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Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

New adapiform primate of Old World affinities from the Devil's Graveyard Formation of Texas

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ARTICLE INFO

Article history:

Received 15 December 2010

Accepted 18 February 2011

Keywords:

Adapidae
 Caenopithecinae
 Cercamoniinae
 Asiadapinae
 Notharctinae
 Eocene
 Uintan
Mescalerolemur
Mahgarita

ABSTRACT

Most adapiform primates from North America are members of an endemic radiation of notharctines. North American notharctines flourished during the Early and early Middle Eocene, with only two genera persisting into the late Middle Eocene. Here we describe a new genus of adapiform primate from the Devil's Graveyard Formation of Texas. *Mescalerolemur horneri*, gen. et sp. nov., is known only from the late Middle Eocene (Uintan) Purple Bench locality. Phylogenetic analyses reveal that *Mescalerolemur* is more closely related to Eurasian and African adapiforms than to North American notharctines. In this respect, *M. horneri* is similar to its sister taxon *Mahgarita stevensi* from the late Duchesnean of the Devil's Graveyard Formation. The presence of both genera in the Big Bend region of Texas after notharctines had become locally extinct provides further evidence of faunal interchange between North America and East Asia during the middle Eocene. The fact that *Mescalerolemur* and *Mahgarita* are both unknown outside of Texas also supports prior hypotheses that low-latitude faunal assemblages in North America demonstrate increased endemism by the late middle Eocene.

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Introduction

The evolution of adapiform primates in North America has been particularly well studied at Wasatchian (early Eocene) and Bridgerian (early middle Eocene) localities in the western interior of the United States (Matthew, 1915; Gazin, 1958; Gingerich and Simons, 1977; Gingerich, 1979, 1995; Covert, 1985; Krishtalka et al., 1990; Gunnell, 1995, 2002; O'Leary, 1996). The earliest adapiform species known from North America, the notharctine *Cantius torresi*, appears at the beginning of the Wasatchian during the carbon isotope excursion that marks the Paleocene–Eocene boundary (Gingerich, 2003). *C. torresi* is almost certainly an immigrant from Eurasia, due to its abrupt appearance in the North American fossil record and the presence of two additional species of *Cantius* in Europe (*Cantius eppsi* and *Cantius savagei*) (Gingerich, 1986, 2003; Godinot, 1998; Beard and Dawson, 1999; Bowen et al., 2002). Furthermore, *Cantius* is probably ancestral to all subsequent North American notharctine genera (*Copelemur*, *Hesperolemur*, *Notharctus*, *Pelycodus*, and *Smilodectes*) (Gingerich and Simons, 1977; Gingerich, 1986; Godinot, 1998). The diversification of notharctines in North America primarily occurred in the Wasatchian, and most genera do not persist

beyond the Bridgerian. Indeed, *Hesperolemur* and *Notharctus* are the only notharctine genera currently known from the Uintan (late middle Eocene) of North America (Gunnell, 1995; Godinot, 1998; Robinson et al., 2004).

Much less is known about adapiform evolution in southwest Texas, where numerous Eocene vertebrate localities have been discovered in the Big Bend region, the Sierra Vieja, and the Gulf Coastal Plain (Wilson, 1986; Runkel, 1988; Westgate, 1990; Robinson et al., 2004; Williams and Kirk, 2008). In the Devil's Graveyard Formation of the Big Bend region (Stevens et al., 1984; Wilson, 1986), notharctine adapiforms are represented by a single genus (*Notharctus*) known locally only from early Uintan (Ui1) localities at the base of the stratigraphic section (West, 1982; Williams and Kirk, 2008). Despite intensive collecting at late Uintan (Ui3) localities in the Devil's Graveyard Formation since 2005, notharctines have not been recovered from higher in the stratigraphic column and are presumed to have become locally extinct after the early Uintan. Nonetheless, adapiforms were again present in the Devil's Graveyard Formation by the early Duchesnean, as documented by the appearance of the adapiform *Mahgarita stevensi* (Wilson and Szalay, 1976; Wilson, 1986; Williams and Kirk, 2008).

M. stevensi is of particular significance to understanding Eocene holarctic primate evolution because for many years it has remained the only adapiform known from North America that is not a notharctine (Wilson and Szalay, 1976; Godinot, 1998). *Mahgarita*

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was initially described on the basis of a crushed cranium and mandible recovered in 1973 from the early Duchesnean Teepee Canyon locality of the Devil's Graveyard Formation (Wilson and Szalay, 1976). Since that time, two additional specimens of *Mahgarita* have been recovered from the early Duchesnean of the Devil's Graveyard Formation – a second crushed cranium and a partial basicranium (Rasmussen, 1990). Additionally, Westgate et al. (2010) have reported the presence of *Mahgarita* at the late Uintan Lake Casa Blanca locality near Laredo on the basis of an isolated upper molar.¹ Most cladistic analyses have supported the hypothesis that *Mahgarita* is an immigrant from the Old World that is most closely related to Eurasian or African adapiforms (Kay et al., 1997; Ross et al., 1998; Seiffert et al., 2009, 2010; Boyer et al., 2010; but see Rasmussen, 1990).

Here we report the discovery of a new Texas adapiform with Old World phylogenetic affinities, *Mescalerolemur horneri*. This new genus and species is known only from the Purple Bench locality of the Devil's Graveyard Formation (Wilson, 1986; Williams and Kirk, 2008). The vertebrate fauna from Purple Bench is late Uintan, dating either to Chrons C20R or C18R with an absolute age of approximately 44–41 Ma (Williams and Kirk, 2008). In the Devil's Graveyard Formation, the Purple Bench locality underlies the early Duchesnean localities that have produced the only definitive specimens of *M. stevensi* (Wilson, 1986; Williams and Kirk, 2008). *Mescalerolemur* shares a number of derived dental features with *Mahgarita*, and is only the second non-notharctine adapiform genus to be described from North America. *Mescalerolemur* thus provides additional evidence of faunal exchange between Eurasia and North America in the Middle Eocene, and reinforces the conclusion that primate faunas from Texas displayed increased endemism by the late Uintan (Simpson, 1947; Black and Dawson, 1966; Beard and Wang, 1991; Beard et al., 1994; Williams and Kirk, 2008).

Materials and methods

The fossils of *Mescalerolemur* and *Mahgarita* described here are housed in the collections of the Texas Memorial Museum at the University of Texas (Austin, Texas, United States). The comparisons made in this paper are based primarily on the study of epoxy resin casts of fossils from other localities. Additionally, published scanning electron micrographs, photographs, and drawings were used to supplement our comparisons (Simons, 1962, 1997; Russell et al., 1967; Szalay, 1971, 1974; Gingerich, 1975, 1977; Gingerich and Sahni, 1979, 1984; Szalay and Delson, 1979; Schwartz and Tattersall, 1983; Russell and Gingerich, 1987; Godinot, 1988, 1998; Thalmann et al., 1989; Hartenberger and Marandat, 1992; Thalmann, 1994; Ducrocq et al., 1995; Qi and Beard, 1998; Gebo, 2002; Franzen, 2004; Beard et al., 2007; Rose et al., 2007, 2009; Chaimanee et al., 2008; Gunnell et al., 2008; Franzen et al., 2009; Seiffert et al., 2009; Marigó et al., 2010). All observations of dental anatomy are our own and are readily observable in casts or published figures unless otherwise noted. Dental measurements (Table 1) were made using either digital calipers or a stereomicroscope fitted with a calibrated reticle.

Abbreviations: BNM = Basel Natural History Museum; MNM = Mainz Natural History Museum; TMM = Texas Memorial Museum; c = mandibular canine; p = mandibular premolar; m = mandibular molar; C = maxillary canine; P = maxillary premolar; M = maxillary molar.

¹ Having examined this specimen, we agree with Westgate et al. (2010) that his molar is clearly that of an adapiform similar to *M. stevensi*. However, the Lake Casa Blanca specimen differs from definitive *M. stevensi* from the Devil's Graveyard Formation in a number of key dental features (e.g., it has a reduced styler region) and thus probably represents a new, more primitive species of *Mahgarita*.

Systematic paleontology

Order Primates Linnaeus, 1758
 Semioorder Strepsirrhini Pocock, 1918
 Suborder Adapiformes Hoffstetter, 1977
Mescalerolemur, gen. nov.
 Type species: *M. horneri*, sp. nov.

Generic diagnosis

Adapiform primate that differs from omomyiforms in having a very small m1 paraconid and in lacking an m1 trigonid basin. Differs from notharctines² in having a cingular hypocone on upper molars. Differs from sivaladapids in having a diminutive m1 hypoconulid that is not twinned with the entoconid. Differs from all other adapiforms except *Mahgarita* in having a simple p4 with the following characteristics: occlusal profile oval and buccolingually compressed; lacks talonid basin; lacks paraconid, metaconid, entoconid, and hypoconulid; hypoconid located directly distal to protoconid³; hypoconid connected to protoconid by a centrally placed (midline) cristid obliqua. Further differs from other adapiforms except *Mahgarita* in having a P3 with a lingual root located directly lingual to the distobuccal root, a flat mesiolingual crown face that is oriented strongly obliquely relative to the buccolingual axis, and an occlusal profile that approximates a right triangle. Differs from notharctines, adapines, sivaladapids, asiadapines, *Donrussellia*, *Anchomomys*,⁴ *Periconodon*, *Pronycticebus*, *Djebelemur*,⁵ *Afradapis*, *Aframoni*, and most species of *Protoadapis* and *Europolemur* in having extremely reduced, single-rooted p2/P2 located mesiolingual to the mesial root of p3/P3. Differs from adapines, notharctines, *Donrussellia*, *Protoadapis*,⁶ *Pronycticebus*, *Marcgodinotius*, *Anchomomys*,⁷ and *Periconodon*⁸ in lacking a p1/P1. Differs from *Adapoides* in having buccolingually broader lower molars, in having an m3 with a shorter mesial shelf, a broader less heel-like hypoconulid, and a smaller more crestiform entoconid, and in having upper molars with broader lingual and distal cingula and a larger hypocone. Differs from *Barnesia* in having a more mesially positioned P4 protocone, in having larger hypocones and a broader distal cingulum on M1–2, and in having a smaller M2 pericone. Differs from *Buxella* in having larger M1–2 hypocones and metaconules, in having complete lingual cingula on M1–3, in lacking an M3 pericone, and in having a shorter, less shelf-like m1 paracristid. Differs from *Mahgarita* in being substantially smaller and in exhibiting the following dento-gnathic features: mandibular symphysis unfused; maxilla with a less prominent rugosity for the

² The adapiform families and subfamilies used here follow Godinot (1998) and Rose et al. (2009).

³ Details of the hypoconid and cristid obliqua are obscured by wear in the only known p4 of *Mahgarita* (TMM 41578-8).

⁴ Following Godinot (1998) and Gebo (2002), we herein treat *Hürzeleris* (Szalay, 1974) and *Fendantia + Laurasia* (Schwartz and Tattersall, 1983) as junior synonyms of *Anchomomys*. Furthermore, Seiffert et al. (2005a) have shown that "*Anchomomys milleri* (Simons, 1997) is not closely related to definitive European members of the genus *Anchomomys*. The type specimen of "*Anchomomys milleri* lacks a p1 but retains a large p2 (Simons, 1997). Assessments of p2/P2 size in definitive *Anchomomys* are based on alveolus size.

⁵ We follow the interpretation of Hartenberger and Marandat (1992) based on alveolar morphology that *Djebelemur* probably lacked a p1 but retained a two-rooted p2.

⁶ In *Protoadapis curvicaudatus* and *P. angustidens*, p1 is variably present or absent (Russell et al., 1967).

⁷ Preserved alveoli strongly suggest that *Anchomomys* retained a p1 (e.g., *A. pygmaeus*; BNM Eh 748) and P1 (e.g., *A. quercyi*; BMN QH 470).

⁸ This assessment is based on the presence of a p1 alveolus in MNM PW-1995/8-LS (Franzen, 2004).

Table 1
Dental dimensions of all known specimens of *Mescalerolemur horneri* and *Mahgarita stevensi*. * = measurement based on root or alveolus; ** = estimated from damaged tooth.

Upper dentition															
Taxon	Catalogue number	C Length	C Width	P2 Length	P2 Width	P3 Length	P3 Width	P4 Length	P4 Width	M1 Length	M1 Width	M2 Length	M2 Width	M3 Length	M3 Width
<i>Mescalerolemur horneri</i>	41672-232 (holotype)	3.23*	2.37*	0.78*	0.68*	2.93	2.50	2.64	3.30	3.13	3.80	3.13	4.10	2.45	3.35
<i>Mahgarita stevensi</i>	41578-9 (holotype)	3.62	2.26	0.98	0.86	3.23	3.10	2.74	3.74	3.62	4.40	3.62	4.89**	3.03	4.41
<i>Mahgarita stevensi</i>	41578-20	4.32	3.15			3.13	3.06	2.84	3.96	3.82	4.96	3.62	5.31	3.23	4.89

Lower dentition															
Taxon	Catalogue number	c Length	c Width	p2 Length	p2 Width	p3 Length	p3 Width	p4 Length	p4 Width	m1 Length	m1 Width	m2 Length	m2 Width	m3 Length	m3 Width
<i>Mescalerolemur horneri</i>	41672-230													3.42	2.05
<i>Mescalerolemur horneri</i>	41672-233		2.15*	0.80*	1.20*	3.13	1.96	3.03	1.96	3.23	2.25				
<i>Mescalerolemur horneri</i>	41672-236							3.13	1.86	2.93	2.05				
<i>Mahgarita stevensi</i>	41578-8	2.93	1.96	1.20*	1.10*	3.23	1.86	3.33	2.11	3.67	2.53	3.67	2.65	4.21	2.40

anterior masseter on the zygomatic process and lacking a well-developed fossa supero-lateral to M2; p4 lacking a continuous lingual cingulid and lacking a lateral protocristid; m3 with a more lingually positioned hypoconulid, a cristid obliqua that meets the protoconid more buccally, and a paracristid that meets the premetacristid to form a complete mesial crest connecting the protoconid and metaconid; P3 lacking a distinct protocone and having a smaller distolingual basin with a deeper invagination of the distal margin; P4 with a more waisted and trapezoidal occlusal profile, a mesiodistally narrower lingual half, lacking a lingual cingulum, with a protocone situated more mesially than the paracone, and with a trenchant and elevated preprotocrista; M1–2 with a less rectangular and more trapezoidal occlusal profile, a narrower stylar region, and lacking mesostyles; M1–3 lacking enamel crenulation; M3 buccolingually narrower than M1 and lacking a hypocone. Also lacks the “twinned” M2 hypocone and accessory cusps in the M1–M2 trigon basins that are variably found in *Mahgarita* (see below).

Etymology

The generic name derives from the *Mescalero* Apache, in combination with *lemur* to acknowledge the strepsirrhine affinities of adapiform primates. The *Mescalero* Apache are a Southern Athabaskan Native American group who occupied the Big Bend region of Texas and adjacent lands in the 18th and 19th centuries.

Mescalolemur horneri, sp. nov. (Figs. 1–5, Table 1)

Holotype

TMM 41672-232, associated left and right maxillae with partial left P3–P4 crowns, complete left M1–M3, right C root, complete right P2–M1, and partial right M2 crown.

Hypodigm

TMM 41672-230, right mandibular fragment with complete m3; TMM 41672-233, right partial mandible with partial c alveolus, complete p2 alveolus, and complete p3–m1; TMM 41672-236, right mandibular fragment with complete p4–m1.

Horizon

Locality TMM 41672 (Purple Bench) of the Devil's Graveyard Formation, Midwestern State University Dalquest Research Site, Brewster County, Texas.

Specific diagnosis

As for genus.

Etymology

In honor of Dr. Norman Horner, Entomologist and Professor of Biology at Midwestern State University, for the many years he has spent undertaking and facilitating scientific research in the Big Bend region of Texas.

Description

Mescalolemur horneri is a relatively small adapiform primate, with teeth broadly similar in size to those of *Cantius torresi* from the early Eocene of North America and *Cantius eppsi* from the early Eocene of Europe. The areas of the maxillary and mandibular first molars of *Mescalerolemur* are approximately 63% of the size of those in the related genus *Mahgarita* (Table 1). Using Conroy's (1987) all-primate regression for m1 area, the body mass of *Mescalerolemur* is estimated to be 371 g (range: 136–1013 g). Although most known adapiform species are estimated to have been considerably larger than 371 g (Fleagle, 1999), several taxa (notably *Donrussellia*, *Anchomomys*, *Periconodon*, *Marcgodinotius*, and *Panobius*) were clearly smaller than *Mescalerolemur* based on dental dimensions (Szalay and Delson, 1979; Godinot, 1988, 1998, Franzen, 2004; Gunnell et al., 2008; Rose et al., 2009).

Corpus depth relative to crown height cannot be assessed in any of the three known mandibular specimens due to damage of the inferior margin of the corpus. Nonetheless, it is clear that corpus depth was more than twice that of m1 crown height (Fig. 2). The number of mental foramina on the external surface of the mandibular corpus is variable. TMM 41672-233 has two oval mental foramina: one larger foramen inferior to the lamina of bone separating the canine and p2 alveoli, and one smaller foramen inferior to the distal root of p3. By comparison, TMM 41672-236 exhibits only a single oval foramen inferior to the position of the p2

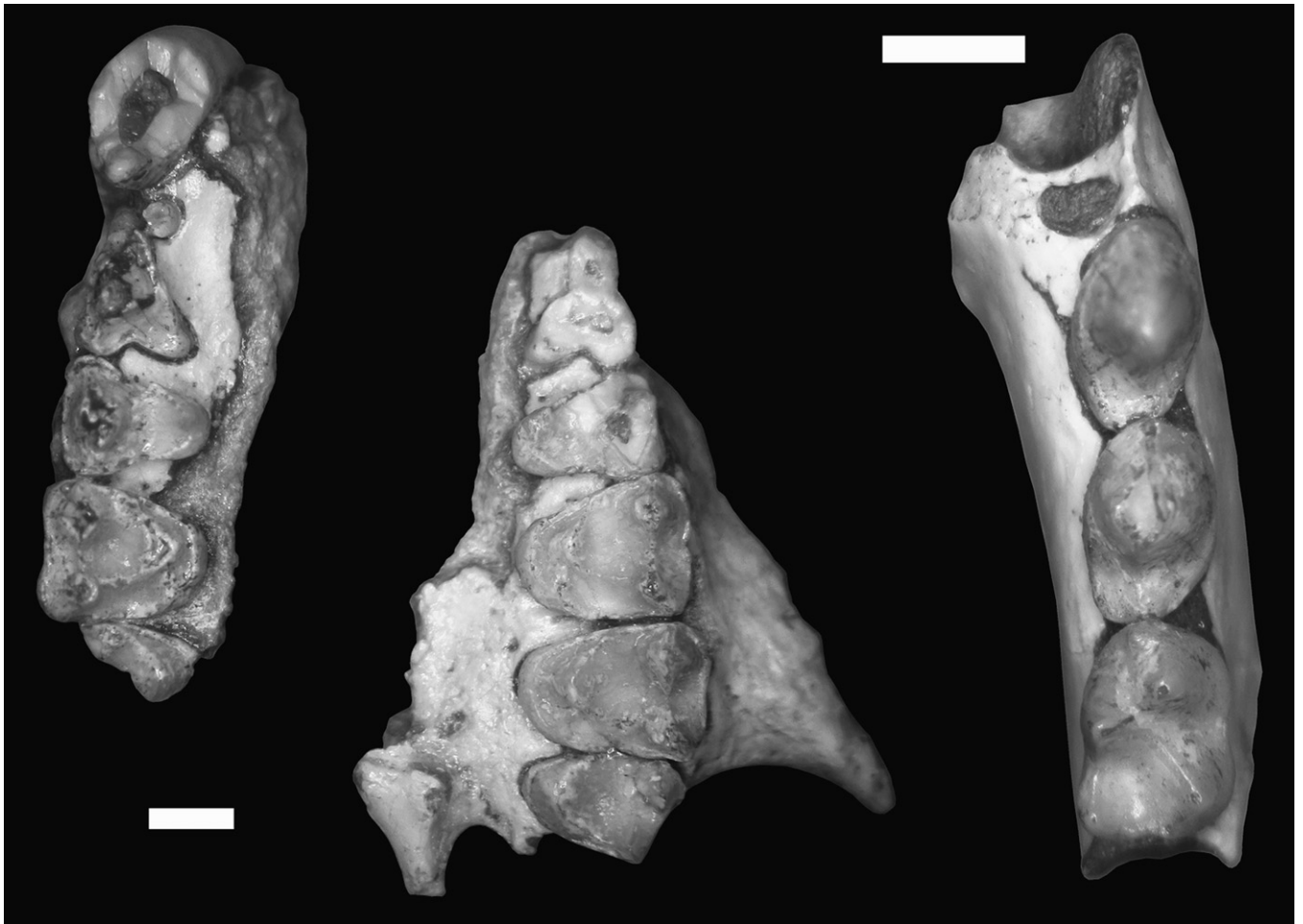


Figure 1. Occlusal views of partial palate (TMM 41672-232 holotype, at left in two parts) and mandible (TMM 41672-233) of *Mescalerolemur horneri*. TMM 41672-232 includes the right C root, right P2-M1, right partial M2, and left P3-M3. TMM 41672-233 includes the c and p2 alveoli and p3-m1. The two specimens are not shown at the same scale. Scale bars for both specimens equal 2 mm.

(which is not preserved). TMM 41672-233 preserves two additional features worthy of comment. First, a portion of the inferior mandibular symphysis is preserved in the specimen, revealing that the reciprocal symphyseal surfaces in the left and right dentaries

were rugose but not fused (Fig. 2). There is no evidence of a superior transverse torus at the symphysis, but the presence or absence of this feature is difficult to ascertain with certainty because the inferior margin of the symphyseal region is not preserved. Second, there is a slight depression of the external surface of the mandibular corpus lateral to the canine and p2 alveoli and superior to the larger mental foramen. The fossa would presumably have accommodated a projecting maxillary canine. The presence of such a canine fossa, combined with the large size of the lower canine alveolus, suggests that both the maxillary and mandibular canines were relatively large in *Mescalerolemur*.

Incisors have not been recovered for *Mescalerolemur*. The mandibular canine and p2 of *Mescalerolemur* are also not preserved in the four known specimens, but the alveoli for both teeth are present in TMM 41672-233 (Figs. 1 and 2). The partial canine alveolus is oval in horizontal cross-section, with its long axis oriented ~40 degrees from the plane of the mandibular symphysis. The canine alveolus is also relatively large and deep, extending at its base to within a millimeter of the surface of the mandibular symphysis. Judging from the size of the alveolus, the root of the mandibular canine was evidently larger at the level of the alveolar process than the roots of any other preserved teeth in this specimen. By comparison, the p2 alveolus is much smaller than the adjacent alveoli for the canine and the p3. The p2 alveolus is elliptical in horizontal cross-section, mesiodistally compressed, and is located mesiolingual to the mesial root of the p3.

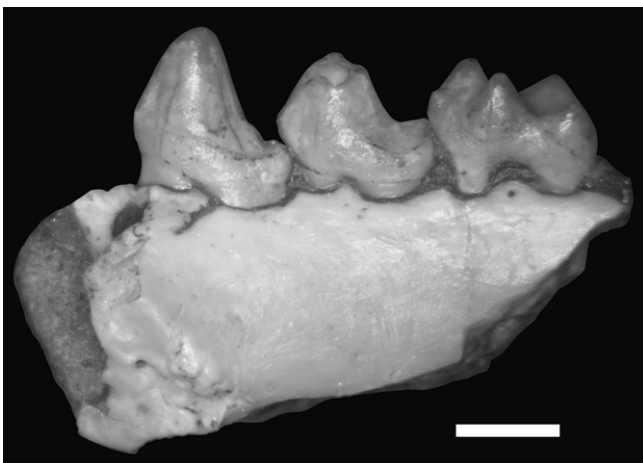


Figure 2. Lingual view of partial mandible with p3-m1 (TMM 41672-233) of *Mescalerolemur horneri*. Scale bar equals 2 mm.

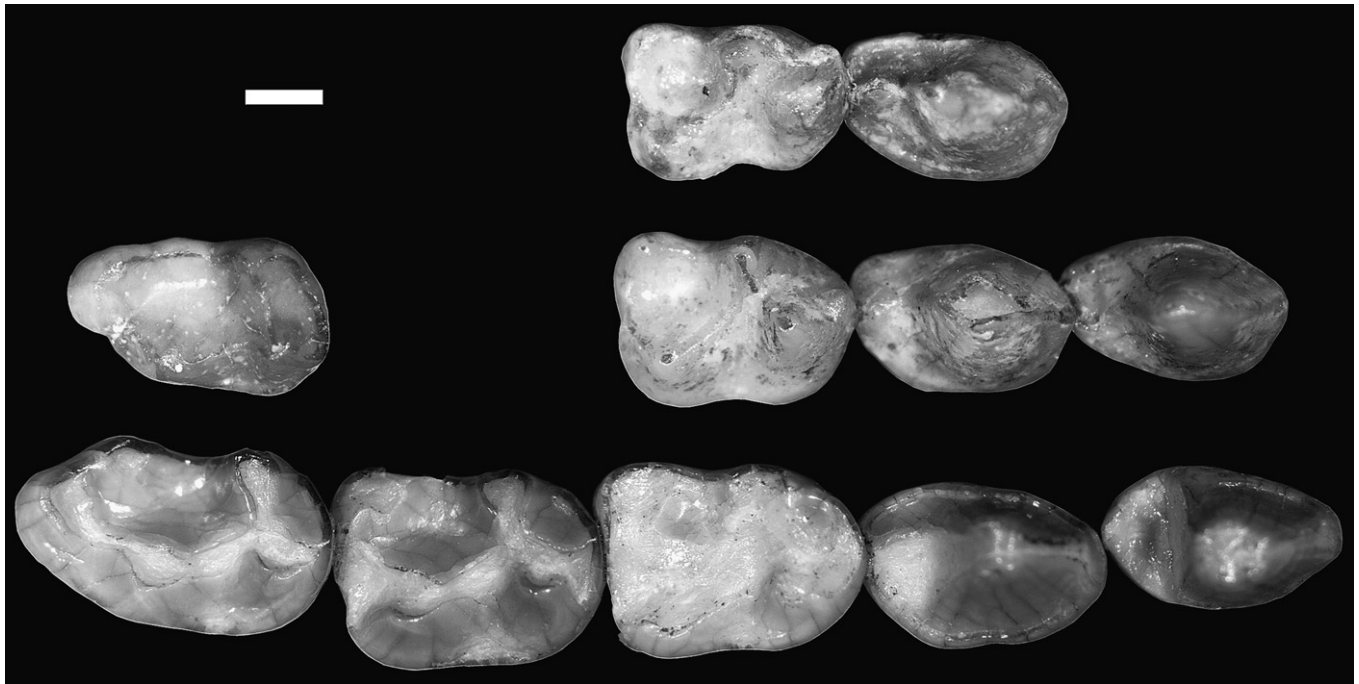


Figure 3. Occlusal view of the mandibular dentitions of *Mescalerolemur horneri* (top two rows) and *Mahgarita stevensi* (bottom row). Top row: TMM 41672-236 (p4–m1); Middle row: TMM 41672-233 (p3–m1) and TMM 41672-230 (m3); Bottom row: TMM 41578-8(p3–m3); Scale bar equals 1 mm.

There is no evidence for diastemata between the canine and p2, or the p2 and p3. The p2 of *Mescalerolemur* was evidently a diminutive single-rooted tooth that was lingually displaced and closely appressed between the much larger canine and p3.

The p3 of *Mescalerolemur* is a simple tooth dominated by a large protoconid (Figs. 2 and 3). It is oval in occlusal profile and buccolingually compressed. The p3 has two roots and the mesial root is displaced buccally. As a result, the mesiodistal (long) axis of the p3 crown is oriented obliquely relative to the mesiodistal axis of the

mandibular corpus. The p3 crown lacks any trace of a paraconid, metaconid, entoconid, or hypoconulid. The only p3 cusp other than the protoconid is a tiny hypoconid, located distobuccally on a very short talonid shelf. Weakly developed crests (the paracristid and protocristid) run directly mesially and distally from the apex of the protoconid. Buccal and lingual cingulids are present but weakly developed.

The p4 of *Mescalerolemur* is a simple but distinctive premolariform tooth (Figs. 2 and 3). Like the p3, the p4 is oval in occlusal profile, buccolingually compressed, has weakly developed

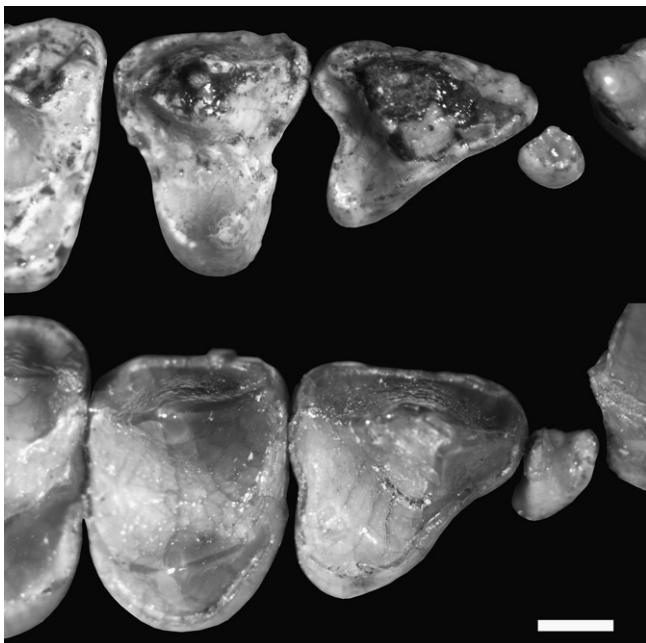


Figure 4. Occlusal view of the maxillary premolars (P2–P4) of *Mescalerolemur horneri* (top row) and *Mahgarita stevensi* (bottom row). Top row: TMM 41672-232 (holotype, right side); Bottom row: TMM 41578-9 (holotype, right side). Scale bar equals 1 mm.

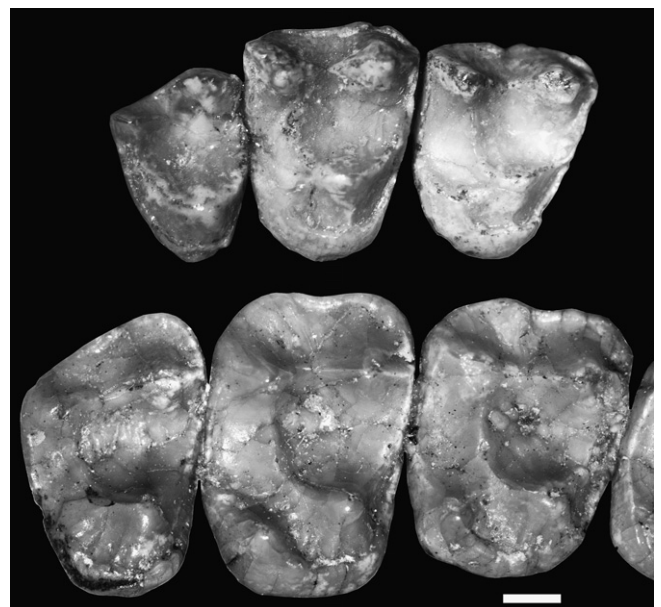


Figure 5. Occlusal view of the maxillary molars (M1–M3) of *Mescalerolemur horneri* (top row) and *Mahgarita stevensi* (bottom row). Top row: TMM 41672-232 (holotype, left side reversed); Bottom row: TMM 41578-20 (right side). Scale bar equals 1 mm.

buccal and lingual cingulids, and lacks any evidence of a paraconid, metaconid, entoconid, or hypoconulid. The p4 crown thus retains only two cusps: a tall protoconid and a smaller hypoconid. These two cusps are located along the central mesiodistal axis of the p4 and are connected by a centrally positioned cristid obliqua that runs to the apices of both cusps. The p4 protoconid is slightly shorter than the p3 protoconid, but slightly taller than the m1 protoconid. A weakly developed paracristid runs directly mesially from the apex of the p4 protoconid. The sizes of the p4 hypoconid and cristid obliqua are variable. In TMM 41672-233, the hypoconid is diminutive and does not stand out above the cristid obliqua. In TMM 41672-236, the hypoconid is cusped and taller than in TMM 41672-233, and the cristid obliqua is more trenchant. In TMM 41672-236 there is also a shallow cleft between the hypoconid and distolingual cingulid that is not present in TMM 41672-233. However, both specimens lack any significant basin in the talonid region. As a result, the p4 talonid of *Mescalerolemur* consists of a centrally placed wedge formed by the hypoconid and cristid obliqua. During Phase I of occlusion, this wedge would have sheared against the trenchant preprotocrista of the P4 (see below).

The m1 trigonid has two principal cusps: a protoconid and a slightly shorter metaconid (Figs. 2 and 3). The metaconid is located distolingual to the protoconid. The paraconid is tiny and located in the midline at the most mesial point of the m1 crown, mesiolingual to the protoconid. The paracristid is weakly developed and the trigonid is completely open mesiolingually. There is no basin in the trigonid region. The m1 trigonid is only moderately taller than the talonid. The m1 talonid also has two principal cusps: a hypoconid and a slightly shorter entoconid. The preentocristid and postmetacristid are moderately well developed, so that the talonid basin is lingually enclosed. The hypoconulid is very small and slightly buccal to the midline of the m1. The medial and lateral postcristids slope down toward the midline of the tooth and are oriented roughly buccolingually. The m1 hypoflexid is deep, reaching nearly to the midline of the tooth. The medial and lateral protocrists are weakly developed, and the postvallid is deeply notched where they meet. The m1 cristid obliqua runs mesiolingually from the hypoconid to meet the base of the postvallid distolingual to the protoconid. There the cristid obliqua turns lingually to run up to the apex of the metaconid. The m1 enamel surface is smooth, and buccal and lingual cingulids are absent.

The m2 of *Mescalerolemur* is unknown. The m3 trigonid has a protoconid and metaconid of approximately equal height, and lacks any trace of a paraconid (Fig. 3). The metaconid is distolingual to the protoconid. The paracristid runs mesially from the apex of the protoconid for a short distance, and then turns to run lingually. Similarly, the premetacristid runs mesially from the apex of the metaconid for a short distance, and then turns buccally to meet the paracristid. Accordingly, the paracristid and premetacristid together form a short, low shelf on the mesial face of the m3 that is unbroken except for a shallow cleft where the two crests meet. These two crests thus enclose a narrow and shallow trigonid basin that is approximately twice the height of the talonid basin. The postvallid is tall, flat, and only slightly notched at the junction of the medial and lateral protocrists. The m3 talonid basin is broad with slightly crenulated enamel. The hypoconid and hypoconulid are large, broad and approximately equal in height, while the entoconid is small and crestiform. The m3 hypoflexid is very shallow, and the cristid obliqua runs mesially from the hypoconid to the apex of the protoconid. The hypoconulid is located far lingual to the midline of the m3, and is separated from the hypoconid by a notch in the lateral postcristid. The medial postcristid, entoconid, preentocristid, and postmetacristid form an unbroken crest that runs mesiodistally along the lingual margin of the talonid, so that the talonid basin is fully enclosed lingually.

The upper dentition of *Mescalerolemur* is known only from the type specimen (TMM 41672-232; Figs. 1, 4 and 5). The upper incisors are not preserved, and the upper canines are represented only by a root that retains a fragment of the dentine from the distal margin of the right canine crown. The canine root is oval in cross-section, with its long axis oriented mesiodistally. The canine root extends superiorly to more than twice the height of the adjacent premolar and molar roots. Based on the preserved anatomy, it is clear that the canine crown of this specimen would have been quite large, projecting well beyond the postcanine occlusal plane and extending presumably to the region of the shallow canine fossa infero-lateral to p2.

The P2 is a tiny, peg-shaped single-rooted tooth located mesiolingual to the mesiobuccal root of P3 (Figs. 1 and 4). The P2 is located immediately adjacent to the P3 crown, but is separated from the top of the canine root by a small gap (~1 mm). Although the tip of the P2 crown is damaged, it is clear that P2 did not extend to the level of the occlusal plane formed by the much larger P3–M3. Nonetheless, it appears that the P2 crown would have contacted the mesial edge of the tall p3 protoconid at centric occlusion.

The P3 of *Mescalerolemur* is a very distinctive tooth with three roots (Figs. 1 and 4). The lingual root of P3 is displaced so far distally that it is situated directly lingual to the distobuccal root. As a result, the flat mesial face of the P3 crown is oriented strongly obliquely rather than buccolingually. The occlusal profile of the P3 crown thus approximates a right triangle, with the oblique mesiolingual crown face forming the hypotenuse. Furthermore, between the lingual and distobuccal roots, the distal margin of the P3 crown is incised by a marked flexus. The P3 crown is dominated by a single large cusp – the paracone. It is not possible to assess the presence or absence of a P3 parastyle due to damage, but the postparacrista is well developed. A buccal cingulum is present but weakly developed. There is no distinct P3 protocone. In its place, there is a shallow basin situated over the lingual root of the P3. Because of the distal position of the lingual P3 root and the existence of a distal flexus, the P3 crown has a small, circumscribed basin projecting distolingual to the large paracone. This distolingual P3 basin evidently contacted the large p4 protoconid during centric occlusion. Running along the mesiolingual margin of the P3 crown is a low crest that is presumably homologous with the preprotocrista. However, due to the unusual configuration of this tooth, this crest effectively forms a tall mesiolingual cingulum along the base of the paracone.

The P4 is less derived than the P3 and exhibits a more typical premolariform morphology (Figs. 1 and 4). In its occlusal profile, the P4 crown is moderately waisted and has a more trapezoidal shape than the P3. The P4 has three roots, and the lingual root is located directly lingual to the paracone. The paracone is large and centrally placed on the mesiodistal axis of the crown's buccal half. Although the details are partly obscured by damage, the paracone is flanked by well developed pre- and postparacristae, a large parastyle, and a complete buccal cingulum. The paraconule is very small and poorly developed. The protocone is distinct and cusped but shorter than the large paracone. The protocone is located mesial to the buccolingual axis of the P4 crown, and is thus situated more mesially than the paracone. Running mesiobuccally from the protocone is a tall and trenchant preparacrista that forms the mesiolingual margin of the P4 crown. This crest and the P4 protocone appear to have occluded with the trenchant complex formed by the cristid obliqua and hypoconid of p4. The holotype palate exhibits a slight left/right asymmetry in the anatomy of the postprotocrista. In both the left and right P4 crowns, the postprotocrista is lower and less trenchant than the preprotocrista. In the left P4, the postprotocrista meets the base of the protocone, where it forms a flexure. However, in the right P4, a small fovea is present at the

junction of the postprotocrista and protocone. In both P4s, this site where the postprotocrista meets the base of the protocone would have accommodated the tiny m1 paraconid at centric occlusion.

The M1 of *Mescalerolemur* has a tall paracone and metacone of similar height (Figs. 1 and 5). The parastyle and metastyle are small. The buccal cingulum is continuous but narrow and weakly developed. There is a shallow M1 ectoflexus, and there is no evidence of a mesostyle. The trigon basin is deep and cone-shaped, reaching its greatest depth at a single point. Although the trigon basin is fully enclosed by crests on all sides, the postparacrista and premetacrista meet at an acute angle and deeply incise the buccal side of the basin at the midpoint between the paracone and metacone. Although not as tall as the paracone and metacone, the protocone is a large cusp with well developed pre- and postprotocristae. The preprotocrista ends at the parastyle, while the terminus of the postprotocrista is at the base of the metacone. The paraconule is large and cusplike, and is located along the preprotocrista at the midpoint between the protocone and parastyle. The paraconule is also situated centrally at the mesial margin of the M1, and is thus more mesially positioned than the paracone. The metaconule is slightly smaller and more crestiform than the paraconule. The metaconule is located along the postprotocrista near its terminus lingual to the metacone. The M1 hypocone is cingular, distolingual to the protocone, and about half the height of the protocone. The hypocone is connected to the base of the protocone by a short but well-developed prehypocone crista that runs mesiodistally. Mesiolingual and distal cingula are very pronounced on the M1. The mesiolingual cingulum runs from the base of the paraconule to the hypocone. It is narrow mesially, and broad lingually. The distal cingulum, between the hypocone and metastyle, is particularly broad and encloses a shallow basin distal to the postprotocrista and metaconule. Although there is a slight swelling of the cingulum lingual to the protocone and a very small crest running a short distance up the base of the protocone from this swelling, there is no distinct pericone.

The M2 is slightly buccolingually broader than M1, but is very similar in its overall occlusal morphology (Figs. 1 and 5). Differences that distinguish the M2 from the M1 are as follows: The paracone is slightly taller than the metacone; the paraconule is larger; the parastyle and metastyle are less well developed; the distal cingulum is narrower; the prehypocone crista is taller, arcuate, and meets the postprotocrista rather than the base of the protocone. In addition to these differences, M2 also has a tiny but distinct pericone located on the lingual cingulum directly lingual to the protocone.

The single left M3 of the *Mescalerolemur* holotype is cracked and missing the base of the paracone, but many details of its morphology are preserved (Figs. 1 and 5). The M3 has three roots, the tips of which are exposed on the infero-lateral floor of the orbit. The M3 crown is smaller in area and has a more triangular occlusal profile than the M1–2 crowns. Also unlike M1–2, the buccal face of the M3 crown is oriented oblique to the mesiodistal axis of the tooth row. The M3 paracone is substantially taller than the metacone, which in turn is substantially taller than the protocone. A hypocone, pericone, and distinct parastyles and metastyles are all absent. The trigon basin of M3 is shallower than in M1–2, but still reaches its greatest depth at a single point rather than being smoothly curved across its floor. The pre- and postprotocristae of the M3 are shorter and less trenchant than those of M1–2. Lingual and distal cingula are present and continuous, but they are narrow and poorly developed. A tiny metaconule is present on the postprotocrista near its terminus at the base of the metacone. The presence or absence of a paraconule and buccal cingulum cannot be assessed due to damage.

Several features of the cranial anatomy of *Mescalerolemur* are preserved in the type specimen, which includes a partial left

maxilla and a fragment of the left palatine (Fig. 1). The palatine bone is separated from the maxilla by a suture running obliquely in the narrow trough (~1.5 mm wide) between the M3 and the pyramidal process of the palatine. The pyramidal process is well developed and projects approximately 1 mm inferior to the level of the hard palate at the infero-lateral angle of the choana, medial to M3. The sphenopalatine canal, connecting the infero-medial orbital fossa with the postero-lateral nasal fossa, is ~1.5 mm long, elliptical in cross section, and about 1 mm in maximum diameter. The sphenopalatine canal is located medial to the M3 and is enclosed entirely within the base of the vertical process of the palatine bone. The root of the zygomatic process of the maxilla is located supero-lateral to M2. There is a weakly developed rugosity at the base of the zygomatic process that marks the site of origin of the anterior masseter, but this rugosity is not projecting. The inferior margin of the orbital aperture is damaged, but it is clear that the maxilla was supero-inferiorly shallow. This conclusion is reinforced by the fact that the lingual roots of M2 and M3 were exposed on the maxillary floor of the orbit. The postero-lateral margin of the orbital floor is thin (approx 1.5 mm thick) and rounded along its free edge between the zygomatic process and M3. The damaged inferior orbital margin has a very shallow curvature, suggesting that the orbital apertures were relatively large in *Mescalerolemur*. This conclusion is also supported by the very shallow maxilla below the orbit and the exposure of molar roots in the orbital floor, but it is not possible to quantify orbital aperture size in existing specimens.

Discussion

In a number of its key dental features (e.g., lack of a pseudohypocone on upper molars, absence of p1/P1, extreme reduction of the p2/P2, and simplified p4 crown morphology), *Mescalerolemur* clearly differs from endemic North American notharctines. By contrast, *Mescalerolemur* shares many derived dental features with *Mahgarita*, a North American genus with presumed Eurasian affinities (Wilson and Szalay, 1976; Figs. 4 and 5). Among Eurasian taxa, *Mescalerolemur* and *Mahgarita* clearly differ from adapines and pronycticebines in lacking a p1/P1, in having a highly reduced p2/P2, and in lacking a molariform or more complex p4/P4. *Mescalerolemur* and *Mahgarita* also lack the more complex p4 and derived twinning of the lower molar entoconid and hypoconulid shared by sivaladapids (Qi and Beard, 1998; Beard et al., 2007; Chaimanee et al., 2008). Accordingly, the adapiform taxa with the greatest dental similarity to both *Mescalerolemur* and *Mahgarita* include various members of the Cercamoniinae, Caenopithecinae, and Asiadapinae.

The absence of a p1 and the presence of a diminutive, single-rooted p2 located between a much larger canine and two-rooted p3 is a derived similarity shared by *Mescalerolemur horneri*, *Mahgarita stevensi*, *Caenopithecus lemuroides*, *Cercamonius brachyrhynchus*, *Europolemur dunaifi*,⁹ *Protoadapis weigelti*,¹⁰ *Godinotia neglecta*, *Darwinius masillae*,¹¹ and *Aframoniens diedes*. By contrast, the p2 is completely lacking in *Afradapis longicristatus* (Seiffert et al., 2009). In *Asiadapis cambayensis*, the p2 was evidently single-rooted and relatively small (based on the p2 alveolus of the *Asiadapis* type specimen GU/RSR/VAS-6), but was still considerably larger than

⁹ Here we follow Godinot (1988), who attributed a partial mandible with a small, single-rooted p2 from Bouxwiller to *Europolemur dunaifi*. Unlike *E. dunaifi*, the p2 of *E. klatti*, *E. koenigswaldi*, and *E. kelleri* has two roots (Franzen et al., 2009).

¹⁰ Unlike *Protoadapis weigelti*, the p2 of *P. angustidens*, *P. curvicaudatus*, *P. igno-ratus* and *P. meuchelensis* has two roots (Russell et al., 1967; Thalmann, 1994; Franzen et al., 2009).

¹¹ Here we follow the interpretation of Franzen et al. (2009), who state that the juvenile type specimen of *Darwinius* possessed a very small, single-rooted adult p2.

that of *Mescalerolemur*. Similarly, in *Asiadapis*, *Aframoni*, *Godinotia*, and *Protoadapis weigelti*, the p2 root was not closely appressed between the canine root and mesial p3 root as it was in *Mescalerolemur*, *Mahgarita*, *Caenopithecus*, and *Cercamoni*. In the latter four genera, crowding of the anterior dentition results in an oblique orientation of the p3 relative to the mesiodistal axis of the mandibular corpus, with the mesial p3 root located more buccally than the distal root. As a result, in *Mescalerolemur*, *Mahgarita*, *Caenopithecus*, and *Cercamoni* the much smaller p2 is located mesiolingual (i.e., rather than directly mesial) to the mesial p3 root.

The p4 of *Mescalerolemur* has a very simple and highly distinctive crown morphology that is most similar to the p4 of *Mahgarita*, *Marcgodinotius*, *Asiadapis*, *Panobius*, *Anchomomys*, *Periconodon*, *Mazateronodon*, and *Djebelemur*. All nine genera share p4s that are buccolingually compressed, and all except *Panobius* and *Djebelemur* have a p4 with an oval occlusal profile. *Mescalerolemur*, *Mahgarita*, *Mazateronodon*, *Panobius*, and *Djebelemur* also have p4s that lack a paraconid and metaconid. By contrast, primitive adapiforms such as *Cantius torresi* and *Donrussellia gallica* have p4 trigonids with distinct paraconids and metaconids. Larger European adapiforms have p4s that either retain metaconids (e.g., *Cercamoni* *brachyrhynchus* and *Protoadapis curvicaudatus*) or retain both metaconids and paraconids (e.g., *Caenopithecus lemuroides*). Very small but distinct p4 paraconids are retained in *Anchomomys* (e.g., BNM En-1) and *Periconodon* (e.g., NHB BCHS 495). In *Asiadapis* and *Marcgodinotius*, the presence and size of the p4 paraconid and/or metaconid are variable (Rose et al., 2009). Some dental specimens that have been identified as p4s of *Asiadapis* have comparatively large and distinct paraconids and metaconids (e.g., GURSR/VAS-745), while others lack a distinct metaconid and have only a tiny paraconid (e.g., GURSR/VAS-38, GURSR/VAS-1627). Similarly, some p4s attributed to *Marcgodinotius* lack paraconids but retain a distinct p4 metaconid (e.g., GURSR/VAS-727), while others lack both paraconid and metaconid (e.g., GURSR/VAS-40) and thus bear a striking resemblance to the p4 of *Mescalerolemur*. This variability in asiadapine p4 morphology cautions against making over-generalizations of dental anatomy based on a limited fossil sample, but it is striking that both known p4s of *Mescalerolemur* retain only two cusps (the protoconid and hypoconid). The p4 of *Mescalerolemur* is also distinctive in lacking any evidence of a talonid basin and in lacking a mesiolingual cingulid. *Asiadapis*, *Marcgodinotius*, *Panobius*, *Anchomomys*, *Mazateronodon*, and *Djebelemur* all have small but discrete talonid basins lingual to the p4 hypoconid/cristid obliqua, and these six genera plus *Periconodon* and *Mahgarita* all have a mesiolingual cingulid on the p4. By the same token, the p4s of *Mescalerolemur* and *Djebelemur* are distinctive in having a hypoconid located directly distal to the protoconid as well as a midline cristid obliqua connecting the apices of the hypoconid and protoconid. As noted above, the p4 cristid obliqua and hypoconid of *Mescalerolemur* form a wedge that shears against the elevated preprotocrista of P4 during occlusion. *Mescalerolemur* also lacks any trace of a lateral protocristid on p4. By comparison, *Anchomomys*, *Periconodon*, and *Asiadapis* have p4s with a distinct lateral protocristid lingual to the cristid obliqua and a hypoconid located buccal to the midline of the crown. The p4s of *Marcgodinotius* and *Panobius* have a hypoconid located along the midline of the tooth, but retain a lateral protocristid. In *Mazateronodon*, the cristid obliqua runs distolingually from the protoconid rather than distally as in *Mescalerolemur*. The position of the p4 hypoconid in *Mahgarita* is obscured by wear in the only known specimen (TMM 41578-8), but a p4 lateral protocristid is visible. The characteristic morphology of the p4 in *Mescalerolemur* thus distinguishes the genus from all other known adapiforms.

As noted above, various details of dento-gnathic anatomy distinguish *Mescalerolemur* from *Mahgarita* (Figs. 3–5). The most

salient of these differences include size (*Mescalerolemur* is smaller than *Mahgarita*), the anatomy of the mandibular symphysis (the symphysis is unfused in *Mescalerolemur* and fused in *Mahgarita*), and the occlusal anatomy of the maxillary postcanine dentition. For example, the P3 of *Mescalerolemur* lacks a protocone and has distal margin with a comparatively deep flexus. In *Mahgarita*, the P3 has a small but distinct protocone and a very shallow distal flexus. The P4 of *Mescalerolemur* has a trapezoidal occlusal profile, lacks a lingual cingulum, and has a protocone that is mesially shifted relative to the paracone. In *Mahgarita*, the P4 has a more oval occlusal profile, has a complete lingual cingulum, and has a protocone that is directly lingual to the paracone. In *Mescalerolemur*, M1–2 have trapezoidal occlusal profiles and comparatively narrow styler regions, narrow lingual cingula, and small hypocones. In *Mahgarita*, M1–2 have rectangular occlusal profiles and comparatively broad styler regions, broad lingual cingula, and large hypocones. Furthermore, in *Mahgarita*, the two known specimens that preserve maxillary teeth demonstrate considerable variation in molar anatomy. In TMM 41572-20, the M2 hypocone is twinned (i.e., it takes the form of two closely-appressed but distinct cusps) on both left and right sides, M1–2 have large mesostyles and well-developed accessory cuspsules in the trigon basins, and M1–3 have highly crenulated enamel. By contrast, TMM 51478-9 (holotype) has a more typical, single-cusped M2 hypocone, lacks accessory cuspsules in the M1–2 trigon basins, has only moderately crenulated enamel on M1–3, and has a small mesostyle on M1.¹² *Mescalerolemur* resembles the *Mahgarita* holotype in lacking twinning of the M2 hypocone and lacks accessory trigon cuspsules, but *Mescalerolemur* also lacks significant enamel crenulation and lacks mesostyles on any molars. Finally, the M3 of *Mescalerolemur* lacks a hypocone, while in *Mahgarita* the M3 has a broad, low hypocone.

Despite these differences, *Mescalerolemur* and *Mahgarita* share a number of derived dental features that collectively distinguish both genera from other adapiforms. As noted above, in *Mescalerolemur* and *Mahgarita* the p4 has a very simple crown morphology. Detailed comparisons are hindered by the advanced state of wear on the only known mandible of *Mahgarita*, but only the presence/absence of a lateral protocristid and mesiolingual cingulid appears to distinguish the p4s of *Mescalerolemur* and *Mahgarita*.

The loss of p1/P1, tiny size of the p2 and P2, and crowding of the antemolar dentition are additional distinctive synapomorphies found in both *Mescalerolemur* and *Mahgarita*. In the only known mandible of *Mahgarita* (TMM 41578-8), the p2 crown is missing bilaterally and there appears to be variation in both root and alveolus size. On the right side of TMM 41578-8, a round p2 alveolus is preserved, but on the left side there is a much smaller and laterally compressed p2 root and alveolus. The size of the p2 in *Mescalerolemur* can only be inferred from the size of the alveolus in TMM 41672-233, which is similar in absolute size to the right p2 alveolus of TMM 41578-8 (*Mahgarita*). Because *Mescalerolemur* is absolutely smaller than *Mahgarita* based on postcanine tooth dimensions, these observations suggest that *Mescalerolemur* may have had a relatively larger p2 than *Mahgarita*. Nonetheless, both genera have a proportionately smaller p2 than in all other adapiforms except perhaps *Caenopithecus lemuroides* (e.g., Eh 597) and *Cercamoni* *brachyrhynchus* (e.g., Basel QV 619). The p2 alveoli of *Mescalerolemur* and *Mahgarita* are absolutely much smaller than that of the larger-bodied *Caenopithecus* and *Cercamoni*, but it is possible that *Mescalerolemur*, *Caenopithecus*, and *Cercamoni* had p2s that were relatively similar in size compared to the dimensions of the adjacent canine and p3. Furthermore, the p2 of

¹² A small mesostyle may have been present on M2, but the buccal cingulum of M2 is damaged.

Mescalerolemur and *Mahgarita* is located mesiolingual to p3, while the mesial root of p3 is displaced buccally. This configuration of the p3 is also shared with *Caenopithecus* and *Cercamoni*, so that in all four genera the p3 is oriented obliquely relative to the mesiodistal axis of the mandibular corpus.

Although P2 crown morphology is unknown in *Mescalerolemur* and *Mahgarita*, more evidence is available regarding the P2 in these genera. In *Mahgarita*, both known crania that preserve maxillary dentitions have small rounded P2 alveoli on the left side. In TMM 41578-20, the right anterior maxilla is damaged, but in TMM 41578-

9, there is a tiny, peg-shaped P2 on the right side (Fig. 4). This P2 in *Mahgarita* is absolutely larger than the only known P2 of *Mescalerolemur* (TMM 41672-232), but the morphology, position, and relative size of the two teeth is very similar. The P2s in both specimens lack the crown tip, but it is not clear whether this condition is due to occlusal wear or damage. Additionally, in both *Mescalerolemur* and *Mahgarita* the P2 is located mesiolingual to the mesial root of P3 and is very tightly appressed between the maxillary canine and P3. Together, these features of the P2 (i.e., very small size, single root, relatively lingual position, and lack of substantial

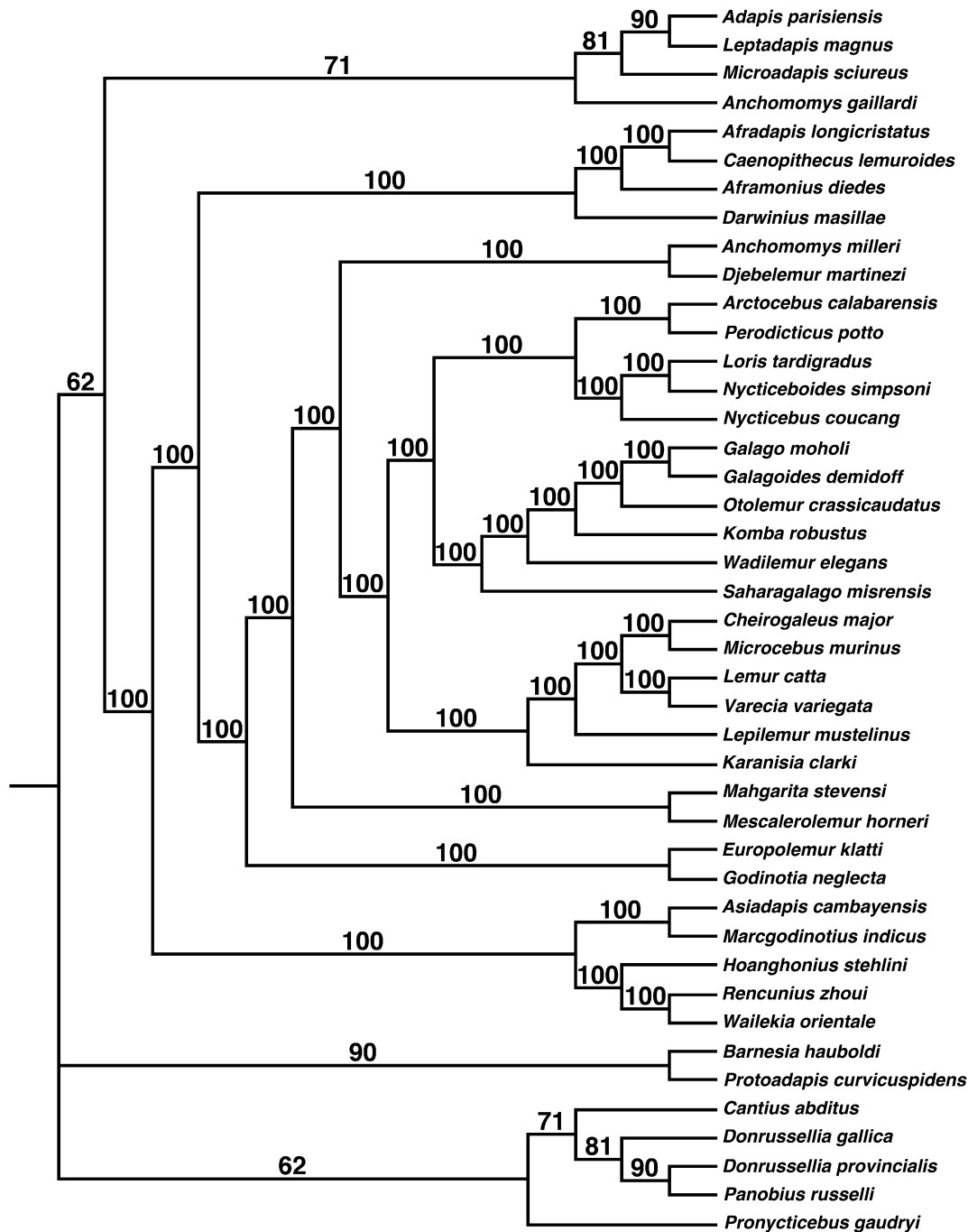


Figure 6. Majority-rule cladogram from “expanded” PAUP analysis, which includes *Mescalerolemur*, *Mahgarita*, and all adapiforms and crown strepsirrhines analyzed by Boyer et al. (2010). Character matrix contained 360 characters scored for 43 taxa. Twenty-one most-parsimonious trees were recovered. The number adjacent to each node represents the percentage of recovered cladograms supporting the node. Tree length = 862.999; consistency index excluding uninformative characters = 0.3517; retention index = 0.5692; rescaled consistency index = 0.2091.

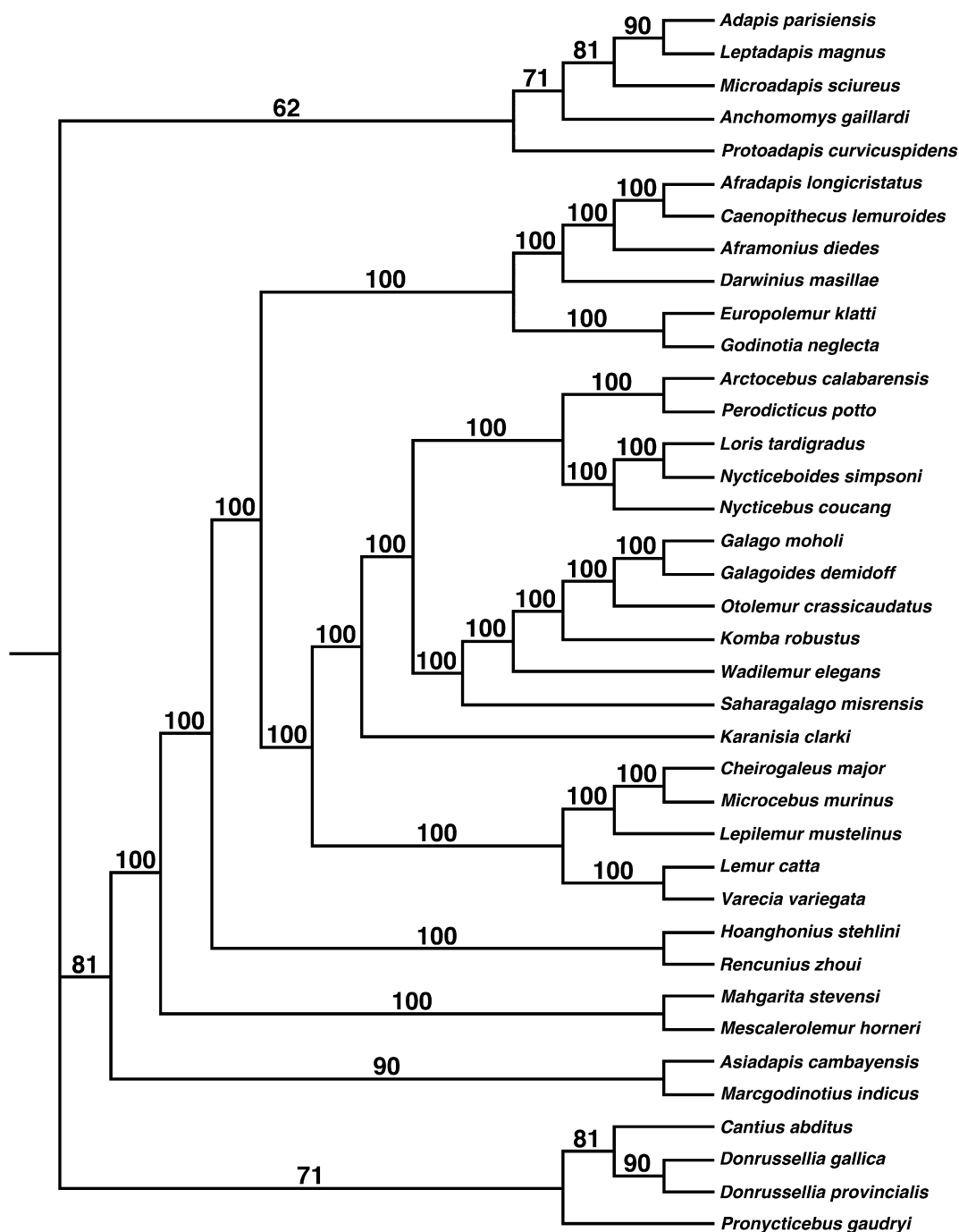


Figure 7. Majority-rule cladogram from “reduced” PAUP analysis, which excludes five taxa with large amounts of missing data (>75%) following Seiffert et al. (2010). Twenty-one most-parsimonious trees were recovered. The number adjacent to each node represents the percentage of recovered cladograms supporting the node. Tree length = 837.610; consistency index excluding uninformative characters = 0.3617; retention index = 0.5703; rescaled consistency index = 0.2153. A bootstrap analysis based on 1200 pseudoreplicates found greater than 50% support for the following clades (bootstrap percentages in parentheses): *Adapis* + *Leptadapis* (85%), *Afradapis* + *Caenopithecus* (61%), *Hoanghoniuss* + *Rencunius* (72%), *Maharita* + *Mescalerolemur* (69%), *Asiadapis* + *Marcgodinotius* (66%), *Donrussellia gallica* + *Donrussellia provincialis* (69%).

adjacent diastemata) distinguish *Mescalerolemur* and *Maharita* from all other known adapiforms.

Although the P3s of *Mescalerolemur* and *Maharita* exhibit some discrete differences in crown morphology (e.g., presence or absence of a protocone), the shape of the P3 crown and configuration of its roots represent additional dental synapomorphies of the two genera. In both *Mescalerolemur* and *Maharita*, the lingual P3 root is shifted distally so that it is directly lingual to the distobuccal P3 root. As a result, the P3 crown has an occlusal profile that approximates

a right triangle, with the flat mesiolingual face of the P3 forming the hypotenuse. The mesiolingual face of the P3 crown thus faces much more lingually in *Mescalerolemur* and *Maharita* than in many other adapiforms (e.g., *Cantius*, *Pronycticebus*). By comparison, the lingual P3 root is also located lingual to the distobuccal P3 root in adapines but the P3 crown has an oval rather than triangular occlusal profile. Similarly, the lingual P3 root is shifted somewhat distally in *Anchemomys*, *Periconodon*, and *Caenopithecus*, but it does not lie directly lingual to the distobuccal P3 root.

Phylogenetic analyses

The many derived dental similarities shared by *Mescalerolemur* and *Mahgarita* favor the conclusion that the two genera are sister taxa. Furthermore, comparisons with other adapiforms reveal that both *Mescalerolemur* and *Mahgarita* generally do not resemble notharctines in their dental morphology. At the same time, *Mescalerolemur* and *Mahgarita* share a number of derived dental features with some asiadapines (e.g., *Marcgodinotius* and *Asiadapis*), caenopithecines (e.g., *Caenopithecus*), and cercamoniines (e.g., *Cercamoniinus*, *Anchomomys*, *Periconodon*, *Mazateronodon*, and *Djebelemur*). In particular, all of these genera demonstrate varying degrees of simplification of the p4 crown and/or reduction and crowding of the anterior premolars compared to the most primitive adapiforms *Donrussellia* and *Cantius*. While it is possible that these dental features evolved in parallel in multiple adapiform clades, such shared derived attributes provide *a priori* support for a hypothesis of common ancestry.

In order to more systematically evaluate the phylogenetic relationships of *Mescalerolemur* and *Mahgarita* vis a vis both adapiforms and crown strepsirrhines, we conducted a parsimony analyses using PAUP* 4.0b10 (Swofford, 1998) software. The analysis included 360 characters and 43 species of extant strepsirrhine primates and adapiforms (i.e., *Mescalerolemur* and all taxa included in Boyer et al., 2010) in an “expanded” analysis, and 38 species in a “reduced” analysis that excluded adapiforms with large amounts of missing data (i.e., taxa included in Seiffert et al., 2010). The matrix used in this study (see Electronic Appendix) was originally established by Ross et al. (1998) and has been modified and supplemented by many authors since then (e.g., Kay et al., 2004; Seiffert et al. 2005b, 2009). The most recently modified version upon which our analysis is based is that of Boyer et al. (2010). Some characters were rescored for *Mahgarita* because original fossil materials were available and morphological details that were obscured in casts could be more clearly observed. These analyses follow Seiffert et al. (2009) in using a molecular scaffold of extant strepsirrhines as a “backbone” constraint and in the use of step matrices to constrain the reacquisition of lost premolars. Some characters were treated as unordered. Characters treated as ordered were scaled so that no character contributed more than one step to tree length. The heuristic search option was employed with random addition sequence and the tree bisection and reconnection branch-swapping algorithm across 1000 replicates. Bootstrap support based on 1200 pseudoreplicates was only assessed for the “reduced” analysis because the “expanded” analysis included large amounts of missing data. Tree statistics are reported in Figs. 6 and 7.

The majority-rule cladogram from our “expanded” phylogenetic analysis is shown in Fig. 6. In 100% of the most parsimonious cladograms that were recovered, *Mescalerolemur* and *Mahgarita* are sister taxa. Both Texas genera comprise the sister group to a larger clade that includes “*Anchomomys milleri* (from the late Eocene of Egypt), *Djebelemur martinezi* (from the early Eocene of Tunisia), and crown strepsirrhines. In turn, all of these taxa are nested within a group of European (*Caenopithecus*, *Darwinius*, *Europolemur*, *Godinotia*) and African (*Afradapis*, *Aframoniinus*) adapiforms.

The majority-rule cladogram from our “reduced” phylogenetic analysis is shown in Figure 7. As in the “expanded” analysis, 100% of the most parsimonious cladograms identify *Mescalerolemur* and *Mahgarita* are sister taxa. Furthermore, the sister-taxon relationship of *Mescalerolemur* and *Mahgarita* received relatively strong support in the bootstrap analysis (bootstrap percentage = 69%). However, unlike the “expanded” cladogram, the “reduced” analysis places the two Texas adapiforms as the sister group to a clade that includes crown strepsirrhines and a large assemblage of European

(*Caenopithecus*, *Darwinius*, *Europolemur*, *Godinotia*), African (*Afradapis*, *Aframoniinus*), and Asian (*Hoanghoniinus*, *Rencuniinus*) adapiforms. After *Mescalerolemur* and *Mahgarita*, the next closest relatives of this group are *Asiadapis* and *Marcgodinotius*. Bootstrap support for these higher-level phylogenetic relationships was relatively low (i.e., below 50%; Fig. 7).

These phylogenetic analyses largely support our two main expectations based on comparative dental morphology. First, both the “expanded” and “reduced” analyses favor the conclusion that *Mescalerolemur* and *Mahgarita* are sister taxa. Second, both analyses strongly suggest that *Mescalerolemur* and *Mahgarita* are more closely related to Eurasian and African adapiforms than to North American notharctines. This latter result provides further support for the early conclusion of Wilson and Szalay (1976) that *Mahgarita* has Old World phylogenetic affinities (see also Kay et al., 1997; Ross et al., 1998; Seiffert et al., 2009, 2010; Boyer et al., 2010). While we regard these two findings as fairly robust, we believe that caution is warranted in drawing more specific conclusions on the basis of the phylogenetic analyses that we have presented here. Although both cladograms (Figs. 6 and 7) are similar in several key respects (e.g., both suggest that the Cercamoniinae as construed by Godinot (1998) is paraphyletic and polyphyletic; both favor a monophyletic Adapinae and Asiadapinae; both favor a clade including *Afradapis*, *Caenopithecus*, *Aframoniinus*, and *Darwinius*), there are substantial differences in tree topology. For instance, the proposed relationships between *Mescalerolemur* + *Mahgarita*, *Europolemur* + *Godinotia*, and hoanghoniines are not concordant in the two cladograms, and yet each analysis found 100% support with regard to the topology of these clades. Furthermore, both cladograms suggest that a number of key derived dental features that have been used to reconstruct adapiform phylogeny (e.g., loss of the p1/P1, extreme reduction in the size of the p2/P2, reduction in the number of p2 roots, and simplification of p4 crown morphology) probably appeared in parallel in multiple adapiform clades. For instance, in both cladograms (Figs. 6 and 7), the asiadapines *Marcgodinotius* and *Asiadapis* form a clade to the exclusion of all other taxa. Within this clade, *Asiadapis* resembles *Mescalerolemur* in lacking a p1 while *Marcgodinotius* retains a p1. Conversely, *Marcgodinotius* more closely resembles *Mescalerolemur* in having a simplified p4 crown morphology. Accordingly, while we are confident in our conclusion that *Mescalerolemur* and *Mahgarita* are not notharctines like other known North American adapiforms, we regard the precise subfamilial affinities of the two Texas genera as unknown based on the data currently available.

Conclusions

Comparisons of dental anatomy and morphological cladistic analyses of stem and crown strepsirrhines indicate that *M. horneri* and *M. stevensi* are closely related sister taxa. Furthermore, none of the craniodental features evident in *Mescalerolemur horneri* would exclude the species from being directly ancestral to *Mahgarita stevensi*. This possibility of an ancestor-descendant relationship is bolstered by biogeographic considerations: both species are known definitively only from the Devil's Graveyard Formation of Texas, with *Mescalerolemur horneri* occurring in the late Uintan and *Mahgarita stevensi* occurring in the early Duchesnean. Further examination of the hypothesis that *Mescalerolemur* and *Mahgarita* are representatives of a single evolutionary lineage will require additional fossil material and improved biostratigraphic resolution in the Devil's Graveyard Formation, as well as clarification of the status of a molar from Lake Casa Blanca that has been attributed to *Mahgarita* (Westgate et al., 2010). Nonetheless, the presence of both *Mescalerolemur* and *Mahgarita* in the Devil's Graveyard Formation adds additional weight to the conclusion that

primate faunas in Texas demonstrate increased endemism in the late Uintan and Duchesnean (Williams and Kirk, 2008).

Our analyses further demonstrate that *Mescalerolemur* and *Mahgarita* are more closely related to Eurasian and African adapiforms than to the endemic radiation of North American notharctines. It is also noteworthy that both *Mescalerolemur* and *Mahgarita* appear in the North American fossil record after the last known occurrences of most species. These findings provide additional evidence of faunal interchange (including primates) between North America and Asia in the middle Eocene (Simpson, 1947; Black and Dawson, 1966; Russell and Zhai, 1987; Beard and Wang, 1991; Beard et al., 1994; Robinson et al., 2004). If *Mescalerolemur* is ancestral to *Mahgarita*, then the earliest representatives of this lineage must have arrived in North America from northeast Asia no later than the late Uintan (U13). However, our results also raise the larger question of why *Mescalerolemur* and *Mahgarita* persisted in the Big Bend region of Texas during the late Uintan and early Duchesnean while notharctines did not. Although it is possible that *Mescalerolemur* and *Mahgarita* were in some way better able than notharctines to cope with a changing environment during the Uintan and Duchesnean (e.g., Janis, 1993; Prothero, 1998; Wing, 1998; Townsend et al., 2010), there is very little evidence with which to evaluate this hypothesis. Nonetheless, it is clear that later-occurring notharctines such as *Notharctus tenebrosus*, *Smilodectes gracilis*, and *Hesperolemur actius* are uniformly much larger than both *Mescalerolemur* and *Mahgarita* (Table 1; Gunnell, 1995; Fleagle, 1999). Because body mass is closely tied to many important ecological factors such as diet, substrate use, and energetic needs (Damuth and MacFadden, 1990), these differences in body mass suggest, at a minimum, that *Mescalerolemur* and *Mahgarita* probably occupied niches that differed from those of the later-occurring notharctines.

Beyond the evidence that we have presented for a close relationship between *Mescalerolemur*, *Mahgarita*, and various Old World adapiforms, the precise higher-level phylogenetic affinities of the two Texas genera are currently unresolved. This consideration makes the subfamilial taxonomic status of *Mescalerolemur* and *Mahgarita* uncertain. At present, it is easiest to conclude that *Mescalerolemur* and *Mahgarita* should not be placed in the Sivaladapinae, Adapinae, or Pronycticebinae. Instead, *Mescalerolemur* and *Mahgarita* are probably most closely related to the Asiadapinae, Cercamoniinae, or Caenopithecinae, although our phylogenetic analyses suggest that the latter two subfamilies are problematic as currently construed (Godinot, 1998). It is also worth noting that a close relationship between *Mescalerolemur* and *Mahgarita* provides additional evidence that adapiforms are not stem anthropoids (Ross, 1994; Seiffert et al., 2009; Williams et al., 2010; but see Franzen et al., 2009; Gingerich et al., 2010). In particular, the unfused mandibular symphysis of *Mescalerolemur* indicates that the fully fused symphysis of *Mahgarita* represents yet another example of the parallel evolution of symphyseal fusion in primates and is therefore not a good indicator of anthropoid affinities (Rasmussen, 1990; Williams et al., 2010).

Acknowledgements

This paper would not have been possible without the generous assistance of Norman Horner, Bill Cook, and the many field crews that have worked to recover fossils at the Dalquest Research Site. The Dalquest Research Site is owned and maintained by Midwestern State University, which has provided invaluable logistical support for paleontological research at the site since 2004. Excellent curatorial, preparatory, and logistical assistance was provided by Tim Rowe, Matt Brown, and Lyn Murray at the Texas Memorial Museum Vertebrate Paleontology Laboratory. Chris Beard, Rachel

Dunn, Gregg Gunnell, Ken Rose, and Bill Sanders kindly provided casts of fossil specimens for this research. Erik Seiffert generously provided the character-taxon matrices that we modified for this analysis. Jim Westgate, Dana Cope, and Chris Beard offered useful comments on the fossils described in this paper and provided access to fossil specimens in their care. This paper was also greatly improved by revisions suggested by Steve Leigh, Erik Seiffert, and two anonymous reviewers.

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