotherium angustidens libycum	Wadi Moghara, Egypt (type)	Moghara Fm.	ca. 18–17 Ma	Fourtau, 1918; Miller, 1996, 1999; Sanders and Miller, 2003
	Ad Dabtiyah, Saudi Arabia	Dam Fm.	Early middle Miocene (alt. ca. 19–17 Ma)	Gentry, 1987; Whybrow et al., 1987; Whybrow and Clements, 1999; Sanders and Miller, 2002
	?Fejej, Ethiopia	Bakate Fm.	>16.18 Ma	Tiffney et al., 1994; Richmond et al., 1998
	Gebel Zelten, Libya	Qaret Jahanneam Mb., Marada Fm.	ca. 16.5 Ma	Hormann, 1963; Savage and Hamilton, 1973; Coppens et al., 1978; Pickford, 2003; Sanders, 2008a
	?Al Jadidah, Saudi Arabia	Hofuf Fm.	Middle Miocene, ca. 14 Ma	Whybrow and Clements, 1999
	Gebel Cherichera, Tunisia	Beglia Fm.	ca. 13–11 Ma	Gaudry, 1891; Robinson, 1974; Robinson and Black, 1974; Pickford, 2003
	Gebel el Hendi, Testour, Tunisia		Late Miocene	Robinson and Black, 1973
Gomphotherium sp. indet.	As-Sarrar, Saudi Arabia	Dam Fm.	Early middle Miocene, 17–15 Ma (alt. ca. 19–17 Ma)	Thomas et al., 1982; Whybrow and Clements, 1999
"'PYGMY' *GOMPHOTHERIUM* GROUP"				
Gomphotherium pygmaeus	Kabylie, Algeria (type)		?Middle Miocene	Depéret, 1897; Bergounioux and Crouzel, 1959; Coppens et al., 1978; Pickford, 2004

TABLE 15.5 (CONTINUED)

Taxon	Occurrence (Site, Locality)	Stratigraphic Unit	Age	Key References
G. pygmaeus continued	Bosluis Pan, South Africa		Middle Miocene, ca. 16 Ma	Senut et al., 1996; Pickford, 2005b
	Ngenyin, Tugen Hills, Kenya	Mb. A, Ngorora Fm.	ca. 13 Ma	Pickford, 2004
Gomphotherium sp. indet.	Ghaba, Oman	Dam Fm.	Latest early Miocene or early middle Miocene	Roger et al., 1994; Pickford, 2003
	Siwa, Egypt		Early Miocene	Hamilton, 1973; Coppens et al., 1978
	Gebel Zelten, Libya	Qaret Jahanneam Mb., Marada Fm.	ca. 16.5 Ma	Arambourg, 1961; Coppens et al., 1978; Gaziry, 1987a; Sanders, 2008a
AMEBELODONTINAE, EARLY–LATE MIOCENE				
Progomphotherium maraisi	Auchas, Namibia (type)	Arrisdrift Gravel Fm.	ca. 20–19 Ma	Pickford, 2003
	? Moroto II		>20.6 Ma (alt. ca. 17.5 Ma)	Gebo et al., 1997; Pickford, 2003; Pickford et al., 2003; Pickford and Mein, 2006
	?Karangu, Kenya	Karangu Fm.	17.8 Ma	Drake et al., 1988; Pickford, 2003
cf. *Archaeobelodon*	?Legetet, Kenya	Legetet Fm.	Early Miocene, ca. 20 Ma	Pickford, 1986b; Tassy, 1986
	?Songhor, Kenya		Early Miocene, 19.5 Ma	Bishop et al., 1969; Pickford and Andrews, 1981; Pickford, 1986b
	Wadi Moghara, Egypt	Moghara Fm.	ca. 18–17 Ma	Miller, 1996, 1999; Sanders and Miller, 2002
	Rusinga, Kenya	Hiwegi Fm.	17.8 Ma	MacInnes, 1942; Tassy, 1979b, 1984, 1986; Drake et al., 1988
		Kulu Fm.; immediately suprajacent to the Hiwegi Fm.	Slightly <17.8 Ma	Pickford, 1981; Tassy, 1986
	Arongo Uyoma (Chianda), Kenya		Early Miocene, cf. Hiwegi and Kulu Fms.	Pickford, 1986b
Archaeobelodon filholi	?Napak, Uganda		Early Miocene, ca. 20.0 Ma	Bishop, 1964; Bishop et al., 1969; Pickford and Andrews, 1981; Pickford, 2003; MacLatchy et al., 2006
	Buluk (West Stephanie), Kenya		18.0–17.2 Ma (alt. 16–15 Ma)	Harris and Watkins, 1974; Pickford, 1981; McDougall and Watkins, 1985; Tassy, 1986
	Mwiti, Kenya	Mwiti 1	ca. 17 Ma	Tassy, 1986; Drake et al., 1988
	?Nachola, Kenya	Aka Aiteputh Fm.	15.5 Ma	Pickford, 2003
Afromastodon coppensi	Arrisdrift, Namibia (type)	Arrisdrift Gravel Fm.	Early middle Miocene, ca. 16.0 Ma (alt. ca. 17.5–17.0 Ma)	Corvinus and Hendey, 1978; Hendey, 1978b; Pickford, 2003

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
Amebelodontinae cf. *A. coppensi*	BUR1, Burji, Ethiopia		ca. 17–15 Ma	Suwa et al., 1991; Pickford, 2003
Protanancus macinnesi	Kalodirr, Kenya	Tiati Grits	ca. 18.0–16.0 Ma (alt. 17.7–16.6 Ma)	Drake et al., 1988
	Maboko, Kenya (type)	Maboko Fm.	ca. 16 Ma (alt. slightly >14.7 Ma)	MacInnes, 1942; Tassy, 1986; Feibel and Brown, 1991
	Kaloma, Kenya	Maboko Fm.	Middle Miocene	Pickford, 1982
	Majiwa, Kenya	Maboko Fm.	Middle Miocene	Pickford, 1981, 1982; Tassy, 1986
	Kipsaraman, Tugen Hills, Kenya	Muruyur Fm.	15.5 Ma	Hill, 1999; Pickford, 2003
	Nyakach, Kenya		ca. 15 Ma	Tassy, 1986; Pickford, 2003
	Ft. Ternan, Kenya	Ft. Ternan Beds	14.0–13.9 Ma	Shipman et al., 1981; Tassy, 1986
	Sinda River area, near Ongoliba (Semliki 531), Democratic Republic of Congo	?Sinda Beds	?Middle Miocene	Lepersonne, 1959; Hooijer, 1963; Boaz, 1994
	?Ombo, Kenya		Middle Miocene	Van Couvering and Van Couvering, 1976; Pickford, 1981; Tassy, 1986
	Alengerr, Kenya		<14.0 Ma, >12.4 Ma	Bishop, 1972; Tassy, 1986
Amebelodon cyrenaicus	Sahabi, Libya (type)	Sahabi Fm.	Late Miocene–early Pliocene, ca. 5.2 Ma	Gaziry, 1982, 1987b; Heinzelin and El-Arnauti, 1987; Tassy, 1999; Bernor and Scott, 2003; Sanders, 2008b
Platybelodon sp.	Loperot, Kenya		Early Miocene, ca. 17 Ma	Maglio, 1969a; Coppens et al., 1978; Tassy, 1986; Pickford, 2003
?Amebelodontinae (?*Platybelodon*)	Ad Dabtiyah, Saudi Arabia	Dam Fm.	Early middle Miocene (alt. ca. 19–17 Ma)	Hamilton et al., 1978; Whybrow and Clements, 1999
?Amebelodontinae gen. et sp. indet.	As Sarrar, Saudi Arabia	Dam Fm.	Early middle Miocene, ca. 17–15 Ma (alt. ca. 19–17 Ma)	Thomas et al., 1982; Whybrow and Clements, 1999
		CHOEROLOPHODONTINAE, EARLY–LATE MIOCENE		
Afrochoerodon kisumuensis	Wadi Moghara, Egypt	Moghara Fm.	ca. 18–17 Ma	Miller, 1996, 1999; Sanders and Miller, 2002
	Maboko, Kenya (type)	Maboko Fm.	ca. 16 Ma (alt. slightly >14.7 Ma)	MacInnes, 1942; Tassy, 1977b, 1979b, 1986; Feibel and Brown, 1991
	Kaloma, Kenya	Maboko Fm.	Middle Miocene	Pickford, 1982
	Majiwa, Kenya	Maboko Fm.	Middle Miocene	Pickford, 1982
	Kipsaraman and Cheparawa, Tugen Hills, Kenya	Muruyur Fm.	15.5 Ma	Bishop, 1972; Tassy, 1986; Hill, 1999; Behrensmeyer et al., 2002; Pickford, 2001, 2003
	Bosluis Pan, South Africa		ca. 16–15 Ma	Senut et al., 1996; Pickford, 2005b

TABLE 15.5 (CONTINUED)

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
Choerolophodon zaltaniensis	Gebel Zelten, Libya (type)	Qaret Jahanneam Mb., Marada Fm.	ca. 16.5 Ma	Savage and Hamilton, 1973; Gaziry, 1987a; Pickford, 1991b; Sanders, 2008a
Choerolophodon ngorora primitive morph.	Tugen Hills, Kenya	Mbs. A–D, Ngorora Fm.	ca. 13–11 Ma	Tassy, 1986
	Ft. Ternan, Kenya	Ft. Ternan Beds	14.0–13.9 Ma	Shipman et al., 1981; Tassy, 1986
Choerolophodon ngorora advanced morph	Tugen Hills, Kenya (type)	Mb. E , Ngorora Fm.	10.5 Ma	Maglio, 1974; Tassy, 1986
	?Mbagathi, Kenya	Kirimun Fm.	?Middle Miocene (alt. ?early Miocene)	Pickford, 1981; Ishida and Ishida, 1982; Tassy, 1986
	Samburu Hills, Kenya	Lower Mb., Namurungule Fm.	ca. 9.5 Ma	Tsujikawa, 2005b
	Nakali, Kenya	Nakali Fm.	9.9–9.8 Ma	Aguirre and Alberdi, 1974; Aguirre and Leakey, 1974; Tassy, 1986; Pickford, 2003; Nakatsukasa et al., 2007
Choerolophodon sp. indet.	Majiwa, Kenya		Middle Miocene	Pickford, 1981; Tassy, 1986
	Gebel Cherichera, Tunisia	Beglia Fm.	ca. 13–11 Ma	Robinson, 1974; Robinson and Black, 1974
	Henchir Beglia, Tunisia	Beglia Fm.	ca. 13–11 Ma	Robinson, 1974; Robinson and Black, 1974
	?Bled Douarah, Tunisia	Beglia Fm.	ca. 13–11 Ma	Robinson and Black, 1974; Geraads, 1989
	?Gebel Krechem el Artsouma, Tunisia	Segui Fm.	Late Miocene, ca. 11 Ma	Geraads, 1989
TETRALOPHODONTINAE				
Tetralophodon sp. nov.	Samburu Hills, Kenya	Lower, Upper Mbs., Namurungule Fm.	ca. 9.5 Ma	Nakaya et al., 1984, 1987; Sawada et al., 1998; Tsujikawa, 2005a, b
Tetralophodon sp. indet.	Gebel Cherichera, Tunisia	Beglia Fm.	ca. 13–11 Ma	Bergounioux and Crouzel, 1956
	?Bled Douarah, Tunisia	Beglia Fm.	ca. 13–11 Ma	Robinson and Black, 1974; Geraads, 1989
	Gebel Krechem el Artsouma, Tunisia	Segui Fm.	Late Miocene, ca. 11 Ma	Geraads, 1989
	?Gebel Sémène, Tunisia		?Late Miocene	Bergounioux and Crouzel, 1956
	?Zidania, Morocco		?Late Miocene	Coppens et al., 1978
	?Smendou, Algeria		?Late Miocene	Coppens et al., 1978
	?Chorora, Ethiopia	Chorora Fm.	Late Miocene, 11–10 Ma	Sickenberg and Schönfeld, 1975; Tiercelin et al., 1979; Geraads et al., 2002
	Kisegi-Nyabusosi area, Uganda	Kakara Fm.	Late Miocene, ca. ?9.0 Ma	Pickford et al., 1993; Tassy, 1999
	Sinda River, Democratic Republic of Congo	Sinda Beds	?Late Miocene	Hooijer, 1963; Madden, 1977, 1982
Gen. and sp. indet. (tetralophodont form)	Tugen Hills, Kenya	Mb. D, Ngorora Fm.	Ca. 11 Ma	Tassy, 1979b, 1986
	?Nakali, Kenya	=Kabarsero Fm.	Ca. 9.5 Ma	Pickford, 2003

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
ANANCINAE, LATE MIOCENE–LATE PLIOCENE				
Anancus kenyensis	Lothagam, Kenya	Lower and Upper Mbs., Nawata Fm.	7.4–5.0 Ma	McDougall and Feibel, 2003; Tassy, 2003
	Toros-Menalla, Chad		ca. 7.0–6.0 Ma	Vignaud et al., 2002
	Tugen Hills, Kenya	Mpesida Beds	ca. 7.0–6.0 Ma	Tassy, 1986; Kingston et al., 2002
		Lukeino Fm.	6.2–5.6 Ma	Hill et al., 1985, 1986; Tassy, 1986; Hill, 2002
	Middle Awash, Ethiopia	Adu Asa Fm.	ca. 6.3–5.6 Ma	Kalb and Mebrate, 1993; Haile-Selassie, 2001; WoldeGabriel et al., 2001; Haile-Selassie et al., 2004
		Kuseralee Mb., Sagantole Fm.	ca. 5.6–5.2 Ma	Kalb and Mebrate, 1993; Renne et al., 1999; Haile-Selassie, 2001; Haile-Selassie et al., 2004
		Haradaso Mb., Sagantole Fm.	ca. 5.0–4.4 Ma (probably about 4.8 Ma)	Kalb and Mebrate, 1993; Renne et al., 1999
	Lemudong'o, Kenya	Lemundong'o Fm.	6.1–6.0 Ma	Ambrose et al., 2003; Saegusa and Hlusko, 2007
	Manonga Valley, Tanzania	Ibole Mb., Wembere-Manonga Fm.	ca. 5.5–5.0 Ma	Harrison and Baker, 1997; Sanders, 1997
	Kossom Bougoudi, Chad		ca. 5.3 Ma	Brunet et al., 2000; Brunet, 2001
	Kanam East (type) and West, Kenya	Kanam Fm.	Late Miocene to earliest Pliocene	MacInnes, 1942; Tassy, 1986; Ditchfield et al., 1999
	Nkondo, Uganda	Nkondo Fm.	ca. 5.0–4.0 Ma	Tassy, 1995
	As Duma, Gona Western Margin, Ethiopia		4.5–4.3 Ma	Semaw et al., 2005
	Endolele, Tanzania	Lower Unit, Laetolil Beds	?ca. 4.3 Ma	Drake and Curtis, 1987; Sanders, in press
	Galili, Ethiopia	Dhidinley Mb., Mt. Galili Fm.	Early Pliocene (alt. ca. 4.17–4.07 Ma)	Kullmer et al., 2008
Anancus sp. nov.	Tugen Hills, Kenya	Chemeron Fm.	ca. 5.0–4.0 Ma	Hill et al., 1985, 1986
	Lothagam, Kenya	Apak Mb., Nachukui Fm., and unknown horizon(s)	5.0–4.2 Ma	McDougall and Feibel, 2003; Tassy, 2003
	Kollé, Chad		5.0–4.0 Ma	Brunet, 2001
	Nkondo-Kaiso Area, Nyaweiga, Uganda	Nyaweiga Mb., Nkondo Fm.	5.0–4.0 Ma	Cooke and Coryndon, 1970; Tassy, 1995
	Aterir, Kenya	Aterir beds	ca. 4.5 Ma (alt. slightly <4.0 Ma)	Bishop et al., 1971; Hill, 1994
	Kiloleli; Ngofila; Beredi South, Manonga Valley, Tanzania	Kiloleli Mb., Wembere-Manonga Fm.	ca. 4.5–4.0 Ma	Harrison and Baker, 1997; Sanders, 1997
	Middle Awash, Ethiopia	Aramis, Beidareem, and Adgantole Mbs., Sagantole Fm.	4.4–4.3 Ma	Kalb and Mebrate, 1993; Renne et al., 1999; White et al., 2006

TABLE 15.5 (CONTINUED)

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
A. sp. nov. continued	Kakesio, Tanzania	Lower Unit, Laetolil Beds	ca. 4.3 Ma	Drake and Curtis, 1987; Harris, 1987b; Hay, 1987; Sanders, 2005, in press
	Kanapoi, Kenya	Kanapoi Fm.	4.2–4.1 Ma	Feibel, 2003; Harris et al., 2003
	Sinda River, Lower Semliki, Democratic Republic of Congo	Sinda Beds	ca. 4.1 Ma	Hooijer, 1963; Yasui et al., 1992; Boaz, 1994
	Ekora, Kenya		ca. 4.0–3.75 Ma (slightly younger than 4.0 Ma)	Behrensmeyer, 1976; Kalb and Mebrate, 1993
	Laetoli, Tanzania	Upper Unit, Laetolil Beds	3.8–3.5 Ma	Drake and Curtis, 1987; Harris, 1987b; Sanders, in press
Anancus capensis	Langebaanweg, South Africa (type)	Quarry E, Quartzose Sand Mb. and Pelletal Phosphorite Mb., Varswater Fm.	Early Pliocene, ca. 5.0 Ma	Hendey, 1981; Sanders, 2006, 2007
Anancus petrocchii	Sahabi, Libya (type)	Sahabi Fm.	Late Miocene–early Pliocene, ca. 5.2 Ma	Petrocchi, 1954; Heinzelin and El-Arnauti, 1987; Bernor and Scott, 2003; Sanders, 2008b
Anancus osiris	Wadi Natrun, Egypt		Late Miocene or early Pliocene	Coppens et al., 1978; Geraads, 1982; Thomas et al., 1982
	Giza, Egypt (type)		Late Pliocene	Arambourg, 1945, 1970
	Grombalia, Tunisia		Late Pliocene	Arambourg, 1970
	Aïn Boucherit, Algeria		Late Pliocene; 2.32 Ma (alt. ca. 2.0 Ma)	Arambourg, 1970; Geraads and Amani, 1998; Geraads, 2002; Sahnouni et al., 2002
	Lac Ichkeul, Tunisia		Late Pliocene	Arambourg, 1970
	Ferryville, Tunisia		Late Pliocene	Depéret et al., 1925; Coppens et al., 1978
	Hamada Damous, Tunisia		Late Pliocene	Fournet, 1971
	Gebel Melah		Late Pliocene	Fournet, 1971
	Ahl al Oughlam, Casablanca, Morocco		Late Pliocene, ca. 2.5 Ma	Geraads and Metz-Muller, 1999; Geraads, 2002
	Fouarat, Morocco		Late Pliocene	Arambourg, 1970
Anancus sp. indet.	Aramis, Middle Awash, Ethiopia	Haradaso Mb., Sagantole Fm.	ca. 4.4 Ma	WoldeGabriel et al., 1994
	Omo, Ethiopia	Mursi Fm.	>4.15 Ma	Beden, 1976; Feibel et al., 1989
	Karonga, Uraha, Malawi	Chiwondo Beds	>4.0 Ma	Mawby, 1970; Bromage et al., 1995
	Makapansgat, South Africa	Mb. 4	<3.1 Ma	Cooke, 1993; Partridge et al., 2000
	Baard's Quarry, South Africa	Lower Level	Late Pliocene	Hendey, 1978a, 1981

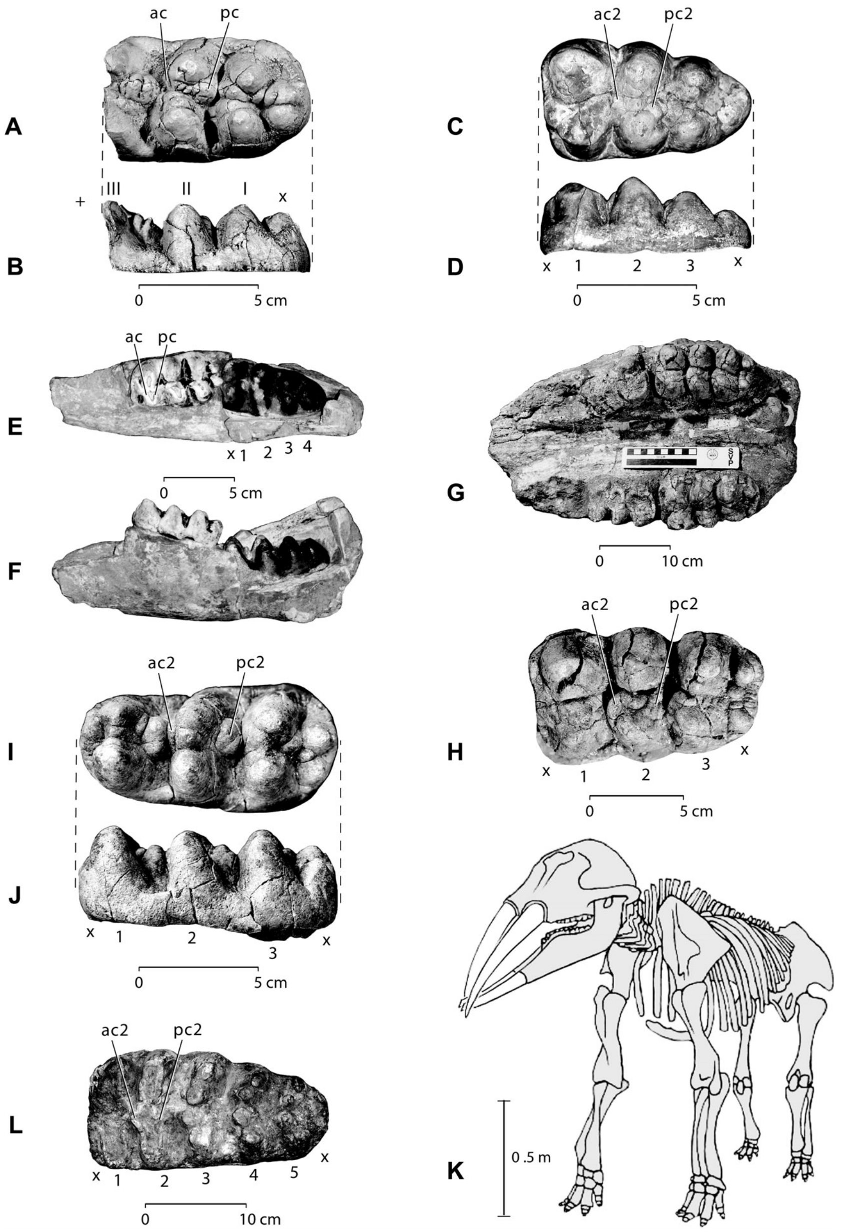

FIGURE 15.11 Aspects of gomphothere dental and skeletal morphology. Anterior is to the left in all specimens. A) Occlusal view, right m3 (cast), CH14-V14, cf. *Gomphotherium* sp. nov., Chilga, Ethiopia. B) Right lateral view, right m3 (cast), CH14-V14, cf. *Gomphotherium* sp. nov., Chilga, Ethiopia (reversed). C) Occlusal view, left M3, M21866, ?cf. *Gomphotherium* sp. nov. D) Right lateral view, left M3, M21866, ?cf. *Gomphotherium* sp. nov. E) Occlusal view, left dentary with m2-m3, DOG87.1, *Eritreum melakeghebrekristosi* (type specimen). F) Right lateral view (reversed), left dentary with m2–m3, DOG87.1, *Eritreum melakeghebrekristosi* (type specimen). G) Occlusal view, palate with right and left M2–M3, KNM-MI 1, *Gomphotherium* sp., Mwiti, Kenya. H) Occlusal view, left M3, KNM-MI 1, *Gomphotherium* sp., Mwiti, Kenya. I) Occlusal view, right m2, DPC 12926. *Gomphotherium angustidens libycum*. J) Left lateral view, right m2, DPC 12926. *Gomphotherium angustidens libycum*. K) Skeletal reconstruction, *Gomphotherium pygmaeus* (modified from Pickford, 2004: figure 3). L) Occlusal view, left M3, KI 6492, *Tetralophodon* sp. nov. K, courtesy of Martin Pickford.

ABBREVIATIONS: ac, pretrite anterior accessory central conule; pc, pretrite posterior accessory central conule; x, anterior or posterior cingulum(id); 1, 2, 3, . . . , first, second, third, . . . loph(id); I, II, III . . ., loph(id)s counted from the posterior end of the crown.

and paleoecological evidence suggest that *Z. aegyptensis* inhabited well-watered, forested landscapes (Said, 1962; Bown et al., 1982; Pickford, 1991b).

Family INCERTAE SEDIS
CF. *GOMPHOTHERIUM* SP. NOV. Sanders, Kappelman and Rasmussen, 2004

Figures 15.11A–15.11D

Age and Occurrence Late Oligocene, eastern Africa, ?northern Africa (table 15.5).

Description Very small elephantoid, at the low end of dental size range for gomphotheres, but with larger molars than palaeomastodonts. Premolars and molars simultaneously in occlusion. Lower third molar with at least three lophids and a prominent postcingulid formed of two stout conelets (figures 15.11A, 15.11B). Molars with small anterior and posterior accessory central conules throughout the pretrite side, and a low cingular ribbon rimming the buccal margin of the crown. Half-lophids composed of a single, large abaxial conelet and a smaller adaxial conelet. No cementum. The upper fourth premolar resembles P4 in *Gomphotherium* in the presence of a central cusp in its posterior loph, and prominent enamel swelling on the anterior face of the last pretrite half-loph (Tassy, 1985; Sanders et al., 2004). An M3 from Gebel Zelten, Libya (M21866) is a good fit morphologically for the m3 from Chilga, Ethiopia, and may belong in this taxon. It is subtriangular in occlusal view, small, and has three lophs and a low, stout heel, lophs composed of massive main conelets superficially subdivided from diminutive mesoconelets, and pretrite accessory central conules accompanying lophs 1 and 2 anteriorly and posteriorly, and loph 3 anteriorly (figures 15.11C, 15.11D).

Remarks Oldest known possible gomphothere, documented with certainty only from the Chilga region, Ethiopia, from sites also containing palaeomastodonts (Sanders et al., 2004). Prior to its discovery, gomphothere-like proboscideans had only been known from Neogene horizons. This new taxon from Chilga, along with *Eritreum*, suggests an autochthonous African origination of elephantoids unrelated to the early Miocene faunal turnover in Afro-Arabia that was marked by an influx of Eurasian taxa (Kappelman et al., 2003).

Genus *ERITREUM* Shoshani et al., 2006
ERITREUM MELAKEGHEBREKRISTOSI Shoshani et al., 2006
Figures 15.7B, 15.11E, and 15.11F

Age and Occurrence Late Oligocene, eastern Africa (table 15.5).

Diagnosis Very diminutive elephantoid (body mass estimate, 600 kg), with molars in size range of palaeomastodonts and smaller than those of other gomphotheres and mammutids (figure 15.7B). Anterior cingulid reduced relative to condition in palaeomastodonts. Further distinguished from palaeomastodonts by presence of fourth lophid in m3, and trefoil wear patterns throughout the length of molar crowns.

Description Lower tusks pyriform in cross section, and higher than wide. Mandibular corpus wider than high; symphysis like that of *Phiomia* in proportions. Intermediate molars trilophodont with a thick postcingulid. Lower third molar with four lophids but no appreciable postcingulid (figure 15.11E). Pretrite anterior and posterior accessory central conules throughout molar crowns contribute to trefoil enamel patterns in wear. Adaxial conelets smaller than abaxial conelets, but more equal in height than in mammutids. No cementum. Emergence of m3 was delayed until intermediate molars were well in wear (figure 15.11F).

Remarks Known from an isolated discovery, *Eritreum* documents an intermediate stage in the evolution of palaeomastodonts to more derived gomphotheres, and further points to the Horn of Africa as a locus of pre-Miocene elephantoid origination.

Family GOMPHOTHERIIDAE Hay, 1922

Arguably the most successful of proboscidean families, of remarkable taxonomic diversity and geographic and temporal extent. Gomphotheriids may have first appeared in the Horn of Africa during the late Oligocene, depending on the affinities of new taxa from Eritrea and Ethiopia (Sanders and Kappelman, 2001; Shoshani et al., 2001b; Kappelman et al., 2003; Sanders et al., 2004; Shoshani et al., 2006), underwent a series of adaptive radiations during the Miocene, and persisted in Africa until the late Pliocene (Kalb and Mebrate, 1993). Along with dramatic molar size increase over that of their palaeomastodont precursors, gomphothere-grade dentition was achieved by substantial enlargement and differentiation of tusk forms, and by elaboration of molars through the addition of loph(id)s, cementum, and accessory central conules. Several gomphothere lineages independently lost lower tusks, and further morphological differentiation among taxa was achieved by occlusal rearrangement of transverse half-loph(id) pairs into anancoid, pseudoanancoid, and chevron patterns. Elephants are thought to have evolved from a gomphotheriid in the late Miocene, a transformation largely achieved through radical reorganization of molar construction and chewing dynamics (Maglio, 1972).

Afro-Arabian constituents of Gomphotheriidae include gomphotheriines, anancines, tetralophodonts, choerolophodontines, and amebelodontines (but see Shoshani, 1996; Tassy, 1996c; Shoshani and Tassy, 2005). These taxa have been tenuously linked only by a small set of traits, such as enlarged central accessory conules, broad narial opening, pyriform cross section of lower tusks, and brachyodont, bunolophodont molars with a tendency for enamel wear figures to incorporate accessory conules into trefoil patterns (Coppens et al., 1978; Shoshani, 1996; Tassy, 1996c).

Subfamily GOMPHOTHERIINAE Hay, 1922

This subfamily, and particularly its core genus *Gomphotherium,* serve as wastebasket taxa, encompassing species that lack specializations (e.g., "shovel tusks") characteristic of more clearly definable gomphotheriids, such as amebelodonts, and which primitively retain features like trilophodonty and lower tusks with pyriform cross sections. *Gomphotherium* has been divided gradistically into a primitive "*G. annectens* group," including *G. annectens* (Asia), *G. cooperi* (South Asia), *G. sylvaticum* (Europe), and *Gomphotherium* sp. (Africa), and a more advanced "*G. angustidens* group," distinguished by differences in cranial vault height, width of the nasal opening, cross-sectional shape of lower tusks, degree of development of accessory conules, and angle of downturn of the symphysis (Tassy, 1985, 1986, 1994a, 1996c). Also included in the subfamily are the so-called pygmy gomphotheres.

Genus *GOMPHOTHERIUM* Burmeister, 1837
["*GOMPHOTHERIUM ANNECTENS* GROUP" Tassy, 1985]
GOMPHOTHERIUM SP. Tassy, 1979a
Figures 15.11G and 15.11H

Partial Synonymy Progomphotherium maraisi (in part), Pickford, 2003:228.

Age and Occurrence Early Miocene, eastern Africa (table 15.5).

Description Primitive trilophodont gomphothere with only nascent development of a fourth loph in M3, and little or no expression of independent accessory central conules (figures 15.11G, 15.11H). Loph(id)s formed of massive, low main conelets accompanied by more diminutive mesoconelets; enamel very thick; no molar cementum. M3s are relatively wide and larger than those of *P. maraisi*. Lower tusks modest in size, pyriform in cross section, and longitudinally torqued.

Remarks This taxon was contemporaneous with other species of the "*G. annectens* group," indicating that these gomphotheres dispersed widely throughout the Old World rapidly after the group first appeared in Africa (Sanders and Miller, 2002). It also overlapped temporally with more advanced congeners, but the early success of the group apparently did not continue into the middle Miocene (table 15.5).

[“*GOMPHOTHERIUM ANGUSTIDENS* GROUP” Tassy, 1985]

GOMPHOTHERIUM ANGUSTIDENS LIBYCUM (Fourtau, 1918)

Figures 15.7, 15.11I, and 15.11J

Partial Synonymy *Mastodon angustidens* var. *libyca*, Fourtau, 1918:84; *Mastodon spenceri*, Fourtau, 1918:89; *Rhyncotherium spenceri*, Osborn, 1936:485; *Trilophodon angustidens* var. *libycus*, Osborn, 1936:260; *Serridentinus* sp., Hormann, 1963:92; *Mastodon angustidens*, Savage, 1971:221; *Gomphotherium angustidens*, Hamilton, 1973:276; *G. angustidens*, Tobien, 1973a:214–215; *G. angustidens*, Coppens et al., 1978:342–343; “*Gomphotherium*” *pygmaeus* (in part), Coppens et al., 1978:344, 346; *G. cooperi*, Gentry, 1987; *G. spenceri*, Savage, 1989:594; *G. cooperi*, Savage, 1989:596; *G. angustidens*, Savage, 1989:594; *Archaeobelodon* aff. *A. filholi*, Tiffney et al., 1994:27; *G. angustidens libycum*, Sanders and Miller, 2002:389; *Afromastodon lybicus*, Pickford, 2003:231, 233; ?*Eozygodon* sp., Pickford, 2003:230–231; *Gomphotherium* sp nov. (in part), Pickford, 2003:233; *Afrochoerodon zaltaniensis* (in part), Pickford, 2003:231, 233.

Age and Occurrence Early–?late Miocene, northern Africa and Arabia (table 15.5).

Diagnosis Sanders and Miller (2002). Differs from more advanced forms of *G. angustidens* by variable expression of fourth loph in M3 and occasional absence of fourth lophid in m3; from *G. steinheimense* and *G. browni* by smaller size (figure 15.7) and lesser subdivision of adaxial and abaxial conelets, and from “pygmy” gomphotheres by larger size and lesser development of cementum. Distinguished from *G. annectens* grade gomphotheres by more pronounced development of anterior and posterior accessory central conules, and less massive structure of loph(id)s (figures 15.11I, 15.11J).

Description Medium-sized gomphothere. The dentition is most like that of European *G. angustidens* in size (figure 15.7) and in the degree of expression of pretrite accessory conules, particularly posterior to loph(id)s, contributing to trefoil enamel patterns with wear. There are no posttrite accessory conules. Half-loph(id)s are separated by a median sulcus, and each is usually composed of a large, outer main conelet accompanied by a much more diminutive mesoconelet. Mesoconelets are aligned transversely side by side and may be slightly more anterior than their main conelets (figure 15.11I). Enamel is thick (as much as 6–7 mm in third molars), and cementum is slight to absent. Intermediate molars are trilophodont.

Remarks The type series and referred specimens from Wadi Moghara, Egypt, have had a varied taxonomic history and have been divided among several species, but there are no compelling reasons to separate these fossils or remove them from *Gomphotherium*. *Gomphotherium angustidens libycum* co-occurs at Moghara with *Archaeobelodon, Zygolophodon, Afrochoerodon*, and *Prodeinotherium* (Harris, 1978; Sanders and Miller, 2002), but these are distinct morphologically. Gomphothere specimens from a handful of other Afro-Arabian sites (table 15.5) identify closely with the Moghara sample, including molars from Ad Dabtiyah, Saudi Arabia. A recent proposal to refer *G. angustidens libycum* to a new species, *Afromastodon libycus* (Pickford, 2003), is baseless. *Afromastodon* clearly belongs in the Amebelodontinae (see later discussion), and unlike molars of *A. coppensi*, in the Moghara and allied material half-loph(id)s are not transversely offset, and there are no posttrite accessory central conules.

An age-grade series of jaws with *Gomphotherium*-type molars from Gebel Zelten clarifies the mandibular morphology of *G. angustidens libycum* and strengthens the connection between the Moghara and Zelten samples (Sanders, 2008a). These jaws have wide symphyseal gutters, symphyseal angulation that increased substantially downward with age, large arterial foramina that communicate medially from the mandibular canal, just posterior to the i2 alveoli, and three mandibular foramina: a large opening below the anteriormost cheek tooth, a smaller foramen lateral to the symphysis, and a capacious (“torpedo-tube”) opening anterior and ventral to that, marking the anteriormost extent of the mandibular canal (Sanders, 2008a). Tassy (1985) speculated that a dentary from Moghara with similar morphology might have choerolophodontine affinities, but the Zelten specimens show that broad guttering and downward angulation of the symphysis are also present in some forms of *Gomphotherium*.

[“‘PYGMY’ *GOMPHOTHERIUM* GROUP”]

GOMPHOTHERIUM PYGMAEUS (Depéret, 1897)

Figures 15.7A, 15.7B, and 15.11K

Partial Synonymy *Mastodon angustidens* var. *pygmaeus*, Depéret, 1897; *Phiomia pygmaeus*, Osborn, 1936:246–247, figures 186, 187A, A1–A4; *Trilophodon olisiponensis* var. *pygmaeus*, Bergounioux and Crouzel, 1959: 102; “*Gomphotherium*” *pygmaeus*, Coppens et al., 1978:343, 346; *Choerolophodon pygmaeus*, Pickford, 2004, 2005a.

Holotype University of Lyon, Institute of Geology, N^{o} 1678, partial r. m3.

Type Locality Kabylie, Algeria.

Age and Occurrence Middle Miocene, northern, eastern, southern Africa (table 15.5).

Referred Specimens (Bosluis Pan, South Africa) SAM-Q 2516, incomplete l. m3; (Ngenyin, Tugen Hills, Kenya) Bar 801’02, l. metacarpal; Bar 802’02, two I2 frags.; Bar 803’02, r. m2; Bar 804’02, l. m2; Bar 805’02, l. and r. m3; Bar 806’02, l. m1; Bar 807’02, l. M1; Bar 808’02, l. M2; Bar 809’02, l. and r. M3; Bar 812’02, r. calcaneum; Bar 814’02, prox. phalanx; Bar 816’02, partial r. femur; Bar 817’02, r. MT IV; Bar 818’02, l. magnum; Bar 821’02, l. trapezoid; Bar 822’02, l. lunate; Bar 823’02, r. lat. cuneiform; Bar 827’02, prox. phalanx frag.; Bar 828’02, prox. phalanx; Bar 829’02, prox. phalanx; Bar 830’02, r. trapezium; Bar 831’02, l. trapezium; Bar 832’02, r. MC IV; Bar 1995’02, Bar 1996’02, l. cuboid; l. navicular; Bar 1998’02, prox. phalanx frag.; Bar 2002’02 r. distal tibia; Bar 2003’02 l. distal fibula.

Diagnosis Gomphothere of small size; molars larger than those of palaeomastodonts but near lower extreme of range for *Gomphotherium* (figure 15.7B); intermediate molars trilophodont and third molars with four loph(id)s; crowns may be well invested with cementum and exhibit choerodonty and ptychodonty; crowding of half-loph(id)s causes main conelets to converge strongly toward the midline apically and produces weak chevroning of posterior loph(id)s (though unlike choerolophodont molars pre- and posttrite mesoconelets are transversely aligned); pretrite accessory central conules present throughout the crown, particularly posterior to loph(id)s.

Description The type specimen, a right m3 missing its anterior lophid, preserves three lophids and a low, substantial distal cingulid composed of several large conelets. Its transverse valleys are filled with cementum, but even so it is apparent that the pre- and posttrite half-lophids are each comprised of a large, outer conelet and more diminutive mesoconelet, and that they are transversely aligned. Also, it is possible to see the outline of pretrite anterior and posterior accessory central conules, which in wear would have contributed to trefoil enamel figures. Because of the narrowness of the crown, the main, outer conelets of each lophid are closely convergent apically.

Morphometrically quite similar to the Kabylie tooth are molars from Bosluis Pan, South Africa, and Ngenyin, Kenya, and particularly in the latter the trefoil arrangement of main conelets and accessory conules can be confirmed. Although crowding of loph(id)s produces weak chevroning in these specimens, they exhibit no sign of the typical choerolophodont occlusal pattern, marked by advancement of the pretrite mesoconelet anterior to the posttrite half-loph(id). An I2 fragment from Ngenyin attributed to this species (Pickford, 2004) is D shaped, typical of *Gomphotherium*, and is too abraded to know whether it originally possessed a band of enamel.

A wealth of postcrania from Ngenyin, Kenya are associated with the dental sample. These are similar to corresponding skeletal elements in *Gomphotherium*, and indicate an animal 1.5 m tall at the shoulder, with graviportal adaptations for support of the body and semicursorial locomotor capabilities (figure 15.11K; Pickford, 2004).

A lower molar from Arrisdrift, Namibia, attributed to this species (Pickford, 2005a) is a dp4 rather than an m1, and as such, its size is not remarkably small. It should be returned to its original assignment in *Afromastodon coppensi* (Pickford, 2003).

Remarks Diminutive gomphothere molars from a number of sites (figures 15.7A, 15.7B) have previously been included in *G. pygmaeus*, based primarily on size (e.g., Coppens et al., 1978). Inclusion of dentition of all small Afro-Arabian gomphotheres, however, would make this an unrealistically heterogeneous species (see later discussion). Roger et al. (1994) considered *G. pygmaeus* a *nomen dubium* due to what they considered the inadequacy of the type specimen, but the addition of the Ngenyin fossils and reconsideration of the peculiar combination of traits in the Kabylie molar demonstrate the validity of the type and taxon. Because of weak chevroning and thick cementum, it has also been suggested that *G. pygmaeus* is a choerolophodont (Tobien, 1973a; Pickford, 2004). This argument is unconvincing, as the former is an artefact of occlusal crowding and small size, and the latter is highly homoplasic among gomphotheriids.

GOMPHOTHERIUM SP. INDET.

Partial Synonymy Trilophodon pygmaeus, Arambourg, 1961:108; *Mastodon pygmaeus*, Savage, 1971:221; *Gomphotherium angustidens*, Hamilton, 1973:276; "*Gomphotherium*" *pygmaeus*, Coppens et al., 1978:344, 346; *Gomphotherium angustidens pasalarensis*, Gaziry, 1987a:76; Elephantoidea gen. et sp. indet., Roger et al., 1994:14, plate I, figures 2–4.

Age Early–middle Miocene, northern Africa and Arabia (table 15.5).

Description Gomphotherium-type molars from a few sites can be grouped together based on their small size and common differences from *G. pygmaeus*, including lesser degree of occlusal crowding and chevroning, and lack of thick cementum. This group has trilophodont intermediate molars and, at least incipiently, four loph(id)s in its third molars. Among this sample, cheek teeth from Ghaba, Oman, are more derived than those of Siwa, Egypt, or Gebel Zelten, Libya, by the greater subdivision of their half-loph(id)s into at least two conelets each, and by a more balanced trefoil pattern of pretrite main conelets and accessory conelets throughout their crowns. Such distinctions may warrant species-level separation of these site samples.

Remarks The occurrences of these specimens and *G. pygmaeus* suggest that "pygmy" gomphotheres were pan-Afro-Arabian in distribution and taxonomically diverse, but not common. It is uncertain whether they represent true cases of dwarfing, or primitively retained an ancestral condition of small size. Among known gomphotheriids, their affinities are unquestionably closest to *Gomphotherium*.

Subfamily AMEBELODONTINAE Barbour, 1927

The origin of amebelodonts and the oldest records of a number of amebelodont genera can be traced to the early Miocene in Africa (MacInnes, 1942; Maglio, 1969a; Tassy, 1984, 1985, 1986; Sanders and Miller, 2002; Pickford, 2003). The group subsequently flourished in early–middle Miocene faunas of Europe (Tassy, 1985), South Asia (Tassy, 1983a), and Asia (Osborn, 1936; Guan, 1996), and it enjoyed particular success in North America during the late Miocene (Osborn, 1936; Fisher, 1996; Lambert and Shoshani, 1998).

The subfamily includes the "shovel tuskers," so called because of the great broadening and dorsoventral flattening of their i2s, accompanied in some instances by internal development of dentinal tubules and rods. Among these are the genera *Amebelodon* and most notably *Torynobelodon* and *Platybelodon* (Osborn and Granger, 1931, 1932; Osborn, 1936; Lambert, 1990, 1992). More plesiomorphic members of the subfamily do not possess these traits to any great extent, if at all.

Along with flattening of i2s, Amebelodontinae is also characterized by tendencies for strong pretrite wear patterns in molars; enlargement of pretrite accessory central conules; presence of posttrite accessory central conules and, in some taxa, of secondary, posttrite trefoils; pseudoanancoid offset of pre- and posttrite half-loph(id)s; relatively narrow molar crowns; and prominent splanchnocrania, especially in the peri- and prenasal regions (Tobien, 1973a; Tassy, 1984, 1985, 1986).

There is little doubt that the success of amebelodonts was largely due to the evolutionary transformation of their lower tusks into powerful tools for the efficient acquisition of plant materials, such as tough subsurface and aquatic browse (Lambert, 1992), that may have been difficult or impossible for other proboscideans to access. Such specialization likely fostered niche displacement between amebelodonts and choerolophodonts, permitting them to widely share early–middle Miocene African habitats (table 15.5). Nevertheless, despite these formidable dental adaptations, by the onset of the Pliocene amebelodonts had disappeared everywhere across their extensive geographic range. Compelling evidence has been presented for the effects of cooler, drier climatic regimes and consequent transition to steppe habitats as prevalent factors contributing to the extinction of the subfamily in North America at the end of the late Miocene (Fisher, 1996). Comparable changes across African landscapes at the close of the Miocene (Cerling et al., 1997; Pagani et al., 1999) may have played a similar role in the demise of amebelodonts on that continent.

Genus *PROGOMPHOTHERIUM* Pickford 2003
PROGOMPHOTHERIUM MARAISI Pickford 2003
Figures 15.12A, 15.12B, 15.13A, and 15.13B

Age and Occurrence Early Miocene, southern and ?eastern Africa (table 15.5).

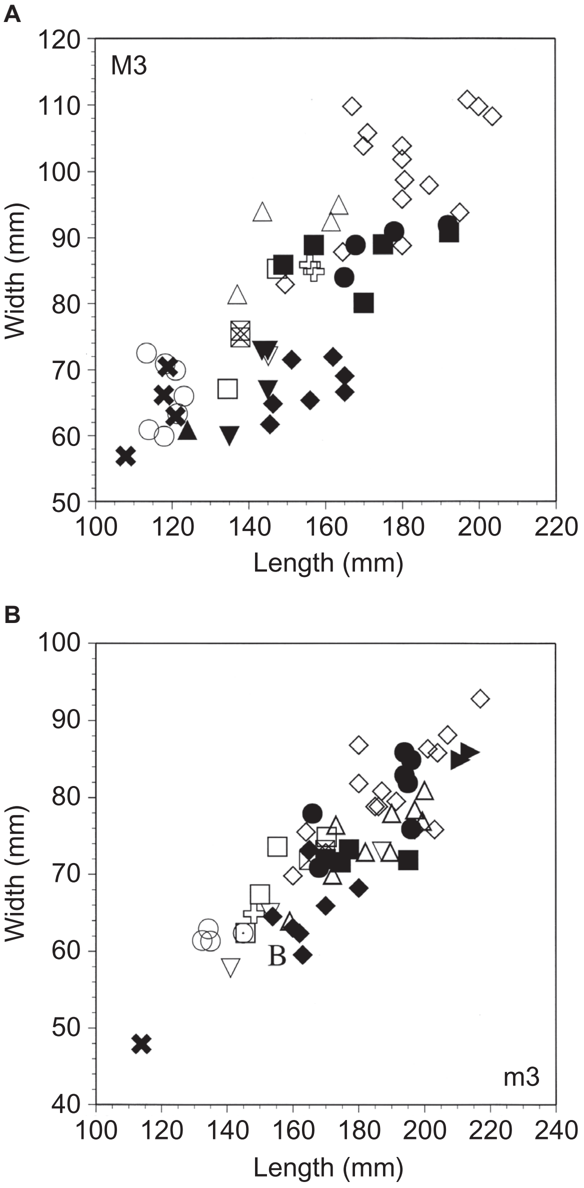

FIGURE 15.12 Bivariate plots of M3 (A) and m3 (B) crown length versus width in African and selected Eurasian amebelodonts and choerolophodonts. Comparative dimensions supplementing original measurements are from Forster Cooper (1922), Tiercelin et al. (1979), Tassy (1983a, 1983b, 1985, 1986), Gaziry (1976, 1987a, 1987b), Suwa et al. (1991), Pickford (2001, 2003), Sanders and Miller (2002), and Sanders (2003).

SYMBOLS: open circle, *Afrochoerodon kisumuensis*; open circle with dot, *"Choerolophodon" palaeindicus;* open square with x, *Choerolophodon zaltaniensis*; open square, *C. ngorora*; open cross, cf. *Choerolophodon* (S. Asia); inverted open triangle, *C. anatolicus*; open triangle, *C. pentelici*; open diamond, *C. corrugatus;* B, Burji gomphotheriid; X, *Progomphotherium maraisi*; inverted closed triangle, cf. *Archaeobelodon*; closed triangle, *A. filholi*; closed diamond, *Protanancus macinnesi*; closed square, *P. chinjiensis*; closed circle, *Afromastodon coppensi*; right-facing closed triangle, *Amebelodon cyrenaicus*.

Diagnosis Pickford (2003). External nares proportionally higher and slightly narrower than in gomphotheriines. Zygomatic process of maxilla projects from face at right angle. Marked angulation between dorsal profile of neurocranium and splanchnocranium. Basicranium nearly in same plane as the palate. Mandibular symphysis relatively brevirostrine, not spatulate anteriorly, and massively constructed for a gomphothere. Molars very small (figures 15.12A, 15.12B).

Description Pickford (2003). Neurocranium heavily pneumatized; rostrum elongated and rostral trough broad; upper tusks socketed parallel to each other; nasals overhang rostrum; external nares about the same width as the rostrum; cranium low and elongated in lateral profile (figure 15.13A). Upper tusks oval in cross section, with greatest diameter dorsoventral and an enamel band ventrolaterally. Lower tusks suboval in cross section, with greatest diameter vertical and mesial face flat or concave. Cheek teeth simultaneously in wear. Molar half-loph(id) s constructed of massive main conelets and poorly differentiated mesoconelets. Lower third molar with four lophids and no appreciable postcingulid; upper third molar variably has three lophs or an incipient fourth loph (figure 15.13B). Intermediate molars trilophodont. Anterior and especially posterior accessory central conules are weakly developed, and enamel trefoil figures may not be distinguishable with wear. Variable development of posttrite accessory central conules (figure 15.13B).

Remarks To Pickford (2003), the craniodental morphology of this diminutive species, barely more advanced than that of palaeomastodonts, suggested its inclusion with primitive early Miocene gomphotheres in the "*Gomphotherium annectens* group." However, features such as facial elongation, close spacing between temporal fossae, low alveolar height of the maxillae, "hourglass" dorsal profile of the cranium, and size and configuration of the nasal opening, as well as development of posttrite accessory conules, suggest that *Progomphotherium* may instead belong in Amebelodontinae. The presence of three lophs in M3, suboval cross sectional shape of the i2s, and inferred short length of the symphysis indicate that if this attribution is correct, *P. maraisi* is the most primitive amebelodont known.

Molars from Moroto II, Uganda, have been assigned to *P. maraisi* (Pickford and Mein, 2006). The pronounced wear asymmentry and angulation between pre- and posttrite molar sides, poor expression of pretrite accessory conules, and development of posttrite accessory conules in the Moroto specimens are features typical of primitive *Archaeobelodon*, supporting the identification of *P. maraisi* as an amebelodont. Molar fragments from Napak, Uganda assigned to *P. maraisi* (Pickford, 2003) have larger accessory conules, and are more similar to *Archaeobelodon filholi* teeth.

Genus *ARCHAEOBELODON* Tassy, 1984
Figure 15.12A

Diagnosis Archaic amebelodonts with relatively slender symphyses that are little angled on mandibular corpora. Lower tusks more flattened than those of *Afromastodon*, but not as wide as those in *Protanancus*, *Amebelodon*, or *Platybelodon*. Upper tusks are robust, without longitudinal torque, and have a band of enamel. P2 is retained. Molars narrow (figure 15.12A) and very brachyodont. Posttrite accessory central conules variably present and diminutive.

CF. *ARCHAEOBELODON* SP. Tassy, 1984

Partial Synonymy Trilophodon angustidens kisumuensis (in part), MacInnes, 1942: plate III, figures 14–16; plate V,

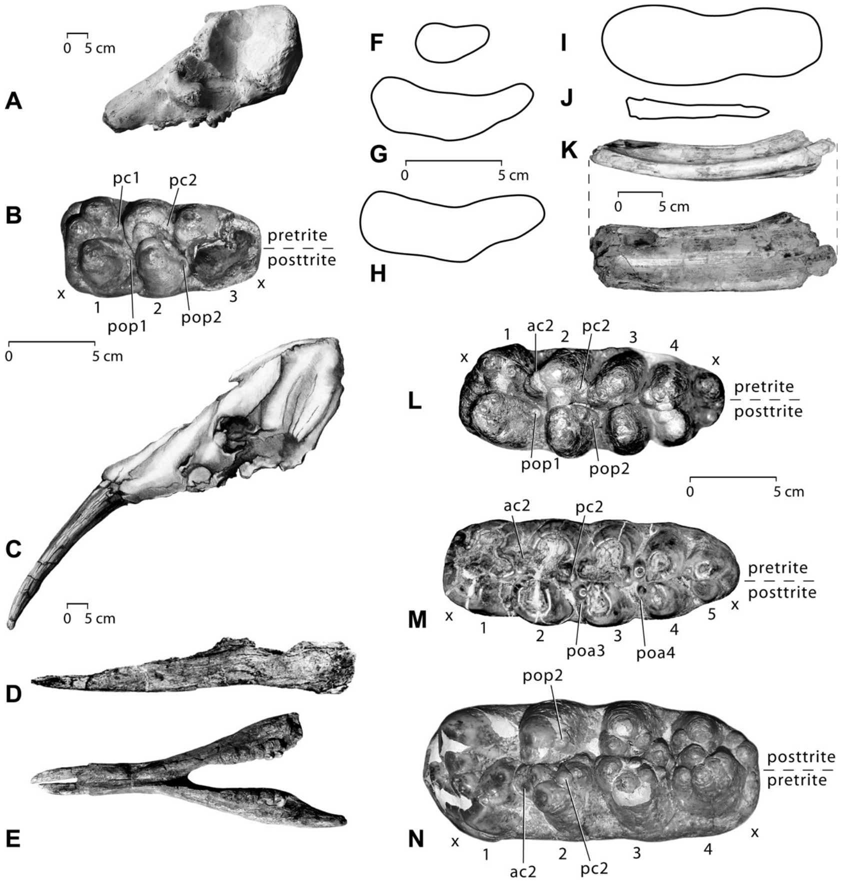

FIGURE 15.13 Aspects of amebelodontine craniodental morphology. A) Right lateral view (reversed), cranium, AM 1'95, holotype of *Progomphotherium maraisi* (see Pickford, 2003: plate 6). B) Right M3, AM 1'95, part of holotype of *Progomphotherium maraisi* (see Pickford, 2003: plate 7). C) Drawing, right lateral view (reversed), cranium, KNM-MI 7532, *Archaeobelodon filholi*. D) Left lateral view, mandible, KNM-MI 7532, *Archaeobelodon filholi*. E) Occlusal view, mandible, KNM-MI 7532, *Archaeobelodon filholi*. F–J, i2 cross sections, medial side to the left, all to same scale. F) KNM-MI 7532, *Archaeobelodon filholi*. G) M15532 (KBA 109), *Protanancus macinnesi*. H) Semliki n° 531A, *Protanancus macinnesi*. I) Sahabi 481P34A, *Amebelodon cyrenaicus* (reversed). J) MCZ 38-64K, *Platybelodon* sp. K) Left i2 fragment, lateral view (top) and dorsal view (bottom), M15533, *Protanancus macinnesi*. L) Occlusal view, right M3, M15525, part of holotype of *Protanancus macinnesi*. M) Occlusal view, right m3, M15438, *Protanancus macinnesi*. N) Occlusal view, left m3, PQAD 257, *Afromastodon coppensi* (see Pickford, 2003: plate 14).

ABBREVIATIONS: ac, pretrite anterior accessory central conule; pc, pretrite posterior accessory central conule; poa, posttrite anterior accessory central conule; pop, posttrite posterior accessory central conule; x, anterior or posterior cingulum(id); 1, 2, 3, . . . , first, second, third, . . . loph(id).

figures 3, 4, 5, 6, 9; plate VI, figure 8; ?Mammutid aff. *Zygolophodon*, Van Couvering and Van Couvering, 1976; cf. *Gomphotherium angustidens* (in part), Coppens et al., 1978.

Age and Occurrence Early Miocene, northern and eastern Africa (table 15.5).

Description Small amebelodont with trilophodont intermediate molars. M3 with four lophs. Molars have massive main conelets. Pretrite accessory conules may be absent (e.g., KNM-RU 4423; Tassy, 1986) or small and contribute to a trefoil arrangement (e.g., CGM 30892; Sanders and Miller, 2002). When present, posttrite accessory conules are diminutive. Worn molars exhibit a distinctive asymmetry between larger, more deeply excavated pretrite half-loph(id)s and posttrite half-loph(id)s. A p3 from Rusinga, Kenya is bilophodont and has tiny accessory conules posterior to its proto- and metaconids (Tassy, 1986).

ARCHAEOBELODON FILHOLI (Frick, 1933)
Figures 15.13C–15.13F

Partial Synonymy *Platybelodon kisumuensis*, Harris and Watkins, 1974; *Gomphotherium kisumuensis*, Savage and Williamson, 1978; *Platybelodon* sp., Pickford, 1981; *Archaeobelodon* aff. *filholi*, Tassy, 1984, 1985, 1986.

Age and Occurrence Early Miocene, eastern Africa (table 15.5).

Description The skull morphology of this taxon is documented in an associated cranium and mandible from Mwiti, Kenya (Tassy, 1986). Compared with the neurocranium, the face is relatively massive, with an elongate prenasal area and wide nasal region. The orbit is low and situated in a line posterior to the molar row; overall, the cranium is low and the basicranium is not very raised (figure 15.13C). The mandible is longirostral, with a transversely narrow symphysis, and is nearly straight along the length of its ventral margin (figures 15.13D, 15.13E).

Upper tusks have a lateral band of enamel and are relatively short and robust; the I2 of the skull has dimensions of L = 610 mm, and W = 110 mm, H = 102 mm at the alveolus (Tassy, 1986). Cross-sectional shape is ovoid. Lower tusks have a flattened pyriform shape in cross section, with a shallow longitudinal sulcus dorsally (figure 15.13F), and are torqued along their length, resembling i2s of *Phiomia major*.

Third and fourth premolars are bilophodont and typical for gomphotheres, with low, narrow cingulae(ids) and cusps much higher and larger anteriorly than posteriorly (Tassy, 1986).

Intermediate molars are trilophodont, and third molars have loph(id) formulas of x4x. Enamel is thick (4.0–6.4 mm), and cusps are low and massive (Tassy, 1986). Cementum is variably present but not extensively distributed on molar crowns. Molars are relatively narrow, with strong development of pretrite anterior and posterior accessory central conules, and much smaller posttrite accessory central conules. Pseudoanancoidy of half-loph(id)s varies but is generally weak.

Remarks The African *Progomphotherium* and *Archaeobelodon* samples mark the beginnings of the Amebelodontinae, and its primitive status is signaled by the retention of features such as low, massive conelets, symphyses projecting horizontally from mandibular corpora, modest flattening of lower tusks, poor or moderate development of accessory central conules, relatively small size, and low crania. *Archaeobelodon* migrated to Europe shortly after its origin in Africa (Tassy, 1985, 1986), and the morphological identity of East African specimens with European material indicates conspecificity.

Genus *AFROMASTODON* Pickford, 2003
AFROMASTODON COPPENSI Pickford, 2003
Figures 15.12A, 15.12B, and 15.13N

Partial Synonymy *Gomphotherium* cf. *angustidens*, Corvinus and Hendey, 1978; Gomphotheriidae, gen et. sp. indet., Hendey, 1978b, *Protanancus macinnesi*, Tassy, 1985, 1986.

Age and Occurrence Middle Miocene, southern Africa (table 15.5).

Diagnosis M3/m3 differ from those of *Protanancus macinnesi* (Tassy, 1986; Pickford, 2003) by their lack of fifth loph(id)s, relatively greater width, and larger size (figures 15.12A, 15.12B), though are similar in occlusal organization. Molars are also larger than those of *Archaeobelodon* (figure 15.12A). Lower tusks lack enamel, are ovoid in cross section (Pickford, 2003, table 11), and have height/width ratios above the proportional range of variation for other amebelodonts (see later discussion). Upper tusks D shaped in cross section, with an enamel band along their lateral surfaces. Differs from South Asian *Protanancus chinjiensis* in having less pronounced pseudoanancoidy of half-loph(id)s, but similar in M3 size and proportions (figures 15.12A, 15.12B).

Description *Afromastodon coppensi* is represented by a modest dental sample, including upper and lower bilophodont deciduous third premolars, trilophodont intermediate molars, and third molars with loph(id) formulas of x4x (figure 15.13N).

Molars are sexually bimodal in size, bunolophodont and very brachyodont, with thick enamel and little or no cementum. Pre- and posttrite half-loph(id)s are separated by deep median longitudinal sulci (Pickford, 2003). In m2, the third lophid is widest; each half-lophid is composed of a main, outer conelet and a more diminutive mesoconelet; pretrite accessory conules are well developed and may be multiplied posteriorly, forming trefoil enamel figures in wear; and small accessory central conules are present posterior to posttrite half-lophids. In M2, crown shape is more rectangular; pretrite half-lophs are located slightly more mesially than their posttrite counterparts; and posttrite posterior accessory central conules are also present. There is also a slight offset of half-loph(id)s in third molars, with the main conelet of the pretrite side anterior to the main conelet of the posttrite side in M3. The condition is reversed in m3. In m3, the main conelets are large and dominate much smaller mesoconelets (which are transversely adjacent to one another); pretrite accessory conules are prominent and may be multiplied posteriorly; and posttrite half-lophids may have small anterior and posterior accessory conules (figure 15.13N; Hendey, 1978b: figure 7). Although third molars develop strong trefoil wear patterns on their pretrite sides, occlusally worn specimens do not develop trefoil enamel figures along the opposing sides, despite the occurrence of accessory central conules in posttrite half-loph(id)s (Pickford, 2003: plate 15, figure 1).

Remarks The slight transverse dislocation of molar half-loph(id)s and occurrence of posttrite accessory central conules led to the initial identification of *A. coppensi* as *Protanancus macinnesi* (Tassy, 1985, 1986). Generic-level distinction of this species is justified only if unassociated lower tusks attributed to *A. coppensi* truly belong to the taxon. In cross section, these are rounded rather than flattened, an unexpected shape for an amebelodont. Otherwise, the morphological resemblance of the molars to those of *P. macinnesi* and proportional similarity with molars of *P. chinjiensis* supports affinity with *Protanancus*. Biochronological correlation of the Arrisdrift fauna with eastern African faunal sets indicates an early middle Miocene date near to that of Maboko, Kenya, ca. 16 Ma (Corvinus and Hendey, 1978; Hendey, 1978b), suggesting that on the continent, evolutionary trajectories of amebelodonts may have diverged regionally.

It is conceivable that an enigmatic elephantoid individual from Burji, Ethiopia, also dated to the early middle Miocene (table 15.5), has affinity with *A. coppensi*. Originally attributed to *Choerolophodon* (Suwa et al., 1991), this proboscidean has features more typical of amebelodonts, including a narrow m3 (figure 15.12B), posttrite accessory conules, and an upper tusk with an enamel band. The lower tusk of this individual is ovoid in cross section, proportionally similar to those of *A. coppensi* (see later discussion).

Genus *PROTANANCUS* Arambourg, 1945
PROTANANCUS MACINNESI Arambourg, 1945
Figures 15.12A, 15.13G, 15.13H, and 15.13K–15.13M

Partial Synonymy *Trilophodon angustidens kisumuensis* (in part), MacInnes, 1942; *Trilophodon angustidens kisumuensis* (in part) Arambourg, 1945; *Protanancus macinnesi*, Arambourg, 1945; *Trilophodon angustidens* cf. *kisumuensis* (in part), Hooijer, 1963; *Protanancus macinnesi*, Leakey, 1967; *Gomphotherium angustidens* (in part), Maglio, 1973: figure 22; *Platybelodon kisumuensis* (in part), Tobien, 1973a; *Platybelodon kisumuensis* (in part), Van Couvering and Van Couvering, 1976; cf. *Gomphotherium angustidens* (in part), Coppens et al., 1978; *Protanancus macinnesi*, Tassy, 1979a; *Platybelodon*, Shipman et al., 1981; *Trilophodon angustidens*, Boaz, 1994.

Age and Occurrence Middle Miocene, eastern Africa (table 15.5).

Diagnosis Tassy (1979a, 1984, 1985, 1986). Amebelodont with powerful upper incisors that curve strongly outwardly and have a band of enamel. Lower tusks flattened and dorsally hollowed, broader than in *Archaeobelodon*, and distinguished from i2s in *Platybelodon* by their lack of dentinal tubules and rods, and less severe compression. Differs from *P. chinjiensis* in having a shorter face, narrower, smaller molars, and less pseudoanancoid dislocation of third molar half-loph(id)s. Has smaller, narrower M3s (figure 15.12A), and wider, flatter i2s than *A. coppensi*. Posttrite accessory central conules are very small and irregularly distributed.

Description A fragmentary cranium from Fort Ternan, Kenya, preserves a small, narrow tympanic bulla, a large glenoid and postglenoid region lacking a postglenoid fossa, a wide palate, and a basicranium only slightly raised. Enough of the cranium is preserved to show the position of the infraorbital foramen above M2, and that the face was short (Tassy, 1986).

In cross section, lower tusks are very compressed dorsoventrally (at midtusk, specimen BMNH 15532 [KBA 109] has W = 83.5 mm and H = 30.0 mm) and are dorsally concave and ventrally convex (figures 15.13G, 15.13H, 15.13K). They are thicker medially, and exhibit polished wear facets at opposing surfaces of the distal end of the tusks, dorsomedially and ventrolaterally. In dorsal view, their tips form a V shape in the midline. Upper tusks are massive (KBA 110 measures L = 1055 mm and has basal diameters of 105 mm × 95 mm) and are pear shaped in cross section, each with an extensive enamel band along the lateral surface and torque about the longitudinal axis (MacInnes, 1942).

Protanancus macinnesi appears to have retained second–fourth deciduous premolars, and third and fourth premolars. The dp2 has two, narrowly transversely appressed anterior cusps, and much lower, paired posterior cusps. The p3 is bilophodont, and intermediate molars are trilophodont with postcingula(ids) formed of several prominent conelets. Lower third molars have lophid formulas of x5x, with very prominent distal cingulids, and may be longitudinally curved (figure 15.13M). In the sample from Maboko, Kenya, M3s have loph formulas of x4x, while M3s from the younger site of Fort Ternan, Kenya, have a nascent fifth loph. In M3, pretrite half-lophs may be slightly anterior to corresponding posttrite half-lophs, and in m3 the reverse occurs, but unlike the condition in choerolophodonts, the mesoconelets of half-loph(id) s are aligned transversely, chevroning is largely absent, and trefoil wear patterns of pretrite half-loph(id)s are generally well developed. On the posttrite side, small anterior accessory central conules may be present in m3s, and diminutive posterior accessory central conules are variably located in M3s (figure 15.13L). Cementum is present in the floor of transverse valleys and occasionally along the sides of loph(id)s; enamel is thick (4.5–6.0 mm) and unfolded; and molars are brachyodont and relatively narrow.

The few postcranials tentatively attributable to *P. macinnesi* include an axis vertebra, several femora distinguished from those of choerolophodonts by relatively small third trochanters, symmetrical condyles, and modest epicondyles, and possibly a radius and several ulnae, all from Fort Ternan, Kenya (Tassy, 1986).

Remarks *Protanancus macinnesi* is the oldest species of the genus, and with *P. chinjiensis* of South Asia constituted an intermediate evolutionary stage between *Archaeobelodon* and *Amebelodon* (Tassy, 1986). The genus extended into the late Miocene in South Asia, but evidently not in Africa (Tassy, 1983a, 1984, 1985, 1986). *Protanancus macinnesi* co-occurs widely with choerolophodonts in East African fossil sites (table 15.5) and is readily distinguishable from them by greater body size and possession of conspicuous lower tusks. However, the pseudoanancoidy of its molars may be mistaken for the offset and chevroning of half-loph(id)s in choerolophodonts; this has led to minor confusion in the assignment of a few specimens from Maboko, Kenya (see later discussion; see also Pickford, 2001:4). Wear patterns and the V-shaped configuration of lower tusk tips in *P. macinnesi* indicates that these teeth were used primarily for slicing through tough vegetation (Lambert, 1992).

Genus *AMEBELODON* Barbour, 1927
AMEBELODON CYRENAICUS Gaziry, 1987
Figure 15.13I

Partial Synonymy *Amebelodon* sp., Gaziry, 1982; "*Amebelodon* sp.," Tassy, 1986; *Amebelodon (Konobelodon) cyrenaicus*, Lambert, 1990.

Age and Occurrence Late Miocene or early Pliocene, northern Africa (table 15.5).

Diagnosis Gaziry, 1987b) A large species of *Amebelodon*, with trilophodont m1, tetralophodont m2, five to six lophids in m3, extensive molar cementum, and lower incisors wider and thicker than those of other Old World congeners, with internal dentinal tubules.

Description The only reliable record of this genus in Africa, and youngest occurrence worldwide (Lambert, 1990) is from Sahabi, Libya (Gaziry, 1982, 1987b). Its presence is marked by i2 fragments that are flat and broad, with ventral and dorsal longitudinal sulci (Sanders, 2008b). Dimensions of the most complete specimen are L = +420 mm; W = 127 mm; H = 44 mm. Proportionally, these are consistent with an attribution to *Amebelodon*, and are less dorsoventally compressed than in *Platybelodon* (figure 15.13I). In cross section, centrally large dentinal tubules and rods are apparent in these tusks, surrounded by dentinal laminae. Ventral tusk surfaces are abraded and polished.

Molars attributed to the species have strongly developed pretrite trefoils, with anterior and posterior accessory central conules, and are relatively long and narrow but lack posttrite accessory conules, and do not exhibit pseudoanancoid offset of half-lophids (Gaziry, 1982, 1987b).

Remarks *Amebelodon* species, best known from North America and Asia, are characterized by elongated, moderately expanded mandibular symphyses, and elongate, flattened lower tusks with dorsal and ventral sulci (Barbour, 1930; Frick, 1933; Osborn, 1936; Tobien et al., 1986; Guan, 1996; Lambert and Shoshani, 1998). Body size estimates for North American *Amebelodon* indicate a weight of ca. 3,000–4,500 kg and height at the pelvis of about 2.3–2.7 m, approximately equivalent to that of the extant Asian elephant (Lambert, 1990; Christiansen, 2004). The cranium is not well-known, but at least in Asian *A. tobieni* it is laterally compressed and anteriorly elongated (Guan, 1996). Dentinal rods and tubules are variably present in i2 (Osborn and Granger, 1931; Lambert, 1990; Lambert and Shoshani, 1998; *contra* Tassy, 1985, 1986), possibly convergent on the condition of i2s in *Platybelodon* and *Torynobelodon* (Lambert, 1990, 1992).

The genus is subdivided into the subgenera *A.* (*Amebelodon*) and *A.* (*Konobelodon*), the latter being distinguished by tetralophodonty of intermediate molars, third molars with six loph(id)s, and lower tusks with dentinal tubules and rods (Lambert, 1990). Based on these criteria, the Sahabi amebelodont belongs in *A.* (*Konobelodon*). The lophid formulas of the Sahabi amebelodonts, and presence of dentinal rods and tubules in their i2s are derived features for *Amebelodon* (Lambert and Shoshani, 1998). These apomorphies are coupled with features that are curiously plesiomorphic for such a late-occurring amebelodont, including absence of posttrite accessory conules, and transversely straight alignment of half-lophids (Tassy, 1985; Lambert and Shoshani, 1998). Alternatively, it is possible that the molars belong to a different, unidentified elephantoid than do the tusks (Sanders, 2008b). Tassy (1999) has pointed out that the flattened Sahabi *A. cyrenaicus* tusks are very similar to those of European and South and western Asian "*Mastodon*" *grandincisivus*, which (unlike the Sahabi sample) also has molars typical for amebelodonts, with features such as pseudoanancoid, offset half-loph(id)s and posttrite accessory central conules. If at least the Sahabi tusks of *A. cyrenaicus* are conspecific with "*Mastodon*" *grandincisivus*, the latter species nomen would have priority (Tassy, 1999).

Wear facets and polishing on the tips of lower tusks in *Amebelodon* have been correlated with a wide range of feeding behaviors, including digging and shoveling in abrasive substrates, vegetation stripping, and bark scraping (Barbour, 1930; Lambert, 1992). Although the tusk fragments of the Sahabi amebelodonts do not preserve their tips, the restriction of abrasion to the ventral side hints at a scooping or shoveling function.

Genus *PLATYBELODON* Borissiak, 1928
PLATYBELODON SP. Maglio, 1969
Figure 15.13J

Partial Synonymy *Platybelodon* sp. cf. *P. grangeri*, Van Couvering and Van Couvering, 1976; ?*Platybelodon*, Coppens et al., 1978; *Platybelodon* sp., Tassy, 1986.

Age and Occurrence Early Miocene, eastern Africa, ?Arabia (table 15.5).

Diagnosis Based on Osborn and Granger (1931, 1932); Osborn (1936). Amebelodonts with highly derived lower tusks and mandibular symphyses that together approximate the form of a shovel. Differ from other amebelodonts in having relatively short, widely flared symphyses that are deeply excavated dorsally, and which accommodate lower incisors uniquely characterized by their extreme degree of dorsoventral compression, breadth, and internal composition of numerous, small and closely compacted dentinal tubules.

Description A single fragment of a lower incisor marks the presence of *Platybelodon* at Loperot, Kenya (Maglio, 1969a). It is extremely flattened dorsoventrally, with dimensions of W = 78.5 mm, and H = 14.6 mm medially and 8.5 mm laterally. The i2 compression index (H × 100/W) for this specimen is 19, well below the range of 35–50 for *P. macinnesi*, 68–84 for *A. coppensi*, 85 for the Burji gomphotheriid, 48–52 for African *Archaeobelodon*, and 35 for *A. cyrenaicus*, but comparable to Asian and North American *Platybelodon* and *Torynobelodon* (Osborn and Granger, 1931, 1932; Osborn, 1936; Guan, 1996). In cross section, the tusk is shallowly concave dorsally, and nearly horizontally flat on its ventral surface (figure 15.13J). Internally, the tusk is composed of a complex system of fine dentinal tubules and rods, invested within and surrounded by laminar dentine (Maglio, 1969a; Coppens et al., 1978). These features, along with the degree of compression, are diagnostic of *Platybelodon*.

Remarks The Loperot *Platybelodon* is the oldest instance of the genus, and it may also be present at Ad Dabtiyah, Saudi Arabia, of similar antiquity (Hamilton et al., 1978; Whybrow and Clements, 1999), indicating an Afro-Arabian origin, though it soon dispersed to Asia (Guan, 1996). By the late Miocene, the genus had reached North America, along with a cohort of other amebelodonts (Frick, 1933; Osborn, 1936; Fisher, 1996; Lambert, 1996; Lambert and Shoshani, 1998). The antiquity of the Loperot *Platybelodon*, combined with penecontemporaneous occurrences of other amebelodont taxa (table 15.5), shows that subfamilial diversity was achieved early on in the phylogenetic history of the group, largely through a temporally condensed adaptive radiation rooted in Africa.

The lower incisors in the "shovel tusker" *Platybelodon* have been hypothesized as functioning to shovel, scoop, dig, and dredge (Osborn, 1936) during feeding on soft vegetation in swampy or lowland aquatic habitats (Coppens et al., 1978). This interpretation was supported by the observation of beveling along the ventral tip of i2 (Osborn and Granger, 1932; Tobien, 1986). The complex of dentinal tubules, surrounded by dentinal laminae, was thought to have resisted abrasion and to have provided strength to the tusk during these sorts of activities (Osborn and Granger, 1931; see Lambert, 1990). A more recent analysis of tusk wear surfaces, however, indicates that the i2s of *Platybelodon* were more likely used as scythes to cut tough vegetation, rather than for shoveling (Lambert, 1992).

Subfamily CHOEROLOPHODONTINAE Gaziry, 1976

Comprised of the genera *Afrochoerodon* and *Choerolophodon*, this subfamily evidently originated in Africa during the early Miocene. By the end of the early Miocene, choerolophodonts had dispersed into South Asia and the eastern Mediterranean region, and persisted throughout much of the Old World until the close of the epoch (Tassy, 1977b, 1983b, 1985; Pickford, 2001; Sanders, 2003). Paleoecological data suggest that African species inhabited primarily closed, wet forest and woodland habitats (Savage and Hamilton, 1973; Pickford, 1985; Jacobs and Kabuye, 1987; Sanders and Miller, 2002; Tsujikawa, 2005a), and presumably were browsers, though choerolophodonts from Fort Ternan, Kenya may have lived in more open conditions (Evans et al., 1981; Shipman et al., 1981; Shipman, 1986).

Subfamilial features include distally upcurved I2s without enamel bands; orbits in line with the posterior end of the last molars; nonflaring zygomatic arches; elongation of the splanchnocranium; deep, wide symphyseal gutters; and loss of i2s and permanent premolars (Tassy, 1985, 1986). Central accessory conules and pretrite mesoconelets are high and large. Molars are specially characterized by chevroning of half-loph(id) pairs and may be choerodont and ptychodont. Half-loph(id)s are transversely offset, with the mesoconelet of each pretrite half-loph(id) projecting anterior to the posttrite half-loph(id) and to its own paired abaxial conelet (Tassy, 1985, 1986). These dental features are less prominently expressed in earlier species. *Choerolophodon* is contrasted with the more primitive *Afrochoerodon* by smaller temporal fossae and less convergent temporal lines, a more elongated basicranium, orbits positioned higher on the cranium, a more horizontal face, more pronounced chevroning, and stronger expression of choero-, ptycho-, and cementodonty, warranting at least generic-level separation (Pickford, 2001; *contra* Shoshani and Tassy, 2005).

Genus *AFROCHOERODON* Pickford, 2001
AFROCHOERODON KISUMUENSIS (MacInnes, 1942)
Figures 15.12A, 15.12B, 15.13J, and 15.14A–15.14D

Partial Synonymy *Trilophodon angustidens kisumuensis* (in part), MacInnes, 1942:51; plate 3, figures 13, 17, 18; plate 4,

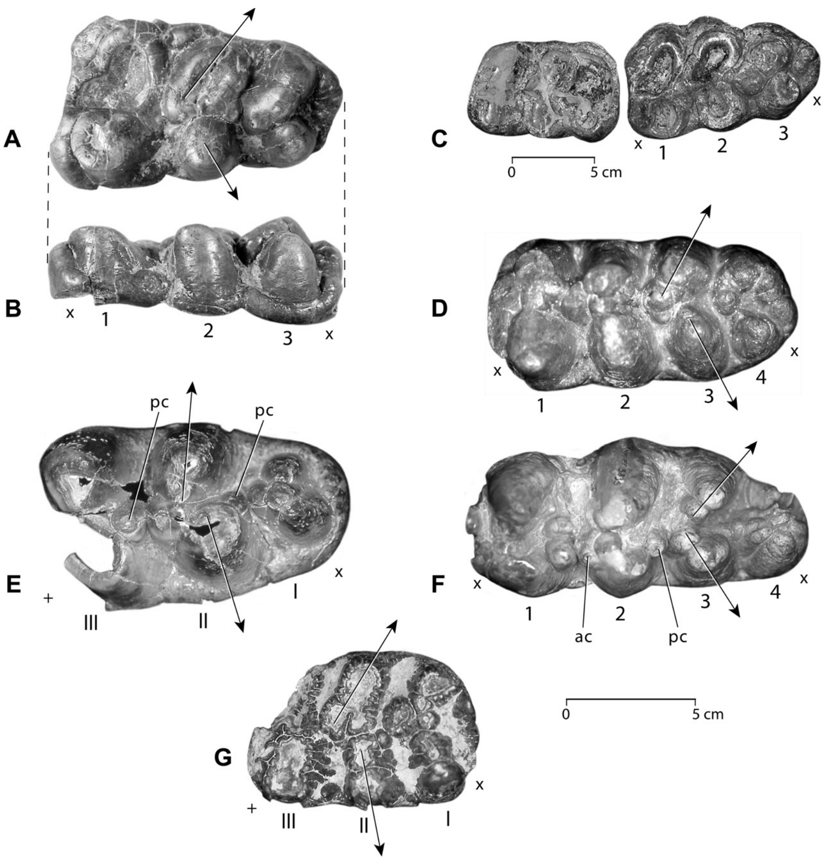

FIGURE 15.14 Aspects of choerolophodont molar morphology. Oblique lines indicate chevroning of pre- and posttrite half-loph(id)s. Anterior is to the left in all specimens. A) Occlusal view, right M3, DPC 14584, *Afrochoerodon kisumuensis*. B) Lateral view, right M3, DPC 14584, *A. kisumuensis*. C) Occlusal view, right M2–3, M15524, *A. kisumuensis* (type). D) Occlusal view, right m3, M15529, *A. kisumuensis*. E) Occlusal view, left ?M3, no number (Gebel Zelten, Libya), *Choerolophodon zaltaniensis*. F) Occlusal view, left m3, KNM-FT 2835, *C. ngorora*. G) Occlusal view, right M1, KNM-NA 4, *C. ngorora*.

ABBREVIATIONS: ac, pretrite anterior accessory central conule; pc, pretrite posterior accessory central conule; x, anterior or posterior cingulum(id); +, indicates a missing portion of a tooth; 1, 2, 3, ..., first, second, third, . . . loph(id).

figures 5, 6, 7, 8; plate 6, figure 7; *Protanancus* (in part), Arambourg, 1945:491; *Platybelodon kisumuensis* (in part), Tobien, 1973a:261; *Choerolophodon kisumuensis*, Tassy, 1977b:2488; *Afrochoerodon kisumuensis*, Pickford, 2001; *Afrochoerodon* aff. *kisumuensis*, Pickford, 2005a.

Age and Occurrence Early to middle Miocene, northern, eastern and southern Africa (table 15.5).

Diagnosis Tassy (1986); Pickford (2001); Sanders and Miller (2002). Small choerolophodont, with third molars below size range for other subfamilials (figures 15.12A, 15.12B; specimen KBA 202 = BMNH 15539, a large m3 from Maboko, belongs instead in *Protanancus macinnesi—contra* Tassy, 1986; see Pickford, 2001; specimen KBA 004 = BMNH 15529, from Maboko, is an m3 and not an M3—*contra* Tassy, 1986). Molar occlusal morphology simple, with little or no choerodonty, ptychodonty, or cementum. Chevroning of lophs modest throughout upper molar crowns. M3 with as few as three lophs. Pretrite half-loph(ids) with greatly enlarged anterior accessory central conules, which may be laterally shifted in m3, and irregular presence of smaller posterior accessory central conules.

Description Cranium high and short, with anteroposteriorly short but steeply inclined facial region; basicranium short; temporal lines converge closely behind the orbits and temporal fossae large; occipital surface nearly as high as wide and flaring laterally (occipital flanges almost platelike); orbits set low; voluminous juga for tusks dominate the facial region; palatines extend beyond distal end of M3s; zygomatic arches massive but not widely prominent; infraorbital foramen positioned above mesial end of M3 (Tassy, 1986; Pickford, 2001). Upper tusks large (diameter 90 mm) and almost circular in cross section, with no enamel band, initially flaring laterally and downward from widely separated alveoli (Tassy, 1986; Pickford, 2001). Nothing is known about symphyseal angulation or lower tusks in this species.

Intermediate molars are trilophodont, with greatest width at second loph(id)s. Cusps are massive, bulbous, and low crowned. Enamel is thick and unfolded. Upper third molars have three lophs or a fourth, smaller loph, and a diminutive posterior cingulum (figures 15.14A–15.14C). Mild chevroning occurs at the posterior end of crown, with pretrite mesoconelets more mesial than principal conelets. Posttrite half-lophs are constructed of a single large conelet or superficially subdivided into two conelets. Lower third molars have four lophids and a small posterior cingulid (figure 15.14D). In m3, pretrite mesoconids are anterior to main conelets and may be separated from them by enlarged, laterally set anterior accessory central conules (Tassy, 1986; Pickford, 2001; Sanders and Miller, 2002).

Proboscidean postcranials from Maboko, Kenya have not been definitively sorted among the taxa present there (table 15.5); however, an isolated elephantoid astragalus from the site has been tentatively attributed to *A. kisumuensis* based on its small size (MacInnes, 1942; Tassy, 1986). In contrast, limb bones and metacarpals from Maboko are slender but from an animal of considerable size, with a pelvic height of about 6–7 feet (MacInnes, 1942).

Remarks The antiquity of this species suggests an African origin for the subfamily. However, it is similar dentally and may be synonymous with *Choerolophodon palaeindicus* from Dera Bugti, Pakistan (Tassy, 1985; Sanders and Miller, 2002), which has nomenclatural priority if this is the case. *Choerolophodon palaeindicus*, whose exact provenance is unknown but is likely of comparable antiquity (Forster Cooper, 1922; Raza and Meyer, 1984; Tassy, 1985, 1986), should be transferred to *Afrochoerodon*. The primitiveness of *A. kisumuensis* among choerolophodonts is evident in the occlusal simplicity, small size, and mild chevroning of its molars (Tassy, 1979a).

Genus *CHOEROLOPHODON* Schlesinger, 1917

CHOEROLOPHODON ZALTANIENSIS Gaziry, 1987

Figures 15.12A and 15.14E

Partial Synonymy *Afrochoerodon zaltaniensis*, Pickford, 2001; *C. zaltaniensis*, Pickford, 2004.

Age and Occurrence Middle Miocene, northern Africa (table 15.5).

Diagnosis Differs from *A. kisumuensis* in variably greater expression of choero- and ptychodonty, slightly more cementum invested in transverse valleys, stronger chevroning of half-loph(id)s, invariant presence of a fourth loph in M3, and larger size of molars (figure 15.12A). In contrast to *Choerolophodon ngorora*, there are in *C. zaltaniensis* no m3s with five lophids, and molar choerodonty and cementum are generally less well developed.

Description Composed primarily of a small sample of teeth from Gebel Zelten, Libya. An adult dentary from the site is too incomplete to accurately ascertain symphyseal angulation or the absence of lower incisors. A juvenile choerolophodont dentary exhibits a wide symphyseal gutter, but is broken anteriorly (Gaziry, 1987a). No cranium has been recovered.

Molars are moderate sized, and in morphology and proportions more resemble teeth of *C. ngorora* than of *A. kisumuensis* (figure 15.12A). Intermediate molars are trilophodont. Upper third molars have a loph formula of x4x, though the fourth loph is narrow, and m3 has four lophids. Enamel is rugose but unfolded. In some molars, multiple accessory conules may be distributed within the transverse valleys (Gaziry, 1987a: figure 5a). In M3, small pretrite accessory conules are present posterior to lophs 1–3 (figure 15.14E). Particularly posterior to the first loph(id), pretrite anterior central accessory conules and mesoconelets are aligned oblique to the main axis of the crown, the main conelets are posterior to the mesoconelets, together contributing to the formation of loph(id)s into markedly anteriorly pointing V's (Gaziry, 1987a).

Remarks The original generic designation is retained for this species, rather than following Pickford's (2001) transfer of it to *Afrochoerodon* (but see Pickford, 2004), because it more closely resembles other species of *Choerolophodon* in chevroning, cementum development, ptychodonty, and upper molar choerodonty. In contrast, in these features and especially in cranial morphology, *A. kisumuensis* stands apart from other choerolophodonts, except its near contemporaries *Afrochoerodon chioticus* from Chios, Greece (Tobien, 1980; Pickford, 2001), and "*C.*" *palaeindicus* (Forster Cooper, 1922; Raza and Meyer, 1984; Tassy, 1985, 1986; Sanders and Miller, 2002).

CHOEROLOPHODON NGORORA (Maglio, 1974)

Figures 15.12A, 15.12B, 15.14F, and 15.14G

Partial Synonymy *Gomphotherium ngorora*, Maglio, 1974; *Gomphotherium*, Andrews and Walker, 1976:300; *Choerolophodon ngorora*, Tassy, 1977b; "*Gomphotherium*" *ngorora*, Coppens et al., 1978; *C. ngorora*, Tassy, 1986; *C. ngorora*, Nakaya, 1993; *Afrochoerodon ngorora*, Pickford, 2001; *Afrochoerodon* sp. nov. [specimens from Mbs. A–D, Ngorora Fm.], Pickford, 2004; *C. ngorora* [specimens from Mb. E, Ngorora Fm.], Pickford, 2004; *Choerolophodon* sp., Tsujikawa, 2005b.

Age and Occurrence Middle to early late Miocene, eastern Africa (table 15.5).

Diagnosis Molars larger and with more complex occlusal morphology than those of *A. kisumuensis* (figures 15.12A, 15.12B, 15.14F, 15.14G), and contrast with those of *C. zaltaniensis* in having folded enamel and (occasionally) greater expression of choerodonty. Variable development of a fifth lophid in m3. Tendency for upper molars to retain a pretrite posterior central accessory conule behind loph 2, and for pretrite anterior accessory central conules to be independent of their corresponding mesoconelets (Tassy, 1986).

Description Symphyseal region of mandible elongate and strongly downturned. Upper tusks curved upward, with no enamel band, but may have an enamel cap; they are ovoid and slightly flattened dorsoventrally in cross section (Tassy, 1986). No cranial remains have been recovered for this species, and there is no evidence of lower tusks.

DP2 is tiny, dominated by an anteriorly situated, mesiodistally compressed loph, and has a diminutive central conule. These features resemble DP2 in Eurasian choerolophodonts (Tassy, 1986). The dp3 is bilophodont and also typical of choerolophodonts: the crown narrows to a point mesially, the cusps of its lophids are offset anteroposteriorly to one another, and it sports large central accessory conules. Intermediate molars are trilophodont. The loph formula for M3 is x4x, and m3 has four-five lophids (figure 15.14F). Mesoconelets are small, but higher than the main conelets, as are the accessory central conules. Anterior accessory conules are massive, while posterior accessory conules are reduced in importance and may be limited to the anterior end of the crown or absent. Chevroning is marked (Tassy, 1986). Enamel is strongly rugose and may be moderately to finely folded (figure 15.14G); cementum may be thick; and in some molars (particularly uppers), multiple enamel tubercles may be present in transverse valleys (see Tassy, 1986: figure 27).

Proboscidean postcrania from Fort Ternan include long bones, carpals, and tarsals (Tassy, 1986). Among those tentatively assigned to *C. ngorora* are femora with salient third trochanters and medial epicondyles, and humeri with reduced trochlear separation between the medial and lateral condyles and with high, capacious epicondyles. The calcaneum is moderate in size for an elephantoid (L = 180.6 mm) but robustly built, with a massive tuber calcanei and a large fibular facet, closely resembling calcanei of Eurasian choerolophodonts (Tassy, 1986).

Remarks The molars of *C. ngorora* are separable into two subsamples (table 15.5): a late middle Miocene morph similar to teeth of *C. zaltaniensis*, and a more advanced, early late Miocene morph. The cheek teeth of the younger morph are larger, higher crowned, and have more finely folded enamel. These differences may signal speciation of the lineage around 11 Ma, but the more advanced subsample is too small and fragmentary for formal acknowledgment of such an event (but see Pickford, 2004). The relationship of similar-aged choerolophodonts from North Africa (table 15.5) to *C. ngorora* has yet to be established.

Despite evolving more complex, durable molars, by ≈9 Ma choerolophodonts had vanished from Africa (Tassy, 1986), but there is no obvious explanation for their demise. While there is evidence for increased aridity and seasonality in Africa from the middle to late Miocene (Pagani et al., 1999), the disappearance of choerolophodonts from the African continent apparently did not coincide with an abrupt shift in vegetation (Cerling et al., 1993; Kingston et al., 1994), or with the emergence of a cohort of new proboscidean rivals, and remains unexplained.

Subfamily TETRALOPHODONTINAE Van der Maarel, 1932
Genus *TETRALOPHODON* Falconer, 1857
TETRALOPHODON SP. NOV. Tsujikawa, 2005
Figures 15.7A, 15.7B, and 15.11L

Partial Synonymy *Tetralophodon longirostris*, Bergounioux and Crouzel, 1956; *Trilophodon angustidens* cf. *kisumuensis*, Hooijer, 1963:32, plate I, figure 2; *Tetralophodon* sp. indet., Madden, 1977; ?*Tetralophodon* cf. *longirostris*, Coppens et al., 1978:346; Proboscidea indet., Tiercelin et al., 1979:257; *Stegotetrabelodon grandincisivum*, Madden, 1982; *Tetralophodon* sp., Nakaya et al., 1984; *Tetralophodon* cf. *longirostris*, Geraads, 1989; *Stegotetrabelodon* n. sp.?, Geraads et al., 2002:114.

Age and Occurrence ?Late middle–early late Miocene, eastern and ?northern Africa (table 15.5).

Diagnosis Based in part on Nakaya et al. (1984, 1987); Geraads (1989); Nakaya (1993). Large gomphotheriid with tetralophodont intermediate molars and third molars with five-six loph(id)s (figure 15.11L). Enamel massively thick. Second-fourth permanent premolars are retained; upper and lower tooth formulae 1-0-3-3, 1-0-2-3, respectively. Occasional development of secondary trefoils on posttrite half-loph(id)s. Differs from anancine gomphotheres in straighter transverse alignment of half-loph(id)s, and from European tetralophodonts by greater angulation of the basicranium, relative to the palate, and absence of cementum.

Description Tetrabelodont, with rounded upper tusks lacking an enamel band and thick lower tusks rounded to pyriform in cross section (the cross sections of putative rostral incisor alveoli from Gebel Sémène are actually those of i2s—*contra* Bergounioux and Crouzel, 1956). The symphysis is long and strongly downturned (Nakaya et al., 1984).

Molar loph(id)s are brachyodont and formed of four to six conelets, with mesoconelets rivaling main conelets in size, and are accompanied by accessory central conules. Lamellar frequency is low (2.3 in m2), enamel thickness is extreme (10.9 mm in m2), and molars are very large (figure 15.7A, 15.7B; Nakaya et al., 1984, 1987). An isolated m3 from Chorora, Ethiopia may also belong in this taxon. It has six lophids, well-developed pretrite posterior accessory central conules, and diminutive posttrite accessory central conules (Coppens and Tassy in Tiercelin et al., 1979).

Permanent premolars P2–4 and p4 have been recovered for this taxon. These are bilophodont teeth (Nakaya et al., 1984; Geraads, 1989), and resemble permanent premolars in *Stegotetrabelodon*.

Remarks *Tetralophodon* is well represented in Eurasia by several late middle–late Miocene (Astaracian-Turolian) species and seems likely to have emigrated from there into Africa (Coppens et al., 1978; Tassy, 1985; Tobien et al., 1988). Morphologically and chronostratigraphically, African *Tetralophodon* is appropriately situated to be ancestral to elephants.

Evidence from the Samburu Hills, Kenya suggests that *Tetralophodon* may have encountered a variety of habitats, including woodlands and savanna (Nakaya, 1993; Tsujikawa, 2005a), but dental isotopic analysis reflects a narrower preference for (possibly xeric) browse with only a small component of C_4 vegetation in its diet (Cerling et al., 2003).

An M3 (KI 64'92) from the Western Rift (table 15.5; figure 15.11L) has been referred to as a primitive elephant (Tassy, 1995). Nevertheless, it should remain in *Tetralophodon* (Pickford et al., 1993), because its overall morphology, including a low number of lophs (x5x), division of the crown by a marked median sulcus, enlarged mesoconelets, presence of anterior and posterior pretrite accessory central conules, wide spacing of lophs (LF = 2.6), brachyodont crown (HI = 53), and low number of conelets per loph (Tassy, 1995), closely resembles the condition of typical tetralophodont gomphotheriid molars.

GEN. ET SP. INDET. (tetralophodont form) Tassy, 1986

Age and Occurrence Late Miocene, eastern Africa (table 15.5).

Description Several specimens from the early late Miocene of eastern Africa appear to be of a different form of tetralophodont than that present at Samburu Hills, notably a partial cranium and incomplete mandible from the Tugen Hills, Kenya. The cranium is reconstructed as having been relatively high, with a short face and angled basicranium (Tassy, 1986). It retains DI2 and I2, as well as DP2–DP4; these latter teeth are bilophodont, trilophodont, and tetralophodont, respectively, and are characterized by a pseudoanancoid offset of pre- and posttrite half-lophs and weak expression of accessory central conules (Tassy, 1986). The mandible is reconstructed as having been brevirostrine with a shallow symphyseal gutter, and carries a p3 typical of tetralophodont elephantoids (Tassy, 1986).

Remarks These specimens superficially resemble anancine gomphothere cheek teeth in the transverse offset of their half-lophs, and the apparent brevirostrine condition of the mandible. They are sufficiently unique and isolated to refrain from assigning them to a particular taxon. Because of their potential phylogenetic role in the emergence of elephants and *Anancus*, it is unfortunate that nonanancine tetralophodonts are so poorly represented in the African fossil record.

Subfamily ANANCINAE Hay, 1922
Figures 15.15A–15.15F

Anancine gomphotheres constitute a monogeneric group (*Anancus* spp.) of Eurasian origin, possibly derived from *Tetralophodon,* that was widely dispersed throughout the Old World during the late Miocene–late Pliocene (Tobien, 1973a; Coppens et al., 1978; Mebrate and Kalb, 1985; Tassy, 1985, 1986, 1996c; Tobien et al., 1988; Metz-Muller, 1995; Kalb et al., 1996a; Shoshani, 1996; Göhlich, 1999; G. Markov, pers. comm.). Immigration of anancines into Africa toward the end of the Miocene coincided with the first appearance of

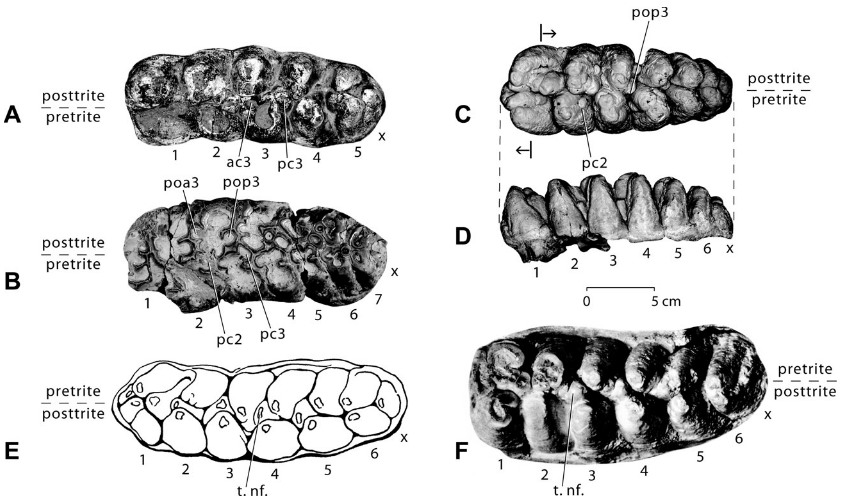

FIGURE 15.15 Aspects of anancine gomphothere molar morphology. Anterior is to the left in all specimens. A) Left m3, KNM-LU 57, *Anancus kenyensis*; B) left m3, EP 197/05, *A.* sp. nov. (type); C) left M3, SAM-PQ-L 41692, *A. capensis* (type), occlusal view (arrows denote relative position of pre- and posttrite half-lophs; in upper molars, pretrite half-lophs are offset anterior to postrrite half-lophs); D) left M3, SAM-PQ-L 41692, *A. capensis* (type), lingual view; E) right m3, Sahabi molar no. 8, *A. petrocchii*; F) right m3, 1956-4: A1, *A. osiris*.

ABBREVIATIONS: ac, pretrite anterior accessory central conule; pc, pretrite posterior accessory central conule; poa, posttrite anterior accessory central conule; pop, posttrite posterior accessory central conule; x, anterior or posterior cingulum(id); t. nf., "tubercle de néoformation" (Arambourg, 1945, 1970); 1, 2, 3, ..., first, second, third, . . . loph(id).

elephants, with whom they remained ubiquitously sympatric until their demise (Tassy, 1986). Although *Anancus* survived well into the late Pliocene in northern and southern Africa, it disappeared elsewhere on the continent during the mid-Pliocene (table 15.5; Tassy, 1986; Kalb et al., 1996b).

African anancines are characterized by short, wide crania with domed, elevated vaults, very raised bases, enlarged tympanic bullae, straight upper tusks lacking enamel, mandibles with brevirostrine symphyses and no lower tusks, and tetralophodont-pentalophodont intermediate molars (Petrocchi, 1954; Coppens, 1967; Coppens et al., 1978; Tassy, 1985, 1986; Kalb and Mebrate, 1993). Their bunolophodont cheek teeth are typified by anancoidy of pre- and posttrite half-loph(id)s: in upper molars, pretrite half-lophs are anterior to their paired posttrite half-lophs, while the reverse occurs in lower molars (figures 15.15A–15.15F; Coppens et al., 1978; Mebrate and Kalb, 1985; Tassy, 1985, 1986; Kalb and Mebrate, 1993). Molar occlusal complexity increased independently in several lineages of *Anancus* and included addition of loph(id)s and elaboration of accessory conules and conelets in transverse valleys and postcingulae(ids) (Coppens et al., 1978; Mebrate and Kalb, 1985; Tassy, 1985, 1986; Kalb and Mebrate, 1993; Sanders, 1997).

The forelimbs of anancine gomphotheres have been reconstructed as habitually flexed, suggesting that they were ground-level feeders (Ferretti and Croitor, 2001, 2005). This conforms with results from stable isotope analyses on tooth enamel from a number of African sites indicating that these proboscideans were grazers with a predominantly C_4-plant-based diet (Cerling et al., 1999, 2003; Zazzo et al., 2000; Harris et al., 2003; Semaw et al., 2005), except at Langebaanweg, where C_3 grasses are inferred to have been prevalent (Franz-Odendaal et al., 2002). Over the course of the Pliocene, this dietary emphasis may have contributed to their eventual decline, placing them in increasingly crowded competition with an expanding cohort of hypsodont elephants and other ungulate grazers (see Cerling et al., 2003).

Genus *ANANCUS* Aymard, 1855
ANANCUS KENYENSIS (MacInnes, 1942)
Figures 15.15A, 15.16A, and 15.16B

Partial Synonymy Pentalophodon sivalensis kenyensis, MacInnes, 1942; *Anancus arvernensis* subsp., Dietrich, 1943; *Anancus kenyensis,* Arambourg, 1947; *Anancus osiris* (in part), Coppens et al., 1978; *Anancus* cf. *A. kenyensis*, Haile-Selassie et al., 2004; *Anancus* sp. indet., Haile-Selassie et al., 2004.

Age and Occurrence Late Miocene to early Pliocene, eastern and Central Africa (table 15.5).

Diagnosis MacInnes (1942); Tassy (1986). Tetralophodont intermediate molars. Anancoidy not pronounced. Enamel unfolded to coarsely folded, and very thick (5.0–7.0 mm in third molars). Crown morphology simple. In lateral view, loph(id)s are bulbous and massive. Posttrite posterior accessory conules restricted to mesial half of crown in m3, and usually in M3, as well. Permanent premolars retained.

Description Crania of *A. kenyensis* from Chad, Kenya, and Ethiopia have vertical basicrania nearly perpendicular to their palates, orbits anterior to the molars, robust, broad zygomatic arches, and lateral alisphenoid processes developed as pillars (Coppens, 1967; Tassy, 1986; Kalb and Mebrate, 1993). Adult upper tusks are rounded in cross section, and exhibit marked interindividual contrasts in size, attributable to sexual dimorphism (Tassy, 1986; Kalb and Mebrate, 1993). Mandibles of *A. kenyensis* have short molar alveolar segments, high rami, and anteroposteriorly narrow, transversely broad condyles (Tassy, 1986; Haile-Selassie, 2001). The forward rotation of

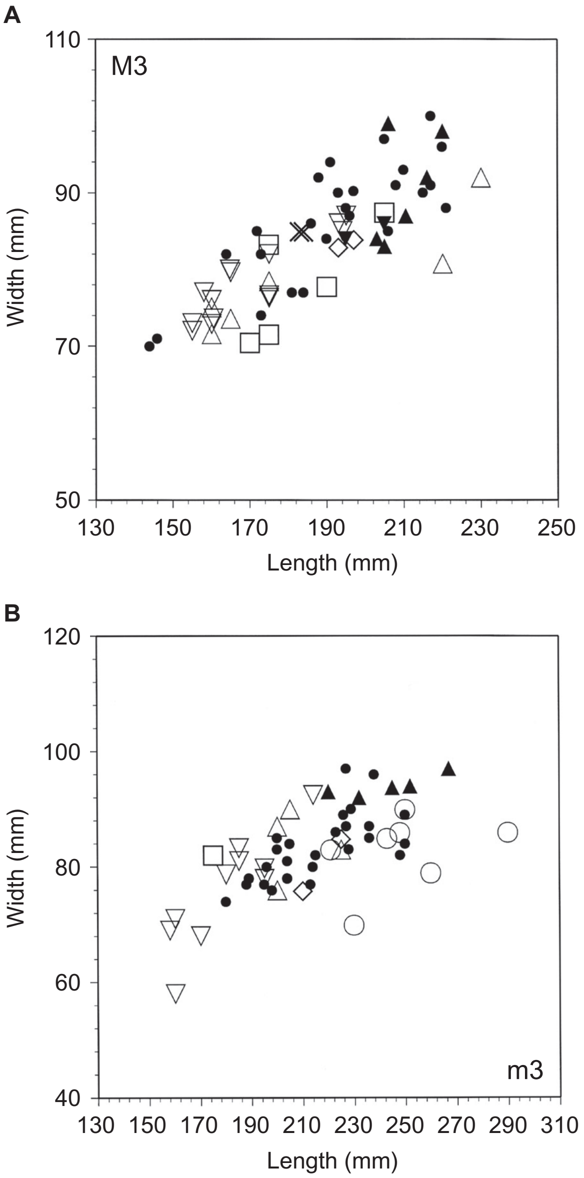

FIGURE 15.16 Bivariate plots of M3 (A) and m3 (B) crown length versus width in African and selected Eurasian anancine gomphotheres. Comparative dimensions supplementing original measurements are from Arambourg (1945, 1970), Petrocchi (1954), Tassy (1986, 1995), Tobien et al. (1988), Boeuf (1992), and Metz-Muller (1995).

SYMBOLS: inverted open triangle, *Anancus kenyensis*; open triangle, *A.* sp. nov. open square, *A. capensis*; open diamond, *A. osiris*; open circle, *A. petrocchii*; X, *A. perimensis*; closed circle, *A. arvernensis*; closed triangle, *A. sinensis*.

emerging cheek teeth precluded the simultaneous occlusion of the entire molar series.

Molar proportions and occlusal morphology vary widely within *A. kenyensis*. Third molar size extends to the low end of the range for the genus, but there is substantial overlap in dimensions among African congeners (figures 15.16A, 15.16B). Pre- and posttrite posterior accessory conules are often present at least in the first three loph(id)s, especially in intermediate molars, but their expression may be more limited in m3. Cementum ranges in thickness from trace amounts to filling transverse valleys. Third molars modally have five and intermediate molars four loph(id)s, with a few exceptions (figure 15.15A; Tassy, 1986, 1995, 2003). Diminutive M3s from the Kuseralee Mb. of the Sagantole Fm., Middle Awash, Ethiopia have six lophs, and have been differentiated from *A. kenyensis* as "*Anancus* sp. indet." (Haile-Selassie, 2001; Haile-Selassie et al., 2004). However, their simple crown morphology and associated tetralophodont intermediate molars suggest instead that they are a variant of *A. kenyensis*.

Remarks *Anancus kenyensis* is the oldest representative of the subfamily in Africa (table 15.5), and constituted a progressively evolving lineage. Evidence for this is documented by directional increase in occlusal complexity, crown size, and loph(id) number in the abundant molar sample from the Middle Awash, Ethiopia, between 6.3 and 4.3 Ma (Mebrate and Kalb, 1985). Schema partitioning the lineage into pseudotaxonomic units include those of Mebrate and Kalb (1985), who divided the Middle Awash sequence into four time-successive stages, and Tassy (1986), who separated the species into an *A. kenyensis* "*kenyensis*-morph" and an *A. kenyensis* "*petrocchii*-morph." It is more appropriate to term these forms "primitive-morph" and "advanced-morph," respectively, to avoid confounding pentalophodont eastern African anancines with the pentalophodont but distinct species *A. petrocchii* from Sahabi, Libya. Differences between these morphs are profound and warrant more formal taxonomic division. Accordingly, they are here assigned to separate species, with the "primitive-morph" retained as *A. kenyensis*.

ANANCUS sp. nov. Sanders, in press
Figures 15.15B, 15.16A, and 15.16B

Partial Synonymy *Trilophodon angustidens* cf. *kisumuensis* (in part), Hooijer, 1963; *Anancus osiris*, Coppens, 1965; *Anancus osiris*, Servant-Vildary, 1973; *Anancus kenyensis* (in part), Coppens et al., 1978; *Anancus kenyensis* (in part; *A. kenyensis* "*petrocchii*-morph"), Tassy, 1986; *Anancus* sp. (Sagantole-type), Kalb and Mebrate, 1993; *Anancus* cf. *Anancus* sp. (Sagantole-type), Sanders, 1997; *Anancus kenyensis*, Harris and Leakey, 2003; *Anancus kenyensis* (in part), Tassy, 2003; *Anancus kenyensis*, Mackaye et al., 2005; *Anancus osiris*, Mackaye et al., 2005.

Age and Occurrence Early–mid-Pliocene, eastern and Central Africa (table 15.5).

Diagnosis Pentalophodont intermediate molars; third molars with six or seven loph(id)s. Anancoidy well expressed. Occlusal morphology usually complex; posttrite and pretrite accessory conules may extend to the back half of molar crowns (figure 15.15B). Accessory conules may be doubled. Talonids may be crowded with many conelets. Moderately worn half-loph(id)s with coarsely to finely folded enamel.

Description An m3 from Laetoli, Tanzania (EP 197/05) is a very advanced specimen, with seven lophids, strong anancoidy, and a complex occlusal pattern of anterior and posterior central accessory conules throughout nearly the entire extent of both the pre- and posttrite sides (figure 15.15B). An M3 from nearby Kakesio, Tanzania, is also strongly anancoid, with thick (4.8–5.5 mm), coarsely folded enamel, seven lophs, posterior accessory conules fused to worn pretrite half-lophs 1–5, and doubled posterior accessory conules associated with posttrite half-lophs 1–4. Cementum is thinly distributed on loph walls and in the transverse valleys. Molars from Kanapoi and Aterir, Kenya, exhibit similar morphological organization. The dental sample from Chemeron differs in having little or no folding of enamel wear figures, thicker enamel, and only six loph(id)s in third molars. Conversely, third molars from the Aramis and

Beidareem Mbs. of the Sagantole Fm., Middle Awash, Ethiopia, are more complex in occlusal morphology, with thinner enamel, greater enamel folding, thicker cementum, and pre- and posttrite accessory conules distributed throughout the length of the crown.

Remarks *Anancus* sp. nov. is largely composed of the "advanced morph" of the *A. kenyensis* lineage (see Tassy, 1986). Progression from tetralophodonty to pentalophodonty in East-Central African anancines occurred in the 5.0–4.5 Ma interval. Division of the lineage, however, is complicated by considerable morphometric overlap among temporally successive site samples (figures 15.16A, 15.16B), as well as by a large degree of intra-site variation, and further taxonomic refinements may be necessary. Nonetheless, striking differences in occlusal complexity leave little doubt about the specific-level separation of *A. kenyensis* and at least the more advanced representatives of *A.* sp. nov.

ANANCUS CAPENSIS Sanders, 2007

Figures 15.15C and 15.15D

Partial Synonymy Gomphotheriidae gen. et sp. indet., Hendey, 1976; *Anancus* sp., Coppens et al., 1978; *Anancus* sp., Hendey, 1981; *Anancus* sp. nov., Sanders, 2006.

Age and Occurrence Early Pliocene, southern Africa (table 15.5).

Diagnosis Sanders (2007). Contrasted with *A. petrocchii* and *A.* new species by its tetralophodont intermediate molars. More advanced than *A. kenyensis* and *A. osiris* in having more complex molars, with greater folding of enamel, six lophs in M3 (figures 15.15C, 15.15D), an incipient seventh lophid in m3, more pronounced anancoidy, and posttrite posterior accessory conules not restricted to the mesial half of crown in third molars (may extend throughout the crown in M3).

Description Sanders (2006, 2007). Cementum coats sides of molar loph(id)s and may fill transverse valley floors. Intermediate molars with four loph(id)s, half-loph(id)s each consisting of two conelets, and posttrite posterior accessory conules to the third or fourth loph(id). Pretrite posterior accessory conules variable, and may occur from loph(id)s 1–3. Enamel thick (about 4.5 mm in M1, 5.0–6.0 mm in M2) and lightly to moderately folded. Third molars low crowned (H = 57–58 mm), with moderately to well folded, thick enamel (4.5–6.0 mm), pre- and posttrite posterior accessories well distributed throughout the crown and occasionally accompanied by multiple additional accessory conules, exhibiting low lamellar frequencies (3.5–4.0), and with a postcingulum(id) formed of three to six conelets.

Remarks Molars of anancine gomphotheres from Langebaanweg exhibit a novel mix of primitive (low crowned, tetralophodonty, thick enamel) and advanced (enamel folding, complex distribution of accessory conules, six to seven third molar loph(id)s, pronounced anancoidy) features (Sanders, 2006). This mix suggests that the progressive evolutionary transformation to *A. capensis* from a primitive, *A. kenyensis*–like molar pattern occurred independently from that in eastern African *A.* sp. nov. in which increasing crown complexity was accompanied by pentalophodonty, and northern African *A. petrocchii*, in which the acquisition of pentalophodonty was not associated with more intricate occlusal morphology (but see below). Overall, the degree of morphological complexity of the Langebaanweg specimens is similar to that in cheek teeth from Kakesio, Tanzania and Aterir, Kenya, ca. 4.5–4.0 Ma. Only a single anancine molar is known from Baard's Quarry at Langebaanweg, and it differs from molars of *A. capensis* in having laterally elongated, anteroposteriorly compressed posttrite half-lophids. Unfortunately, it is too fragmentary to assign more precisely than to *Anancus* sp. (table 15.5). Further study is necessary to determine if specimens from Karonga and Uraha, Malawi attributed to *A. kenyensis* and *A.* sp. (table 15.5; Mawby, 1970; Bromage et al., 1995) might instead belong in *A. capensis*.

ANANCUS PETROCCHII Coppens, 1965

Figures 15.15E and 15.16B

Partial Synonymy *Pentalophodon sivalensis*, Petrocchi, 1943; *Anancus (Pentalophodon) petrocchii*, Coppens, 1965; *Anancus osiris* (in part), Arambourg, 1970.

Age and Occurrence Late Miocene, northern Africa (table 15.5).

Diagnosis Distinguished from *A. kenyensis, A. capensis*, and *A. osiris* by its pentalophodont intermediate molars, and from *A.* sp. nov. by the simplicity of its occlusal morphology (no accessory conules in m3) and massiveness of its pyramidal lophids. Lower third molars relatively narrow and range to substantially larger size than those of other African congeners (figure 15.16B).

Description Mandible brevirostrine, with no lower tusks. Apices of lower molar conelets converge strongly toward the midline of the crown. Third molars are composed of six lophids and a simple postcingulid formed of a large, single conelet (Petrocchi, 1954; Coppens, 1965; Coppens et al., 1978). Posttrite half-lophids have two conelets each; corresponding pretrite half-lophids have one. A low, narrow cingular ribbon surrounds the molar crowns (figure 15.15E). Molars are very brachyodont. Anancoidy is not marked.

Remarks Represented solely by lower teeth and jaws from the latest Miocene–earliest Pliocene site of Sahabi, Libya, as depicted by Petrocchi (1943, 1954), this species is advanced only in the pentalophodonty of its intermediate molars. Otherwise, the simplicity of its molar crowns clearly distinguishes it from *A.* sp. nov. (the "*A. kenyensis* '*petrocchii*-morph'" of Tassy, 1986) and mediates against any special relationship between the taxa. However, reexamination of Sahabi anancine molars shows that the occlusal morphology is more complex than previously described. Small pre- and posttrite accessory conules are present throughout upper and lower molar crowns, and may be accompanied by coarsely folded enamel in worn specimens (Sanders, 2008b). *Anancus petrocchii* has been posited as the terminal derivation of *A. osiris* (Coppens, 1965; Coppens et al., 1978), but this idea is untenable, as the latter species is primarily known from younger deposits (table 15.5).

ANANCUS OSIRIS Arambourg, 1945

Figure 15.15F

Partial Synonymy *Mastodon arvernensis*, Depéret et al., 1925; *Anancus arvernensis*, Dietrich, 1943; *Anancus (Mastodon) arvernensis*, Ennouchi, 1949.

Age and Occurrence Late Pliocene, northern Africa (table 15.5).

Diagnosis Modified from Coppens (1965); Coppens et al. (1978); Tassy (1986). Tetralophodont intermediate molars; molars with heavy, pyramidal loph(id)s and simple crowns (third molars with few pretrite and no posttrite accessory conules), but with conspicuous anancoidy of half-loph(id)s. Higher crowned than *A. petrocchii*.

Description The type M3, from Gizeh, Egypt, has five lophs and plain crown morphology, lacking posterior accessory conules. Each pretrite half-loph is formed of a large outer conelet and diminutive mesoconelet, and has a large "tubercle de néoformation" (figure 15.15F; Arambourg, 1945, 1970), or anterior accessory conule, that projects anterior to the accompanying posttrite half-loph. This feature is occasionally seen in other species of *Anancus*, particularly *A. kenyensis*. Cementum is not apparent, and the postcingulum is uncomplicated, of only a few conelets. Cementum may be more heavily distributed in molars from other localities (Pickford, 2003). Other third molars, such as those from Aïn Boucherit, Algeria, have equally basic occlusal organization, though they possess five and a half or six loph(id)s (Arambourg, 1970). Second molars, in contrast, may have pretrite posterior accessory conules throughout the crown, and even posttrite accessories (Arambourg, 1970).

Remarks *Anancus osiris* is primarily a late Pliocene North African species (table 15.5; Tassy, 1986) that did not attain the occlusal complexity of sub-Saharan congeners, and whose relationship to other African members of the genus remains obscure. Although it has been hypothesized that *A. osiris* and *A. kenyensis* derived from different Eurasian ancestors (Tassy, 1986), the phylogenetic analysis on which this is based is less than satisfactory, as presumed synapomorphies linking particular African and Eurasian species are prone to homoplasic expression. Nonetheless, even though the fossil record is presently too incomplete to resolve these relationships, its emerging pattern is sufficient to infer independent evolution of African anancines within at least three major zones: North, East-Central, and South African.

Family STEGODONTIDAE Osborn, 1918

The family Stegodontidae is composed of the archaic genus *Stegolophodon* ("stegolophodonts"), and the more derived genus *Stegodon* ("stegodonts"). The oldest representative of the family is *Stegolophodon nasaiensis* from the early Miocene of Thailand (Tassy et al., 1992), and the youngest is *Stegodon orientalis,* which survived until the Holocene in China (Ma and Tang, 1992; Saegusa, 1996). It is predominantly an Asian family geographically and in terms of faunal importance (Coppens et al., 1978; Saegusa et al., 2005). *Stegodon* also occurred in the latest Miocene-Pliocene of Africa, where it was rare and limited in distribution (table 15.6). Although the oldest example of *Stegodon* was reported to be from ~7-Myr-old sediments in Kenya (Sanders, 1999), stegodont localities in Yunnan, China, are now correlated to 9 Ma (Saegusa et al., 2005), strengthening the position that these proboscideans are immigrants to Africa.

Stegodon is characterized by extremely brachyodont molars convergent on those of elephants in having platelike loph(id)s. These may be composed of numerous, bilaterally compressed conelets ("mammillae") and mesiodistally separated by transverse valleys that are Y shaped in cross section (Osborn, 1942; Coppens et al., 1978; Kalb et al., 1996a; Saegusa, 1996). In addition, *Stegodon* crania have high nasal openings, which separate short foreheads from long lower faces, reduced facial crests, and steeply vertical lateral walls of infraorbital canals (Osborn, 1942; Saegusa, 1987). Apart from the development of molar plates, numerous other homoplasies are shared by elephants and stegodonts, including anteroposterior compression of the cranium, elevation of the parietals and occipital, loss of lower tusks and concomitant shortening of the mandibular symphysis, lack of median molar sulci, inflation of mesoconelets, and absence of accessory central conules (Osborn, 1942; Saegusa, 1987, 1996; Kalb et al., 1996a). Molar wear analysis indicates that, as in elephants, stegodont mastication was achieved via fore-aft shearing (Saegusa, 1996). Because of these similarities to elephants, stegodonts have played a significant role in the development of ideas about the origin of elephants since the time of Clift (1828), who first described these proboscideans as intermediates between "mastodonts" and elephants.

More recently, stegodontids were regarded as a group close to mammutids (Maglio, 1970a, 1973; Tobien, 1975; Coppens et al., 1978), but now are considered a sister taxon of tetralophodont gomphotheres and elephants (Tassy and Darlu, 1986; Tassy, 1990, 1996c; Kalb and Mebrate, 1993; Shoshani, 1996; Shoshani et al., 1998). Given their early Miocene divergence from the dental morphological pattern conserved in gomphotheriids, one of us (W.J.S.) feels that it is alternatively possible that stegodontids are the sister taxon to all gomphotheriids + elephants (figure 15.20, later). Monophyly of the family has been defended by Tassy (1990, 1996c), Saegusa (1987, 1996), Shoshani (1996), and Shoshani et al. (1998). By contrast, Kalb and Mebrate (1993) and Kalb et al. (1996a) allocate *Stegodon* to the Elephantinae. Both hypotheses are only weakly supported by parsimony analysis, because of heavy reliance on dental features. Chronostratigraphy and biogeography of stegodontids and early elephants, however, are concordant with monophyly of the Stegodontidae and Asian origin of stegodonts. Advanced stegolophodonts are stratigraphically succeeded by primitive, morphologically similar stegodonts in late Miocene formations in Thailand and Myanmar (Saegusa et al., 2005; Takai et al., 2006), while African proboscideans initially reported as stegolophodonts (Petrocchi, 1954; Singer and Hooijer, 1958; Hooijer, 1963) have been reidentified as early elephants (Maglio and Hendey, 1970; Maglio, 1973; Coppens et al., 1978).

Stegodonts have been thought of as forest-dwelling browsers (Osborn, 1921, 1942), an interpretation supported by their extreme brachyodonty and by dental isotopic analysis of late Miocene South Asian material (Cerling et al., 1999). Their relatively short, massive bodies and closely parallel, gently upcurved tusks have also been described as adaptations to dense forest (Osborn, 1921). However, carbon isotopic studies of fossil teeth reveal stegodonts from Central Africa to have been surprisingly eclectic feeders, ranging from browsers to grazers during the late Miocene, to early Pliocene mixed feeders and grazers, to grazers during the mid-Pliocene (Zazzo et al., 2000). This apparent shift in dietary preferences may signal increased ecological pressures over time to compete for C_4 resources, particularly with more hypsodont ungulates, including elephants, possibly the ultimate cause of their disappearance from the continent.

Genus *STEGODON* Falconer and Cautley, 1847
STEGODON KAISENSIS Hopwood, 1939
Figures 15.17A and 15.17B

Partial Synonymy *Stegodon fuchsi*, MacInnes, 1942; *S. kaisensis*, Cooke and Coryndon, 1970; *Primelephas gomphotheroides* (in part; Nyawiega, Uganda), Maglio, 1973:20; *Stegodon* sp., Beden, 1975; *S. kaisensis* "Nkondo stage" and "Warwire stage," Tassy, 1995.

Age and Occurrence Late Miocene–late Pliocene, eastern and Central Africa (table 15.6).

Diagnosis Emended diagnosis based on observations by H. Saegusa. While nearly all of the stegodont specimens from

TABLE 15.6
Major occurrences and ages of Afro-Arabian stegodonts and elephants
? = attribution or occurrence uncertain; alt. = alternatively.

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
STEGODONTIDAE, LATE MIOCENE–LATE PLIOCENE				
Stegodon cf. *S. kaisensis*	Tugen Hills, Kenya	Mpesida Beds	Ca. 7.0 Ma	Sanders, 1999; Kingston et al., 2002
Stegodon kaisensis "Nkondo stage"	Shoshomagai 2, Inolelo 3, Manonga Valley, Tanzania	Ibole Mb., Wembere-Manonga Fm.	Ca. 5.5–5.0 Ma	Harrison and Baker, 1997
	Kossom Bougoudi, Chad		Ca. 5.3 Ma (alt. 6.0–5.0 Ma)	Brunet et al., 2000; Zazzo et al., 2000; Brunet, 2001; Fara et al., 2005
	"Kaiso Village," south of the Howa River, probably Nkondo area, Uganda (type)	?Nkondo Fm.	Ca. 5.0 Ma	Hopwood, 1939; Cooke and Coryndon, 1970; Coppens et al., 1978; Sanders, 1990; Tassy, 1995
	Kaiso Central; Kisegi Wasa/N. Nyabrogo; Nyawiega site I, Uganda	Lower Kaiso Fm. (= Nkondo Fm.)	Ca. 5.0 Ma (alt. 6.0 Ma)	Cooke and Coryndon, 1970; Sanders, 1990, 1999; Pickford et al., 1993
	Kazinga-Kisenyi Area, Kazinga Channel, Uganda	Kazinga Beds	Ca. 5.0 Ma	MacInnes, 1942; Cooke and Coryndon, 1970; Sanders, 1990; Pickford et al., 1993; Tassy, 1995
	Nkondo-Kaiso Region, Uganda	Nkondo Fm.	Ca. 5.0 Ma	Pickford et al., 1993; Tassy, 1995
	Kollé, Chad		Ca. 5.0–4.0 Ma	Brunet et al., 1998
Stegodon kaisensis "Warwire stage"	Nkondo-Kaiso Region, Uganda	Warwire Fm.	Ca. 3.5–3.0 Ma	Pickford et al., 1993; Tassy, 1995
	Koro Toro, Chad		Ca. 3.5–3.0 Ma	Brunet, 2001; Fara et al., 2005
	Omo, Ethiopia	Upper Mb. B, Shungura Fm.	2.95–2.85 Ma	Beden, 1975, 1976; Alemseged, 2003
Stegodon sp. indet.	Sinda River, Lower Semliki, Democratic Republic of Congo	Sinda Beds	Ca. 4.1 Ma	Yasui et al., 1992
	Laetoli, Tanzania	Upper Unit, Laetolil Beds	3.8–3.5 Ma	Drake and Curtis, 1987; Sanders, 2005, in press
	Ishango 11 and Senga near Sn1, Upper Semliki, Democratic Republic of Congo	Lusso Beds	Late Pliocene	Sanders, 1990
ELEPHANTIDAE, LATE MIOCENE–PRESENT				
STEGOTETRABELODONTINAE, LATE MIOCENE–EARLY PLIOCENE				
Stegotetrabelodon orbus	Lothagam, Kenya (type)	Lower and Upper Mbs., Nawata Fm.; Apak Mb., Nachukui Fm.	At least 7.4–5.0 Ma; 6.5–5.0 Ma; 5.0–4.2 Ma	Maglio, 1970a, 1973; Maglio and Ricca, 1977; McDougall and Feibel, 2003; Tassy, 2003
	Tugen Hills, Kenya	Mpesida Beds	Ca. 7.0 Ma	Hill et al., 1985, 1986; Kingston et al., 2002

TABLE 15.6 (CONTINUED)

Taxon	Occurrence (Site, Locality)	Stratigraphic Unit	Age	Key References
S. orbus continued		Lukeino Fm.	6.2–5.6 Ma	Hill et al., 1985, 1986; Tassy, 1986; Hill, 2002
	Manonga Valley, Tanzania	Ibole Mb., Wembere-Manonga Fm.	Ca. 5.5–5.0 Ma	Harrison and Baker, 1997; Sanders, 1997
Stegotetrabelodon syrticus	Sahabi, Libya (type)	Sahabi Fm.	Late Miocene–early Pliocene, ca. 5.2 Ma	Petrocchi, 1943, 1954; Maglio, 1970; de Heinzelin and El-Arnauti, 1987; Bernor and Scott, 2003; Sanders, 2008b
Stegotetrabelodon sp. indet.	?Lemudong'o, Kenya	Lemundong'o Fm.	6.1–6.0 Ma	Ambrose et al., 2003; Saegusa and Hlusko, 2007
	Shuwaihat and Jebel Barakah, Abu Dhabi	Baynunah Fm.	Late Miocene, ca. 6.0 Ma	Glennie and Evamy, 1968; Madden et al., 1982; Hailwood and Whybrow, 1999; Tassy, 1999
	Kanam East and Central, Kenya	Kanam Fm.	Late Miocene to earliest Pliocene	MacInnes, 1942; Ditchfield et al., 1999
	Nyabusosi, Uganda	Kakara Fm., Lower and Upper Oluka Fm.	Late Miocene	Pickford et al., 1993; Tassy, 1995
ELEPHANTINAE, LATE MIOCENE–PRESENT				
Primelephas korotorensis	Lothagam, Kenya	Lower and Upper Mbs., Nawata Fm.; Apak Mb., Nachukui Fm.	At least 7.4–5.0 Ma; 6.5–5.0 Ma; 5.0–4.2 Ma	Maglio, 1970a, 1973; Maglio and Ricca, 1977; Leakey et al., 1996; McDougall and Feibel, 2003; Tassy, 2003
	Toros Menalla, Chad		7.0–6.0 Ma	Brunet et al., 2000; Mackaye et al., 2008
	Tugen Hills, Kenya	Lukeino Fm.	6.2–5.6 Ma	Hill et al., 1985, 1986; Tassy, 1986; Hill, 2002; Sanders, 2004
		Lower part, Chemeron Fm.	5.3–4.0 Ma	Hill et al., 1985, 1986; Deino et al., 2002
	Middle Awash, Ethiopia	Saraitu, Adu Dora, and Asa Koma Mbs., Adu-Asa Fm.	6.3–5.6 Ma	Mebrate, 1983; Kalb and Mebrate, 1993; Kalb, 1995; Haile-Selassie, 2001; WoldeGabriel et al., 2001; Haile-Selassie et al., 2004
		Kuseralee Mb., Sagantole Fm.	5.6–5.2 Ma	Mebrate, 1983; Kalb and Mebrate, 1993; Renne et al., 1999; Haile-Selassie, 2001; WoldeGabriel et al., 2001; Haile-Selassie et al., 2004
	"Galili Area," Mulu Basin, Ethiopia	Asa Koma Mb., Adu-Asa Fm.	5.8–5.6 Ma	Haile-Selassie, 2000; WoldeGabriel et al., 2001
	Manonga Valley, Tanzania	Ibole Mb., Wembere-Manonga Fm.	Ca. 5.5–5.0 Ma	Harrison and Baker, 1997; Sanders, 1997

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
P. korotorensis continued	Nyabusosi, Uganda	Lower Oluka Fm.	Late Miocene	Pickford et al., 1993; Tassy, 1995
	North and South Nyabrogo, Uganda	Lower horizons, Kaiso Fm.	Late Miocene–early Pliocene	Cooke and Coryndon, 1970
	Kossom Bougoudi, Chad		Ca. 5.3 Ma (alt. 6.0–5.0 Ma)	Brunet et al., 2000; Zazzo et al., 2000; Brunet, 2001; Fara et al., 2005; Mackaye et al., 2008
	Kollé, Chad		Ca. 5.0–4.0 Ma	Brunet et al., 1998; Mackaye et al., 2008
	Koulà, Chad (type)		?Early Pliocene	Coppens, 1965; Maglio, 1970a, 1973; Coppens et al., 1978
	Kolinga, Chad		?Early Pliocene (alt. latest Miocene)	Coppens, 1967; Maglio, 1973; Coppens et al., 1978
Stegodibelodon schneideri	Menalla, Chad (type)		?Early Pliocene	Coppens, 1972; Coppens et al., 1978
	Kolinga I, Chad		?Early Pliocene (alt. latest Miocene)	Coppens, 1972; Coppens et al., 1978
	Kollé, Chad		5.0–4.0 Ma	Brunet, 2001; Fara et al., 2005; Mackaye et al., 2005
		“*LOXODONTA ADAURORA* GROUP”		
Loxodonta adaurora adaurora	?Kanam East, Kenya	Kanam Fm.	Latest Miocene–earliest Pliocene	MacInnes, 1942; Ditchfield et al., 1999
	?Bugoma, Kaiso Central, Nyawiega, Uganda	Lower Kaiso Beds (= Nkondo Fm.)	Ca. 5.0 Ma (alt. 6.0 Ma)	Cooke and Coryndon, 1970; Sanders, 1990; Pickford et al., 1993; Boaz, 1994
	Tugen Hills, Kenya	Chemeron Fm.	Early Pliocene (within 5.3–4.0 Ma interval)	Maglio, 1973; Hill et al., 1985, 1986; Deino et al., 2002
	Middle Awash Valley, Ethiopia	Aramis and Beidareem Mbs., Sagantole Fm.	4.4–4.3 Ma	Mebrate, 1983; Kalb and Mebrate, 1993; Renne et al., 1999
	Kanapoi, Kenya (type)	Kanapoi Fm.	4.2–4.1 Ma	Maglio, 1970a, 1973; Feibel, 2003; Harris et al., 2003
	Omo, Ethiopia	Mursi Fm.	Early Pliocene, >4.15 Ma	Heinzelin, 1983; Beden, 1987a; Feibel et al., 1989
		Mb. B, Shungura Fm.	3.4–2.85 Ma	Heinzelin, 1983; Beden, 1987a; Alemseged, 2003
	West Turkana, Kenya	Kataboi and lower Lomekwi Mbs., Nachukui Fm.	Ca. 4.10–3.0 Ma	Harris et al., 1988a, 1988b
	Ekora, Kenya		Ca. 4.0–3.75 Ma (slightly younger than 4.0 Ma)	Maglio, 1970a, 1973; Behrensmeyer, 1976
	Allia Bay, Kenya	Moiti and Lokochot Mbs., Koobi Fora Fm.	Ca. 3.9–3.4 Ma	Beden, 1983; Harris, 1983; Brown, 1994
	Lothagam, Kenya	Kaiyumung Mb., Nachukui Fm. (=Unit 3)	Ca. 3.5–3.0 Ma	Coppens et al., 1978; Feibel, 2003; McDougall and Feibel, 2003

TABLE 15.6 (CONTINUED)

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
L. adaurora adaurora; continued	Hadar, Ethiopia	Sidi Hakoma and Denen Dora Mbs., Hadar Fm.	3.40–3.18 Ma	White et al., 1984; Bonnefille et al., 2004
L. adaurora kararae	Koobi Fora, Kenya (subspecies type)	Upper Burgi Mb., Koobi Fora Fm.	2.0–1.88 Ma	Beden, 1983; Feibel et al., 1989
	Karonga, Malawi	Chiwondo Beds	Ca. 2.4–2.3 Ma	Bromage et al., 1995
	Omo, Ethiopia	Mb. E, Shungura Fm.	2.40–2.36 Ma	Heinzelin, 1983; Beden, 1987a; Alemseged, 2003
	?Middle Awash, Ethiopia	Matabaietu Fm.	Ca. 2.3–2.0 Ma	Kalb and Mebrate, 1993
“*LOXODONTA EXOPTATA–L. AFRICANA* GROUP”				
Loxodonta sp. indet.	Toros Menalla, Chad		7.0–6.0 Ma	Brunet et al., 2000
	Tugen Hills, Kenya	Lukeino Fm.	6.2–5.6 Ma	Hill et al., 1985, 1986; Tassy, 1986; Hill, 2002
	Lothagam, Kenya	Apak Mb., Nachukui Fm.	5.0–4.2 Ma	McDougall and Feibel, 2003; Tassy, 2003
	Kollé, Chad		5.0–4.0 Ma	Brunet et al., 1998; Brunet, 2001
	Konso, Ethiopia	Intervals 1 and 4, Konso Fm.	Ca. 1.91 Ma and 1.43 Ma	Suwa et al., 2003
	West Turkana, Kenya	Kaitio Mb., Nachukui Fm.	1.9–1.6 Ma	Brugal et al., 2003
Loxodonta cookei	Tugen Hills, Kenya	?Lukeino Fm.	6.2–5.6 Ma	Hill et al., 1985, 1986; Tassy, 1986; Hill, 2002
		Chemeron Fm.	5.3–4.0 Ma	Hill et al., 1985, 1986; Deino et al., 2002
	Nkondo-Kaiso Region, Uganda	Nkondo Fm.	Ca. 5.0 Ma (alt. ca. 6.0 Ma)	Pickford et al., 1993; Tassy, 1995
	Langebaanweg, South Africa (type)	Quarry E, Quartzose Sand Mb. and Pellatal Phosphate Mb., Varswater Fm.	Early Pliocene, ca. 5.0 Ma	Hendey, 1981; Sanders, 2006, 2007
	?Endolele, Tanzania	?Lower Unit, Laetolil Beds	?>4.3 Ma	Sanders, 2005, in press
Loxodonta exoptata	?Manonga Valley, Tanzania	Kilolei Mb., Wembere-Manonga Fm.	Ca. 4.5–4.0 Ma	Harrison and Baker, 1997; Sanders, 1997
	Kakesio (and Esere, Emboremony, and Noiti), Tanzania	Lower Unit, Laetolil Beds	Ca. 4.3–3.8 Ma	Drake and Curtis, 1987; Harris, 1987b; Hay, 1987; Sanders, 2005
	Kanapoi, Kenya	Kanapoi Fm.	4.2–4.1 Ma	Feibel, 2003; Harris et al., 2003
	Karonga, Uraha, Malawi	Chiwondo Beds	Ca. 4.0–3.0 Ma	Bromage et al., 1995
	Allia Bay, Kenya	Lokochot and Tulu Bor Mbs., Koobi Fora Fm.	~3.5–2.6 Ma	Beden, 1983; Harris, 1983; Brown, 1994
	Laetoli, Tanzania (type)	Upper Unit, Laetolil Beds; Upper Ndolanya Beds	3.8–3.5 Ma; ~2.7–2.6 Ma	Beden, 1987b; Drake and Curtis, 1987; Harris, 1987b; Harrison, 2002; Sanders, 2005, in press
	Koro Toro, Chad		3.5–3.0 Ma	Brunet et al., 1995; Brunet, 2001

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
L. exoptata continued	West Turkana, Kenya	lower Lomekwi Mb., Nachukui Fm.	Ca. 3.36–3.0 Ma	Harris et al., 1988a, 1988b
	Omo, Ethiopia	Mb. A, Shungura Fm.	Ca. 3.5–3.4 Ma	Heinzelin, 1983; Beden, 1987a; Alemseged, 2003
	Hadar, Ethiopia	Denen Dora Mb., Hadar Fm.	3.22–3.18 Ma	White et al., 1984; Bonnefille et al., 2004
	?Middle Awash, Ethiopia	Matabaietu Fm.	Ca. 2.3–2.0 Ma	Kalb and Mebrate, 1993; Kalb, 1995
Loxodonta atlantica angammensis	Omo, Ethiopia	Mbs. D, F, Shungura Fm.	2.52–2.40 Ma and 2.36–2.33 Ma	Beden, 1987a; Feibel et al., 1989; Alemseged, 2003
	Angamma-Yayo, Chad (subspecies type)		?Early Pleistocene	Coppens, 1965; Beden, 1987a
L. atlantica atlantica	Ternifine, Algeria (type)		Middle Pleistocene	Pomel, 1879; Osborn, 1942; Maglio, 1973; Coppens et al., 1978
	Oued Constantine, Algeria	Maison Carrée Fm.	Middle Pleistocene	Maglio, 1973; Coppens et al., 1978
	Sablière de Palekao, Algeria		Middle Pleistocene	Maglio, 1973
	Sidi Abderrahmane, Algeria		Middle Pleistocene	Maglio, 1973; Coppens et al., 1978; Raynal et al., 2004a
L. atlantica zulu	Elandsfontein, South Africa		Ca. 1.0–0.6 Ma (alt. ca. 0.7–0.4 Ma)	Maglio, 1973; Klein and Cruz-Uribe, 1991; Klein et al., 2007
	Zululand, southeast coast of Africa, South Africa (subspecies type)		Middle Pleistocene	Scott, 1907; Osborn, 1942; Maglio, 1973
Loxodonta africana (type locality probably Cape Colony, South Africa [Osborn, 1942: p. 1197])	Middle Awash, Ethiopia	?Wehaietu Fm.	Between 0.8 and 0.2 Ma	Kalb and Mebrate, 1993
	Ounaianga Kebir I, Chad		?Middle Pleistocene	Joleaud and Lombard, 1933a, 1933b; Coppens, 1967
	Kanjera, Kenya	Apoko Fm.	Ca. 0.5 Ma	Plummer and Potts, 1989; Behrensmeyer et al., 1995
	Duinefontein 2, Elandsfontein, South Africa		270 Ka	Klein et al., 2007
	Omo, Ethiopia	Mb. III, Kibish Fm.	130–75 Ka	Assefa et al., 2008
	Elands Bay Cave, Elandsfontein, South Africa		13,600–7,900 y BP	Klein et al., 2007
	Bone Circle assemblage, Elandsfontein, South Africa		12,000–10,000 y BP	Klein and Cruz-Uribe, 1991
	Omo, Ethiopia	Mb. IV, Kibish Fm.	<10 Ka	Assefa et al., 2008
Mammuthus subplanifrons	Middle Awash, Ethiopia	?Kuseralee and Aramis Mbs., Sagantole Fm.	5.77–5.18 Ma; ca. 4.4 Ma	Mebrate, 1983; Kalb and Mebrate, 1993; Renne et al., 1999; Haile-Selassie, 2001
	Langebaanweg, South Africa	Quarry E, Quartzose Sand Mb., Varswater Fm.	Early Pliocene, ca. 5.0 Ma	Maglio and Hendey, 1970; Hendey, 1981; Sanders, 2006, 2007

TABLE 15.6 (CONTINUED)

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
M. subplanifrons continued	?Nyawiega, Uganda	Lower Kaiso Beds (= Nkondo Fm.)	Ca. 5.0 Ma (alt. 6.0 Ma)	Cooke and Coryndon, 1970; Pickford et al., 1993
	?Nkondo-Kaiso Area, Uganda	Lower Kaiso Beds (= Nkondo Fm.)	Ca. 5.0 Ma (alt. 6.0 Ma)	Pickford et al., 1993; Tassy, 1995
	Vaal River, South Africa (type)	Middle Terrace	?Early Pliocene	Osborn, 1928, 1934
	Virginia, Orange Free State, South Africa		?Early Pliocene	Meiring, 1955; Maglio, 1973
	?Uraha, Malawi	Chiwondo Beds	Ca. ≥4.0 Ma	Mawby, 1970; Bromage et al., 1995
	?Ishasha River, Virunga National Park, Democratic Republic of Congo	Kaiso Group sediments	Early Pliocene	Vanoverstraeten et al., 1990
Mammuthus africanavus	Lac Ichkeul, Tunisia (type)		Mid–late Pliocene	Arambourg, 1970; Coppens et al., 1978
	Aïn Brimba, Tunisia		Mid–late Pliocene	Arambourg, 1970
	Kebili, Tunisia		Mid–late Pliocene	Maglio, 1973; Coppens et al., 1978
	Garet et Tir, Algeria		Mid–late Pliocene	Arambourg, 1970; Coppens et al., 1978
	Aïn Boucherit, Algeria	Oued Boucherit Fm.	Late Pliocene; 2.32 Ma (alt. ca. 2.0 Ma)	Arambourg, 1970; Coppens et al., 1978; Geraads and Amani, 1998; Sahnouni and Heinzelin, 1998; Geraads, 2002; Sahnouni et al., 2002
	Oued Akrech, Morocco		Mid–late Pliocene	Arambourg, 1970; Coppens et al., 1978
	Fouarat, Morocco		Mid–late Pliocene	Arambourg, 1970
	Goz-Kerki, Chad (70 km SE of Koro-Toro)		Ca. 3.5–3.0 Ma	Coppens, 1965; Brunet, 2001; Fara et al., 2005
	Koulà, Chad		Ca. 3.5–3.0 Ma	Coppens, 1965; Maglio, 1973; Coppens et al., 1978; Brunet, 2001; Fara et al., 2005
	Ouadi-Derdemy, Chad		Ca. 3.5–3.0 Ma	Coppens, 1965; Maglio, 1973; Coppens et al., 1978; Brunet, 2001; Fara et al., 2005
	Toungour, Chad (30–50 km W of Koro-Toro)		Ca. 3.5–3.0 Ma	Coppens, 1965; Maglio, 1973; Coppens et al., 1978; Brunet, 2001; Fara et al., 2005
Mammuthus meridionalis	Aïn Hanech, Algeria	Aïn Hanech Fm.	Between 1.95 and 1.78 Ma (alt. ca. 1.2 Ma)	Arambourg, 1970; Maglio, 1973; Sahnouni and Heinzelin, 1998; Geraads et al., 2004; Sahnouni et al., 2002, 2004
Mammuthus sp. indet.	Djebel Bel Hacel, Algeria		Early Pleistocene	Arambourg, 1970
	Hadar, Ethiopia	Sidi Hakoma and Denen Dora Mbs., Hadar Fm.	3.40–3.18 Ma	White et al., 1984; Bonnefille et al., 2004

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
Elephas ekorensis	?Lothagam, Kenya	Apak Mb., Nachukui Fm.	5.0–4.2 Ma	Beden, 1985; McDougall and Feibel, 2003; Tassy, 2003
	Kanapoi, Kenya	Kanapoi Fm.	4.2–4.1 Ma	Maglio, 1970a, 1973; Feibel, 2003; Harris et al., 2003
	Ekora, Kenya (type)		Ca. 4.0–3.75 Ma (slightly younger than 4.0 Ma)	Maglio, 1970a, 1973; Behrensmeyer, 1976
	Dikika, Ethiopia (DIK-1)	Sidi Hakoma Mb., Hadar Fm.	3.40–3.22 Ma	Wynn et al., 2006
	Hadar, Ethiopia	Sidi Hakoma and Denen Dora Mbs., Hadar Fm.	3.40–3.18 Ma	White et al., 1984; Bonnefille et al., 2004
	Omo, Ethiopia	Usno Fm.	Within 3.6–2.7 Ma interval	Butzer, 1971; Heinzelin, 1983; Beden, 1987a
Elephas recki brumpti	Bolt's Farm, South Africa		Ca. 5.0–4.0 Ma (alt. 3.4–2.9 Ma)	Maglio, 1973; Cooke, 1993; Sénégas and Avery, 1998
	?Middle Awash, Ethiopia	?Aramis Mb., Sagantole Fm.	Ca. 4.4 Ma (alt. 4.1–3.8 Ma)	Kalb and Mebrate, 1993; Renne et al., 1999
	Koobi Fora and Allia Bay, Kenya	Lokochot Mb., Koobi Fora Fm. (= "Kubi Algi Fm., Zone B")	~3.50–3.36 Ma	Beden, 1983, 1985; Harris, 1983; Brown, 1994
	?Goz-Kerki, Chad (70 km SE of Koro-Toro)		Ca. 3.5–3.0 Ma	Coppens, 1965; Maglio, 1973; Brunet, 2001; Fara et al., 2005
	?Koulà, Chad		Ca. 3.5–3.0 Ma	Coppens, 1965; Maglio, 1973; Brunet, 2001; Fara et al., 2005
	?Ouadi-Derdemy, Chad		Ca. 3.5–3.0 Ma	Coppens, 1965; Maglio, 1973; Coppens et al., 1978; Brunet, 2001; Fara et al., 2005
	Omo, Ethiopia (subspecies type)	Upper Mb. A, Mb. B, Shungura Fm.	Ca. 3.5–2.85 Ma	Beden, 1980, 1987a; Feibel et al., 1989; Alemseged, 2003
	Dikika, Ethiopia (DIK-1)	Sidi Hakoma Mb., Hadar Fm.	3.40–3.22 Ma	Wynn et al., 2006
	West Turkana, Kenya	lower and upper Lomekwi Mb., Nachukui Fm.	3.36–2.5 Ma	Harris et al., 1988a, 1988b
	Hadar, Ethiopia	Denen Dora Mb., Hadar Fm.	3.22–3.18 Ma	White et al., 1984; Bonnefille et al., 2004
E. recki shungurensis	Koobi Fora and Allia Bay, Kenya	Tulu Bor and Upper Burgi Mbs., Koobi Fora Fm.	3.36–1.88 Ma	Beden, 1980, 1983; Harris, 1983; Feibel et al., 1989; Brown, 1994
	Hadar, Ethiopia	Kada Hadar Mb., Hadar Fm.	3.18–2.9 Ma	White et al., 1984; Bonnefille et al., 2004; Wynn et al., 2006
	Tugen Hills, Kenya	Chemeron Fm. (loc. 91)	Ca. 2.85–2.40 Ma	Beden, 1985
	West Turkana, Kenya	Upper Lomekwi and Lokalalei Mbs., Nachukui Fm.	2.9–2.3 Ma	Harris et al., 1988a, 1988b

TABLE 15.6 (CONTINUED)

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
E. recki shungurensis continued	Omo, Ethiopia (subspecies type)	Mbs. C-lower F, Shungura Fm.	2.9–2.3 Ma	Beden, 1980, 1987a; Feibel et al., 1989; Alemseged, 2003
	Kigagati, Kaiso Village, Uganda	Upper Kaiso Fm., cf. Mbs. C-lower F, Shungura Fm.	Ca. 2.9–2.3 Ma	Cooke and Coryndon, 1970; Sanders, 1990
	Bouri, Ethiopia	Hata Mb., Bouri Fm.	2.5 Ma	Heinzelin et al., 1999
	Karonga, Uraha, Malawi	Chiwondo Beds	Ca. 2.4–1.8 Ma	Bromage et al., 1995
E. recki atavus	Upper Semliki River, Democratic Republic of Congo	Lusso Beds	Ca. 2.36–1.90 Ma (equivalent to Mbs. F, G, Shungura Fm.)	Sanders, 1990
	?West Turkana, Kenya	Kalochoro Mb., Nachukui Fm.	2.35–1.90 Ma	Brugal et al., 2003
	Omo, Ethiopia (subspecies type)	Mbs. upper F–G, Shungura Fm.	2.34–1.90 Ma	Beden, 1980, 1987a; Feibel et al., 1989; Alemseged, 2003
	Fejej FJ-1 Site, Kenya	Unit III	Ca. 2.34–1.90 Ma	Moullé et al., 2001
	Koobi Fora and Ileret, Kenya	Upper Burgi Mb., Koobi Fora Fm. (just under and above the KBS Tuff)	2.0–1.88 Ma	Beden, 1980, 1983; Harris, 1983; Feibel et al., 1989; Brown, 1994
	Konso, Ethiopia	Intervals 1–3, Konso Fm.	Ca. 1.91–1.50 Ma	Suwa et al., 2003
	Olduvai Gorge, Tanzania	Beds I and lower II	~1.87–1.6 Ma (alt. 2.10–1.75 Ma)	Hay, 1976; Beden, 1980, 1985; Brown, 1994; Tamrat et al., 1995
E. recki ileretensis	?West Turkana, Kenya	Kaitio Mb., Nachukui Fm.	1.9–1.6 Ma	Harris et al., 1988a, 1988b
	Omo, Ethiopia	Mbs. ?J, K, and lower L, Shungura Fm.	~?1.74–1.30 Ma	Beden, 1980, 1985, 1987a; Feibel et al., 1989; Alemseged, 2003
	Koobi Fora and Ileret, Kenya (subspecies type)	KBS and Okote Mbs., Koobi Fora Fm. (below and above the Okote Tuff)	~1.7–1.5 Ma	Beden, 1980, 1983, 1985; Harris, 1983; Feibel et al., 1989; Brown, 1994
	Barogali, Republic of Djibouti		Ca. 1.6–1.3 Ma	Berthelet, 2001; Berthelet and Chavaillon, 2001
	Chesowanja, Kenya		>1.42 Ma	Hooker and Miller, 1979; Beden, 1985
	Olduvai Gorge, Tanzania	Upper Bed II	~1..60–1.15 Ma (alt. 1.75 Ma–?)	Hay, 1976; Beden, 1980, 1985; Brown, 1994; Tamrat et al., 1995
E. recki recki	Koobi Fora and Ileret, Kenya	Okote Mb., Koobi Fora Fm. (below the Chari Tuff)	1.64–1.39 Ma	Beden, 1980; 1983; Harris, 1983; Feibel et al., 1989; Brown, 1994
	Konso, Ethiopia	Intervals 4–6, Konso Fm.	Ca. 1.43–1.39 Ma	Suwa et al., 2003
	Omo, Ethiopia	Upper Mb. L, Shungura Fm.	<1.39–1.16 Ma	Beden, 1980, 1987a; Feibel et al., 1989; Alemseged, 2003
	West Turkana, Kenya	Nariokotome Mb., Nachukui Fm.	Ca. 1.3–1.0 Ma	Harris et al., 1988a, 1988b

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
E. recki recki continued	Olduvai Gorge, Tanzania (type)	Beds III, IV	1.15–0.60 Ma (alt. ?–1.1 Ma)	Hay, 1976; Beden, 1985; Brown, 1994; Tamrat et al., 1995
	Melka Kunture (Garba IV), Ethiopia	Melka Kunture Fm.	>0.78 Ma, ca. 1.0 Ma	Beden, 1980, 1985; Raynal et al., 2004b
	Olorgesailie, Kenya	Olorgesailie Fm.	Ca. 1.0–0.5 Ma (alt. 0.93–0.70 Ma)	Beden, 1980, 1985; Bye et al., 1987; Deino and Potts, 1990
	Busidima-Telalak region, Afar, Ethiopia	?Wehaietu Fm.	Between 0.8 and 0.2 Ma	Alemseged and Geraads, 2000
	Kathu Pan, South Africa	Acheulean deposit	Middle Pleistocene, sometime in interval of 0.7–0.4 Ma	Klein, 1984, 1988
	Namib IV, Namibia		0.7–0.4 Ma interval (alt. late Lower or early Middle Pleistocene)	Shackley, 1980; Klein, 1984, 1988
	Power's Site, South Africa	lower terrace, Vaal River sequence, Rietputs Fm.	Middle Pleistocene, similar in age to Kathu Pan	Klein, 1988
	Kanjera, Kenya	Apoko Fm.	Ca. 0.5 Ma	Plummer and Potts, 1989; Behrensmeyer et al., 1995
E. recki subsp. indet. (*E. r. shungurensis* or *E. r. brumpti*)	Makapansgat, South Africa	Mb. 4	<3.110 Ma (alt. 2.7–2.5 Ma)	Cooke, 1993; Partridge, 2000; Partridge et al., 2000
	Sterkfontein, South Africa	Mb. 4	2.8–2.4 Ma (alt. 2.5–1.5 Ma)	Cooke, 1993; Berger et al., 2002
(?*E. recki shungurensis*)	Ahl al Oughlam, Morocco		Late Pliocene, ca. 2.5 Ma	Geraads and Metz-Muller, 1999
(?*E. recki shungurensis*)	Salé, Morocco		?Early Pleistocene (alt. late Pliocene)	Arambourg, 1970
	Marsabit Road, Kenya		Early Pleistocene	Gentry and Gentry, 1969
(*Elephas* sp.)	Mansourah (Constantine), Algeria		Early Pleistocene	Chaid-Saoudi et al., 2006
(*Elephas* sp.)	Swartkrans, South Africa	Hanging Remnant Mb. 3	Ca. 1.8–1.5 Ma Ca. 1.5–1.0 Ma	de Ruiter, 2003 Cooke, 1993; Partridge, 2000
	Dandero, northern Danakil Depression, Eritrea	Upper Danakil Fm.	Ca. 1.0 Ma	Shoshani et al., 2001c
(intermediate between *E. r. ileterensis* and *E. r. recki*)	Buia, Eritrea	Upper Danakil Fm.	Ca. 1.0 Ma	Ferretti et al., 2003
Elephas iolensis	Sidi Abderrahmane, Algeria		?Close to middle Pleistocene/late Pleistocene boundary	Arambourg, 1960; Maglio, 1973; Coppens et al., 1978; Raynal et al., 2004
	Omo, Ethiopia	Kibish Fm.	Close to middle Pleistocene/late Pleistocene boundary	Maglio, 1973; Coppens et al., 1978; McDougall et al., 2005
	Vaal River, South Africa	Lower (younger) terraces	Middle–late Pleistocene	Dart, 1927, 1929; Osborn, 1928; Maglio, 1973; Coppens et al., 1978
	Beausejour Farm, Algeria (type)		?Late Pleistocene	Maglio, 1973; Coppens and Gaudant, 1976
	Port de Mastaganem, Algeria		Late Pleistocene	Maglio, 1973; Coppens et al., 1978

TABLE 15.6 (CONTINUED)

Taxon	*Occurrence (Site, Locality)*	*Stratigraphic Unit*	*Age*	*Key References*
E. iolensis continued	Zouerate, Mauritania		Late Pleistocene	Maglio, 1973; Coppens et al., 1978
	El Douira, Tunisia		90–75,000 y BP	Coppens and Gaudant, 1976
	Kaiso Village and Behanga I, Western Rift, Uganda	?Rwebishengo Beds	Latest Pleistocene	Cooke and Coryndon, 1970; Sanders, 1990; Pickford et al., 1993
	Natodameri, Sudan		35,000 y BP	Maglio, 1973; Coppens et al., 1978

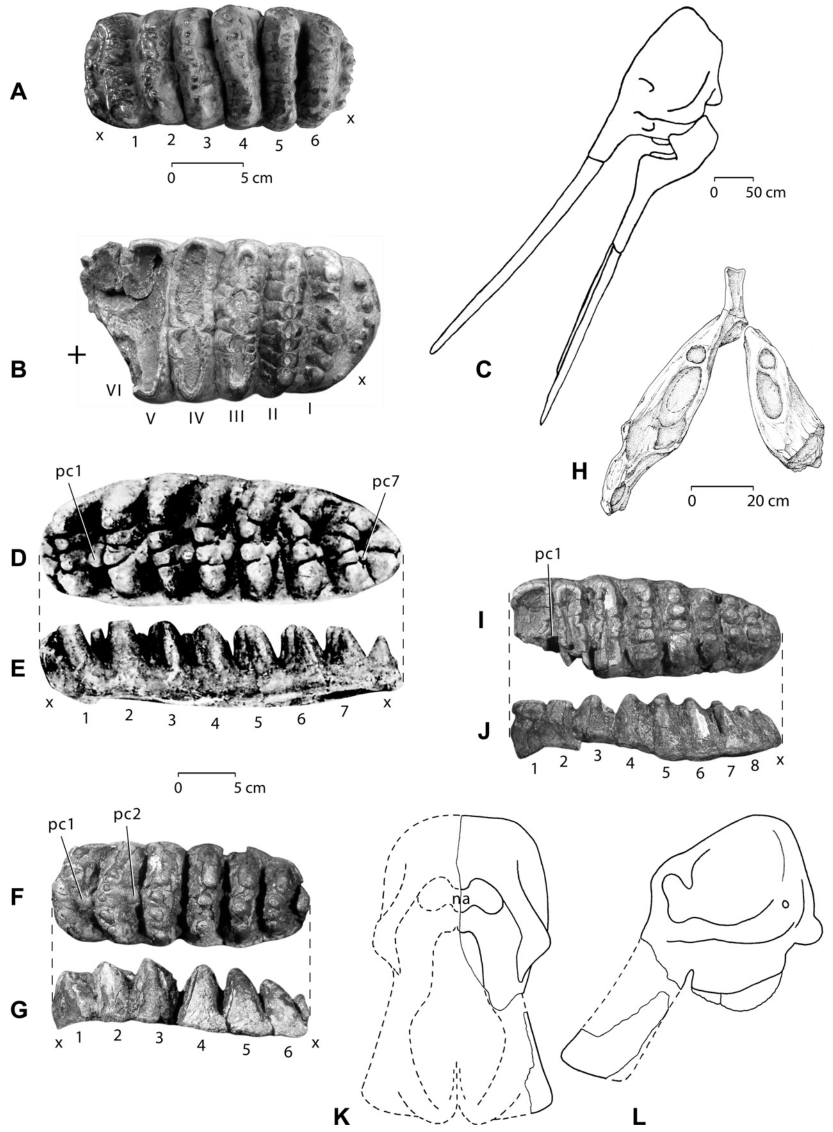

FIGURE 15.17 Aspects of stegodont and elephant cranial, mandibular, and dental morphology. Anterior is to the left except where specified. A) Occlusal view, M2, M15408 (Kazinga Channel, Uganda), *Stegodon kaisensis*. B) Occlusal view, M3, NK92'88 (Nkondo Fm., Uganda), *Stegodon kaisensis*. C) Reconstruction of skull, *Stegotetrabelodon syrticus* (cover illustration, Garyounis Scientific Bulletin, Special Issue No. 4, 1982). D) Occlusal view (reversed), m3, unnumbered (Sahabi, Libya), *Stegotetrabelodon syrticus* (Maglio, 1973: plate I, figure 3). E) Left lateral view (reversed), m3, unnumbered (Sahabi, Libya), *S. syrticus* (Maglio, 1973: plate I, figure 3). F) Occlusal view, M3, KNM-LT 354, part of holotype of *Stegotetrabelodon orbus*. G) Right lateral view, M3, KNM-LT 354, part of holotype of *S. orbus*. H) Dorsal view, mandible, L176-1, *Primelephas korotorensis*, originally attributed to *Stegodibelodon schneideri* (Kalb and Mebrate, 1993: figure 23); anterior is to the top. I) Occlusal view, m3, KNM-LT 351, *P. korotorensis*. J) Left lateral view, m3, KNM-LT 351, *P. korotorensis*. K) Anterior view, reconstruction of cranium of *Loxodonta adaurora*, based on KNM-LT 353 and KNM-KP 385 (Maglio, 1970b: figure 2A). L) Left lateral view, reconstruction of cranium of *L. adaurora*, based on KNM-LT 353 and KNM-KP 385 (Maglio, 1970b: figure 2). C, courtesy of Noel Boaz. D, E, H, permission of the American Philosophical Society. K, L, permission of the Museum of Comparative Zoology, Harvard University.

Africa have been attributed to *S. kaisensis*, previous diagnoses (e.g., Hopwood, 1939; Cooke and Coryndon, 1970) did not distinguish the species from other congeners, or were based on erroneous identification of molars. Tassy's (1995) separation of specimens from Uganda into two stages, without specifying the synapomorphies uniting these forms, further complicated the situation. Thus, the justification for this species has been largely geographic, rather than morphological.

Nonetheless, the species appears to be distinguished by apically anteroposteriorly compressed loph(id)s; deep grooves separating apical digitations (mammillae) that reach the bottom of transverse valleys (figures 15.17A, 15.17B); and strong steplike wear configuration of enamel wear figures combined with weak enamel folding.

Description No skulls of African stegodonts have been conserved (see MacInnes, 1942:85). The species is best documented from the Western Rift, where it has been chronostratigraphically subdivided into two morphs, a primitive "Nkondo stage" and a more progressive "Warwire stage," based on dental differences (Tassy, 1995). The Nkondo stage includes all of the older collections of Western Rift material attributed to the species (Cooke and Coryndon, 1970; Sanders, 1990), as well as a more recent sample from this region (Tassy, 1995) and specimens of similar age from Chad (table 15.6; Brunet, 2001). Molars of this stage are wide (M3 W = 100–114 mm), with a thin covering of cementum over the plate sides; enamel is thick (ET ≈ 4.6–5.1 mm); lamellar frequency is low (M3 LF = 3.0–4.0); and crown height is very low (HI ≈ 55) (Tassy, 1995). There are no accessory central conules, and apically loph(id)s are anteroposteriorly narrow. Except for thicker enamel and more massive plates, a partial M3 from Kenya (KNM-MP 46; Sanders, 1999) is otherwise morphometrically similar to molars of the Nkondo stage of *S. kaisensis*.

The best preserved specimen of this morph is a complete right M2 from the Kazinga Channel, Uganda (BMNH 15408; Fuchs, 1934), originally the type of *S. fuchsi* (MacInnes, 1942).

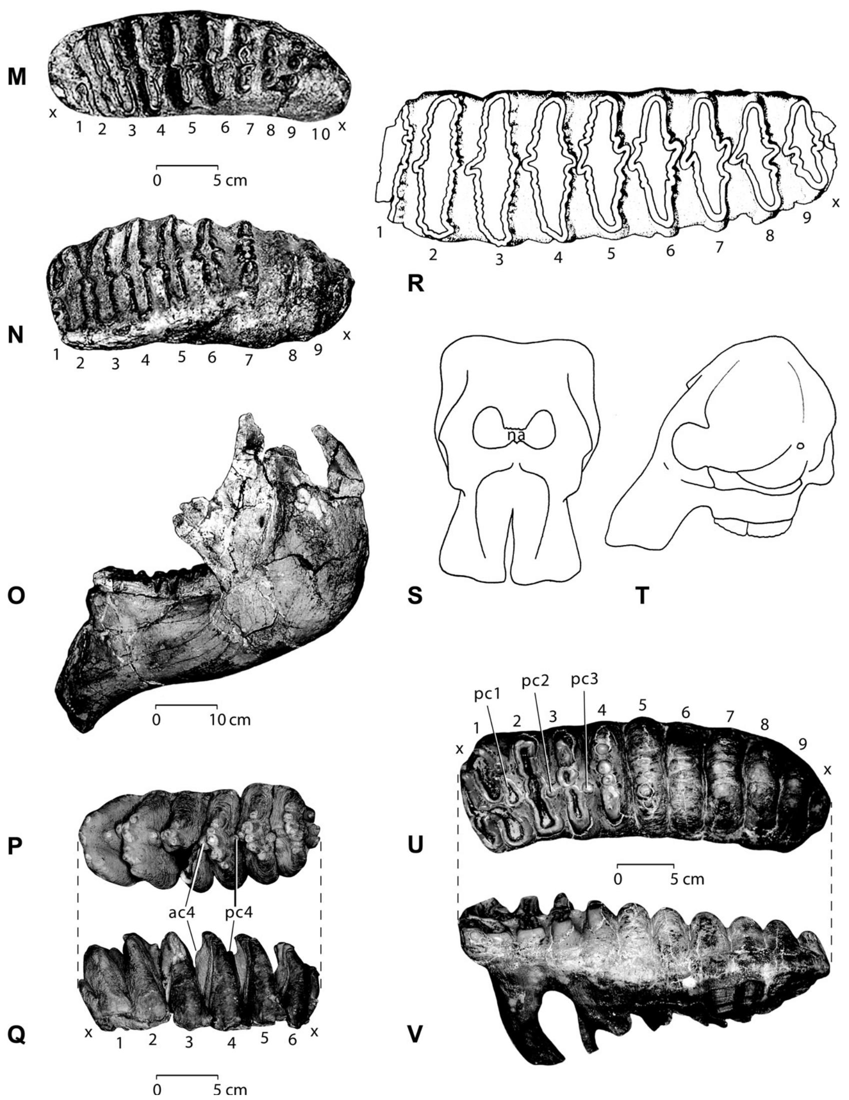

FIGURE 15.17 (CONTINUED)

M) Occlusal view, m3, KNM-KP 385, part of holotype of *L. adaurora*. N) Occlusal view, M3, KNM-KP 385, part of holotype of *L. adaurora*. O) Left lateral view, mandible, KNM-KP 385, part of holotype of *L. adaurora*. P) Occlusal view, M2, SAM-PQ-L45627, holotype of *Loxodonta cookei*. Q) Right lateral view, M2, SAM-PQ-L45627, holotype of *L. cookei*. R) Occlusal view, M3, L 161.19a (Omo Shungura, Ethiopia), *Loxodonta atlantica angammensis* (Beden, 1987a: figure 8). S) Anterior view, cranium, *Loxodonta africana* (Maglio, 1970b: figure 2B). T) Left lateral view, cranium, *L. africana* (Maglio, 1970b: figure 2B). U) Occlusal view, m3, SAM-PQ-L12723, *Mammuthus subplanifrons*. V) Left lateral view, m3, SAM-PQ-L12723, *M. subplanifrons*. R, permission of Editions du Centre National de la Recherche Scientifique. S, T, permission of the Museum of Comparative Zoology, Harvard University.

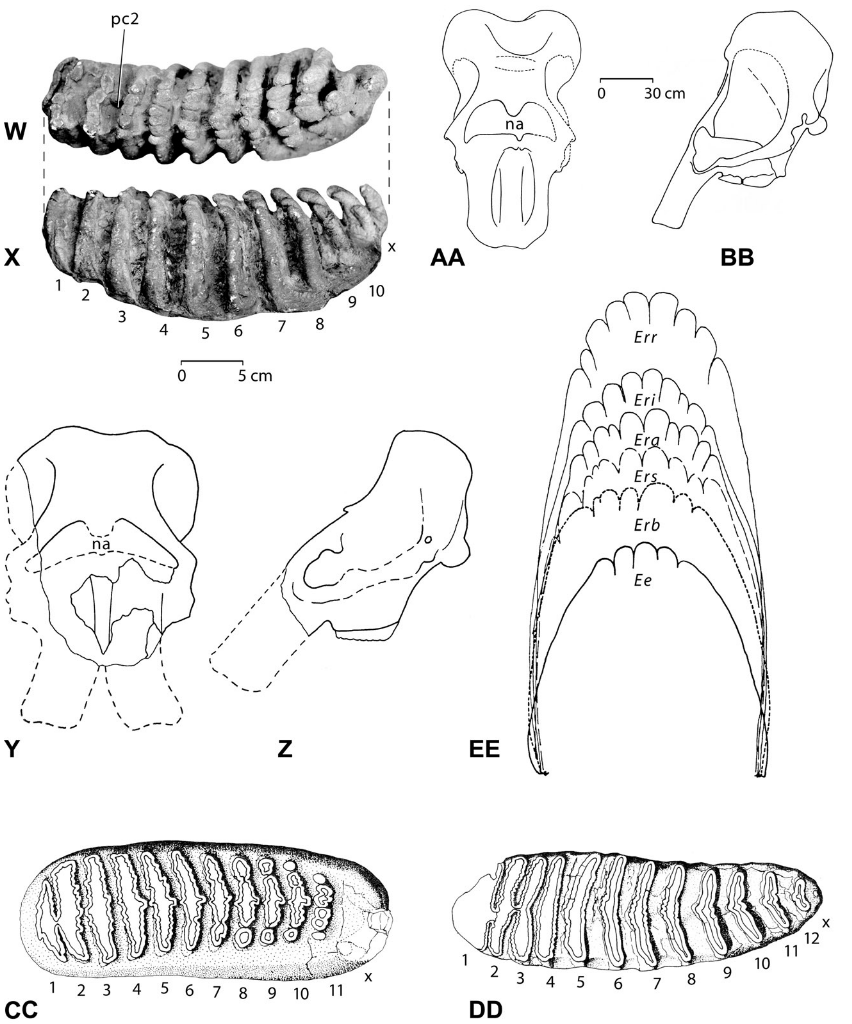

FIGURE 15.17 (CONTINUED)

W) Occlusal view, m3, 1950-1: 12 (Lac Ichkeul, Tunisia), *Mammuthus africanavus*. X) Left lateral view, m3, 1950-1: 12 (Lac Ichkeul, Tunisia), *M. africanavus*. Y) Anterior view, reconstruction of cranium of *Mammuthus meridionalis*, based on Geological Institute of Florence Nos. 1049, 1051, and 1054 (Maglio, 1970b: figure 3A). Z) Left lateral view, reconstruction of cranium of *M. meridionalis*, based on Geological Institute of Florence Nos. 1049, 1051, and 1054 (Maglio, 1970b: figure 3A′). AA) Left lateral view, reconstruction of cranium of *Elephas recki atavus*, KNM-ER 5711 (Beden, 1983: figure 3.17A). BB) Anterior view, reconstruction of cranium of *E. recki atavus*, KNM-ER 5711 (Beden, 1983: figure 3.17B). CC) Occlusal view, m2, lectotype of *E. recki recki* (Beden, 1980: plate IE). DD) Occlusal view, m3, *E. recki atavus* (Beden, 1980: plate IC). EE) Transverse profiles of *E. ekorensis* and *E. recki* molars, showing progessive, time-successive increases in hypsodonty within the lineage (Beden, 1987a: figure 22). Y, Z, permission of the Museum of Comparative Zoology, Harvard University. AA, BB, permission of Oxford University Press, Inc. CC, DD, copyright © 2010 Elsevier, B.V. EE, permission of Editions du Centre National de la Recherche Scientifique.

ABBREIVATIONS: ac, anterior accessory central conule; *Ee, Elephas ekorensis*; *Era, Elephas recki atavus*; *Erb, E. recki brumpti*; *Eri, E. recki ileretensis*; *Err, E. recki recki*; *Ers, E. recki shungurensis*; na, nasal aperture; pc, posterior accessory central conule; x, anterior or posterior cingulum(id); 1, 2, 3, . . ., first second, third, . . . plate.

It has a plate formula of x6x, with 9–11 apical digitations per plate; plates are transversely straight and separated by Y-shaped transverse valleys, wide (W = 92.8) and low (H = 54 mm), and are not closely spaced (LF = 3.75); enamel is thick (5.0 mm); a trace of cementum coats the valleys and is invested around plate apices; and the crown is rectangular in occlusal view (figure 15.17A). Other molars of Nkondo stage stegodonts are morphologically similar, with as many as 13 mammillae per plate (see Tassy, 1995: figure 2), and weakly folded enamel accompanied by pronounced steplike wear configurations of enamel. Plate formulae dp4 = 6; m1 = x6x; M1 = x6x; M2 = x6x; M3 = 7x (Tassy, 1995).

"Warwire stage" molars are also wide (M3/m3 W = 99–105 mm), with numerous bilaterally compressed apical digitations per plate (10–13) (Tassy, 1995). They are primarily distinguished from "Nkondo stage" molars by slighly greater hypsodonty (HI = 63–66) and evidently by more plates, but otherwise are quite similar. Plate formula: m3 = 9 (Tassy, 1995).

Remarks The greater representation of *Stegodon kaisensis* in the Western Rift may be related to humid conditions and proximity of lowland rainforest locally during the late Miocene–Pliocene (Pickford et al., 1993; Boaz, 1994). In overall morphology, *S. kaisensis* Nkondo stage most closely resembles the penecontemporaneous Asian species *S. zdanskyi*, and "Warwire stage" is similar to Javan *S. trigonocephalus* (see Saegusa et al., 2005). *Stegodon kaisensis* is dentally convergent on the primitive elephant *Primelephas korotorensis*, and where one is common, the other is rare or absent (table 15.6).

Further sampling of dental isotopes needs to be undertaken to more widely assess habitat and dietary similarities for these taxa. They both have extremely brachyodont crowns, a low number of plates, few or no accessory central conules in third molars, transversely rectilinear, pyramidal-shaped plates, V-shaped transverse valleys that may be "pinched" at their bases, cementum not completely infilling transverse valleys, thick enamel, and numerous apical digitations in deciduous premolars. This has led to some confusion in identification of specimens. Molars referred to various stegodont species from the Middle Awash, Ethiopia (Kalb and Mebrate, 1993; Tassy, 1995), and Koulà and Kolinga, Chad (Coppens, 1965, 1967) instead belong in *P. korotorensis* (Haile-Selassie, 2001).

Family ELEPHANTIDAE Gray, 1821

Arising in Afro-Arabia during the late Miocene, by the late Pliocene elephants had dispersed throughout the Old World and into North America, and for most of their existence were considerably more taxonomically diverse and widespread than today (Todd and Roth, 1996; Shoshani and Tassy, 1996). The decline of mammutids and gomphotheriids, and increased distribution of C_4 plants (grasses and sedges) (Cerling et al., 1993) created ecological opportunities that were exploited by several successive Mio-Pliocene adaptive radiations of elephants. The first radiation of elephants, in the interval 9.0–7.0 Ma, included *Stegotetrabelodon*, *Primelephas*, and archaic loxodonts, and was followed in the early to mid-Pliocene by a cohort of more progressive species of *Loxodonta* and the first appearance of unequivocal *Mammuthus* and *Elephas* (Maglio, 1973; Sanders, 2004; *contra* Tassy, 2003). These last three genera endured to the Recent as the main, crown lineages of Elephantidae (Maglio, 1973; Todd and Roth, 1996).

At the heart of the rise of elephants was a reconfiguration of craniodental anatomy, correlated with a shift from the grinding-shearing mastication of gomphotheres to a dedicated fore-aft power-shearing translation of the jaws during feeding (Maglio, 1972, 1973) and an emphasis on grazing (Cerling et al., 1999). Anatomical changes included re-organization of molar loph(id)s into transverse lamellae (plates), forward displacement of temporalis muscles, and elevation of parietals and occipitals (Maglio, 1972, 1973; Coppens et al., 1978). The efficiency of this power-shearing adaptation was subsequently improved by loss of lower tusks, anterior shortening of the mandible, increased number of plates and lamellar frequency, enhanced hypsodonty, greater complexity of enamel folding, increased cranial elevation, and delayed serial appearance of molars, all or nearly all of which occurred independently in multiple lineages of elephants (Sikes, 1967; Aguirre, 1969; Maglio, 1973; Froehlich and Kalb, 1995; Todd and Roth, 1996).

Subfamily STEGOTETRABELODONTINAE Aguirre, 1969

Stegotetrabelodonts originated in Afro-Arabia during the late Miocene, and are primarily known from that region. These primitive elephants retained long mandibular symphyses and impressive, projecting lower tusks. In addition, their molars exhibit a host of plesiomorphic features, including strong median longitudinal molar sulci, or clefts; few, low-crowned lamellae, each formed of a small number of conelets; thick, unfolded enamel; and prominent posterior accessory central conules, often throughout the extent of the crown (Maglio, 1973; Coppens et al., 1978). However, their molars also possess traits common to elephant cheek teeth, such as true plates, loss of trefoil wear patterns, and obliteration of longitudinal sulci by the formation of complete transverse enamel loops in moderate occlusal wear. As well, stegotetrabelodontine crania evidently had a raised, anteroposteriorly compressed skull profile typical of more advanced elephants (Maglio, 1973; see also Tassy, 1999: figure 18.1; *contra* Maglio, 1972).

Despite the low-crowned condition of their molars, stegotetrabelodontines were grazers, a preference shared with other early elephants (Cerling et al., 1999, 2003). This behavior is linked with a late Miocene worldwide pattern of increased seasonality and aridity (Pagani et al., 1999) and widespread expansion of C_4 ecosystems (Cerling et al., 1993). Domination of open grasslands at the expense of heterogenous environments, however, appears to have been more of a Pliocene phenomenon in Africa (Cerling et al., 1993, Kingston et al., 1994), synchronous with further alterations to the elephant masticatory system beyond that of the first radiation of the family.

Often portrayed as broadly ancestral to elephantine elephants as a whole (e.g., Maglio, 1973; Coppens et al., 1978; Beden, 1983), it is alternatively possible that the phylogenetic role of stegotetrabelodontines was limited to being part of an early, side branching of elephants which also included *Primelephas* and *Stegodibelodon* (Tassy and Debruyne, 2001; Sanders, 2004).

Genus *STEGOTETRABELODON* Petrocchi, 1941
STEGOTETRABELODON SYRTICUS Petrocchi, 1941
Figures 15.17C–15.17E

Partial Synonymy *Stegotetrabelodon lybicus*, Petrocchi, 1943, 1954; *Stegolophodon sahabianus*, Petrocchi, 1943, 1954; *Stegodon syrticus*, Petrocchi, 1954; *Stegotetrabelodon lybicus*, Maglio, 1973; *Stegolophodon sahabianus*, Gaziry, 1982; *Stegotetrabelodon lybicus*, Gaziry, 1982, 1987b; *Stegotetrabelodon syrticus*, Tassy, 1995; *Stegotetrabelodon syrticus*, Sanders, 2008b.

Age and Occurrence Latest Miocene or earliest Pliocene, northern Africa (table 15.6).

Diagnosis Based in part on Maglio (1973). Large elephant with long, straight upper and lower tusks (length reaches over 2,000 mm for both; i2 projecting length >50% of jaw length) that are relatively slender; lower tusks closely appressed to one another; mandibular symphysis elongate and downturned; median longitudinal sulci divide molars; prominent posterior accessory conules may extend nearly throughout the extent of crowns (figures 15.17C, 15.17D).

Description The lone recovered cranium of *S. syrticus* is heavily damaged dorsally, but its preserved morphology suggests an elephantine-like configuration (figure 15.17C; Petrocchi, 1954; Maglio, 1973; Coppens et al., 1978). Upper tusks are rounded in cross section, and lower tusks have ovoid cross sections that are higher than wide. Both lack enamel.

Third and fourth permanent premolars were retained (Gaziry, 1987b), and the dental formula is 1-0-2-3/1-0-2-3 for upper and lower tooth quadrants, respectively, likely preceded by three deciduous premolars in each. Molars are low-crowned, and organized into rows of lamellae, or plates, each composed of a small number of conelets (four–six). Enamel is thick and unfolded, and plates are coated with cementum. Plate formulae dp4 = x4x; m1 = x4x; m3 = x7x; P4 = x2x; M2 = x5–x5x; M3 = x6x.

Lamellar frequency is low (m3 = 2.7; M3 = 3.0). Although unworn molar crowns are longitudinally divided by median clefts and superficially resemble molars of gomphotheriids, with moderate wear plates occlusally form complete transverse enamel loops. In lateral view, plates are pyramidal in shape, and transverse valleys are correspondingly V-shaped (figure 15.17E).

STEGOTETRABELODON ORBUS Maglio, 1970
Figure 15.17F

Partial Synonymy *Primelephas gomphotheroides* (in part), Coppens et al., 1978; cf. *Primelephas gomphotheroides*, Tassy, 1986; Elephantidae gen. et sp. indet. (in part), Tassy, 2003; Elephantidae gen. et sp. incertae sedis A (in part), Tassy, 2003; *Elephas nawataensis* (in part), Tassy, 2003: figure 8.8, plate 4; *Elephas* cf. *E. ekorensis* (in part), Tassy, 2003: figure 8.8, plate 5; Elephantidae gen. and sp. indet., Tassy, 2003: figure 8.5, plates 4–5; Elephantidae gen. et sp. indet., Saegusa and Hlusko, 2007.

Age and Occurrence Late Miocene–early Pliocene, eastern Africa (table 15.6).

Diagnosis Based in part on Maglio (1970b, 1973); Maglio and Ricca (1977); Coppens et al. (1978). Smaller than *S. syrticus*, with less massive mandible; lower tusk length ≤1,000 mm and projecting length less than 50% of overall jaw size; M3 with posterior central accessory conules usually limited to first two plates (figure 15.17F); crown height low but slightly greater than in *S. syrticus* (figure 15.17E, G).

Description The cranium is unknown for this species. Lower tusks relatively slender (KNM-LT 354 L = 1000 mm; H = 70 mm; W = 58 mm), closely parallel to one another, and strongly downturned in their alveoli. Mandibular symphysis extensive, with surprisingly thin alveolar bone for support of such elongate i2s.

Inferred presence of second-fourth deciduous premolars and upper and lower third and fourth premolars; the adult dental formula is 1-0-2-3/1-0-2-3. Plate formulae: dp3 = x3x; p3 = x3x; p4 = x3x; m2 = 5x-x6; m3 = x7x; dP2 = 3x; dP3 = x3x; P4 = x2x; M2 = x5x; M3 = x6x. Molar morphology similar to that in *S. syrticus*, with thick enamel (5.0–8.0 mm in third molars), low hypsodonty indices (66–71) and lamellar frequency (2.75–3.0), and median clefts in unworn crowns.

Remarks Proposed incorporation of *S. orbus* into *S. syrticus* (Gaziry, 1987b) merits consideration, since morphological differences between the species are slight and tusk size distinctions may be ontogenetic. In addition to the type series from Libya, fossils from Abu Dhabi have also been added to *S. syrticus*, including a partial skeleton with a cranium, mandible, and tusks, and a modest sample of molars (Andrews, 1999; Tassy, 1999). The cranium exhibits typical elephant features (see Tassy, 1999: figure 18.1), and the upper and lower tusks are elongate and relatively thin (I2 L = 1,020 mm; i2 projecting length = 530 mm; Tassy, 1999). The m3, however, has eight massive, low plates formed of three to four conelets each, with anterior and posterior pretrite accessory central conules closely appressed to several of them, suggesting that the Abu Dhabi elephant belongs to a different species (Sanders, 2004). An isolated lower molar (?m2) from Jebel Barakah, Abu Dhabi, was allocated by Madden et al. (1982) to *Stegotetrabelodon grandincisivus*, and later was placed by Tassy (1999) in Elephantoidea indet. ?"*Mastodon*" *grandincisivus*. The taxon "*grandincisivus*" appears to be an amebelodont (Tassy, 1985, 1986, 1999); however, the occlusal morphology of the Jebel Barakah specimen exhibits no amebelodont features, and likely does not belong to this taxon. Contrary to Tassy's (1999) assertion, the Jebel Barakah molar does possess features in common with the stegotetrabelodont documented by other specimens at Jebel Barakah and at Shuwaihat: it is very brachyodont, lophids are composed of few conelets (four), a median longitudinal sulcus is persistent with wear, cementum coats the plates and partially fills the transverse valleys, and posterior accessory central conules were apparently present throughout the pretrite side of the crown (see Tassy, 1999: figure 18.15).

A stegotetrabelodont (not *Primelephas*, *contra* Coppens et al., 1978; Beden, 1985; Pickford, 1987a) is present in the heterogeneous elephant assemblage from Kanam, Kenya (MacInnnes, 1942; Maglio, 1973), evidenced by molars (M 15409, 15410, 15411) with low lamellar frequencies, wide plates, small number of robust conelets, presence of accessory conules nearly throughout m3, and persistence of median clefts. M3s in this sample have seven plates. A stegotetrabelodont is also present in the Oluka Fm. of the Western Rift, Uganda (Tassy, 1995), with eight plates in m3. This elephant apparently succeeded locally a more primitive species of *Stegotetrabelodon* from the Kakara Fm. (Tassy, 1995). While an isolated m2 (KNM-NK 42396) from Lemudong'o, Kenya, has been described as belonging to a new, indeterminate genus and species of elephant (Saegusa and Hlusko, 2007), one of us (W.J.S.) does not think the evidence is sufficient to warrant a new taxon and prefers to place the specimen in *Stegotetrabelodon* for now. It has a plate formula of 5x, pyramidal plate shape in lateral view, and posterior accessory conules throughout the crown, all features found in *Stegotetrabelodon*; the value of features such as uniformity of width of the crown and appression of conules on plates for diagnosing a new taxon may be overstated. Similarly, Tassy (2003:346) has assigned a small number of gnathic and dental remains from the Lower and Upper Nawata Fm. at Lothagam, Kenya to "Elephantidae gen. and sp. indet.," but their morphological departure from the type seems acceptable for a normally variable, dimorphic species, and they should be retained in *S. orbus*.

Deriving crown elephant genera (*Loxodonta, Elephas*, and *Mammuthus*) from this primitive subfamily requires a reversal to the dental morphology of gomphotheres, which have free anterior as well as posterior accessory conules associated with their loph(id)s. These are present to some degree in early species of each crown genus, but not in stegotetrabelodonts and other primitive elephant taxa. In nearly all other ways, however, *Stegotetrabelodon* is sufficiently primitive to represent a good model for the ancestral elephant (Coppens et al., 1978).

Subfamily ELEPHANTINAE Gray, 1821

More advanced elephants lacking lower tusks and appreciable median sulci, and with less prominent mandibular symphyses than in stegotetrabelodonts. Minimum number of third molar plates is seven (Kalb and Mebrate, 1993; Kalb et al., 1996a). Tendency for molar crowns to become hypsodont, enamel thinner and folded, plates more closely spaced and numerous, and for accessory conules to become incorporated into plates, except in the earliest forms. Trends in these features are strongly directional over time and occurred independently within the main elephantine lineages (Maglio, 1973).

This subfamily had its origins in Africa in the late Miocene, contemporaneous with stegotetrabelodonts, and includes the last extant representatives of the Proboscidea. As pointed out by Maglio (1973), the rapid evolution and wide geographic distribution of elephantine species make them particularly valuable for biochronological correlation and the study of evolutionary phenomena.

Genus *PRIMELEPHAS* Maglio, 1970
PRIMELEPHAS KOROTORENSIS (Coppens, 1965)
Figures 15.17H–15.17J, 15.18A, and 15.18B

Partial Synonymy *Stegodon korotorensis*, Coppens, 1965:343; *Stegodon kaisensis* Coppens, 1967:I, figure 2; *Mammuthus* (*Archidiskodon*) *subplanifrons* (in part), Cooke and Coryndon, 1970:123; *Primelephas gomphotheroides*, Maglio, 1970b:10; *Primelephas korotorensis*, Maglio, 1970b:12, and Maglio, 1973:22; *Stegotrabelodon orbus*, Kalb and Mebrate, 1993:40–44; cf. *Stegodibelodon schneideri*, Kalb and Mebrate, 1993:44–46; *Mammuthus subplanifrons* (in part), Kalb and Mebrate, 1993:59–63; *Elephas nawataensis* (in part), Tassy, 2003:343–345: figure 8.8, plates 1–3; *Primelephas korotorensis*, Mackaye et al., 2008:227.

Age and Occurrence Late Miocene-early Pliocene, East and Central Africa (table 15.6).

Diagnosis Monospecific genus. Distinguished from other elephants by extreme brachyodonty and from contemporaneous elephant species by narrowness of cheek teeth (East African sample; figures 15.18A, 15.18B) third molar mean W < 100 mm). Differs from *Stegotetrabelodon* by absence of lower tusks and superficial expression or absence of median sulci in molar crowns, less robust molar crown features, and restriction of accessory central conules to the anterior end of the crown in m3. In occlusal view, plates usually more rectilinear than the convex-convex plates of *Stegodibelodon*.

Description Based on Maglio (1970b, 1973); Maglio and Ricca (1977); Coppens et al. (1978); Tassy (1986, 1995, 2003); Sanders (1997, 2004); Haile-Selassie (2001). A partial cranium from the Oluka Fm. of the Western Rift, Uganda, has a convex forehead with small concavities at the lateral corners, weakly divergent, narrow tusk alveoli (W = 80 mm), a large and bulging nasal process of the premaxillary, and massive zygomatic process of the frontal. In addition, the face is anteroposteriorly short, the orbits are situated above the anterior end of the M1s, and the basicranium is semivertical and raised well above the height of the palate (see Tassy, 1995: figure 4, plate III). In lateral profile, the cranium is rounded and the forehead appears convex.

Adult dental formula 1-0-2-3/0-0-2-3; deciduous formula 1-0-3/0-0-3. Mandibular symphysis a distinct, projecting "spout" with no incisor alveoli (figure 15.17H). Molars very low crowned (third molar HI < 70) and composed of few plates. Plate formulae: dp2 = x3x; dp3 = x4x; dp4 = x5 to 6x; p3 = x3; p4 = x3x; m1 = x5x; m2 = x6x; m3 = 7x to 8x; dP2 = x3x; dP3 = x4x; dP4 = x5x; P4 = x3x; M1 = x5x; M2 = x5x; M3 = x7x. Accessory central conules only on the posterior side of plates. Enamel thick, unfolded. Cementum coats plates to apices, but does not completely fill the transverse valleys. In lateral view, plates are pyramidal in shape and widely spaced by V-shaped transverse valleys (figure 15.17J). In occlusal view, plates are usually transversely rectilinear or anteriorly convex (figure 15.17I). Molar plates typically superficially subdivided into four-eight apical digitations. The East African sample of this species has relatively narrow molars; width of third molars is usually < 100 mm (figures 15.18A, 15.18B). Mackaye et al. (2008) state that the new molars from Chad assigned to *Primelephas* generally fit metrically with the East African sample; however, they range to greater width (figures 15.18A, 15.18B).

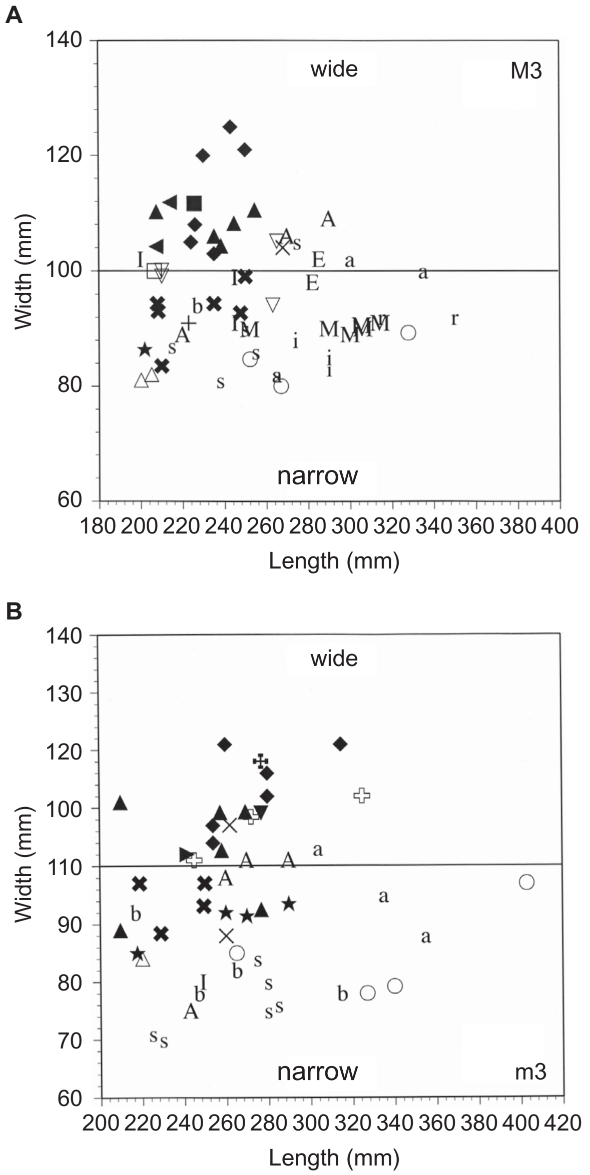

FIGURE 15.18 Bivariate plots of M3 (A) and m3 (B) crown length versus width in African tetralophodonts, stegodonts and elephants. Comparative dimensions supplementing original measurements are from Scott (1907), MacInnes (1942), Petrocchi (1954), Coppens (1965, 1972), Arambourg (1970), Maglio (1973), Beden (1983, 1987a), Harris et al. (1988a, 2003), Kalb and Mebrate (1993), Tassy, (1995, 1999), Sanders (1997, 2007), Haile-Selassie (2001), Tsujikawa (2005b), and Mackaye et al. (2008).

SYMBOLS: closed square, *Tetralophodon* sp. nov.; open square, *Stegodon kaisensis*; closed diamond, *Stegotetrabelodon syrticus*; closed triangle, *S. orbus*; inverted closed triangle, *Stegotetrabelodon* sp., Abu Dhabi; right-facing closed triangle, *Stegotetrabelodon* sp., Kanam; left-facing closed triangle, *Stegotetrabelodon* sp., Nyabusosi, Western Rift; heavy X, *Primelephas korotorensis*; light X, *P. korotorensis*, Toros Menalla, Chad; cross, *Stegodibelodon schneideri*; inverted open triangle, *Loxodonta adaurora adaurora*; open triangle, *L. adaurora kararae*; star, *L. cookei*; +, *L. exoptata*; open circle, *L. atlantica*; open cross, *Mammuthus subplanifrons*; A, *M. africanavus*; M, *M. meridionalis*; E, *Elephas ekorensis*; b, *Elephas recki brumpti*; s, *E. recki shungurensis*; a, *E. recki atavus*; i, *E. recki ileretensis*; r, *E. recki recki*; I, *Elephas iolensis*.

Remarks Originally erected as a temporal and morphological intermediate between *Stegotetrabelodon* and elephantine elephants, the taxonomic homogeneity and legitimacy of the taxon have been questioned (Coppens et al., 1978; Beden, 1979, 1983, 1985). Recent addition of considerable new material to the original hypodigm (Mebrate, 1983; Tassy, 1986, 1995, 2003; Kalb and Mebrate, 1993; Sanders, 1996, 1997; Brunet et al., 2000; Haile-Selassie, 2000, 2001; WoldeGabriel et al., 2001; Mackaye et al., 2008) and comprehensive restudy of *Primelephas* (Mundinger and Sanders, 2001; Sanders, 2004), however, have more clearly delineated the taxon and confirmed its validity. Supposed tusk sockets on symphyseal fragment KNM-LT 358 (Maglio, 1970b; Maglio and Ricca, 1977) articulate with KNM-LT 378 to form closed anterior chambers of the mandibular canal (Mundinger and Sanders, 2001; Sanders, 2004). A mandible from the Middle Awash with a projecting symphyseal "spout" and no incisor alveoli (figure 15.17H), a juvenile mandible with a similar symphysis (the type of "*Elephas nawataensis*"; Tassy, 2003), and mandibles from Toros Menalla, Chad (Mackaye et al., 2008) demonstrate the absence of lower tusks in *Primelephas*. The molars of the juvenile mandible differ from other early *Elephas* taxa (e.g., *E. ekorensis, E. recki brumpti*) but closely match molars of *Primelephas* in having posterior but not anterior accessory central conules, and in overall plate construction. In addition, no features were provided to differentiate it from other elephant species in the publication that formally named "*E. nawataensis*" (Tassy, 2003). There is no compelling reason to accept this as a new species. Conversely, an m3 from Lukeino (KNM-LU 7597) with nine plates that was originally placed in *Primelephas* (Tassy, 1986) does not belong in this genus and may be an archaic mammoth (see later discussion).

Maglio (1970b) originally named two species of *Primelephas*, *P. gomphotheroides*, and *P. korotorensis*, the latter based on two distal molar fragments from Koulà and Kolinga, Chad that were originally placed in *Stegodon* by Coppens (1965, 1967). Sanders (1997), Mundinger and Sanders (2001), and Sanders (2004) suggested that *Primelephas korotorensis* should be subsumed into *P. gomphotheroides* as the supposed greater molar hypsodonty of the former is an artefact of measurements taken only on the narrow distal heel of molars—there is no proportional difference between the molars of these species. Mackaye et al. (2008) recently agreed with this assessment and pointed out that in this case, *P. korotorensis* has priority, since Coppens named *(Stegodon) korotorensis* in 1965, well before Maglio's (1970b) erection of *P. gomphotheroides*. Unfortunately, this means that the type reverts to a broken distal molar from Koulà, Chad, rather than the more complete, associated dentition from Lothagam, Kenya, selected as the original type by Maglio (1970b).

Chronostratigraphic refinements at Lothagam, Kenya (Feibel, 2003; McDougall and Feibel, 2003) show that *Primelepha*s was contemporaneous with *Stegotetrabelodon* (table 15.6; Tassy, 2003; Sanders, 2004). With new evidence of *Loxodonta* from similar-aged deposits (see later discussion; Tassy, 1995, 2003; Vignaud et al., 2002; Sanders, 2004), it is apparent that *Primelephas* was part of an initial evolutionary radiation of elephants in the late Miocene. Alternately posited as centrally positioned phylogenetically vis-à-vis other elephantines (Todd and Roth, 1996), or as the sister taxon to a more restricted clade of *Elephas* + *Mammuthus* (Beden, 1983; Tassy, 1995), it is more likely that *Primelephas* was part of an early, side branching of elephants separate from the origination of Recent elephant genera (Tassy and Debruyne, 2001; Sanders, 2004).

Genus *STEGODIBELODON* Coppens, 1972
STEGODIBELODON SCHNEIDERI Coppens, 1972

Partial Synonymy *Loxodonta schneideri,* Beden, 1983, 1985; *Selenetherium kolleensis*, Mackaye et al., 2005.

Age and Occurrence Early Pliocene, Central Africa (table 15.6).

Diagnosis Based in part on Coppens (1972); Sanders (2004); Mackaye et al. (2005). Differs from *Stegotetrabelodon* in absence of lower tusks, shorter symphysis, thinner enamel, higher molar plates, and virtual absence of median sulci. Similar to *Primelephas* in mandibular and dental morphology, but has wider molars and apparently higher-crowned M3s. Distinguished from other elephantine elephants in the length of its mandibular symphysis, low number of plates, enamel thickness (5.0–8.0 mm), and low lamellar frequency (2.1–3.0) in M3/m3.

Description Coppens (1972); Mackaye et al. (2005). Plate formulae: m3 = x7x; M3 = x7x. Poorly known from dental, mandibular, and a small number of postcranial remains, including new specimens from Kollé, Chad. Molars are large, wide, and moderately low crowned (M3 HI = 79). Enamel is thick and unfolded. Plates are well spaced, and pyramidal in lateral view; transverse valleys are correspondingly V shaped and well coated with cementum. In occlusal view, plates of m3 are anteriorly convex, and it is not possible to ascertain if there were accessory central conules present at earlier stages of wear. Upper tusks are large and slightly curved.

Remarks Originally placed in Stegotetrabelodontinae because of the elongation of its symphysis, compared with those of extant elephants (Coppens, 1972). Although exclusion of *Stegodibelodon* from the Elephantinae persists uncritically in the literature (e.g., Kalb et al., 1996b; Shoshani, 1996; Tassy and Shoshani, 1996; Shoshani and Tassy, 2005), there is no reason to continue this arrangement. The lack of lower tusks and reduction of median sulci are synapomorphies of Elephantinae.

In the absence of any other evidence to mark its presence, a mandible lacking teeth from the Middle Awash, Ethiopia, with symphyseal morphology identical to that of the *Stegodibelodon* mandible from Menalla, Chad (Kalb and Mebrate, 1993), is more reasonably attributed to *Primelephas*, which is common there. New specimens from Kollé, Chad, including third molars with *more* than six plates, *contra* Mackaye et al. (2005), are indistinguishable from the modest original *Stegodibelodon* sample, and thus do not warrant erection of a new species. As more becomes known about its overall anatomy, it is possible that *Stegodibelodon* will be recognized as a larger congener of *Primelephas*. Contrary to Beden (1983, 1985), there are no features of the occlusal morphology of *S. schneideri* that would support its placement as a basal member of the *Loxodonta* clade.

Genus *LOXODONTA* Cuvier, 1825
(anonymous emendation, 1827)

The phylogeny of *Loxodonta* includes the living African elephants and extends back to the late Miocene (table 15.6). Isolated molars from Toros Menalla, Chad (Vignaud et al., 2002) and the Lukeino Fm., Tugen Hills, Kenya (including KNM-LU 916) constitute the earliest evidence of the genus: these teeth have as few as eight plates in m3, are low crowned with thick enamel and low lamellar frequencies, and exhibit propeller- or lozenge-shaped enamel wear figures distinctive of the genus.

Compared with *Elephas* and *Mammuthus*, loxodont elephants are morphologically and geographically conservative, with a wholly African evolutionary history (Coppens et al., 1978). For the greater part of the Pleistocene, however, they were supplanted in the eastern part of the continent by

Elephas recki and apparently retreated to northern and southern refugia, and possibly to West–Central African forests. Although Mio-Pliocene species were grazers or mixed feeders with a high proportion of C_4 plants in their diet, in the middle Pleistocene *Loxodonta africana* emerged from exile as a preferential browser (Koch et al., 1995; Cerling et al., 1999, 2003; Zazzo et al., 2000; Harris et al., 2003; Schoeninger et al., 2003; Kingston and Harrison, 2007).

Among the distinctive features shared by most members of the genus, including archaic species, are a globular cranium with a biconvex vault, unexpanded parietals, and distally divergent tusk alveoli; mandibles with long, straight corpora, prominent symphyses, and strongly convex and anteroventrally canted condyles; and "lozenge"-shaped enamel molar occlusal wear figures, incorporating anterior and posterior central accessory conules that are usually present throughout molar crowns (Maglio, 1973; Beden, 1983).

There has been some debate about the relationship of *Loxodonta* to other elephant genera, though morphology based cladistic analyses usually position *Loxodonta* as the sister taxon to an *Elephas-Mammuthus* clade (e.g., Kalb and Mebrate, 1993; Shoshani, 1996; Tassy, 1996c; Shoshani et al., 1998). These results were criticized by Thomas et al. (2000), who felt that features linking *Elephas* and *Mammuthus* are homoplasic. More recent cladistic analyses relying largely on craniodental characters of basal members of elephant genera (Mundinger and Sanders, 2001; Sanders, 2004), however, support the traditional view. Mitochondrial DNA sequence analysis, using the American mastodon as an outgroup, concluded that *Loxodonta* is the sister taxon to *Elephas* + *Mammuthus* (Rohland et al., 2007), a result supported by other analyses (e.g., Yang et al., 1996; Ozawa et al., 1997; Krause et al., 2005; Rogaev et al., 2006), but some genetic studies are contradictory, alternatively finding evidence for a *Loxodonta-Mammuthus* clade (Hagelberg et al., 1994; Noro et al., 1998; Barriel et al., 1999; Thomas et al., 2000; Thomas and Lister, 2001; Debruyne et al., 2003). The phylogenetic connection of *Loxodonta* to archaic elephants remains unresolved: while molars of the earliest loxodonts retain the anterior and posterior accessory conules of the gomphothere "trefoil" throughout their crowns, the molars of *Stegotetrabelodon, Primelephas, and Stegodibelodon* lack anterior accessory conules, and therefore in this feature seem unsuitable for the ancestry of these crown elephants (Sanders, 2004).

LOXODONTA ADAURORA Maglio, 1970

Figures 15.17K–15.17O, 15.17S, 15.17T, 15.17Z, and 15.17BB

Partial Synonymy *Archidiskodon planifrons nyanzae* (in part), MacInnes, 1942; *Archidiskodon* cf. *meridionalis*, MacInnes, 1942; *Elephas* cf. *planifrons*, Arambourg, 1947; *Loxodonta* cf. *africanava* (in part), Cooke and Coryndon, 1970: plate I, figures D, E; *Loxodonta exoptata*, Kalb and Mebrate, 1993: figure 30.

Age and Occurrence Early–late Pliocene, eastern and southern Africa (table 15.6).

Diagnosis Based in part on Maglio (1970b); Maglio and Ricca (1977); Beden (1983); Harris et al. (2003). Cranium similar to that of *Loxodonta africana* but with a longer frontal, broader forehead, more elongate prenasal region, more flaring tusk alveoli, and prominent frontoparietal ridges lateral to the narial opening (figures 15.17K, 15.17L, 15.17S, 15.17T). As in modern African elephants but differing from *Elephas* spp., the occipital condyles are located below the level of the glenoid fossa. Mandible also similar to the lower jaw of the extant African elephant, except for a more prominent symphyseal "beak" and broader corpus to accommodate wide molars (figure 15.17O). Molars mesodont to slightly hypsodont, with unfolded or coarsely undulating enamel, and modest number of well spaced plates. Anterior and posterior accessory central conules present throughout molar crowns and incorporated into enamel loops with wear, but do not form prominent median loxodont sinuses ("lozenges"; figures 15.17M, 15.17N); lateral arms of plates may remain anteroposteriorly compressed well into occlusal wear (Tassy, 2003). Posterior accessory conules may be doubled, and crowns may sport marginal accessory conules as well (Kalb and Mebrate, 1993).

Molars more massive than in *Elephas ekorensis* and *L. exoptata*, and with less developed median sinuses than in the latter.

Description *Loxodonta adaurora* resembles *L. africana* in cranial morphology in its convex frontoparietal surface, unexpanded parietals and occipital region, and slight temporal constriction. As in the extant species, the cranium of *L. adaurora* is only slightly compressed anteroposteriorly, and in lateral view has a more rounded profile than in either *Elephas* or *Mammuthus* (figures 15.17L, 15.17Z, 15.17BB; Maglio, 1970b). The nasal aperature is exceptionally large, the occipital condyles are posteriorly prominent, and the incisor alveoli are widely separated and flare distally. The alveoli held massive upper tusks that curved gently upward with no longitudinal torque (Maglio, 1973).

There are no lower tusks or vestigial incisor cavities in the mandible (*contra* Maglio, 1970b, 1973; Beden, 1983). Rather, these cavities form the antechambers of the mandibular canal for nerve plexuses and arteries that supplied the face. The symphyseal gutter is narrow and very deep. The ramus is tall, with a narrow neck, transversely elongated condyle, and coronoid process that leans outward and exhibits a capacious masseteric fossa (Beden, 1983). These features are typical of modern African elephants.

Molars are broadest basally, with crown height slightly less than width (Beden, 1983). In lateral view, plates are subparallel to one another and separated by U-shaped valleys that may be filled with cementum. In the third molars, lamellar frequency ranges from 3.2 to 5.0, and enamel thickness varies from 2.8 to 4.5 mm (Beden, 1983). Plates are comprised of five to six conelets (five to eight in advanced forms), and taper laterally and anteroposteriorly toward the apex. The adult dental formula appears to have been 1-0-0-3/0-0-0-3, with three deciduous precursors in each quadrant of the upper and lower jaws. No permanent premolars are known for *L. adaurora*.

Plate formulae: (*L. adaurora adaurora*) dp2 = 4x; dm3 = 6x; m1 = 6–7; m3 = x10x; dP2 = 3x; dP4 = x8x; M2 = x6x; M3 = x9x–10x; (*L. adaurora kararae*) m3 = 11–12; M2 = x9x; M3 = x10x.

The species is well represented by a nearly complete skeleton from Kanapoi (Maglio, 1973), which anatomically resembles the postcranium of the modern African elephant and is distinct from that of *Elephas* spp. (Maglio and Ricca, 1977). There are at least 18 thoracic, 3 or 4 lumbar, and 4 sacral vertebrae; the long bones exhibit numerous graviportal adaptations and indicate an animal of very large size (femur L = 136.5 cm; humerus L = 116.2 cm); manus and pes elements are especially *Loxodonta africana*–like, except for being larger and more robust (Maglio and Ricca; 1977).

Remarks While skull morphology links *Loxodonta adaurora* with other loxodont elephants (Maglio, 1970b, 1973; Beden, 1983), it is an atypical member of the genus because its enamel wear figures do not develop strong median sinuses (Tassy, 2003). For this reason, it is unlikely that this species was part of the main loxodont lineage leading to *L. africana*.

Beden (1983) divided the species into early to mid-Pliocene *L. adaurora adaurora*, and late Pliocene *L. a. kararae*, based on slight differences in enamel thickness, number of plates in m3, and lamellar frequency. Compared with *L. a. adaurora*, in *L. a. kararae* the cranium also has a shorter premaxillary, orbits that protrude less laterally, and zygomatic arches that are taller and less massive (Beden, 1983). An M2 from the Matabaietu Fm., Middle Awash, Ethiopia attributed to *L. exoptata* (L77-1; Kalb and Mebrate, 1993: figure 30) appears instead to belong to *L. a. kararae*, based on its number of plates (eight), twinned accessory conules, degree of enamel folding, enamel thickness (ET = 2.0–4.0 mm), and moderate plate spacing (LF = 5.0), in addition to its lack of prominent loxodont sinuses.

These elephants appear to have existed in a mosaic of closed woodlands to open savannas (Harris et al., 2003; Schoeninger et al., 2003), with morphological transformation of their craniodental features during the late Pliocene perhaps a response to increase of open habitats and grazing competition due to cooler, drier climates (Behrensmeyer et al., 1997; Alemseged, 2003). No longer included in *L. adaurora* are specimens returned to *Loxodonta exoptata* (Beden, 1987b; Sanders, 2005, in press), particularly the fossil sample from Laetoli, Tanzania. These specimens were once partitioned among *L. adaurora* and *Elephas recki* (Maglio, 1969b, 1973; Coppens et al., 1978), but the molar variation that led to this division is an artifact of differences in the contribution of accessory conules to occlusal plate shapes at successive wear stages (see later discussion).

LOXODONTA COOKEI Sanders, 2007
Figures 15.17P and 15.17Q

Partial Synonymy *Mammuthus subplanifrons*, Hendey, 1976, 1981; Elephantinae indet., cf. *Loxodonta*, Tassy, 1986; *Loxodonta* sp. "Lukeino stage," Tassy, 1995; *Loxodonta* sp. nov., Sanders, 2006.

Age and Occurrence Late Miocene-early Pliocene, southern and eastern Africa (table 15.6).

Diagnosis Sanders (2007). Primitive loxodont with permanent third and fourth premolars. Distinguished from *L. adaurora*, *L. exoptata*, *L. atlantica*, and *L. africana* by fewer molar plates, especially in posterior teeth, and lower hypsodonty indices, and from nonloxodont elephants by presence of anterior and posterior accessory conules (figures 15.17P, 15.17Q) and tendency for plates to apically form median sinuses with wear, throughout molar crowns. The only crown elephant species known to retain permanent premolars.

Description Tassy (1995); Sanders (2007). Skull unknown. Morphological details of the entire molar sample are similar: plates are formed of five to eight conelets, converge anteroposteriorly and laterally toward the apex, and are not very closely spaced (m3 LF = 3.4–4.2); crown height is usually less than width (m3 HI = 81–102); transverse valleys are U shaped. In more worn specimens, enamel is thick (m3 ET = 4.1–6.2 mm) and unfolded or coarsely folded, and wear figures form median loxodont sinuses that may touch in the midline. Cementum usually nearly fills transverse valleys. Accessory conules are lower than unworn plates and apically free (figure 15.17Q) and only become incorporated into plates with moderate wear. Deciduous premolars are miniature versions of adult molars, except for dp2s, which are tiny, triangular teeth with three closely appressed plates.

Permanent premolars were in occlusion at the same time as adult molars, without a strong wear gradient between them. In occlusal view, P3 is rounded, of nearly equal length and width, while p3 is more ovoid and longer than wide. Fourth permanent premolars are larger, relatively more elongate, and have better expression of accessory central conules. Cementum is well developed in these teeth.

Plate formulae: dp2 = 3x; dp3 = x4x; dp4 = x6x; p3 = x3x–x4x; p4 = x4x; m1 = x5x; m2 = x7x; m3 = x7x–x8x; DP3 = x4; DP4 = x5x or x6; P3 = x3x–x4; P4 = x4; M1 = 5x–x6; M2 = x5x-x6x; M3 = 7–8.

Remarks This species, best represented at Langebaanweg, South Africa, encompasses late Miocene–early Pliocene specimens that exhibit strong development of anteroposterior median enamel expansions ("loxodont sinuses") and are characterized by mesodont molar crowns with a low number of plates (Sanders, 2006). The morphology of these specimens suggests affinity with a subsequent *L. exoptata*–*L. africana* lineage (see Tassy, 1995). Possibly the oldest representative of *L. cookei* is an m3 reportedly from the Lukeino Fm., Tugen Hills, Kenya (KNM-LU 67; Tassy, 1986). The actual provenance of this specimen is uncertain (M. Leakey, pers. comm.), and its preservation and morphology are a good match for other specimens referable to *L. cookei* from the younger Chemeron Fm.

LOXODONTA EXOPTATA (Dietrich, 1941)

Partial Synonymy *Palaeoloxodon antiquus recki*, Hopwood, 1936; *Archidiskodon exoptatus*, Dietrich, 1941, 1942; *Elephas antiquus recki*, Hopwood in Kent, 1941; *A. subplanifrons*, Cooke, 1960; *E. recki*, Leakey, 1965; *Loxodonta exoptata*, Coppens, 1965; *E. (Archidiskodon) exoptatus*, Arambourg, 1969; *Loxodonta* sp. (in part), Maglio, 1969b; *E. recki* (in part), Maglio, 1969b; *Loxodonta* sp. "C" (in part), Maglio, 1970a; *E. recki* (in part), Maglio, 1970a; *L. adaurora* (in part), Maglio, 1970b; *Mammuthus (Archidiskodon) recki* (in part), Cooke and Coryndon, 1970; *L. adaurora* (in part), Maglio, 1973; *L. adaurora* (in part), Coppens et al., 1978; *L. exoptata*, Beden, 1987b.

Age and Occurrence Early–late Pliocene, eastern Africa (table 15.6).

Diagnosis Based in part on Beden (1987b). Molars with anterior and posterior accessory conules that fuse with enamel wear figures of plates to form loxodont median sinuses the length of the crown when in wear, and slightly hypsodont, with maximum width a little above the base of the tooth. Lateral borders of molar crowns converge toward the apex, and the median part of each plate is highest. Cementum thick and fills the transverse valleys. Higher crowned with thinner enamel, more plates, and greater lamellar frequencies than molars of *L. cookei* and Miocene *Loxodonta*. Molars with narrower plates, stronger median sinus development, and less robustly constructed than in contemporaneous *L. adaurora*.

Description Cranium unknown. Adult dental formula is 1-0-0-3/0-0-0-3, with three deciduous premolars preceding the eruption of adult molars in each dental quadrant; there are no known permanent premolars. Molars with parallel-sided plates and U-shaped transverse valleys. Enamel thickness moderate (m3 = 2.54.0 mm; M3 = 2.0–4.0 mm); lamellar frequency ranges from 4.1 to 5.5 in third molars; and third molar crown height is usually slightly greater than width (HI > 100). Accessory conules are lower than plate conelets, closely appressed to plates, and have their greatest diameter at about the midheight of the crown. For this reason, they may not be apparent and do not contribute to the formation of median sinuses until the crown is well in wear, and disappear with heavy occlusal wear. In the early stages of occlusal wear, plate apices may form "propeller" shapes, with the center of the enamel figure prominent and rounded, and the lateral "arms" more anteroposteriorly compressed (Kalb and Mebrate, 1993; Sanders, 1997).

Plate formulae: dp2 = x3x–x4x; dp3 = x6x; dp4 = 7; m1 = x7x or x8; m2 = 8–9x; m3 = 11–12; DP2 = x3x–x4; DP3 = x5x–6x; DP4 = x6 or x7x; M2 = 8x–9x; M3 = 11–12 (Beden, 1983, 1987b; Harris et al., 2003).

The postcranial sample for the species from the Upper Unit of the Laetolil Beds and the Upper Ndolanya Beds at Laetoli is primarily composed of isolated bones of the manus and pes. These closely resemble comparable elements in the extant African elephant (Beden, 1987b).

Remarks Although this species, best known from the Laetolil and Upper Ndolanya Beds (table 15.6), has a long and complicated taxonomic history (Beden, 1987b) and has been subdivided and subsumed into *Loxodonta adaurora* and *Elephas recki* (Maglio, 1969b, 1973; Coppens et al., 1978), it is clear that its constituent specimens belong to a distinct species of *Loxodonta* that is on or close to the evolutionary lineage of the extant African elephant. Chronostratigraphic refinements and an expanded fossil record indicate that *L. exoptata* is an early–late Pliocene collateral rather than descendant species of *L. adaurora*, with antecedents more likely in earliest Pliocene *L. cookei*.

From the absence at Laetoli of *Elephas recki*, presumed to be an habitué of dry wooded savannas, Beden (1987b) inferred that *Loxodonta exoptata* lived in humid/wet wooded savannas. While contrasting paleoecological reconstructions of Pliocene Laetoli varying from semiarid bushland (Kovarovic et al., 2002) to habitats "dominated by closed woodlands with a substratum of C_4 grasses or open woodland interspersed with grassy patches" (Kingston and Harrison, 2007:299) have not helped to refine this hypothesis, isotopic studies showing that *all* early elephant species were grazers or mixed feeders with a strong dietary preference for C_4 plants (see earlier discussion) contradict the idea that *L. exoptata* was singularly adapted for feeding in such a specialized ecological niche (Kingston and Harrison, 2007).

LOXODONTA ATLANTICA (Pomel, 1879)
Figure 15.17R

Partial Synonymy *Elephas atlanticus*, Pomel, 1879; *E.* (*Loxodon*) *zulu*, Scott, 1907; *Loxodonta zulu*, Osborn, 1942; *E. pomeli* (in part), Arambourg, 1947, 1952:413, figures 7 and 8, plate 1, figure 4; *Loxodonta (Palaeoloxodon) antiquus recki*, Singer and Crawford, 1958; *Loxodonta atlantica*, Cooke, 1960.

Age and Occurrence ?late Pliocene–early Pleistocene eastern and Central Africa; ?early–middle Pleistocene, northern and southern Africa (table 15.6).

Diagnosis Based on Maglio (1973); Coppens et al. (1978). Largest and most advanced loxodont elephants, subdivided into at least two geographically separate subspecies. Enamel wear figures do not include median sinuses as prominent as those in modern African elephants, and enamel may be finely folded or crimped (Scott, 1907; Osborn, 1942). *Loxodonta atlantica atlantica*: median molar plate loops often bifurcated. Irregular, small enamel loops may occur around worn lozenge-shaped molar plate wear figures. Distinguished from other loxodont elephants by greater number of plates, higher crowns, and plicated enamel. *Loxodonta atlantica zulu*: differentiated from *L. a. atlantica* by thinner enamel.

Description The species is best known from northern Africa. The skull of *L. a. atlantica* is morphologically similar to that of *L. africana*, except for exceptionally large occipital condyles and a narrower premaxillary region (Coppens et al., 1978). Molars of this subspecies are among the most derived of all loxodont elephants, with hypsodonty indices exceeding 200, coarsely folded, moderately thick enamel (2.2–3.6 mm in third molars), and more plates per molar than in other species of *Loxodonta*. Plate formulae: m1 = 7–8; m2 = 11–12; m3 = 10–15; M1 = 8–9; M2 = 9–11; M3 = 14 (Maglio, 1973).

Molars of *L. a. zulu*, from southern Africa, have even thinner enamel (2.0–2.8 in third molars) and are also high crowned (range of HI > 200). Plate spacing is similar to that of the northern subspecies (third molar LF = 3.4–5.4). Enamel is folded, and a right m3 described by Scott (1907) has bifurcated accessory conules that are much more prominent posteriorly, as is the case in molars from Elandsfontein, South Africa (Maglio, 1973). Plates may have trifoliate lateral tips and are anteriorly concave and posteriorly convex (unlike the condition in *L. a. atlantica*, in which m3 plates occlusally exhibit narrow median sinuses and are slightly anteriorly and posteriorly convex). The occlusal morphology of *L. a. zulu* recalls that of *Elephas recki*, particularly in the greater expression of the posterior median plate projections. Plate formulas: m1 = 10; m3 = x11x–13x; M2 = 12; M3 = 12 (Scott, 1907; Osborn, 1942; Maglio, 1973).

Remarks Coppens (1965) named a third subspecies of *L. atlantica*, *L. a. angammensis*, based on craniodental material from the early Pleistocene of Chad, to which Beden (1987a) later added molar specimens from the late Pliocene of the Omo, Ethiopia (see figure 15.17R). Morphometrically, the cranial and dental remains of this subspecies are quite similar to those of *L. africana*, and except for some gross enamel folding, exhibit no special similarity to those of *L. atlantica atlantica* or *L. a. zulu*. Plate formulae are less advanced than those of *L. a. atlantica* and *L. a. zulu*: dp3 = 5x; dp4 = x8; DP3 = 5x; M2 = x8x–9; M3 = x12x. Third molar LF = 3.5–5.0 and HI = 154; enamel thickness ranges from 2.3 to 3.1 mm (Coppens, 1965; Beden, 1987a). It is debatable whether this fossil material belongs in *L. atlantica* (Maglio, 1973; Coppens et al., 1978).

Too derived to be considered a lineal precursor of *Loxodonta africana* (Maglio, 1973), *L. atlantica atlantica/zulu* appear to have been grazing specialists whose demise paralleled that of *Elephas recki* at the end of the middle Pleistocene, attributed at least in part to global environmental change (see Klein, 1988). The relationship between the geographically discontinuous subspecies *L. a. atlantica* and *L. a. zulu* requires further exploration.

LOXODONTA AFRICANA (Blumenbach, 1797)
Figures 15.17S and 15.17T

Partial Synonymy *Elephas africana*, Blumenbach, 1797; *E. capensis*, Cuvier, 1798; *Loxodonta africana*, Gray, 1843; *E. (Loxodonta) oxyotis*, Matschie, 1900; *E. africanus capensis*, Lydekker, 1907; *E. a. cyclotis*, Lydekker, 1907; *E. a. oxyotis*, Lydekker, 1907; *E. a. knochenhaueri*, Lydekker, 1907; *Loxodonta africana africana*, Heller and Roosevelt, 1914; *L. prima*, Dart, 1929; *L. africana* var. *obliqua*, Dart, 1929; *L. africana pharaohensis*, Deraniyagala, 1948; ?*L. atlantica angammensis*, Coppens, 1965; ?*L. atlantica angammensis*, Beden, 1987a.

Age and Occurrence Early Pleistocene–present, widespread throughout the central, eastern, and southern regions of sub-Saharan Africa (table 15.6).

Diagnosis Based in part on Maglio (1973). Distinguished from *L. adaurora* by cranium with more reduced premaxillaries and tusks, by higher, narrower molar crowns, and by substantial development of anteroposterior median expansions of molar plate wear figures ("loxodont sinuses"). Greater number of molar plates than in *L. adaurora* and *L. cookei*; intermediate molars with more plates than in *L. exoptata*.

Description Based in part on Osborn (1942); Sikes (1971); Maglio (1973). Cranium is rounded in lateral profile and highly pneumatized, with comparatively widely spaced, distally divergent premaxillae, a biconvex frontoparietal surface, no median parietal depression, and with a nearly vertical occipital region (figures 15.17S, 15.17T). Mandible with a long, relatively slender horizontal corpus and forward-leaning ramus. Condyles are convex and usually wider transversely than anteroposteriorly; masseteric fossae are capacious. *Contra* Maglio (1973), the mandibular canal terminates in an antechamber lateral to the symphysis (see Sikes, 1971: figure 43).

The most distinctive feature of *L. africana* is the formation with wear of enamel figures with strong anteroposteriorly projecting median sinuses (anteriorly ∧ shaped and posteriorly ∨ shaped), throughout the occlusal surface of molars. Plates are moderately well spaced (third molar LF = 4.0–5.0). Molar enamel is without plications and has moderately thick borders. HI > 100, but not as extremely hypsodont as in more derived species of *Elephas* and *Mammuthus*, and lower than in *L. atlantica*.

Molars in each quadrant may be numbered M1–M6 or MI-MVI (e.g., Laws, 1966; Sikes, 1967) but are actually DP2–DP4, M1–M3, with no permanent premolars (Roth, 1992); upper tusks have a small deciduous precursor, and curve gently upward and slightly inward, without longitudinal torque.

Plate formulae: dp2 = 3–5; dp3 = 6–8; dp4 = 8–10; m1 = 7–10; m2 = 9–12; m3 = 10–14; DP2 = x3x–5; DP3 = 6–7; DP4 = 8–10; M1 = 8–9; M2 = 11–12; M3 = 11–13. This is very conservative compared with plate formulae of Recent species of *Elephas* and *Mammuthus*.

The postcranium is that of an immense animal that must bear the heft of considerable daily forage (up to 5%–6% of body weight, along with as much as 50 gallons of water; Sikes, 1971). The neck is short; there are 20–21 strong, compact thoracic vertebrae and only 3–4 short lumbars with massive centra, linking the thorax closely to the pelvis; the scapular glenoid and acetabulum of the innominate face downward; the pelvic ilia flare broadly and are united by a sturdy sacrum of four elements; the feet are pseudoplantigrade with thick pads; the legs are thick and pillarlike; and the long anterior thoracic spinous processes and high pelvic girdle anchor a dorsal vertebral suspensory bridge ("swayback") for support of the substantial viscera (Sikes, 1971).

LOXODONTA CYCLOTIS (Matschie, 1900)

Partial Synonymy *E. cyclotis*, Matschie, 1900; *E. africanus pumilio*, Noack, 1906; *E. a. albertensis*, Lydekker, 1907; *L. cyclotis*, Morrison-Scott, 1947; *L. cyclotis*, Grubb et al., 2000; *L. cyclotis*, Roca et al., 2001.

Age and Occurrence Recent, western half of sub-Saharan Africa up to lake region of the Western Rift Valley.

Diagnosis In comparison with the African bush elephant *L. africana*, the African forest elephant *L. cyclotis* varies to appreciably smaller body size and has paler, more finely wrinkled skin, relatively more slender, straighter tusks, smaller, more rounded ears, a greater number of toenails, a more flattened, relatively broader cranium with more widely separated temporal ridges, shorter, less divergent tusk alveoli, and less arched zygomatics, and a mandible with lower rami and a more prominent, narrow spoutlike symphysis (Lydekker, 1907; Allen, 1936; Morrison-Scott, 1947; Grubb et al., 2000; but see Backhaus, 1958).

Description Except for the differences listed in the diagnosis, African forest elephants are similar morphologically to African bush elephants.

Remarks African elephants are the largest living terrestrial animals, exceeding 6,000 kg and 4 m in shoulder height in some individuals (Laursen and Bekoff, 1978). Once inhabitants of all Africa except the most arid areas of the Sahara, competition with humans and poaching for ivory has severely reduced the distribution of these last proboscideans on the continent, and they are now endangered (Kingdon, 1997). The geographic range of *L. cyclotis* extends from western Africa (Sierra Leone) across the Congo forest belt to the lake region of the Western Rift Valley, and *L. africana* is unevenly dispersed throughout sub-Saharan areas of Central, East, and southern Africa (Allen, 1936; Kingdon, 1997).

Although these species have been considered subspecies with hybrid zones, and study of mitochondrial genes suggested gene flow between forest and savanna populations and incomplete speciation (Eggert et al., 2002; Debruyne, 2005), sequence analysis of nuclear genes in African elephants revealed that their mitochondrial and nuclear genomes have very different evolutionary histories and that there is deep, species-level genetic disparity partitioning the forest and bush forms, interpreted as a consequence of strong reproductive isolation between *L. africana and L. cyclotis*; this supports their separation at the species level (Roca et al., 2001, 2005; Comstock et al., 2002). Dissociation between mitochondrial and nuclear gene patterns in African elephants is evidence of ancient episodes of hybridization between forest females and savanna males, and a long history of backcrossing of female hybrids to savanna males has obliterated the forest nuclear genome in savanna elephant populations (Roca et al., 2005).

Modern African elephants are mixed feeders whose diet is generally dominated by C_3 browse (Cerling et al., 1999); however, this may vary considerably and include heavy reliance on grazing, reflecting local and seasonal availability of foods (Kingdon, 1979; Buss, 1990; Tchamba and Seme, 1993; White et al., 1993; Koch et al., 1995; Cerling et al., 2006; Codron et al., 2006). Forest elephants may consume a greater amount of fruit than their bush cousins, but there is no evidence that they consistently rely on a higher percentage of browse across their range (see Tchamba and Seme, 1993; White et al., 1993). The suggestion that modern elephants may be filling a niche vacated by other browsing ungulates during the Pleistocene (Kingston and Harrison, 2007) is intriguing.

The antiquity of the species is uncertain. Craniodental specimens from the Omo, Ethiopia and Angamma-Yayo, Chad may extend the temporal span of *L. africana* beyond middle Pleistocene East and Central African occurrences (table 15.6) to as early as the late Pliocene–early Pleistocene, or could belong to an ancestral segment of the African elephant lineage, such as *L. cookei* (table 15.6). Originally placed in *L. atlantica angammensis* (Coppens, 1965; Beden, 1987a), these specimens differ from *L. africana* only in subtle features and are not especially like typical middle Pleistocene examples of *L. atlantica* (Maglio, 1973; Coppens et al., 1978). There is no fossil record of forest elephants.

Genus *MAMMUTHUS* Brookes, 1828

Mammuthus encompasses the mammoths, popularly exemplified by the woolly mammoth, *M. primigenius* (Lister and

Bahn, 2007). Following an early to mid-Pliocene African origin, mammoths migrated to Eurasia during the mid-late Pliocene and reached North America by the early Pleistocene (Dudley, 1996; Fisher, 1996; Lister, 1996; Lister and van Essen, 2003), where they thrived until the end of the epoch. In Eurasia and North America, mammoths underwent multiple episodes of speciation and profound evolutionary changes in craniodental anatomy (Lister, 2001; Lister et al., 2005; Lister and Bahn, 2007). Many of these changes paralleled progressive modifications of the skull and molars in *Elephas*, particularly in features correlated with increased hypsodonty and shearing efficiency during mastication, presumably in association with availability of grasslands and adaptation to grazing (Maglio, 1973; Dudley, 1996; Lister and Sher, 2001; but see Koch, 1991; Fisher, 1996). The later species from the Northern Hemisphere were the most derived elephants of all, with more than 25 plates crowded together in third molars whose crown heights exceed twice their width. In addition, these elephants had very raised, extremely foreshortened crania festooned with prodigious, spirally twisted and curved tusks (Maglio, 1973).

Mammoths did not fare as well in Africa, apparently going extinct there before the end of the early Pleistocene (Maglio, 1973). *Mammuthus* skulls are characterized by dorsally expanded parietals and vertically concave, transversely convex frontoparietal surfaces (lacking a midsagittal depression), strong temporal constriction, widely separated orbits, and proximally closely spaced premaxillary sheaths that curve outward distally (Maglio, 1973). Most of these features are also present in crania of early species, which has proven invaluable for positive identification of the genus in Africa.

MAMMUTHUS SUBPLANIFRONS (Osborn, 1928)

Figures 15.17 U and 15.17V

Partial Synonymy *Archidiskodon subplanifrons*, Osborn, 1928; *A. andrewsi*, Dart, 1929; *A. proplanifrons*, Osborn, 1934; *Mammuthus (Archidiskodon) scotti*, Meiring, 1955; *Stegolophodon* sp., Singer and Hooijer, 1958; *Mammuthus (Archidiskodon) subplanifrons*, Cooke and Coryndon, 1970; *Mammuthus subplanifrons*, Maglio and Hendey, 1970; *M. subplanifrons*, Maglio, 1973; *Primelephas gomphotheroides* (in part), Tassy, 1986.

Age and Occurrence Latest Miocene, early Pliocene, eastern and southern Africa (table 15.6).

Diagnosis Large elephant with broad, brachyodont to mesodont molars, low number of thick plates (leading to low LF = 3.2–3.75), moderately thick (ET = 4.0–5.8 mm), unfolded enamel, and accessory conules limited to the posterior side of plates in the mesial half of the crown. There are no loxodont sinuses formed by the enamel loops with wear.

Description Based in part on Maglio and Hendey (1970); Sanders (2006, 2007). The cranium is unknown for this species. The corpus of a mandible (SAM-PQ-L 12723) from Langebaanweg, South Africa, is relatively long and not heavily constructed. The ramus is high and has a more restricted masseteric fossa than in loxodont elephants. Anterior chambers of the mandibular canal open externally via mandibular foramina; these are lateral to where incisive alveoli would be if lower tusks existed, though there are no signs of these. The anterior chambers never contain incisive tooth buds in proboscideans that do have i2s, so there is no reason to speculate that they once contained vestigial tusk buds in *M. subplanifrons* (*contra* Maglio and Hendey, 1970).

A large tusk from Virginia, South Africa, associated with a molar comparable morphometrically with others assigned to *M. subplanifrons*, displays the spiral twisting typical of the genus (Meiring, 1955; Maglio, 1973). An enigmatic isolated upper tusk from Langebaanweg, South Africa (SAM-PQ-L 40430), with a length of >830 mm and cross sectional height of 103 mm near its midpoint, although flattened throughout, also retains a distinct longitudinal torque and curves upward at its distal tip. Longitudinal torque is typical of mammoths but not of the other proboscidean taxa found at Langebaanweg (*Anancus* and *Loxodonta*); however, the tusk is unusual for an elephant in that it also has lateral sulci that run its length. In the absence of crania, tentative reliance must be placed on these tusks to justify allocating this species to *Mammuthus*.

The m3s of the Langebaanweg mandibular specimen are low crowned (HI = 67–69) with nine robustly built plates composed of three to five conelets (figures 15.17U, 15.17V). The anterior and posterior cingulids are prominent. Posterior accessory central conules are limited to the first three plates, and plates are transversely straight with a dominant central conelet. The plates are less pyramidal in cross section than in *Primelephas,* and the transverse valleys are sub–U shaped. Cementum coats the plates but does not fill the transverse valleys. Several specimens from the Middle Awash, Ethiopia (table 15.6) are morphologically similar, but with one less plate in m3, and greater crown height (m3 HI = 76; M3 HI = 89).

An m3 from the Lukeino Fm., Tugen Hills, Kenya that was originally assigned to *P. gomphotheroides* (KNM-LU 7597A; Tassy, 1986) has nine plates and a distinctive dominant central conelet in each plate, typical of early mammoths. Morphometrically, though well worn, this molar resembles specimens in the Langebaanweg + Middle Awash sample of *M. subplanifrons*. Dated between 6.2 and 5.6 Ma (table 15.6), the Lukeino molar may be the oldest known mammoth fossil.

Plate formulae: m3 = x8x–x9x; M2 = x6x; M3 = 8x–9 (Maglio and Hendey, 1970; Kalb and Mebrate, 1993; Haile-Selassie, 2001).

Remarks As traditionally composed, this species is quite heterogeneous morphologically (Maglio, 1973), and likely is a wastebasket taxon. The holotype, a partial m3 from the Vaal River, South Africa (MMK 3920, *"Archidiskodon subplanifrons"*; Osborn, 1928), and molar specimens of other, synonymized taxa from the Vaal River (*"Archidiskodon proplanifrons," "A. andrewsi"*; Dart, 1929; Osborn, 1934; Maglio, 1973) differ in important occlusal details from the Middle Awash + Langebaanweg sample and more closely resemble primitive *Loxodonta* (Sanders, 2006, 2007). At the same time, the Middle Awash + Langebaanweg sample cannot be fit into any other existing proboscidean taxon, and anatomically anticipates at least part of the younger *M. africanavus* hypodigm. For these reasons, the species *M. subplanifrons* is maintained. In the absence of associated crania, however, there is no certainty that this species is a mammoth.

MAMMUTHUS AFRICANAVUS (Arambourg, 1952)

Figures 15.17U–15.17X

Partial Synonymy *Elephas meridionalis*, Pomel, 1895; *E. planifrons*, Deperet and Mayet, 1923; *E. africanavus*, Arambourg, 1952, 1970; *Loxodonta africanava*, Cooke, 1960; *L. africanava*, Coppens, 1965; *Mammuthus africanavus*, Maglio, 1973.

Age and Occurrence Mid- to late Pliocene, northern and Central Africa (table 15.6).

Diagnosis Based in part on Arambourg (1970); Maglio (1973). Primitive species of *Mammuthus* with a low number of third molar plates, occasionally undulating but unfolded, moderately thick enamel, modest plate spacing, and retention in anterior half of molar crowns of accessory central conules. Sides of molars taper strongly toward the apex of the crown (figure 15.17W). Cranium and I2s typical for the genus.

Description Based in part on Arambourg (1970); Maglio (1973); Coppens et al. (1978). The upper tusks are massive in cross section (Garet et Tir specimen, W = 136 mm; H = 140 mm), long (L = +2,310 mm), and recurved upward and inward distally (Arambourg, 1970). An associated cranium is reportedly morphologically similar to that of *M. meridionalis* (Maglio, 1973).

Isolated molars are difficult to distinguish from those of archaic *Elephas*. Accessory conules are retained in the anterior portion of the crown and may be particularly prominent posterior to plates. These do not contribute to loxodont sinuses, however. Plates are formed of five to seven conelets, are parallel to one another in lateral view, and are separated by U-shaped transverse valleys that are abundantly filled with cementum (figure 15.17X). In third molars, lamellar frequency varies from 3.0 to 5.2; enamel thickness ranges from 2.6 to 4.3 mm; and crowns are modestly high, reaching hypsodonty indices of 120 (Maglio, 1973). Plate formulae: dp3 = x6x; dp4 = 6–x7x; m1 = 7–x8x; m2 = 8–9; m3 = 10–13; DP2 = x5; DP3 = 5–6; DP4 = 6; M1 = 6–7; M2 = 8–9; M3 = 9.

Remarks The earliest unambiguous evidence of the genus *Mammuthus* in Africa, the age and morphology of this species are close to those for the oldest European mammoths (*M. rumanus*, dated to ca. 3.5–2.5 Ma; Lister and van Essen, 2003; Lister et al., 2005). If there is a connection between this species and its putative precursor *M. subplanifrons*, it might be evidenced by the similarity of specimens such as m3 1950-1:12 from Lac Ichkeul, Tunisia to m3s from early Pliocene Langebaanweg, South Africa, in restriction of accessory conules to the posterior of the first few plates, and relatively rectilinear, simple plates, though with one more plate (10) and higher crowned (figures 15.17U–15.17X). In addition, mammoth dental specimens from Hadar, Ethiopia, of mid-Pliocene age (White et al., 1984) are reportedly morphometrically intermediate between *M. subplanifrons* and *M. africanavus* (Beden, 1985).

MAMMUTHUS MERIDIONALIS (Nesti, 1825)
Figures 15.17Y and 15.17Z

Partial Synonymy Elephas meridionalis, Nesti, 1825; *E. planifrons*, Doumergue, 1928; *Elephas* aff. *meridionalis*, Arambourg, 1952; *E. moghrebiensis*, Arambourg, 1970; *Mammuthus meridionalis*, Maglio, 1973; "*E. moghrebiensis*" = *E. recki ileretensis*, Geraads and Metz-Muller, 1999.

Age and Occurrence Early Pleistocene, northern Africa (table 15.6).

Diagnosis Based on Maglio (1973). Species with characteristic mammoth cranium showing dorsally expanded occipital and parietals, a strongly anteriorly concave frontoparietal surface that is flat to convex transversely, without parietal crests (figures 15.17Y, 15.17Z). Molars moderately derived for the genus, with hypsodont crowns lacking significant development of accessory conules, and slightly more plates than in *M. africanavus*.

Description Molars of this species from Africa are morphologically similar to those from Europe, but with greater hypsodonty (third molar HI = 157–176) and more plates (Arambourg, 1970). In the African specimens, lamellar frequency ranges from 4.0 to 5.0 and enamel thickness from 2.0 to 3.5 mm (Arambourg, 1970). Molars are long but not particularly wide. Greatest width of the crown is located one-third to halfway above the cervix. Enamel may be slightly folded to undulating, and enamel loops are simple and comprised of five to seven conelets. There are no appreciable accessory central conules. Plate formulae (Africa): ?dp4 = ?12; m3 = 16; DP4 = 9; ?M2 = ?15; M3 = 14–16 (Arambourg, 1970); (Europe): dp2 = 3–4; dp3=5-6; dp4 = 8–9; m1 = 9–10; m2 = 8–10; m3 = 10–14; DP2 = 3–4; DP3 = 5–6; DP4 = 7–8; M1 = 8–10; M2 = 9–11; M3 = 12–14 (Maglio, 1973).

Remarks This species is best known from Europe, and only tentatively documented in North Africa. Geraads and Metz-Muller (1999) place the specimens from Aïn Hanech, Algeria, in *Elephas recki ileretensis*, and it is possible that Arambourg's (1970) "*E. moghrebiensis*" may not be synonymous with *M. meridionalis* (G. Markov, pers. comm.). Because the African specimens are more advanced in crown height and plate number, it is possible that they are derived from the European deme of the species, which in turn almost certainly descended from *M. rumanus* (see Lister and van Essen, 2003; Lister et al., 2005). Nonetheless, the progressive quality of molar morphology and younger geological age of African "*M. meridionalis*" in comparison to *M. africanavus* suggest that these species might be useful for future biochronological sequencing of North African sites, especially if considered along with *Loxodonta atlantica atlantica*, which replaced *Mammuthus* in North Africa during the middle Pleistocene.

Genus *ELEPHAS* Linnaeus, 1758
Figures 15.17AA–15.17EE

Now endangered, in terms of biogeography, longevity, diversity, and impact on faunas, *Elephas* was the most successful Old World elephant taxon. The genus originated in Africa in the early Pliocene and by the late Pliocene migrated out of the continent into more temperate zones (Maglio, 1973; Todd and Roth, 1996). Once out of Africa, these proboscideans diversified quickly across the Near East, Europe, Asia, and South Asia to become the most speciose of the elephant genera (Coppens et al., 1978). Today, the genus is represented only by the Asian elephant, *E. maximus*, which is widely distributed across Asia and South Asia, though in increasingly fragmented areas and declining numbers (~55,000 individuals; Shoshani and Eisenberg, 1982; Sukumar and Santiapillai, 1996; Fleischer et al., 2001; Blake and Hedges, 2004). The species has been sorted into three subspecies (Shoshani and Eisenberg, 1982; Sukumar and Santiapillai, 1996), with genetic variability evidencing two major clades that appear to have experienced extensive gene flow between populations in the past (Fernando et al., 2000; Fleischer et al., 2001; Vidya et al., 2005).

Even primitive species of *Elephas* are readily recognizable from their cranial morphology, which clearly contrasts with that of *Loxodonta*, and to a lesser degree with that of *Mammuthus*: the skull is high and anteroposteriorly compressed; the frontoparietal surface is flat to concave; there are usually distinct parietooccipital bosses; and the upper edges of the temporal fossae are bordered by sharp, prominent ridges (figures 15.17AA, 15.17BB; Maglio, 1973; Coppens et al., 1978). In derived species, the molars are very high crowned, may have a large number of plates, thin, very plicated enamel, thick cementum, and accessory conules are absent or persist only as larger folds in enamel loops (figures 15.17CC, 15.17DD). These features are convergent on molar structure in advanced forms of *Mammuthus*. In more primitive species, the greater expression of accessory conules is shared by a number of elephant genera, and may cause difficulty for identification of isolated specimens.

There is no consensus on how to more finely partition the African *E. ekorensis–E. recki–E. iolensis* lineage (see Maglio, 1973; Beden, 1980; Todd, 2005). Nevertheless, the geographic and temporal extent of this lineage, particularly *E. recki*, its occurrence in radiometrically well-dated sites, and its progressive morphometric changes over time (figure 15.17EE), make this one of the most useful African mammalian taxa for biochronological correlation. More difficult to understand is the precipitous disappearance of this lineage, after nearly three million years of dominating East African faunas.

ELEPHAS EKORENSIS Maglio, 1970

Partial Synonymy *Elephas africanavus*, Arambourg et al., 1969; primitive *E. recki*, Howell et al., 1969; *Loxodonta adaurora*, Coppens and Howell, 1974:2275; *E. recki,* Coppens and Howell, 1974:2275.

Age and Occurrence Early to mid–Pliocene, eastern Africa (table 15.6).

Diagnosis Based in part on Maglio (1970b); Beden (1987a). Less pronounced expression of typical "*Elephas*" features in the cranium than other congeners, with only modest bossing of the parietooccipital region and a flatter forehead without much anterior expansion of the parietals. Prominent, widely separated tusk sockets. Large external nasal opening. Differs from *Loxodonta* in having a more anteroposteriorly compressed cranium with a flat rather than rounded forehead, and distally less flaring tusk sockets.

Description This is a primitive member of the genus, as evidenced by the low number of molar plates, moderate hypsodonty (HI ranges from 100 to 175), intermediate plate spacing (third molar LF = 3.8–4.8), and moderately thick, unfolded or coarsely undulating enamel (third molar ET = 3.3–4.0 mm; Maglio, 1973). In addition, molar plates retain anterior and larger posterior accessory conules throughout much of the crown. These are apically free though incorporated as mesiodistal median projections in enamel wear figures, but they do not form strong median sinuses as in *Loxodonta*. Only a small number of conelets (four to six) form each plate, which are broadest near the base of the crown. Third molars are broadest anteriorly, taper drastically posteriorly, and are less massive than in sympatric *L. adaurora*. In lateral view, plates are parallel-sided and separated by cementum-filled, U-shaped transverse valleys.

Plate formulae: m1 = 8; m2 = x9; m3 = 12; DP2 = 3x; DP3 = 6x; DP4 = 8x; M1 = 7–7x; M2 = 9; M3 = 11–11x (Coppens et al., 1978; Beden, 1980, 1987a).

Remarks This is the most ancient unequivocal representative of the genus *Elephas*. Although an older putative congener, *Elephas nawataensis*, was named from the Upper Mb. of the Nawata Fm. and Apak Mb. of the Nachukui Fm. at Lothagam, Kenya (Tassy, 2003; see also Tassy and Debruyne, 2001), its holotype is more sensibly synonymized with *Primelephas korotorensis* and the rest of its type series with *Stegotetrabelodon orbus* (see above; Mundinger and Sanders, 2001; Sanders, 2004).

Morphologically, *E. ekorensis* seems a good ancestral model from which to derive *Elephas recki* and the first Eurasian representative of the genus, *E. planifrons* (Maglio, 1970b; Coppens et al., 1978).

ELEPHAS RECKI Dietrich, 1915

Figures 15.17AA–15.17EE

Partial Synonymy See Beden (1983) for a more complete synonymy. *Elephas antiquus recki,* Dietrich, 1915; *E. zulu*, Hopwood, 1926; *E. recki*, Arambourg, 1942; *Palaeoloxodon antiquus recki,* MacInnes, 1942:42, plate 8, figures 4–5; *Palaeoloxodon recki*, Osborn, 1942; *Omoloxodon*, Deraniyagala, 1955; *Elephas Palaeoloxodon recki*, Beden, 1983.

Age and Occurrence Early Pliocene–middle Pleistocene, primarily eastern Africa (rare occurrences in northern, Central, and southern Africa; table 15.6).

Diagnosis Based in part on Maglio (1973); Coppens et al. (1978); Beden (1980). Medium-sized elephant with hypsodont molars that in later forms have finely folded, thin enamel, and a greater number of closely spaced plates than in *Loxodonta*. Unlike *Mammuthus*, tusks are not spirally twisted, and the forehead is demarcated from the temporal fossae by sharp, acute ridges. Frontoparietal surface more vertical than in *E. ekorensis*.

Description Based in part on Maglio (1973); Coppens et al. (1978); Beden (1980). Cranium raised and anteroposteriorly flat or concave, with a strong frontal crest, large external nasal opening, rectangular prenasal region, deep, wide incisive fossa, nearly parallel, and drawn out zygomatic processes of the frontal; massive incisor alveoli that are closely proximate at their openings; and parietooccipital bosses (which are profound in more advanced subspecies) (figures 15.17AA, 15.17BB). Orbits widely spaced but small. Tusks are gently curved upward in a single plane.

Mandible short, massive, very brevirostrine, with a more rocker-shaped ventral corpus than in *Loxodonta*. The ramus is broad, and the condyles are rounded and set on a short condylar neck. There are no lower tusks.

Differences in molar proportions, plate spacing, enamel thickness, hypsodonty indices, enamel folding, and plate number in different stages or subspecies of *E. recki* are enumerated by Maglio (1973) and Beden (1980, 1983, 1987a). Generally, in earlier forms (e.g., *E. r. brumpti*) enamel is thicker (M3/m3 = 2.8–4.0 mm) and unfolded to coarsely folded, hypsodonty is modest (M3/m3 = 101–116), plates are not particularly closely spaced (M3/m3 LF = 4.0–5.5), and accessory central conules may be retained, particularly in the anterior half to two-thirds of the crown, though median sinuses are absent or only weakly developed (figures 15.17CC, 15.17DD). In more advanced subspecies (e.g., *E. r. recki*), accessory conules are completely absorbed into the plate loops, plate spacing is closer (M3/m3 LF = 4.6–6.0), enamel is thinner (M3/m3 = 1.8–3.0 mm) and well plicated, and molar crowns are relatively higher (M3/m3 HI = 161–200)(Beden, 1980).

Plate formulae: (*E. r. brumpti*) dp2 = x3x–x4; dp3 = 6x–x6x; dp4 = x7x–9; m3 = x11x–14; DP2 = 4x; DP3 = 6x; DP4 = x7x; *(E. r. shungurensis)* dp2 = x3–x4; dp3 = x6–7x; dp4 = 9–10x; m1 = 10x; m2 = 10–x10x; m3 = x12x–15; DP2 = x4–5; DP3 = x5x–x7x; DP4 = x9; M1 = 8x; M2 = 11x; M3 = x12x–15; *(E. r. atavus)* dp2 = 4–4x; dp3 = 6x–x8; dp4 = x8x–10; m1 = 10–11; m2 = 10–12x; m3 = 13x–x17; DP2 = 5–x5; DP3 = 6x–7x; DP4 = 9–9x; M1 = 9–x11x; M2 = 9–11x; M3 = 14x–17; *(E. r. ileretensis)* dp3 = 7x–8x; m1 = x10x; m2 = 11–11x; m3 = x14x; M2 = 12; M3 = x15x–x16; *(E. r. recki)* dp2 = 3x–x3x; dp3 = 7x–8; m2 = x12; m3 = 14x–18x; M2 = x10; M3 = x13x–19 (Beden, 1980, 1983, 1987a).

Remarks A highly successful species of great longevity, *Elephas recki* was the dominant elephant in East Africa during the late Pliocene-–middle Pleistocene (Beden, 1985) and apparently evolved anagenetically for a period of over three million years. Phyletic transformation of the dentition in this species was directional, and involved increases in molar hypsodonty (figure 15.17EE), number of plates, and enamel folding, accompanied by closer spacing of plates, thinner enamel, and complete incorporation of accessory conules into plates (Maglio, 1973; Coppens et al., 1978; Beden, 1980, 1985). Although the species continued to evolve progressively into the late Pleistocene in the form of *E. iolensis* (see later discussion), by the middle Pleistocene *Loxodonta* had reappeared in East Africa and begun to replace *Elephas* there (Beden, 1985).

The morphological continuum across successive generations of *E. recki* resembles that of a ring species rolled out over time, with the end members as distinct from one another as any two living species, but with morphological changes between intervening generations nearly imperceptible. Although overall differences could warrant partitioning the lineage into a number of species (see Todd, 2005), serial phases have been subdivided into time-successive stages (1–4; Maglio, 1970a, 1973; Coppens et al., 1978) or subspecies (*E. r. brumpti, shungurensis, atavus, ileretensis*, and *recki;* Beden, 1980), whose divisions are largely governed by chronostratigraphic unit boundaries, most notably in the Omo Shungura Formation (table 15.6; Beden, 1980, 1987a). It has been suggested that temporal overlap of these subspecies (see table 15.6) invalidates the hypothesis of anagenetic change (e.g., Todd, 2005). These taxonomic subdivisions are artificial, however, and the arbitrary partitioning of specimens may have typologically overemphasized subspecific or stage demarcations and downplayed variability. When the names or stages are ignored, the emergent pattern is one of a continuously, directionally evolving lineage with robust variation and substantial morphometric overlap between successive generations.

The disappearance of this once widespread, abundant elephant is unlikely to have resulted from direct competition with reemergent loxodonts. There is evidence for the decline of the species toward the end of the Acheulean industrial phase, and absence from subsequent Middle Stone Age faunas, though not necessarily because of overhunting by humans. It is alternatively possible that shifts in temperature and rainfall patterns due to changes in the intensity and periodicity of glacials and interglacials may have upset competitive balances among grazers and given other ungulate taxa an edge over these elephants (Klein, 1988). If the *E. recki* lineage is considered to have terminated in *E. iolensis*, then its extinction prior to the late Pleistocene is illusory.

ELEPHAS IOLENSIS Pomel, 1895

Partial Synonymy *Archidiskodon sheppardi*, Dart, 1927; *A. transvaalensis*, Dart, 1927; *A. broomi*, Osborn, 1928; *A. hanekomi*, Dart, 1929; *A. yorki*, Dart, 1929; *Pilgrimia yorki*, Dart, 1929; *P. wilmani*, Dart, 1929; *P. kuhni*, Dart, 1929; *P. archidiskodontoides*, Haughton, 1932; *P. subantiqua*, Haughton, 1932; *Elephas pomeli* (in part), Arambourg, 1952; *E. iolensis*, Arambourg, 1960.

Age and Occurrence Late Pleistocene, northern, eastern, and southern Africa (table 15.6).

Diagnosis Based in part on Maglio (1973); Coppens and Gaudant (1976); Coppens et al. (1978). Medium- to large-sized species, with more hypsodont molars than *E. recki*, lacking significant development of median loops or sinuses in molar enamel wear figures.

Description Based in part on Dart (1929); Maglio (1973); Coppens and Gaudant (1976); Coppens et al. (1978). The skull is unknown. The molars are more hypsodont than those of other African elephants (HI ranges to nearly 300). Despite this advanced condition, molars have only a modest number of plates (m1 = 8; m2 = 12; M3 = 13–14). Sectioned molars show that anterior and posterior accessory central conules are completely "captured" by the enamel loops, producing little anteroposterior midline expansion of the wear figures (see Coppens and Gaudant, 1976: plate 3). Enamel is only moderately thin (third molar ET = 2.0–3.5), and plates are thick in lateral view, yet they are crowded together, yielding lamellar frequencies of 5.0–6.3. Enamel is irregularly but strongly folded. Plate breadth is greatest about midheight and may exceed 100 mm in third molars. Plates are parallel sided in lateral view and separated by very narrow, U-shaped transverse valleys that are abundantly filled with cementum.

Remarks *Elephas iolensis* occurred widely across Africa but is not abundant in the fossil record (Maglio, 1973). Nonetheless, it is temporally well constrained between the close of the middle Pleistocene to nearly the end of the epoch (table 15.6), and it constitutes the closing phase of the *E. ekorensis*–*E. recki* lineage (Maglio, 1973). With its demise, *Loxodonta africana* and *L. cyclotis* were left as the lone proboscidean inhabitants of Africa. Presumably a grazer, *E. iolensis* might have become extinct for causes ecologically linked with the reasons that the modern African elephant survived as a mixed-feeder/browser.

Summary

EVOLUTIONARY PHASES

Due to their robust fossil record, dynamic course of evolution, and ability to traverse great distances, proboscideans are among the most useful of African mammals for correlative dating of fossil sites and refining the chronology and geographic pattern of regional migratory events. There is now considerably more evidence of their phylogeny, from a greater reach of geological history, than there was at the time of the last major review of African proboscideans (in Maglio and Cooke, 1978). Since then, the proboscidean fossil record has been extended back more than 20 million years, to >55 Ma, and has yielded many new taxa (table 15.1). Temporal range distributions of genera indicate that proboscideans underwent at least eight major phylogenetic diversification events (figure 15.19). These may prove useful for subdividing African mammalian faunas into biochronological stages (see Pickford, 1981), but the relationship between these episodes and biotic, physical, and climatic phenomena is still being investigated.

The earliest documented phase of African proboscidean evolution occurred at the end of the Paleocene and produced the oldest known members of the order, including phosphatheres and daouitheres. This phase coincided with the Paleogene thermal maximum, the warmest period of the Cenozoic (Kennett, 1995; Denton, 1999; Feakins and deMenocal, this volume, chap. 4). At this time, Africa and southern Arabia constituted an island continent separated from Eurasia by the Tethys Sea, and its mammalian fauna was strongly endemic (Cooke, 1968; Coryndon and Savage, 1973; Maglio, 1978; Krause and Maas, 1990; Holroyd and Maas, 1994; Gheerbrant, 1998). Regional differences in climate and ecology were far smaller than they are today (Denton, 1999), and forests were probably widespread across the continent. The connection between this climatic event and proboscidean origins is uncertain, as the diversity of these archaic taxa suggests an even older

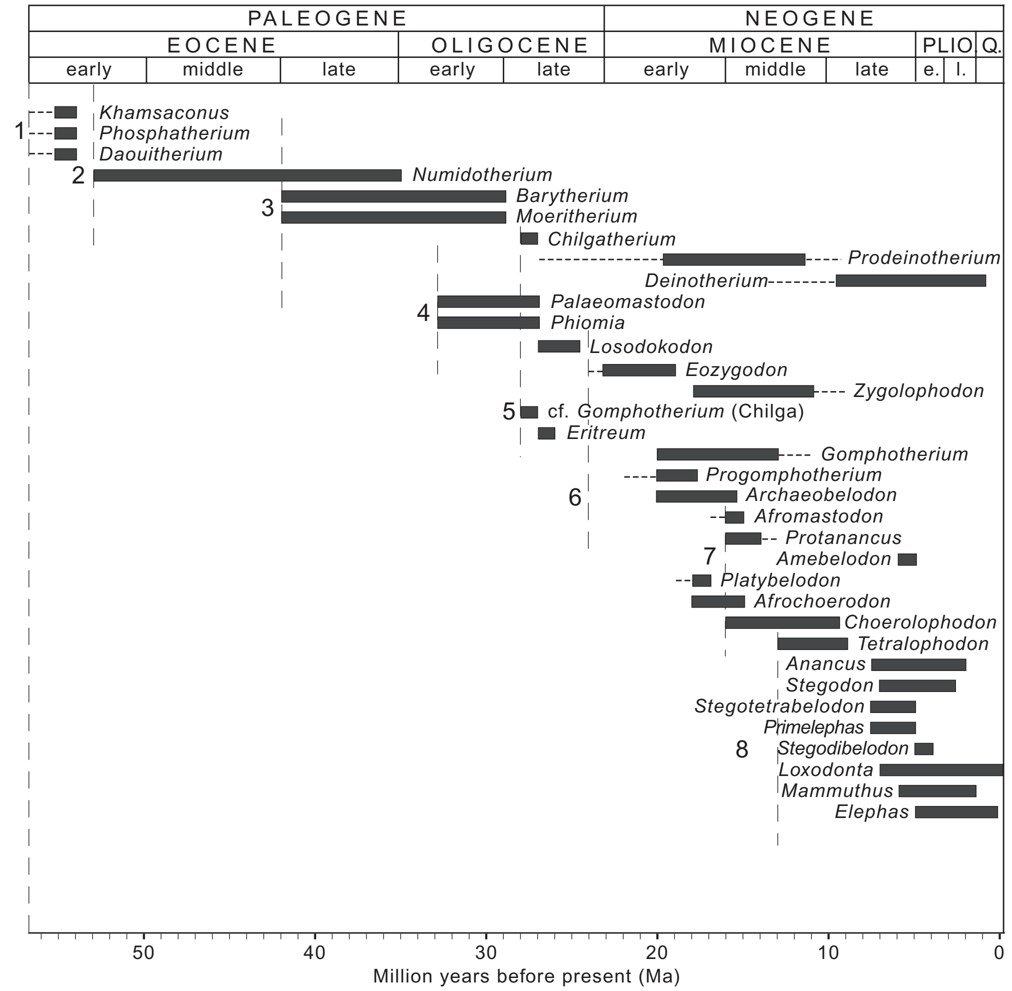

FIGURE 15.19 Temporal distribution of African proboscidean genera, based on tables 15.2–15.6. Bars represent known chronological ranges of taxa; horizontal dotted lines represent uncertain dates of occurrence. Numbers 1–8 indicate major proboscidean evolutionary episodes.

divergence from other paenungulates. Subsequent to their first appearance, proboscideans remained indigenous to Afro-Arabia until the end of the Paleogene (Antoine et al., 2003). It is likely that the predominantly North African distribution of proboscideans from nearshore and shallow water environments during the Eocene is an artefact of poor preservation of Paleogene sub-Saharan sites (Sanders et al., 2004).

By the end of the early Eocene (ca. 50 Ma), phosphatheres and daouitheres had been supplanted by numidotheres, of greater body size and more derived skeletal anatomy. The timing of this replacement coincided with the start of a cooling trend, but climate was still quite equable (Denton, 1999; Feakins and deMenocal, this volume, chap. 4), and reasons for the succession are obscure.

In the latter half of the Eocene (ca. 40–37 Ma), a greater diversity of proboscidean taxa came to coexist, including more advanced numidotheres, barytheres, and moeritheres. These taxa were considerably larger in body size, with more specialized, outsized anterior dentitions than their predecessors, and with adaptations for a semiaquatic existence. Habitat specializations likely helped to ensure their survival into the Oligocene.

Barytheres and moeritheres were joined at the start of the Oligocene by palaeomastodonts, the first of the elephant-like proboscideans, possessing trunks, projecting tusks, and terrestrial graviportal postcranial adaptations. This proboscidean assemblage, along with taxa such as creodonts, early anthropoids, saghatheriid hyraxes, anthracotheriid artiodactyls, and arsinoitheres, comprised the typical mammalian "Fayumian" fauna of the African Oligocene (Simons, 1968; Gagnon, 1997). Although in the early Oligocene the collision of the Indian plate with Asia closed off the eastern Tethys Sea, Africa remained separated from Eurasia by the western Tethys and Paratethys Seas (Rögl, 1998), and its fauna continued to be isolated. Global temperatures also declined precipitously (Denton, 1999), but palaeomastodonts were shielded in low latitudes from the extreme effects of global cooling, and they existed in warm, well-watered forested and woodland conditions (Wight, 1980; Bown et al., 1982; Bown and Kraus, 1988; Jacobs et al., 2005).

Distinct global warming trends occurred during the late Oligocene and early Miocene (Miller et al., 1987; Kennett, 1995; Denton, 1999), the former accompanied by the first appearance of elephantoids and chilgatheriine deinotheres, in the Horn of Africa. Palaeomastodonts appear to have been unaffected by these changes, but by the early part of the Miocene and the second warming episode, they and many of the other Fayumian mammals had vanished and the most significant phase of African proboscidean evolution had begun, with the diversification of elephantoids into mammutids, gomphotheriines, amebelodonts, and choerolophodonts, and replacement of chilgatheriines by deinotheriines. Distribution of early Miocene proboscidean sites is more extensive throughout Africa than are Paleogene occurrences (tables 15.1–15.5; Pickford, 2003) and shows that some species had epicontinental ranges.

During this time, Africa and the Arabian plate rotated northward to contact the Anatolian plate, establishing a land bridge between Afro-Arabia and Eurasia (Rögl, 1999). Gomphotheriines, deinotheres, amebelodontines, and mammutids exploited the new intercontinental connection to immigrate to Eurasia in the 20–18 Ma interval (Tassy, 1989), and made their way even earlier to South Asia (Bernor et al., 1987; Antoine et al., 2003). At the same time, a host of Eurasian mammals (rhinos, fissiped carnivores, suids, insectivores, chalicotheres, rodents) invaded Afro-Arabia (Andrews and Van Couvering, 1975; Bernor et al., 1987; Agustí and Antón, 2002; Guerin and Pickford, 2003). Competition with new herbivorous ungulate taxa may have played an important role in the early Miocene morphological specialization and phyletic diversification of elephantoids, and in the demise of the palaeomastodonts (Sanders et al., 2004).

In the early middle Miocene, ca. 16.5–16.0 Ma, at the climax of Neogene warming (Kennett, 1995; Denton, 1999), archaic amebelodonts and choerolophodonts were replaced by more advanced subfamilials, perhaps catalyzed by the immigration into Africa of a second wave of Eurasian mammals (horned bovids, antlered giraffoids, and listriodont suids; Pickford, 1981). There is evidence of continued, progressive evolutionary change, particularly by these taxa, throughout phases of subsequent middle Miocene global cooling in the interval of 15.6–12.5 Ma (Kennett, 1995; Denton, 1999).

The most recent major proboscidean evolutionary episode in Africa occurred in the late Miocene. This involved the local extinction of most gomphotheres and mammutids, immigration into the continent of stegodonts, anancine gomphotheres, and tetralophodonts, perhaps made easier by the beginning of the Messinian Crisis, or closing off of the Mediterranean Sea, which enhanced land connections between Africa and Eurasia via the Gibralter Strait and the Gulf of Aden (Rögl, 1999), and the origin of elephants. Around this time, strong uplift of rift shoulders in eastern Africa began to affect local climate, enhancing seasonal temperature variability, and producing more arid conditions through rainshadow effects (Partridge et al., 1995a). Simultaneously, uplift of the Tibetan Plateau changed wind patterns and also contributed to drier conditions, and global decrease in the worldwide CO_2 content of the atmosphere favored the spread of C_4 plants, including grasses (Cerling et al., 1993; Partridge et al., 1995b). Elephants were among the first African mammals to exploit these new circumstances by evolving craniodental adaptations specialized for grazing. Increased fragmentation and heterogeneity of ecosystems due to climatic deterioration and greater geomorphological relief created conditions favorable to speciation (Partridge et al., 1995a) and may be linked with the initial radiation of archaic elephants ca. 7.0–5.0 Ma. Elephants underwent a series of subsequent diversifications as they continued to refine these adaptations against the pressures of increased competition for C_4 resources (see Cerling et al., 2003). The wide distribution of fossil elephants, and rapid pace of progressive alterations of their craniodental grazing adaptations have proven especially useful for biochronological correlation of sites from the late Miocene to the present, and for the study of evolutionary processes (Cooke and Maglio, 1972; Maglio, 1973).

PHYLOGENY

Most major phylogenetic events in proboscidean evolution occurred in Africa, including the first appearance of the order and the origin of most subsequent major taxa (barytherioids, moeritheres, deinotheres, palaeomastodonts, mammutids, gomphotheres, and elephants). Phylogenetic analyses have now established that moeritheres, barytheres, and deinotheres belong in the Proboscidea (Tassy, 1979b, 1981, 1982, 1985, 1996c; Shoshani et al., 1996; Gheerbrant et al., 2005), linked by a small series of unremarkable traits such as anteroposterior flattening of the femur, loss of the first lower premolar, and hypertrophy of second incisors (Shoshani and Tassy, 1996). Recent discoveries of older, Paleocene and Eocene taxa from North Africa such as *Eritherium, Phosphatherium, Daouitherium*, and *Numidotherium* (Mahboubi et al., 1986; Gheerbrant et al., 1996, 2002, 2005; Court, 1995) have more clearly delineated the primitive condition for the order: relatively small animals lacking graviportal adaptations, with low-slung crania, nearly full dentitions, no trunks or projecting tusks, and bilophodont molars. Addition of these taxa to phylogenetic analyses has reconfigured proboscidean relationships (figure 15.20). As a result, moeritheres, once posited as basal proboscideans (Tassy and Shoshani, 1988; Shoshani et al., 1996; Tassy, 1996c), have been replaced in this position by phosphatheres and barytherioids, and they are now hypothesized to be the sister taxon to Deinotheriidae + Elephantiformes (Gheerbrant et al., 2005). Recovery of more ancient moerithere fossils from Algeria (Delmer et al., 2006) suggests that they are descended from lophodont proboscideans, supporting this hypothesis.

While their relationships are now clearer and better supported (figure 15.20; Shoshani et al., 2001; Shoshani, 1996; Tassy, 1996c; Sanders, 2004; Gheerbrant et al., 2005), problems remain for the interpretation of African proboscidean phylogeny, partly because of strong tendencies for homoplasy within the order, as illustrated by several notable examples. First, the nature of the connection between palaeomastodonts, mammutids, and gomphotheres requires further investigation. Although cladistic analysis has indicated that *Palaeomastodon* is the sister taxon to *Phiomia* + Elephantoidea (Tassy, 1988, 1990; Shoshani, 1996), new fossils of late Oligocene palaeomastodonts and mammutids (Sanders et al., 2004; Gutiérrez and Rasmussen, 2007) suggest instead that *Palaeomastodon* and mammutids have an ancestor-descendant relationship. This would necessitate drastic reclassification of Palaeomastodontidae and Elephantoidea.

A second phylogenetic problem concerns stegodont relationships. *Stegodon* is highly convergent craniodentally on elephants, and has been placed in Elephantidae by some (Arambourg, 1942; Kalb and Mebrate, 1993; Kalb et al., 1996a). Nonetheless, advances in stegodont biogeography and chronostratigraphy show this to be unlikely (Saegusa et al., 2005). Alternatively, stegodonts are often designated as close sister taxa to elephants (e.g., Shoshani, 1996), but new fossil material from Kenya (Tassy, 1995; Tsujikawa, 2005a) indicates a derivation of elephants from *Tetralophodon* and a more immediate relationship of those taxa. Despite their eventual evolution of elephant-like features, it is possible that stegodontids diverged from other elephantoids as long ago as the early Miocene. If so, they would instead be a sister taxon of Gomphotheriidae (figure 15.20).

Third, the relationships of deinotheres remain poorly understood. New fossil finds from Ethiopia (Sanders et al., 2004)

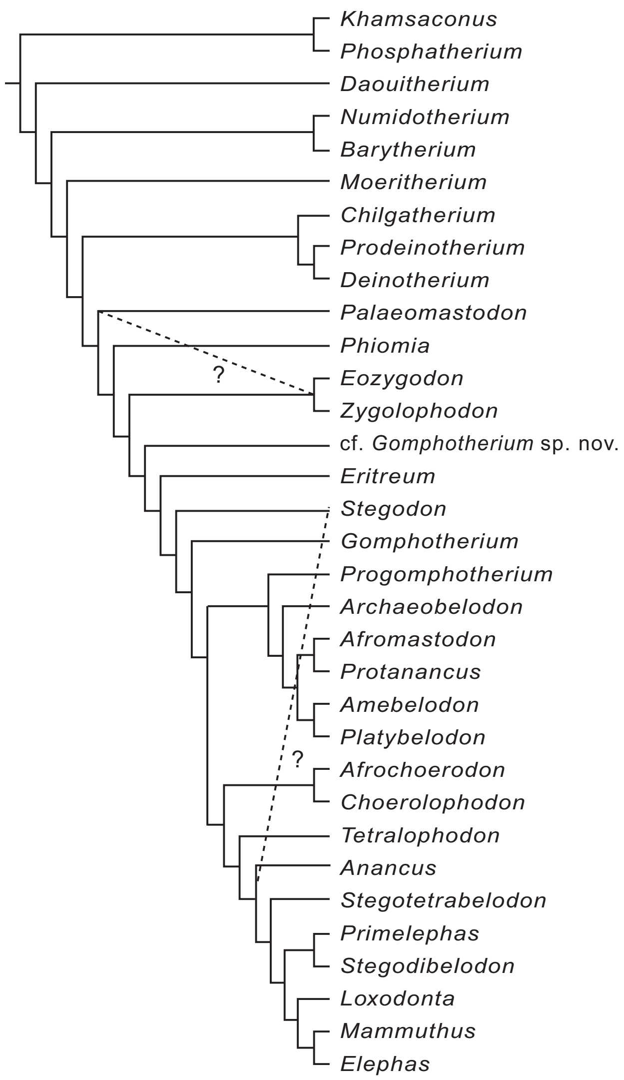

FIGURE 15.20 Cladogram of African proboscidean genera, based in part on Shoshani (1996), Tassy (1996c), Sanders (2004), and Gheerbrant et al. (2005). Dotted lines indicate alternative hypotheses about sister group relationships of taxa.

support an earlier hypothesis of derivation from a moerithere-like ancestor (Harris, 1969, 1975, 1978). Cladistic treatment indicates that while deinotheriines are strongly convergent in cheek tooth morphology with barytheres (Harris, 1978), they are more closely related to Elephantiformes (Gheerbrant et al., 2005). However, recovery of chilgatheriine skulls is critical for more informative testing of these hypotheses.

Finally, despite thorough efforts at description and diagnosis (e.g., Maglio, 1973; Maglio and Ricca, 1977; Kalb and Mebrate, 1993; Tassy, 1995; Sanders, 1997, 2007), elephant relationships remain tangled. The traditional separation of *Loxodonta* from *Elephas* + *Mammuthus* (Coppens et al., 1978; Kalb and Mebrate, 1993; Shoshani, 1996; Tassy, 1996c) has been challenged on morphological and molecular grounds (Hagelberg et al., 1994; Noro et al., 1998; Barriel et al., 1999; Thomas et al., 2000; Thomas and Lister, 2001; Debruyne et al., 2003), and proposed ancestral-descendant relationships between late Miocene–early Pliocene archaic genera and these crown elephantines seems more tenuous now (Sanders, 2004) than they were thought to be 30 years ago (Coppens et al., 1978). Nonetheless, the taxonomic and temporal continuity of crown elephantines within their own lineages is now much better documented, and for *Loxodonta* can be traced back nearly continuously from the present to at least 7 Ma (Sanders, 2007). Genetic studies provide support for the division of modern African elephants into distinct forest and savanna species (Roca et al., 2001, 2005; Comstock et al., 2002).

TRENDS

The pattern of African proboscidean evolution is widely branching, as a result of repeated adaptive radiations, with the greatest variety of taxa in the Miocene (Shoshani and Tassy, 1996). From their inception, proboscideans exhibited surprising diversity, with phosphatheres and more advanced daouitheres found together. In the early and middle Miocene, it was not unusual for multiple species of proboscideans to co-occur at the same localities, as for example at Wadi Moghara, where the fauna includes deinotheres, mammutids, gomphotheriines, amebelodontines, and a species of choerolophodont (Sanders and Miller, 2003). Given the impact of *Loxodonta africana* on modern African ecosystems, it is difficult to imagine the richness of an environment that could support so many megaherbivores, and yet this seems to have been fairly common in Miocene times. As recently as the late Pliocene, multiple species of elephants, stegodonts, deinotheres, and anancine gomphotheres still shared much of the African landscape, but were finally reduced to a single surviving species, largely because of the ecological ascendance of hominids, and increasing competition with other herbivores in the Pleistocene.

Throughout most of their existence, proboscideans have been the largest or among the largest animals in African terrestrial faunas, with repeated tendencies for gigantism. Although the earliest known members of the order were small, by the latter part of the early Eocene numidotheres had become pig sized, and soon thereafter barytherioids reached elephantine proportions. Most Miocene proboscideans probably weighed several tons and were at least the size of small elephants, with late Miocene deinotheres being the most immense terrestrial mammals to have inhabited the continent (Christiansen, 2004). The long trunk, tusks, and serially replaced dental battery of 2- to 7-ton modern elephants give them the ability to eat a varied and impressive daily amount of forage, thereby maintaining their large mass, and were likely the key adaptations that also maintained the impressive early–middle Miocene radiation of gomphotheres. Common to such huge animals is a suite of graviportal adaptations such as short, stout feet; pillarlike, elongated long bones (particularly proximal elements) with vertically facing articular surfaces, broad innominates with downward facing acetabulae; and shortened lumbar vertebral regions that bring the thorax in close approximation with the pelvis. These adaptations were present in even the first elephantiforms, by the beginning of the Oligocene.

An important factor in the evolution of horizontal, serial emplacement of cheek teeth was loss of teeth, probably associated with timing of tooth development and their rotation into occlusion, so that most lineages of large-bodied proboscideans exhibited a reduced dental formula in comparison with the first members of the order. The first phases of tooth loss in proboscideans, however, appear to have been linked with rostral elongation and/or specialization of incisors for acquisition of forage, and not with horizontal tooth succession. In these phases, canines and anteriormost premolars were diminished in importance or lost, and some incisors were hypertrophied, while the remaining premolars became more molariform. Starting with a dental formula of I3/2-C1/1-P4/3-M3/3 in *Phosphatherium*, the tooth complement in the sirenian- and hippolike moeritheres and barytheres was modestly reduced to I3/2-C1/0-P3/3-M3/3 and I2/2-C0/0-P3/3-M3/3, respectively.

With the evolution of the first of the elephant-like proboscideans, the palaeomastodonts, the rostrum and symphysis were further elongated, in concert with greater hypertrophy of second incisors, leaving no room or need for additional anterior teeth, and the tooth formula was again reduced, to I1/1-C0/0-P3/2-M3/3. Elephants underwent a secondary reduction of the anterior mandible and lost their lower incisors, as part of a mechanical reorganization of the skull for greater effectiveness of fore-aft mastication, and although more archaic elephant species retained permanent premolars, most crown elephants have a very reduced tooth formula of I1/0-C0/0-P0/0-M3/3, with three deciduous premolars preceding the emergence of molars (Laws, 1966; Sikes, 1967; Roth, 1992). The convergent loss of the lower tusks in choerolophodonts, anancine gomphotheres, and *Stegodon* suggests that they also could have been lost multiple times among elephantines.

The proboscidean tendency for convergent or parallel development of features is best documented in the dentition. The earliest proboscideans, including phosphatheres, daouitheres, and barytherioids, had lophodont cheek teeth with chisellike crests, employed in tapirlike vertical shearing; this masticatory mechanism was evidently separately evolved by deinotheres, and also to some extent by mammutids. Gomphotheres developed a different, rotary grinding and shearing system for chewing that became progressively more effective independently in different lineages through the addition of accessory conules, acquisition of cementum, increase in number of conelets per loph(id), and multiplication of loph(id)s per tooth. Mechanisms to enhance locking precision of molars in occlusion, such as lateral offset of half-loph(id)s, also were developed multiple times by different proboscidean taxa (e.g., choerolophodonts, *Protanancus*, *Anancus*). Crown elephant lineages responded to selective pressure for greater efficiency in grazing by independently evolving molars with more plates, greater lamellar frequency, higher crowns, and thicker cementum, perhaps the most compelling example of parallelism in the development of proboscidean dentitions. The temporally coordinated and progressive, directional pattern of this change across multiple lineages during a time of increasingly widespread open conditions suggests that these elephants evolved via anagenesis.

EPILOGUE OR EPITAPH?

The surviving African elephant are among the most recognizable mammals on the continent, sharing with humans the traits of great intelligence and complex social behavior (Sikes, 1971), and are likely the terminal members of an order that dominated Paleogene and Neogene ecosystems. Maintenance of open woodlands and savannas, and associated herbivore assemblages, is critically dependent on the presence of elephants (Eltringham, 1992), whose absence would likely permanently alter the biotic composition of habitats throughout sub-Saharan Africa. Despite their ecological versatility, however, there is no guarantee that these representatives of one of the most successful orders of African mammals will long survive into the future. Poaching of elephants for ivory has exacted a terrible toll on elephant populations, and the encroachment of human settlements and domestic livestock on their ranges looms as an even greater threat to their survival (Kingdon, 1979; Buss, 1990). Elephants in particular may have helped ensure the initial fortunes of hominids by opening up ecosystems, and it would be tragically ironic if this most African of mammalian orders is brought unnecessarily to extinction, after surviving the rigors of physical, biotic, and climatic upheavals for over 55 million years, by unbounded human fecundity.

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