New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia

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Newly recovered fossil proboscideans and embrithopods from Chilga, Ethiopia are described and evaluated taxonomically. They are dated to ca. 28–27 Ma (late Oligocene), temporally intermediate between late Eocene–early Oligocene Afro-Arabian faunas dominated by archaic, endemic taxa, and replacement faunas of the early Miocene marked by a massive influx of Eurasian migrants. The paucity of similar-aged sites in Afro-Arabia makes Chilga critical for delineating the initiation and sequence of this faunal turnover. While most of the genera present at Chilga persist from older Afro-Arabian localities, at higher elevation and farther inland than elsewhere, there are no Eurasian mammals in the fauna. However, the archaic endemics from Chilga differ morphometrically from their older congeners, and include a new embrithopod, *Arsinoitherium giganteum* sp. nov., and novel species of elephantiform proboscideans, *Phiomia major* sp. nov., aff. *Palaeomastodon* sp. nov. A, and aff. *Palaeomastodon* sp. nov. B. New, primitive deinotheres and gomphotheres also occur at Chilga, extending the fossil records of these proboscideans considerably back in time. The Chilga deinothere, *Chilgatherium harrisi* sp. nov., differs sufficiently from *Prodeinotherium* and *Deinotherium* to be placed in its own subfamily, Chilgatheriinae subfam. nov. The Chilga gomphothere is smaller than Miocene elephantoids, and is referred to cf. *Gomphotherium* sp. nov. Together, this evidence suggests that indigenous Afro-Arabian taxa had greater ecological versatility than previously suspected and continued to enjoy successful evolutionary trajectories into the late Paleogene. Thus, as they spread into Afro-Arabia, new immigrants from Eurasia may have encountered vibrant local mammalian communities. The demise of many endemic inhabitants followed and remains poorly understood.

Key words: Arsinoitheriidae, Deinotheriidae, Gomphotheriidae, Palaeomastodontidae, Paleogene, Afro-Arabia.

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Introduction

This paper provides formal taxonomic treatment of large-bodied mammals from a new faunal assemblage recovered between 1998–2003 from late Paleogene deposits in the Chilga region of Ethiopia (Fig. 1; Kappelman et al. 2003). The Chilga fauna is comprised of taxa belonging predominantly to the paenungulate orders Hyracoidea, Embrithopoda, and Proboscidea, and is noteworthy as a diverse and well sampled fossil collection from a time interval poorly represented in Afro-Arabia. It is temporally interpolated between archaic, endemic Afro-Arabian faunas of the late Eocene and early Oligocene, mainly known from the Fayum, Egypt (Simons 1968; Coryndon and Savage 1973; Gagnon 1997), and early Miocene replacement faunas, principally documented in East Africa, containing Eurasian migrants such as suids, giraffids, rhinos, bovids, and fissiped carnivores (Maglio 1978; Bernor et al. 1987). As such, the Chilga fauna is valuable for delineating the taxonomic composition and adaptive profile of mammals in Afro-Arabia closely preceding major faunal turnover, and for assessing paleogeographic-based hypotheses about the chronology of that biologic event (see Bernor et al. 1987; Rögl 1998; Adams et al. 1999).

Geology and geochronology.—The Chilga fossils derive from the Western Plateau of Ethiopia, a major highland region composed mostly of massive Oligocene flood basalts (Hofmann et al. 1997). At Chilga, the dominant basalt landscape is interrupted in places by outcrops of sedimentary rocks on weathered basalt surfaces, in association with block faulting and possibly minor rifting activity. The sediment is exposed in a series of stream and gully cuts along the Guang and Hauga Rivers (Yemane et al. 1985, 1987a, 1987b), and consists of siltstones and other fine-grained rock, in places containing tuffs and lignites (Assefa and Saxena 1983; Feseha 2002; Kappelman et al. 2003).

Most of these sediments represent fluvial deposits, including both channel fills and overbank floodplain deposits, the latter with some development of paleosols to varying degrees of maturity (Feseha 2002). The total thickness of the deposits is about 130 meters. Most of the fossils described

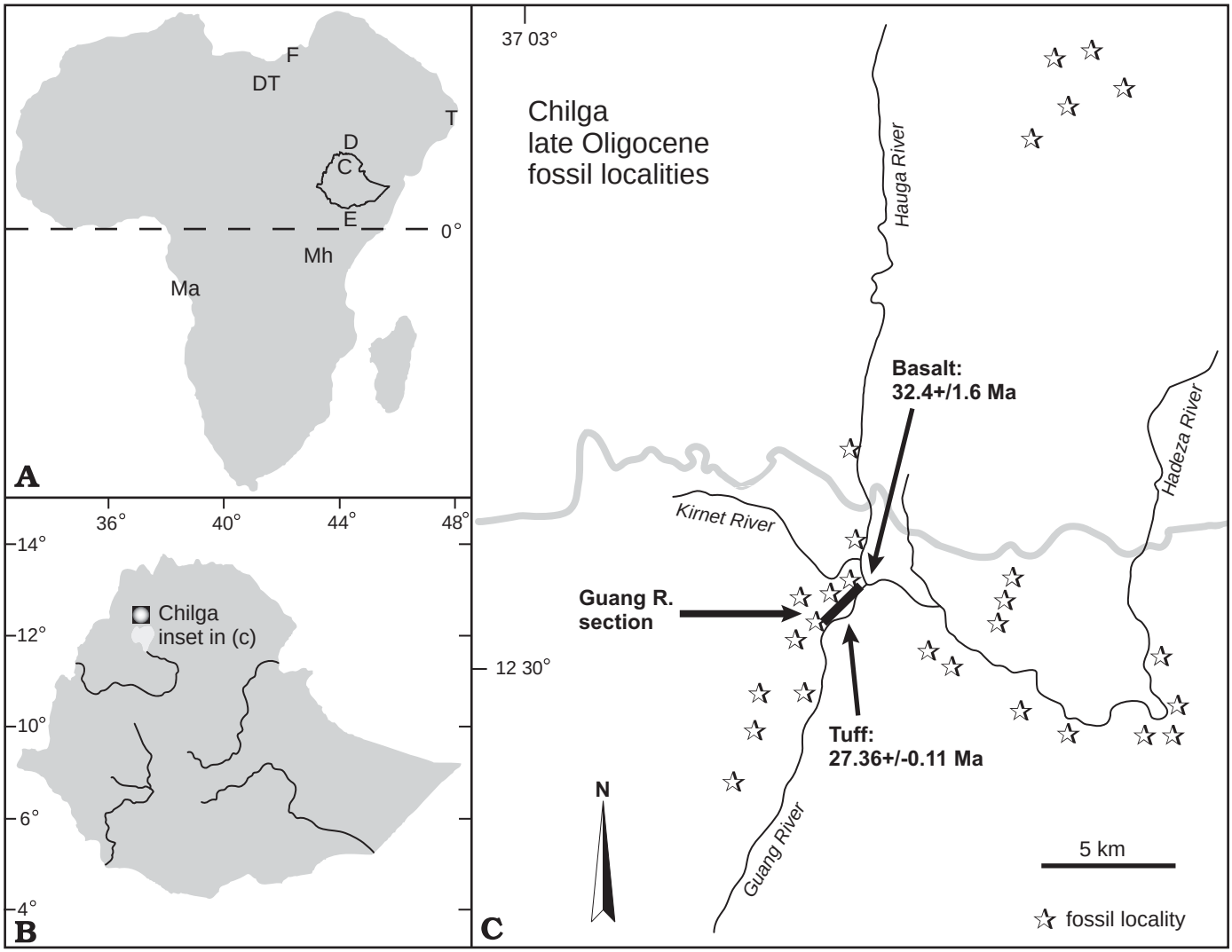

Fig. 1. **A**. Map of Afro-Arabia with several important Paleogene terrestrial mammal sites (underlined characters denote abbreviations for the localities marked on the map), including Chilga (Ethiopia), Dogali (Eritrea), Lothidok (Eragaleit Beds, Kenya), Fayum (Egypt), Dor el Talha (Libya), Malembe (Angola), Mahenge (Tanzania), and Thaytini and Taqah (Oman). Outline of Ethiopia is inset. **B**. Map of Ethiopia showing the location of Chilga, north of Lake Tana. **C**. Detailed map of the Chilga area showing the fossil localities, geologic section (Fig. 2), and dated rock sample localities, along the Guang and Hauga Rivers.

here occur in one of three general outcrops of sediment: (1) an extensive Upper Guang Section, in the southwestern part of the study area, which is better exposed than other outcrop areas; (2) a Gahar Valley Section, more northerly and accessible only by a long hike down into a 400-meter deep valley; and (3) a Middle Guang Area, an easterly area of smaller and more isolated outcrops widespread over an area of lesser topographic relief (Fig. 1C). No evidence suggests the three regions are of significantly different ages.

Whole rock K-Ar dating of unweathered basalt underlying the base of the sedimentary section provides a maximum age of about 32 Ma for the fossil beds. Tuffs from within the vertebrate-bearing portion of the section produced K-Ar and ^{40}Ar-^{39}Ar dates of 28–27 Ma, further refining the age of the new fauna. Radiometric dating of the Chilga sediments is supported by preliminary results of paleomagnetic reversal stratigraphy (Kappelman et al. in review). Most of the Chilga section is normally magnetized, except for two brief reversal events, which is consistent with fitting the sedimentary section wholly in Chron C9n (Fig. 2), dated to between 27.972 and 27.027 Ma (Cande and Kent 1995). The reversals in the Chilga section may be equivalent to a pair of cryptochrons recorded by Cande and Kent (1995) within Chron C9n. Earlier work by Yemane et al. (1985) incorrectly concluded that a much younger Miocene basalt occurred at the base of this section, but our work shows that this particular younger flow is in a faulted but not conformable relationship with the sediment.

There are few other mammalian faunas of similar age known from what is now sub-Saharan Africa. Aside from a late Oligocene collection from Lothidok, Kenya (Boschetto et al. 1992; Leakey et al. 1995), the only other Paleogene mam-

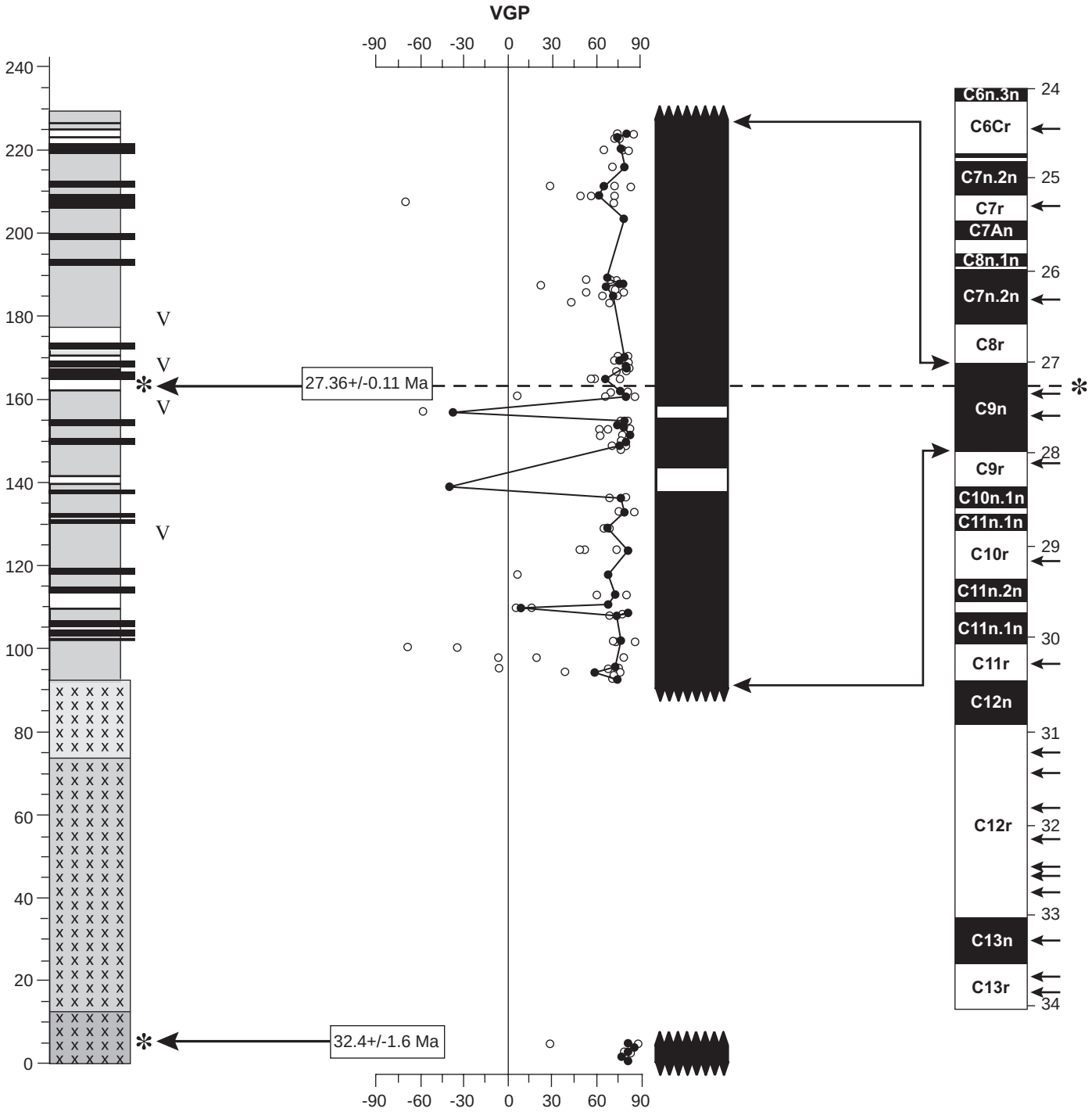

Fig. 2. Diagram of the Chilga stratigraphic section. The section has more than 90 m of volcanics at its base that are overlain by at least 130 m of fluvial and alluvial sediments. Stepwise alternating-field demagnetization was carried out on 118 samples with generally three samples per stratigraphic level. Paleomagnetic reversal stratigraphy demonstrates a dominance of normal polarity, and an $^{40}Ar/^{39}Ar$ age of 27.36 ± 0.11 Ma for a tuff in the upper portion of the sedimentary sequence at about 165 m provides an absolute tie point to Chron C9n (27.946-27.004 Ma). Small arrows to the far right of the geomagnetic polarity time scale of Cande and Kent (1995) represent "tiny wiggles," and the two brief reversal events within Chron 9 may be present at Chilga, providing additional but more indirect support for this correlation. Together these data suggest that this section is probably limited to the duration of this Chron (<1 Myr). Vertebrate-bearing horizons (V) occur primarily through the middle part of the section.

malian fossil occurrences from this vast area are a small assemblage of fragmentary material from Malembe, Angola (Pickford 1986a), a single bat from Mahenge, Tanzania (Gunnell et al. 2003), and an isolated proboscidean mandible from Dogali, Eritrea (Shoshani et al. 2001) (see Fig. 1A). This perspective makes especially clear the importance of the Chilga

fauna for documenting the nature and timing of faunal succession in Afro-Arabia near the close of the Paleogene.

Taxonomic background.—Most of the mammals from Chilga are classified within Simpson's (1945) superorder Paenungulata. Of these, the embrithopods and proboscideans are presented here. The rest of the Chilga mammal fauna, which includes isolated anthracothere and creodont specimens and a diverse collection of hyracoids comprised of new species of the saghatheriids *Bunohyrax*, *Megalohyrax*, and *Pachyhyrax*, will be described later (Rasmussen et al. in preparation).

Traditionally, the order Embrithopoda has been placed within Paenungulata (Andrews 1906; Gregory 1910; Simpson 1945). A major departure from this arrangement was that of McKenna (1975), who instead classified Embrithopoda together with Articodactyla and Dinocerata in a new taxon, Eparctocyona, without empirical justification. Nevertheless, Court (1989, 1990, 1992a) presented substantial evidence linking embrithopods with other paenungulates. His cranial analyses robustly favor placing *Arsinoitherium*—and by extension, Embrithopoda—near Proboscidea (Court 1990, 1992a). Thus, embrithopods appear to belong comfortably within Paenungulata. A host of other morphological evidence, and among the extant taxa molecular studies, powerfully support retention of Paenungulata (Rasmussen et al. 1990; Novacek 1992; Shoshani 1992; Springer et al. 1997; Stanhope et al. 1998; Liu and Miyamoto 1999; Eizirik et al. 2001; Madsen et al. 2001; Murphy et al. 2001; O'Brien et al. 2001).

Relatively primitive taxa of Embrithopoda are known from the Eocene of Europe (Sen and Heintz 1979; Rădulescu and Sudre 1985; Kappelman et al. 1996; Court 1992b). The best known and most derived genus in the order is *Arsinoitherium*, from the Oligocene of the Fayum, Egypt, with dental specimens of broadly similar age also recorded from Taqah, Oman, Dor el Talha, Libya, and Malembe, Angola (Andrews 1906; Tanner 1978; Wight 1980; Pickford 1986a; Shoshani et al. 1996; Thomas et al. 1999). There is no fossil record of embrithopods postdating the Oligocene.

The order Proboscidea contrasts with Embrithopoda in the great scope of neontological and paleontological work that has been conducted on its phylogeny, function, and evolution (e.g., Shoshani and Tassy 1996). Higher level phylogenetic questions about Proboscidea have traditionally focused on the relationship of the order to other paenungulates, as outlined above. The oldest unequivocal fossil record of proboscideans is from the early Eocene of Morocco (Gheerbrant et al. 1996, 1998, 2002; Gheerbrant 1998). Other Paleogene records come from Algeria, Libya, Senegal, Mali, Tunisia, Egypt, and Oman, pointing to Afro-Arabia as the likely place of origin of the order and as the locus of basal radiations that produced such archaic, widely divergent forms as numidotheres, barytheres, moeritheres, and palaeomastodonts (Andrews 1906; Matsumoto 1922, 1924; Osborn 1936; Arambourg et al. 1951; Gorodisky and Lavocat 1953; Savage 1969; Harris 1978; Coiffait et al. 1984; Mahboubi et al. 1984; Court 1995; Shoshani et al. 1996). Following the Paleogene, the most important evolutionary radiation of proboscideans was among the elephantiforms, the result of a complex diversification and dispersal of elephantoid taxa that began in the early Miocene of Africa (Coppens et al. 1978; Tassy 1979, 1985, 1994a). In the Paleogene, however, elephantiform proboscideans were restricted to a small number of palaeomastodont taxa, and the derivation of Miocene elephantoids (gomphotheres and mammutids) from them remains uncertain. The fossil record suggests that deinotheres also arose in Africa, and underwent phylogenetic and geographic expansion during the early Miocene; however, their relationships to Paleogene forms are even more obscure than those of elephantoids (Harris 1978; Shoshani et al. 1996).

Prior to the Chilga discoveries, virtually nothing was known about mammals from Afro-Arabia during the interval between the early Oligocene and early Miocene, including proboscideans and other paenungulates. Of particular interest are questions about the persistence of archaic endemics into the late Oligocene, and what competitive role, if any, Eurasian migrants played in their disappearance. Comparative morphological and metric analyses of the new assemblage demonstrate that these indigenous Afro-Arabian forms not only survived but continued to evolve and speciate well into the late Oligocene, and that the faunal turnover strikingly evidenced in the early Neogene of Afro-Arabia occurred diachronously rather than in a single episode.

Accession abbreviations.—AMNH, American Museum of Natural History, New York; CGM, Cairo Geological Museum, Cairo; CH, Chilga specimens housed in the National Museum of Ethiopia, Addis Ababa.

Dental abbreviations and definitions.—Measurements in millimeters (mm). Upper teeth are denoted with capital letters, lower teeth with lower case letters: D/d, deciduous premolar; I/i, incisor; M/m, molar; P/p, premolar; 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 in the transverse valleys, partially blocking them centrally (Tobien 1973); adaxial conelet(s), the inner, or meso-, conelet(s) in each half-loph(id) (Tassy 1996a); choerolophodonty, molar crowns covered with tubercles (Osborn 1942); crescentoids, enamel crests running from the apices of the abaxial conelets of the pretrite half-loph(id)s to the bottom of the transverse valleys, and ending near the middle axis of the crown (Tobien 1975); hypolophid, second lophid; metaloph, second loph; pretrite, refers to the more worn half of each loph(id), which is buccal in lower and lingual in upper molars (Vaček 1877); protoloph(id), first loph(id); posttrite, refers to the less worn half of each half loph(id), which is lingual in lower and buccal in upper molars (Vaček 1877); ptychodonty, plication or infolding of enamel borders with grooving of the sides of the molars (Osborn 1942); tritoloph(id), third loph(id); 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

Class Mammalia Linnaeus, 1758
Superorder Paenungulata Simpson, 1945
Order Embrithopoda Andrews, 1906
Family Arsinoitheriidae Andrews, 1904
Genus *Arsinoitherium* Beadnell, 1902
Arsinoitherium giganteum sp. nov.

Fig. 3, Table 1.

Holotype: CH69-1, maxilla with M2-3 (Fig. 3A).

Referred specimens: CH3-1, distal half of upper molar, probably M3; CH3-2, maxilla with P3-4; CH3-8, right deciduous premolar (d2 or d3); CH3-16, lower molar fragment; CH3-52, left m1; CH3-60, upper molar; CH3-63, upper molar fragment; CH3-94, partial mandible with right p2-m1, left p2-m2; CH3-95, left M3 (Fig. 3E); CH5-12, left P4; CHS6-V-1, proximal femur; CH7-1, right deciduous premolar (d4?); CH9-9, left p4 (Fig. 3C); CH9-12, right p1; CH9-14, right upper premolar; CH9-15, molar fragment; CH9-16, upper molar fragment; CH10-3, left? p1?; CH10-5, juvenile mandible with two deciduous? premolars (Fig. 3B); CH10-6, M1; CH15-V-6, right I1; CH16-133, mid-cervical vertebra; CH17-5, axis; CH18-133, cervical vertebra; CH18-134, cervical vertebra (axis); CH19-6, thoracic vertebra; CH25-17, left m2? (Fig. 3F); CH25-18, right p2 or p3; CH26-10, partial left nasal horn core (Fig. 3D); CH26-12, acetabulum; CH33-9, left femur; CH33-22, cranial fragment; CH35-7, premolar inside nodule; CH35-13, molar inside nodule; CH35-14, right m2; CH35-16, molar inside nodule; CH35-18, tooth fragment inside nodule; CH35-19, molar inside nodule, CH35-21, molar inside nodule; CH35-35, thoracic vertebra; CH35-36, femoral head; CH35-37, distal femur; CH35-39, left tibia; CH51-1, right m3; CH51-2, left m2; CH51-3, distal femur; CH56-1, proximal humerus; CH76-1, parts of both lower jaws and one maxilla, each bearing two or three cheek teeth, embedded in a solid stone block, associated with multiple other blocks containing postcranial remains (CH76-3).

Etymology: From the Greek *gigantos*, gigantic.

Type locality: Chilga 69, Gahar Valley, Chilga region, northwest Ethiopia. Referred specimens are from other localities of the Gahar Valley, Upper Guang Section, and Middle Guang Area.

Age and distribution: Late Oligocene, 28–27 Ma. Only known from the Chilga region.

Diagnosis.—Differs from other species of *Arsinoitherium* in its larger tooth size (Table 1).

Description.—The M2 of the holotype is fully erupted and in occlusion, while the M3 is incompletely erupted and has endured no occlusal wear (Fig. 3A). These are massive teeth, exceeding in size those of large "*Arsinoitherium andrewsi*" of the Fayum. Because of damage to the back of the maxilla, the entire, unworn crown of the distal loph in M3 can be measured—it is an impressive 120 mm high. Other lightly worn or intact distal lophs of upper molars measure 115 mm (CH3-60), 131 mm (CH3-95; Fig. 3E), and 132 mm high (CH3-1). Crown height is also remarkably tall in other maxillary teeth (Table 1). In two moderately to heavily worn specimens of P4, CH3-2 and CH5-12, buccal crown height measures 73 and 76 mm, respectively. The lingual crown heights of the same premolars are only 10–14 mm high. As Andrews (1906) pointed out, this suggests that the teeth pivot as they erupt, wearing unequally along the edges of the crown.

The lower molars are also extremely high-crowned (Table 1), with typical development of the distinctive form of arsinoithere bilophodonty (Court 1992b). Teeth identified as m1 rise relatively straight from their bases, while m2 and m3 show greater degrees of curvature on the buccal side of the lophid pillars. All molars have a slight fossa and paracristid located in front of the mesial lophid representing a relictual trigonid (see CH25-17, Fig. 3F).

Comments.—*Arsinoitherium giganteum* sp. nov. is the largest and the geologically youngest species of arsinoithere. It is the second sub-Saharan record of the genus, the other being tooth fragments from Malembe, Angola, that are apparently of Oligocene age (Pickford 1986a). The geographically disparate occurrences at Malembe, and in Arabia (Thomas et al. 1989a, 1999), Egypt (Andrews 1906), Libya (Wight 1980), and highland Ethiopia, indicate that *Arsinoitherium* was a widespread herbivore in Afro-Arabia during the early Tertiary. This distribution is unexpected given detailed functional morphological study of the postcranium suggesting that *Arsinoitherium* was adapted to semi-aquatic swampland environments (Court, 1993). The lower adult and deciduous premolars from Chilga (Fig. 3B, C) resemble those known from Fayum arsinoitheres. The deciduous premolars are nearly perfect small replicas of the adult molars. The dental specimens of arsinoitheres from Chilga, however, are larger than all specimens from the Fayum, with one exception: the holotype of the Fayum's controversial large species, "*A. andrewsi*" (Lankester 1903; Andrews 1906; El-Khashab 1977), which overlaps the lower range of variation seen in the Chilga arsinoitheres. The largest specimen examined by us attributed to the common Fayum species, *A. zitteli* (CGM 8802), has an m1 length about eight millimeters shorter than the smallest Chilga m1 (Table 1). The longest Chilga lower molar is over 90 mm long, while no specimen of *A. zitelli* exceeds 67 mm.

It seems likely that the large holotype of "*A. andrewsi*" simply represents the largest known individual of *A. zitteli*. Large herbivores are almost always sexually dimorphic in body size, especially those with head ornaments indicating mating competition (Fig. 3D). If "*A. andrewsi*" were a legitimate species, one might still expect variation in *A. zitteli* to exceed CV values of 8–10, an amount easily accommodated in monomorphic and moderately dimorphic species (Plavcan and Cope 2001). However, excluding the holotype of "*A. andrewsi,*" the CV for remaining specimens of *A. zitteli* is quite low (ranging from 5.0 to 8.2 for those dental measures with $n \geq 8$). With the holotype of "*A. andrewsi*" added in to the calculations, CVs for the same tooth dimensions increase to a range of 7 to 15, not too high to encompass within a single species, and indeed, comfortably within the range expected for dimorphic species (Plavcan and Cope 2001). The early justification to recognize "*A. andrewsi*" as a distinct

Table 1. Comparative cheek tooth dimensions of *Arsinoitherium*. All dimensions are in mm.

Taxon/ Specimen number	p1		p2		p3		p4		m1			m2			m3		
										width			width			width	
	length	width	length	width	length	width	length	width	length	mesial	distal	length	mesial	distal	length	mesial	distal
Arsinoitherium giganteum sp. nov.																	
CH9-12	30.5	29.2															
CH10-3	+23.2	+25.7															
CH25-18			31.2	23.5													
CH3-94 (right)					32.3	30.4	38.5	32.5									
CH3-94 (left)			–	31.2	30.0	31.6	37.5	33.5	61.8		+43.8						
CH9-9							39.9	–									
CH3-52									70.5	53.4	49.3						
CH25-17												84.0	–	55.5			
CH35-14												88.0	54.0	53.0			
CH51-2												93.0	63.7	60.2			
CH51-1															81.6	54.3	58.6
"Arsinoitherium andrewsi"																	
n			1		1		1		1			1			1		
mean			34.0	–	36.0	–	41.0	–	69.0	–		78.0		–	82.0	–	
range																	
s.d.																	
Arsinoitherium zitteli																	
n			3	1	4	2	4	2	11	4		13		10	8	9	
mean			25.9	17.3	28.2	22.3	32.4	26.2	48.8	36.1		61.9		43.4	59.3	44.5	
range[a]			24.9–26.7		26.0–31.9	19.5–25.0	29.5–35.4	24.1–28.3	43.4–54.0	33.6–38.6		58.0–66.9		37.9–47.4	52.0–63.7	40.2–52.1	
s.d.			0.9		2.6	3.9	3.1	3.0	3.9	2.6		3.2		3.2	4.7	3.6	

Taxon/ Specimen number			P2		P3		P4		M1			M2			M3		
										width			width			width	
			length	width	length	width	length	width	length	mesial	distal	length	mesial	distal	length	mesial	distal
Arsinoitherium giganteum sp. nov.																	
CH3-2					36.0	–	43.5	44.3									
CH5-12							43.0	38.0									
CH9-14							39.4	46.5									
CH76-1												77.0	62.0	59.0			
CH69-1												76.0	60.0	53.0	70.0	–	–
CH3-1															–	–	59.4
CH3-95															73.6	–	63.0
"Arsinoitherium andrewsi"																	
n			1		1		1		1								
mean			35.0	–	37.0	–	41.0	–	72.0	–							
range																	
s.d.																	
Arsinoitherium zitteli																	
n			2	2	3	3	2	2	1	1		1	1		1	2	
mean			26.2	26.4	29.2	32.9	30.1	37.0	52.5	48.6		70.5	57.4		60.5	55.0	
range[a]			26.2–26.2	23.6–29.2	27.4–31.5	29.1–35.0	28.6–33.0	35.5–38.4	–	–		–	–		–	55.0–55.0	
s.d.			0.0	4.0	2.1	3.3	3.1	2.1	–	–		–	–		–	0.0	

[a] width of loph(id) of greatest breadth.

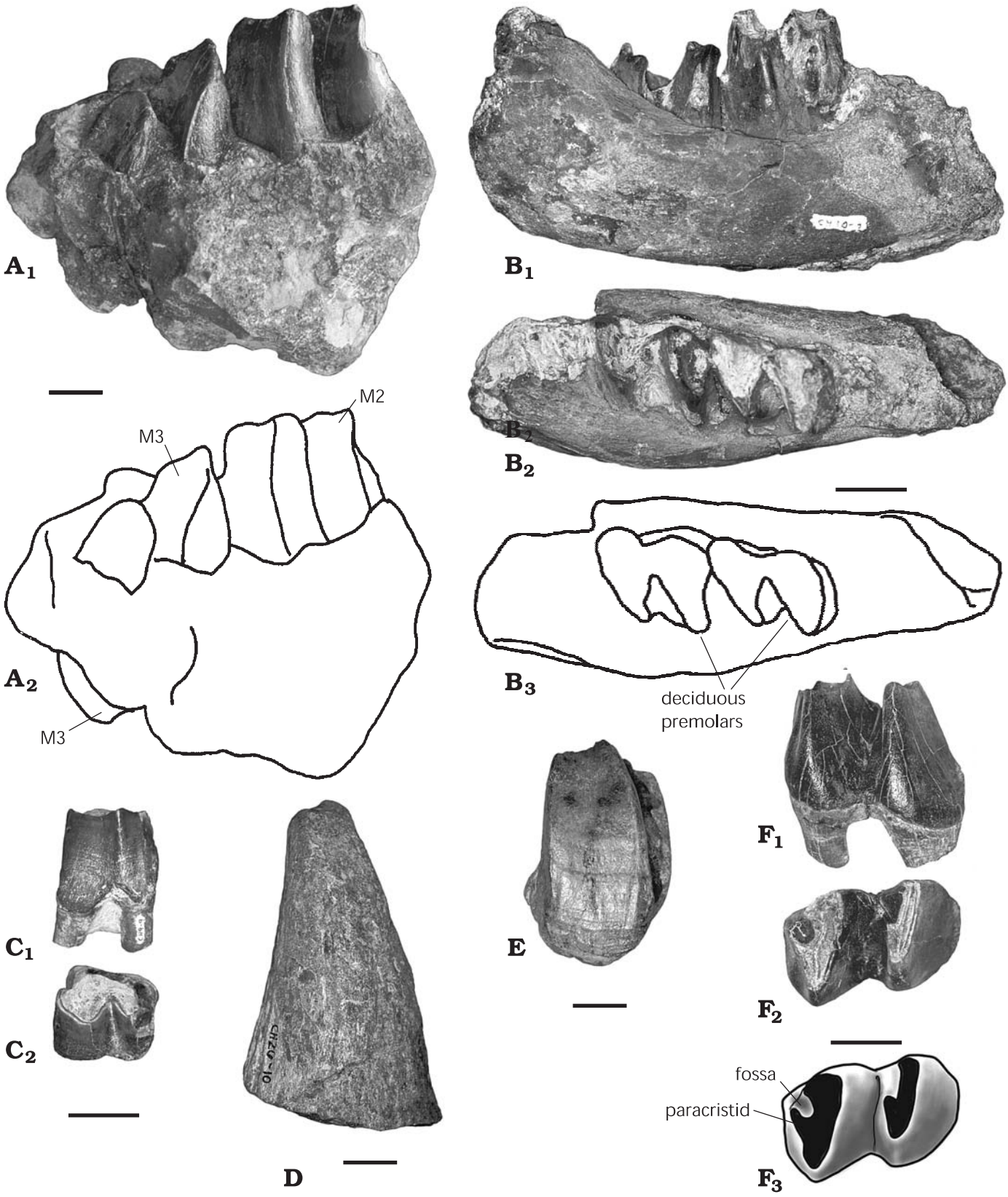

Fig. 3. Cranio-dental remains of *Arsinoitherium giganteum* sp. nov. **A**. Maxilla fragment with M2-3, CH69-1, holotype, in lateral view; anterior is to the right. (A_2, diagram of A_1). **B**. Juvenile dentary with two deciduous premolars, CH10-5, in buccal (B_1) and occlusal (B_2, B_3) views; anterior is to the right. **C**. Left p4, CH9-9, in buccal (C_1) and occlusal (C_2) views; anterior is to the left. **D**. Partial left nasal horn core, CH26-10. **E**. Left M3 in posterior view, CH3-95. **F**. Left m2, CH25-17, in buccal (F_1) and occlusal (F_2, F_3) views; anterior is to the left. Scale bars 3 cm.

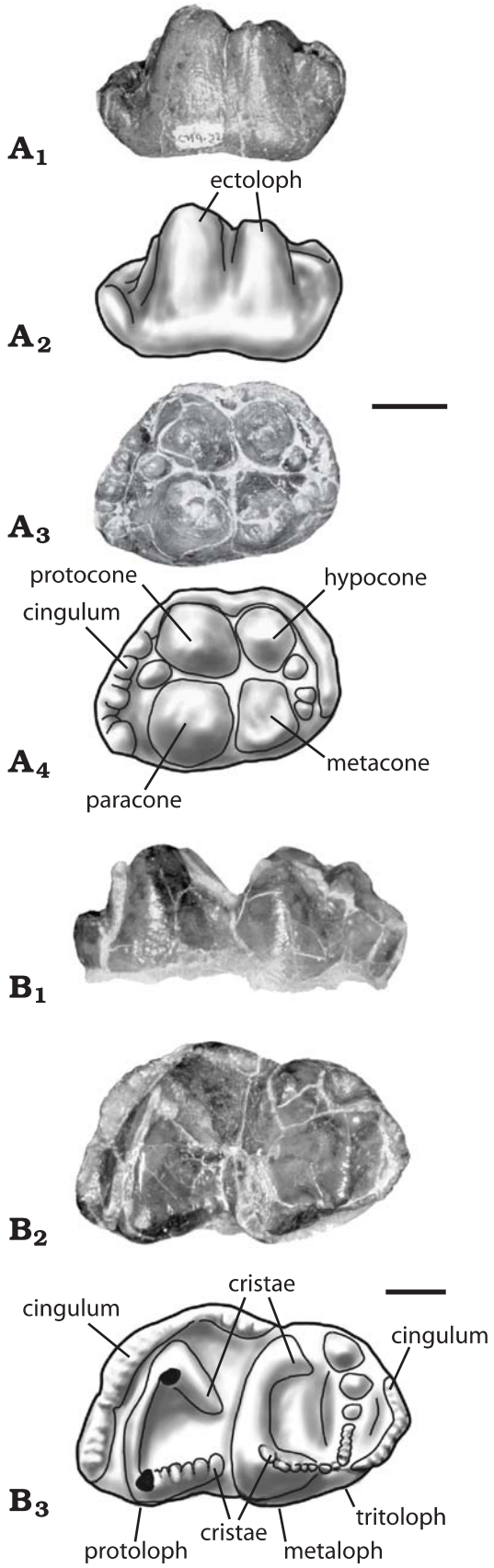

Fig. 4. Cheek teeth of *Chilgatherium harrisi* sp. nov. **A**. Right P3, CH9-22, in buccal (A_1, A_2) and occlusal (A_3, A_4) views. **B**. Right M3, CH35-1, in buccal (B_1) and occlusal (B_2, B_3) views. Anterior is to the left. Scale bars 1 cm.

species was that it was "nearly half again as large" (Andrews, 1906) as *A. zitteli*, but this ratio is not compelling. Similar size disparities are expected in large herbivores; e.g., among extant rhinocerotids the largest adult individuals are well over 50% larger than the smallest (Nowak and Paradiso, 1983).

The fairly large sample of arsinoithere teeth from Chilga allow us to conclude that the population from Chilga was greater in body size than that from the Fayum, with slight overlap between only the largest specimen from the Fayum and the smallest from Chilga, suggesting that there is a specific distinction between the two samples.

Order Proboscidea Illiger, 1811
Suborder Deinotherioidea Osborn, 1921
Family Deinotheriidae Bonaparte, 1845
Subfamily Chilgatheriinae nov.

Type genus: *Chilgatherium* gen. nov.

Etymology: As for the type genus.

Diagnosis.—As for the type species.

Genus *Chilgatherium* nov.

Type species: *Chilgatherium harrisi* sp. nov.

Etymology: The genus name is derived from the Greek word *therion* for wild animal, and the site name of Chilga.

Diagnosis.—As for the type species.

Chilgatherium harrisi sp. nov.

Figs. 4 and 5, Table 2.

Holotype: CH35-3a-e, associated partial right m1 (d), right m2 (a) (Fig. 5A), partial right m3 (e), partial left m2 (b), left m3 in crypt (c) (Fig. 5B).

Referred specimens: CH4-2a,b, left p4 (a), left m1 (b); CH9-7, left P3; CH9-22, right P3 (Fig. 4A); CH12-3, upper right molar fragment; CH12-4, upper left molar fragment; CH15-3, upper right molar fragment; CH35-1, right M3 (Fig. 4B).

Etymology: In recognition of the many important contributions of Dr. John M. Harris to the study of deinothere evolution.

Type locality: Chilga 35, Gahar Valley, Chilga region, northwest Ethiopia. Referred specimens from Upper Guang and Gahar Valley Sections.

Age and distribution: Late Oligocene, ca. 28–27 Ma. Only known from the Chilga region.

Diagnosis.—Diminutive deinotheres; teeth smaller than homologs in *Prodeinotherium* and *Deinotherium* (Fig. 6). Differ from deinotheriines (*Deinotherium* and *Prodeinotherium)* in the following features: P3 with bunodont cusps that are more independent in occlusal distribution and that crowd the trigon basin, and with a weakly formed ectoloph; m2 with poor expression of cristids; m2, m3, and M3 with incipient development of a tritoloph(id). Distinguished from barytherioids (*Phosphatherium, Daouitherium, Numidotherium, Barytherium*, all with bilophodont molars) by development of the m2 distocristid into an incipient third lophid; by development of a postentoconulid in m3; by greater expression of lingual cusps in P3 (shared with other

deinotheres); and by the bunodont (P3) and bunolophodont (molars) condition of cheek teeth.

Description.—There are only a small number of deinothere cheek teeth in the Chilga sample. Typical deinothere features in these specimens include transversely continuous, sharp-crested loph(id)s, tapiroid "chisel-like" wear on loph(id) apices, and cristae(ids) extending posteriorly from the lateral edges of upper molar lophs and anteriorly from the lateral edges of lower molar lophids (Figs. 4 and 5; see Bergounioux and Crouzel 1962; Harris 1975, 1978).

In deinotheres, D2 and P3 are very comparable morphologically and probably served similar masticatory functions (Harris 1975). Specimens CH9-7 and CH9-22 are identified as P3 by their size relative to M1/m1 and to P3 in other deinotheres; they are too large to be D2 in this species (Fig. 6A, B). The P3 specimens from Chilga differ from those of other deinothere species in having their buccal cusps connected only weakly by a postparacrista and premetacrista to form an incipient ectoloph (Fig. 4A; see Roger 1886; Gräf 1957; Bergounioux and Crouzel 1962; Harris 1975). These premolars have four inflated main cusps which largely fill the crown, rather than crested lophs. A narrow median sulcus divides the lingual and buccal halves of the crown, and a constricted transverse valley separates the lingual cusps from one another. Each buccal cusp is superficially subdivided into three apical digitations.

M3 is also distinguished from those of other deinothere species, by the nascent development of its tritoloph. The M3 tritoloph is composed of a transverse row of mammillons and is not fully independent of the metaloph (Fig. 4B). It is also narrower transversely and mesiodistally than the proto- and metalophs. The protoloph and metaloph are both well formed, anteriorly convex, and have transverse ridges with chisel-like wear along their anterior margins. The protoloph has a strong crescentoid on its lingual side that extends well into the transverse valley, and a narrow crest that runs along the posterior face of the buccal cusp toward the metaloph. Similarly, the metaloph has short cristae on its lingual and buccal sides that extend posteriorly toward the tritoloph. These features are characteristic of upper molars in deinotheres.

Lower cheek teeth of deinotheres from Chilga contrast with those of other confamilials, as well, particularly in the expression of their third lophids. Specimen CH35-3a is the antimere of CH35-3b (based on similar width; Table 2), which is identified as an m2 because it is serially associated anterior to an m3 in its crypt. In occlusal view, the tooth in crypt is identified as an m3 by its distally tapered profile (Fig. 5B). The proto- and hypolophids of the m2 are dominated by large, rounded cusps located at the buccal and lingual edges of the crown that are transversely connected by sharp, anteroposteriorly narrow crests. The crests are anteriorly concave and are worn in a chisel-like manner on their posterior faces, as in other deinothere species. The buccal cusp (hypoconid) of the hypolophid has a long, low crescentoid that projects into the first transverse valley. However, there are no other cristids apparent on the crown. Differing from

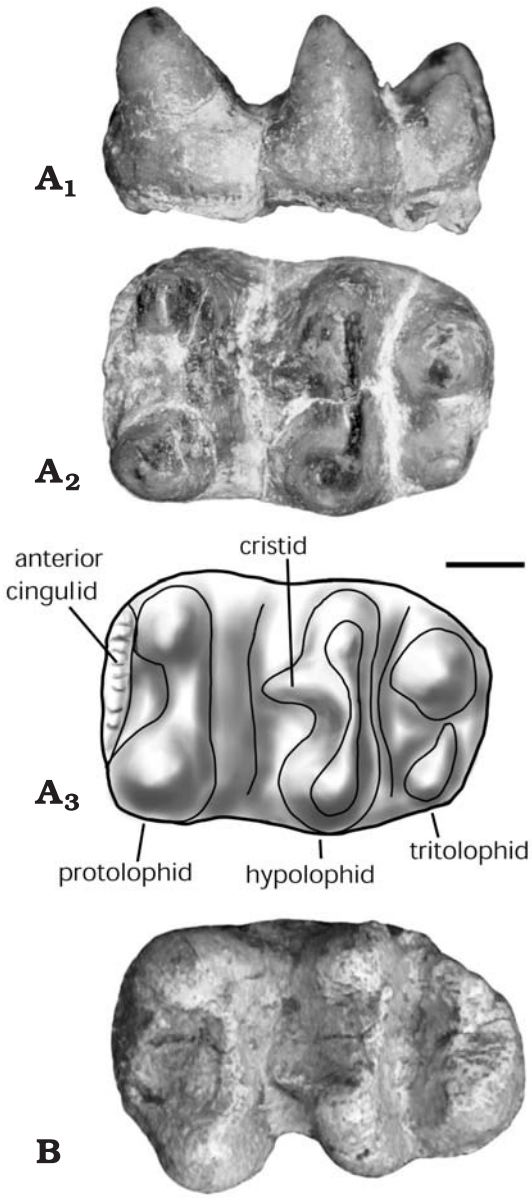

Fig. 5. Cheek teeth of *Chilgatherium harrisi* sp. nov. **A**. Right m2, part of type specimen, CH35-3a, in lingual (A_1) and occlusal (A_2, A_3) views; anterior is to the left. **B**. Left m3, part of type specimen, CH35-3c, in occlusal view. Scale bar 1 cm.

the condition in *Prodeinotherium* and *Deinotherium* m2 (which lacks a tritolophid) and d4 and m1 (which have complete tritolophids), the m2 tritolophid in *Chilgatherium* is composed of two rounded cusps (hypoconulid and postentoconulid) that are not connected by a transverse ridge and that are lower than the cusps in the first two lophids (Fig. 5A). The tritolophid has no accompanying distal cingulid. There is no ectoflexus laterally demarcating the boundary between the hypolophid and tritolophid.

Like m2, m3 has a weakly developed tritolophid; the cusps of the third lophid are low, narrow, and only tenuously connected by several mammillons, rather than a crest (Fig. 5B).

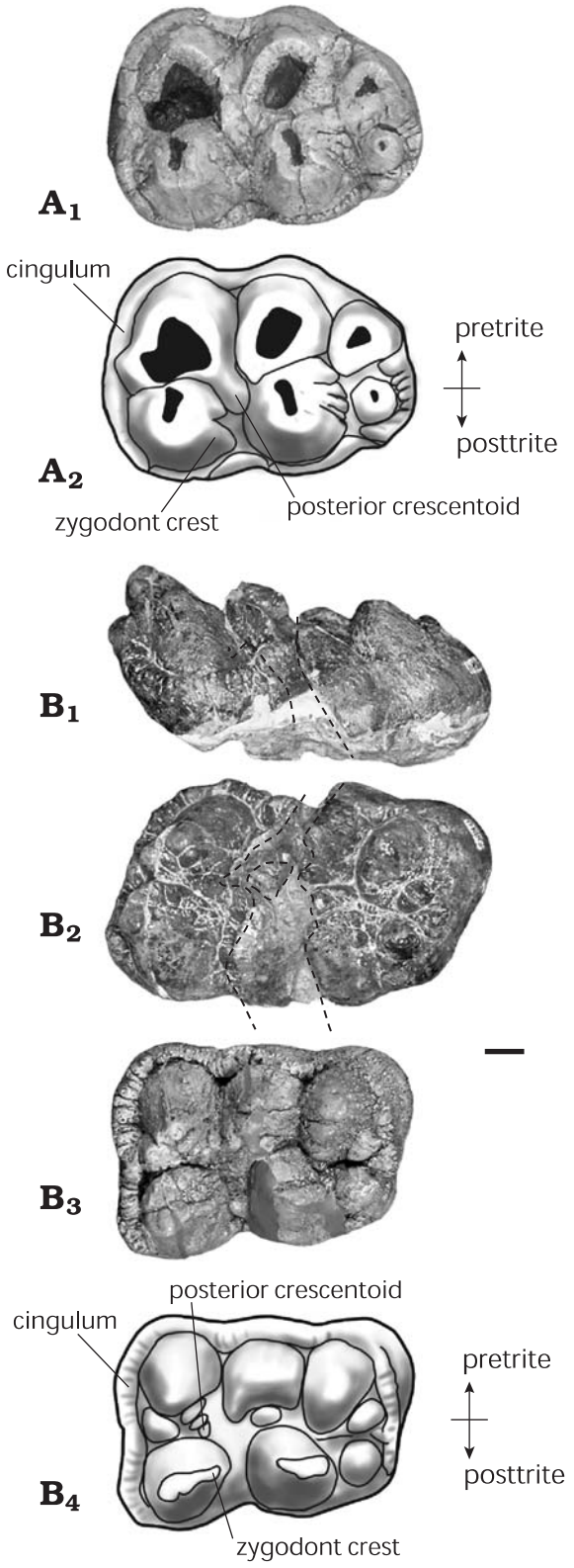

Fig. 14. Dental specimens of Chilga palaeomastodonts, aff. *Palaeomastodon*. **A**. Right M3, CH35-V-23, aff. *Palaeomastodon* sp. nov. A. in occlusal view. **B**. Right M3, CH14-11, aff. *Palaeomastodon* sp. nov. B. Original specimen in buccal (B_1) and occlusal (B_2) views; note step fractures and separation of crown segments, indicated by dotted lines. Reconstructed cast specimen in occlusal view (B_3, B_4). Anterior is to the left. Broken areas indicated by dotted lines. Scale bar 1 cm.

side, and has a low posterior accessory central conule that connects it with the posterior cingulum.

A moderately worn upper molar (CH25-16), probably M2, with large anterior and small posterior interproximal facets, is morphologically and dimensionally conformable with CH14-11 and is therefore also included in the hypodigm of this taxon.

Comments.—Specimen CH14-11 defies precise taxonomic allocation. Its occlusal configuration generally resembles M3 of *Palaeomastodon*, including aff. *Palaeomastodon* sp. nov. A (Figs. 13A, B, 14A). However, it differs from *Palaeomastodon* M3 by its more rectangular occlusal outline, greater enamel rugosity, more pronounced development of posterior posttrite cristae and cingula, and by its considerably greater size (it is approximately half again larger than M3 in Fayum palaeomastodonts, and is about 20 percent larger than CH14-V-12 and CH35-V-23; Fig. 12 and Table 2; Andrews 1906; Matsumoto 1924; Lehmann 1950). While sexual dimorphism could account for size variation among CH14-11, and CH14-V-12, CH35-V-23, and CH71-20, their morphological contrasts are great enough to warrant allocation to different species.

In the ways that CH14-11 differs from or is more pronounced than *Palaeomastodon* molars, it anticipates the dental morphology of early Miocene mammutids. The oldest recognized mammutid is *Eozygodon morotoensis*, dated to ca. 23 Ma at Meswa Bridge, Kenya (Bishop et al. 1969; Pickford and Tassy 1980; Pickford and Andrews 1981; Tassy and Pickford 1983; Pickford 1986b) and >20.6 Ma at Moroto, Uganda (Gebo et al. 1997; but see Pickford et al. 1986 and Pickford et al. 1999, who feel that Moroto I and II are ca. 17–15 Ma based on biochronological comparison). Its similarity to CH14-11 in cingular, posterior crescentoid, and posterior posttrite cristae ("zygodont crest") morphology is conspicuous. For this reason, prior to its restoration CH14-11 was initially considered mammutid (Sanders and Kappelman 2001). However, in *Eozygodon* and *Zygolophodon*, another mammutid which first occurs in the early Miocene (in Europe and North Africa), molar tritolophs are complete and (in M3) associated with a pronounced posterior cingulum, meta- and tritolophs are transversely straighter and their half-lophs are not offset, and crown height and molar size are greater (Fig. 12; Tobien 1975, 1996; Tassy and Pickford 1983; Tassy 1985; Göhlich 1998, 1999; Sanders and Miller 2002).

Other aspects of crown organization in CH14-11 (ptychodonty, transverse offset of pre- and posttrite half-lophs, oblique orientation of pretrite half-lophs, and anterior advancement of pretrite mesoconelets relative to posttrite half-lophs) more closely resemble molar morphology in the oldest known choerolophodont, *Afrochoerodon kisumuensis*, documented from the early-mid Miocene sites of Wadi Moghara, Egypt (Sanders and Miller 2002), and Cheparawa and Maboko, Kenya (MacInnes 1942; Tassy 1977a, 1985, 1986; Pickford 2001). This species is possibly synonymous with *Choerolophodon palaeindicus*, presumably from the early Miocene levels of the Bugti Beds, Pakistan (Cooper

1922; Raza and Meyer 1984; Tassy 1985, 1986; see Welcomme et al. 1997, 2001). As with mammutids, however, archaic choerolophodonts also have M3s of larger size and that are more advanced in the greater development of their tritolophs and posterior cingula than CH14-11. While CH14-11 approximates M3 of *Hemimastodon* (also presumably from the early Miocene levels of the Bugti Beds, Pakistan) in size (Fig. 12), it differs from that obscure elephantoid as well in lacking full trilophodonty and in the offset of its half-lophs (Pilgrim 1912; Tassy 1988).

Because of its primitive loph formula and lack of further evidence with which to more comprehensively assess its affinities, for now we prefer to conservatively refer CH14-11 to *Palaeomastodon*. Nonetheless, the intriguing morphological and temporal intermediacy of CH14-11 between palaeomastodonts and these early Miocene taxa suggests that recovery of additional fossil material of aff. *Palaeomastodon* sp. nov. B might prove useful for refining current hypotheses (e.g., Tassy 1994a, 1996b; Shoshani 1996) about sister-group relationships between particular palaeomastodont and elephantoid taxa.

Superfamily Elephantoidea Gray, 1821
Family Gomphotheriidae Hay, 1922
cf. *Gomphotherium* sp. nov.

Figs. 15 and 16, Table 2.

Referred specimens: CH14-V-14, partial r. m3 (Fig. 16B); CH25-3, r. p4 (Fig. 15A; in same dentary as CH25-V-12a); CH25-V-12a, r. m2 (Fig. 16A; in same dentary as CH25-3; antimere of CH25-V-12b); CH25-V-12b, l. m2 (antimere of CH25-V-12a); CH25-V-12c, r. P4 (Fig. 15B).

Age and distribution: Late Oligocene, ca. 28–27 Ma. Only known from the Upper Guang and Gahar Valley Sections, Chilga region, northwest Ethiopia.

Description.—Broken anteriorly, enough of the crown of CH14-V-14 remains to show that it had at least three lophids (Fig. 16B). It also is damaged by compression fractures, but they have little affected crown dimensions and morphology. Enamel is thick (Table 2) and marked by fine horizontal striations. There is no cementum. The posterior cingulid is expanded into a stout "heel" comprised of two large conelets, an anterior accessory central conule, and a low enamel ribbon on the pretrite side. The occlusal shape of the crown posteriorly, lack of a distal interproximal facet, narrowness relative to length, and slight longitudinal occlusal concavity of the crown indicate that CH14-V-14 is an m3.

In lateral view, the lophids are torpedo-shaped, rather than pyramidal as in palaeomastodonts (Fig. 16B). The transverse valleys are occupied on the pretrite side by large posterior central accessory conules and smaller anterior central accessory conules. Pre- and posttrite half-lophids are each formed of a large, outer main conelet accompanied by a smaller, lower mesoconelet. The accessory central conules are located on the postero- and anteromedial sides of the main conelets, and at least in the last pretrite half-lophid would have formed a trefoil enamel figure with wear. Vestiges of buccal and lingual cingulids are present only as low enamel ribbons at the entrances of the transverse valleys.

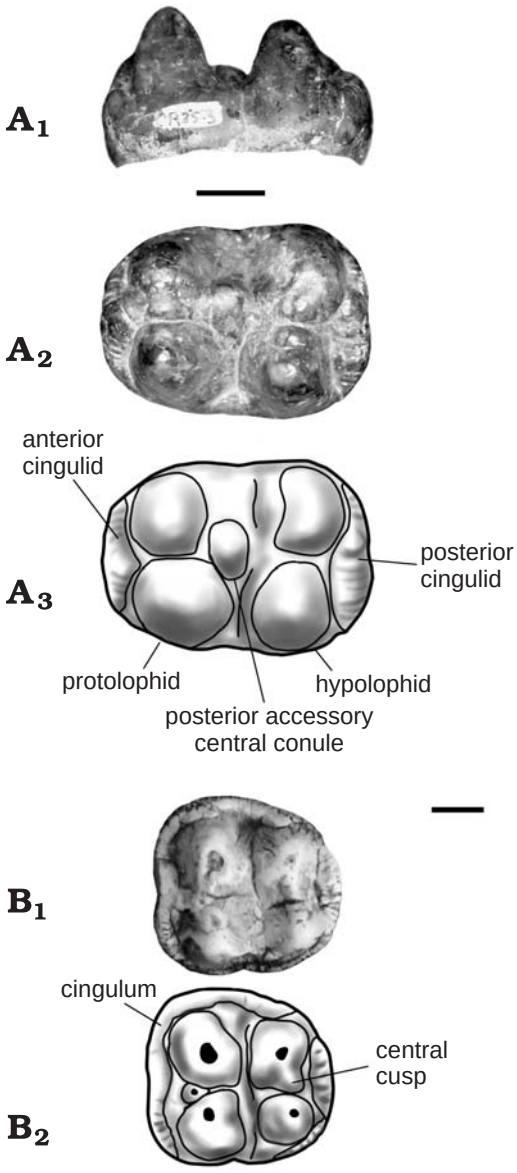

Fig. 15. Dental specimens of Chilga elephantoids, cf. *Gomphotherium* sp. nov. **A**. Right p4, CH25-3, in lingual (A_1) and occlusal (A_2, A_3) views. **B**. Right P4, CH25-V-12c, in occlusal view. Anterior is to the left. Scale bars 1 cm.

The presence of an elephantoid at Chilga is confirmed by CH25-V-12a (Fig. 16A) and b, right and left m2 antimeres. These specimens are complete, with three full lophids, and virtually unworn. They are small compared to m2 in other elephantoids (Fig. 12B). In each, the pretrite half-lophid is accompanied by anterior and posterior accessory central conules, which would have formed trefoil enamel figures with wear. Each half lophid is formed of a large main, outer conelet and a smaller, lower mesoconelet. Anterior and posterior cingulids are narrow, low, and closely appressed to their nearest lophids. As in m3, the buccal and lingual cingulids are present only as low enamel ribbons restricted to the entrances

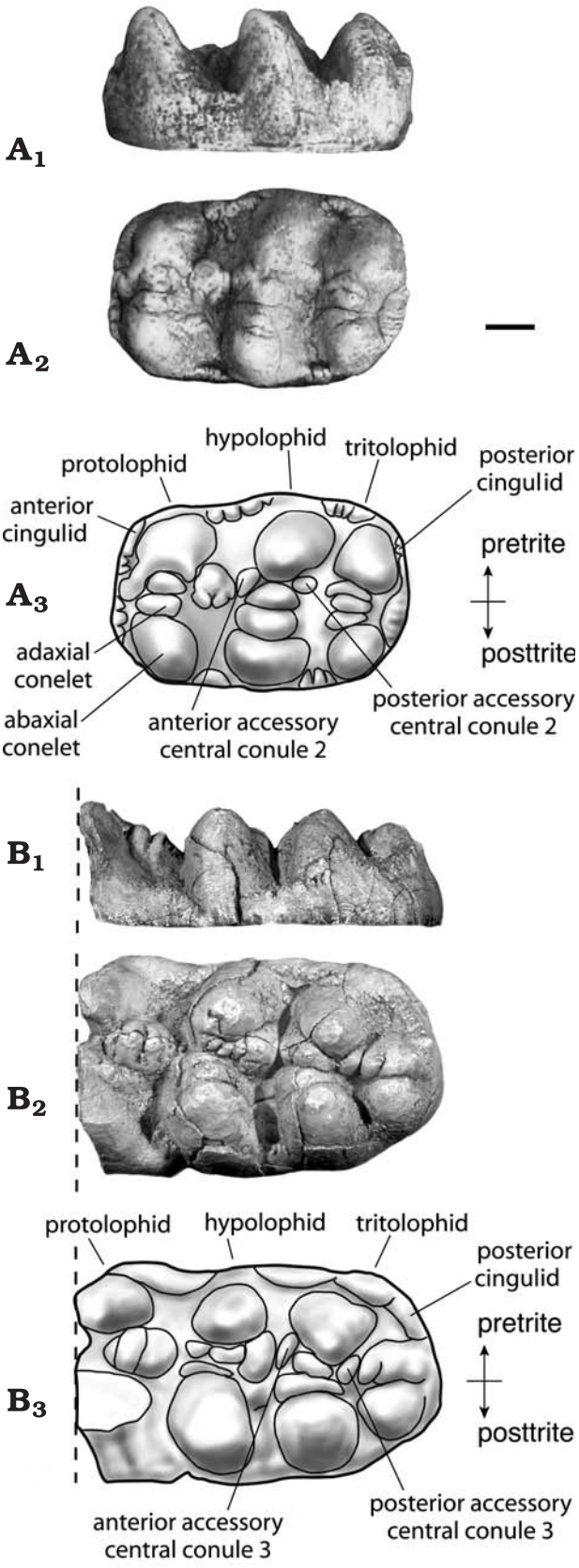

Fig. 16. Dental specimens of Chilga elephantoids, cf. *Gomphotherium* sp. nov. **A**. Right m2, CH25-V-12a, in lingual (A_1) and occlusal (A_2, A_3) views. **B**. Partial right m3, CH14-V-14, in buccal (B_1) and occlusal (B_2, B_3) views. Anterior is to the left. Broken areas indicated by dotted lines. Scale bars 1 cm.

of the transverse valleys. In occlusal view, the crown widens abruptly at the metaloph. There is a broad interproximal facet on the mesial face of the crown, and a much smaller, less distinct facet at the distal end. The alveolus anterior to the right m2 has a length of 58.6 mm and a width of 33.9 mm. The corpus below the m2 measures 94 x 94 mm.

A bilophodont right p4, CH25-3 (Fig. 15A), is in place in the same dentary as CH25-V-12a. It differs from p4 in *Phiomia major* sp. nov. in its larger size (Table 2) and greater expression of accessory conules, which with wear would have formed trefoil enamel figures on the pretrite side of the crown. The space between p4 and m2 in this individual shows that m1 would have measured 66.5 mm in length.

A right P4 (CH25-V-12c; Fig. 15B) is also likely from the same individual. It is morphologically similar to P4 in *Phiomia major* sp. nov., but is larger (Table 2) and has a better developed central cusp in its posterior loph. Also, the prominent enamel swelling on the anterior face of the second pretrite half-loph resembles the condition of P4 in *Gomphotherium* (Fig. 15B; see Tassy 1985).

Comments.—These specimens are morphologically distinct among Chilga elephantiform teeth. They differ from cheek teeth of palaeomastodonts and resemble elephantoid teeth by the prominent posterior "heel" in m3, in having highly reduced bucco-lingual cingulids, lophids that are torpedo-shaped rather than pyramidal in lateral view, last lophids with distinct abaxial and adaxial conelets on both pre- and posttrite sides, and by the presence of anterior and posterior accessory central conules throughout the length of the crown. Overall, they most closely resemble cheek teeth of *Gomphotherium*, particularly by their rounded conelets, transverse continuity of half-lophs, and trefoil arrangement of outer main conelets and accessory conules on the pretrite side.

It is difficult to more precisely assess the affinities of these specimens because the m3 (CH14-V-14) is incomplete and many features diagnostic of Elephantoidea are cranial (Shoshani 1996; Tassy 1996b). Although the presence of a fourth lophid in m3 is considered a defining trait of elephantoids by Shoshani (1996), this feature is variable in *Gomphotherium* (Tassy 1996c; Lambert and Shoshani 1998; Sanders and Miller 2002). Consequently, although the number of lophids originally present in CH14-V-14 is uncertain, even with only three it could still be elephantoid.

These teeth constitute the earliest appearance of the superfamily Elephantoidea, and considerably extend its temporal range. The oldest prior record of elephantoids is that of *Eozygodon* from the earliest Miocene (see above); the most ancient certain occurrences of *Gomphotherium* are slightly younger and penecontemporaneous in Africa and Eurasia, from the interval ca. 20–18 Ma (Tassy 1985, 1986, 1989, 1994b, 1996c; Pickford 1986b; Welcomme 1994; Mazo 1996; Sanders and Miller 2002). If a molar from the Aquitanian of Sicily is really that of *Gomphotherium* (Checchia-Rispoli 1914), the genus would be older yet by several million years, but still geologically younger than the Chilga specimens.

Specimen CH14-V-14 is also the smallest m3 formally attributed to Elephantoidea, though m3 of a proboscidean of similar morphological grade from slightly younger deposits at Dogali, Eritrea is even more diminutive (Shoshani et al. 2001). If CH14-V-14 had three lophids, it could reasonably be reconstructed to a length of approximately 100 mm, slightly shorter than the smallest, early–mid Miocene "pygmy" gomphotheres from Ghaba, Oman (Roger et al. 1994), Siwa, Egypt (Hamilton 1973), Gebel Zelten, Libya (Arambourg 1961; Gaziry 1987), and Kabylie, Algeria (Depéret 1897). CH14-V-14 thus resembles other elephantiform molars in the Chilga assemblage in being intermediate between earlier Oligocene palaeomastodonts and Miocene elephantoids not only in age but in size.

Discussion

The new fossil assemblage from the late Paleogene site of Chilga is similar to mammalian faunas of the older, well-known localities of the Fayum in the shared occurrence of many of the same hyrax, embrithopod, and palaeomastodont genera (Andrews 1906; Matsumoto 1924, 1926; Meyer 1978; Tanner 1978; Court 1989; Rasmussen 1989; Gagnon 1997; Kappelman et al. 2003). This similarity is remarkable in light of their tremendous differences in geological time, distance, and elevation (Kappelman et al. 2003). The presence of Fayum taxa at Chilga and at Malembe, Angola (Pickford 1986a), as well as in the Arabian Peninsula (Thomas et al. 1989a, b, 1999) and across North Africa (Coryndon and Savage 1973), indicates a pan-Afro-Arabian distribution of this archaic, endemic mammalian fauna throughout the Oligocene. As the climate of eastern Africa was wetter during the late Oligocene–early Miocene than now, it is possible that expansion of Fayum-type mammals into highland Ethiopia was promoted by concomitant eastward extension of western evergreen forests throughout the region (Andrews and Van Couvering 1975). The emerging biogeographic evidence could also be interpreted to suggest that these archaic endemics had broader ecological tolerances than previously suspected.

The paenungulate herbivores and other mammals comprising the Chilga fauna are all large-to-very large in body size (Gagnon 1997), suggesting taphonomic bias against the preservation of small- and medium-sized animals at the localities sampled thus far, possibly caused by diagenetic leeching of bone (Kappelman et al. 2003). This is unfortunate, as recovery of small- and medium-sized mammals from the time period represented by Chilga would be of great value for resolving questions about the phylogeny and timing of first appearances of several important taxa whose inaugural Afro-Arabian records are in or near the beginning of the early Miocene. For example, the earliest record of hominoids is at Lothidok, Kenya at the very end of the Oligocene (Leakey et al. 1995), but they are widely separated in morphology and by a temporal gap of about eight million years from basal catarrhine precursors in the Fayum sequence (Simons and Rasmussen 1994).

Morphological and metrical analyses of the Chilga fossil mammals demonstrate not only the persistence of an archaic, endemic Afro-Arabian assemblage into the late Oligocene, but continued evolution of the groups represented. All Chilga taxa are either new or differ at the species level from those present in the Fayum sequence, marked particularly in the embrithopods and palaeomastodonts by increased size compared with their older congeners. Moreover, compared with Fayum predecessors, the Chilga paenungulates exhibit novel dental adaptations for processing and acquiring food, such as the formation of additional crests in hyrax cheek teeth (Rasmussen et al. in prep.), greater molar hypsodonty in the arsinoithere, and disproportionate elongation of tusks in at least one palaeomastodont species. Most notably, the Chilga fauna includes the oldest known deinotheres and elephantoids, whose prior fossil records did not extend before the early Miocene (Shoshani and Tassy 1996). These proboscideans are typical members of early Miocene Afro-Arabian replacement faunas, but their evolutionary connections to older proboscideans—numidotheres, barytheres, moeritheres, and palaeomastodonts—are sketchy, particularly for deinotheres (Harris 1978; Shoshani et al. 1996). The recovery of elephantoids and deinotheres from Chilga, then, constitutes a potentially important step in reconstructing their phylogenetic histories. For instance, dental features of the Chilga deinotheres point to a bunolophodont ancestry. This supports the hypothesis that deinotheres derived from moerithere-like progenitors (Harris 1978), and suggests that their acquisition of tapiroid, lophodont teeth by the Miocene occurred in convergence to earlier development of a similar occlusal morphology in barytherioid proboscideans (barytheres + numidotheres; Court 1995; Gheerbrant et al. 2002).

In contrast, there is no evidence in the Chilga assemblage of other large-bodied mammals, with Eurasian pedigrees, such as rhinos, suids, and bovids, that also distinguished faunal turnover in the early Miocene of Afro-Arabia (Coryndon and Savage 1973; Van Couvering and Van Couvering 1976; Maglio, 1978). This helps constrain the dating of the Eurasian immigration event, and suggests an autochthonous African origination of deinotheres and elephantoids predating and not initially influenced by that occurrence.

Afro-Arabia appears to have been geographically isolated from Eurasia throughout most of the early Paleogene, leading to the establishment of mammalian communities characterized by a high degree of endemicity (Coryndon and Savage 1973; Maglio 1978; Holroyd and Maas 1994). Consequently, late Eocene–early Oligocene mammalian faunas of Arabia and North Africa, and probably much of the rest of Africa as well, were populated by a distinct mix of taxa, such as creodonts, saghatheriids, arsinoitheres, moeritheres, barytheres, palaeomastodonts, early anthropoid primates, and anthracotheriid artiodactyls (Coryndon and Savage 1973; Fleagle 1986; Thomas et al. 1989a,b; 1999; Simons and Rasmussen 1994; Gagnon 1997; Holroyd 1999).

Biogeographic separation of Afro-Arabia from Eurasia was apparently maintained into the late Paleogene by the interposition of the Mediterranean and Paratethys seas between these landmasses and continued lack of a land bridge between the regions (Rögl 1998; Harzhauser et al. 2002). Movement of animals between these regions (see Rasmussen 1994) was probably limited to sweepstakes dispersal (Holroyd and Maas 1994). There is some debate about the timing of contact between the Arabian and Anatolian plates and establishment of a stable, long-term land connection of Eurasia with Afro-Arabia (Adams et al. 1999). Land corridors are alternatively hypothesized to have been available during the mid-Oligocene (Haq et al. 1987; Janis 1993), latest Oligocene–earliest Miocene (Drooger 1979, 1993; Adams et al. 1983, 1999; Whybrow 1984), or late Burdigalian (late early Miocene; Steininger and Rögl 1979; Rögl and Steininger 1983, 1984; Thomas 1985; Rögl 1998, 1999; Harzhauser et al. 2002).

Likewise, questions have been posed about whether replacement of archaic, endemic Afro-Arabian faunas largely by Eurasian taxa was truly episodic or occurred progressively (Pickford 1981; Thomas 1985; Tchernov et al. 1987). The introduction of Eurasian large mammal forms into Afro-Arabian faunas may have been phased, becoming significant only by MN3b-equivalent times (ca. 18 Ma; Andrews and Van Couvering 1975; Tchernov et al. 1987), or later (Van Couvering and Van Couvering 1976). With the possible exception of a tragulid, the earliest Miocene mammalian fauna of East Africa, as represented at Meswa Bridge, Kenya (ca. 23 Ma), was composed of new endemics (Pickford 1986b; Agustí and Antón 2002) that may have evolved locally from earlier taxa like those known from the Fayum (e.g., the giant creodont *Hyainolouros*, which appears to be closely related to Fayum *Pterodon* [Holroyd 1999]). It was succeeded by faunas rich in Eurasian taxa including rhinos, fissiped carnivores, suids, insectivores, chalicotheres, and rodents at sites such as Songhor, Kenya, and Napak I, Uganda, ca. 20–19 Ma (Andrews and Van Couvering 1975; Bernor et al. 1987; Agustí and Antón 2002; Guérin and Pickford 2003). Gomphotheres, mammutids, and deinotheres entered Eurasia from Afro-Arabia in successive migrations around this time or slightly after (Tassy 1989). An increase in ruminant (pecoran and tragulid) diversity is documented in East Africa during the interval 20–18 Ma (Pickford 2002). The entry of Eurasian horned bovids, antlered giraffoids, and listriodont suids into Afro-Arabian communities appears to represent a subsequent, late early–middle Miocene wave of immigration (ca. 17–16 Ma; Pickford 1981).

Along with the results of previous research, the new finds from Chilga focus attention on the interval between 28 and 20 Ma for resolving questions about mid-Tertiary Afro-Arabian mammalian turnover. At the beginning of this time span in Afro-Arabia, Fayum genera persisted and there is no sign of an influx of large-bodied Eurasian mammals; however, it also marks the first appearance of deinotheres and elephantoids, proboscideans usually identified with the replacement faunas of the Miocene. This suggests that their genesis preceded and was unrelated to paleobiogeographical and ecological factors driving the immigration of Eurasian large-bodied mammals into Afro-Arabia. Toward the end of this interval, palaeomastodonts, many of the hyraxes, arsinoitheres, and other archaic endemics disappeared from the fossil record, and Eurasian forms were in ascendancy in Afro-Arabian faunas. Despite this biochronological refinement, important questions remain about the fate of these archaic endemics toward the end of this interval, especially regarding the relative contributions to their extinction of global and regional climatic change (Flower and Kennett 1994) versus competition with immigrant taxa. We believe that further collection and study of mammalian assemblages from Chilga and similar-aged sites (such as the Erageleit Beds at Lothidok, Kenya) will better elucidate the paleobiological factors that influenced differential survival of archaic endemics and engendered immigrant success at the start of the Neogene in Afro-Arabia.

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