New omomyoids (Euprimates, Mammalia) from the late Uintan of southern California, USA, and the question of the extinction of the Paromomyidae (Plesiadapiformes, Primates)

Sergi López-Torres, Mary T. Silcox, and Patricia A. Holroyd

ABSTRACT

Paromomyidae has been thought to represent the longest-lived group of stem primates (plesiadapiforms), extending from the early Paleocene to late Eocene. We analyzed primate material from the late-middle Eocene of southern California that had initially been ascribed to cf. *Phenacolemur shifrae*. This material falls at the lowest end of the size range for the family. The Californian specimens also exhibit several dental features that are atypical for paromomyids, such as a strong paraconid on the third lower molar, and differ from early Eocene species of *Phenacolemur* in lacking a distally expanded distolingual basin on upper molars. This combination of traits is more typical of earlier paromomyids with more plesiomorphic morphologies (e.g., *Paromomys*) and as such is inconsistent with the late age of these specimens. The purported paromomyids *Ph. shifrae* and *Ignacius mcgrewi* known in deposits of similar age are comparably tiny and share many of the characteristics found in the southern California material that distinguish them from typical early Eocene paromomyids. However, these traits are shared with some trogolemurin omomyoid euprimates that are of similar size. We argue that the material from southern California, along with *Ph. shifrae* and *I. mcgrewi,* should be transferred to a new genus of trogolemurin omomyoid. Purported European records of paromomyids later than the earliest middle Eocene are reconsidered and found to be non-diagnostic. After the early middle Eocene, only a single tooth of a paromomyid can be confirmed, indicating that the group suffered near-extinction, possibly correlated with the Early Eocene Climatic Optimum.

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INTRODUCTION

The Paromomyidae is a family of extinct fossil mammals known from the early Paleocene (Torrejonian 1) to the late Eocene (late early Chadronian) of North America (Silcox and Gunnell, 2008; Silcox et al., 2008; Clemens and Wilson, 2009; Kihm and Tornow, 2014), the early through middle Eocene of Europe (Russell et al., 1967; Godinot, 1984; Estravís, 2000; Aumont, 2003; Hooker, 2010; Marigó et al., 2012, 2014), and the early Eocene of Asia (Tong and Wang, 1998). Paromomyids have been characterized dentally as possessing enlarged lower incisors that are inclined nearly-horizontally (i.e., sub-horizontal); P_4 with a tall, pointed, broad-based protoconid; low crowned molars; and a large hypoconulid lobe on M_3 (Silcox and Gunnell, 2008, Silcox et al., 2017; e.g., *Phenacolemur citatus* in Figure 1). Cranially, paromomyids have a long snout, small and widely spaced orbits, absence of postorbital bar, wide zygomatic arches, and inflated auditory bullae ossified from the entotympanic (Silcox and Gunnell, 2008). The postcranial skeleton of Paromomyidae suggests arborealism and vertical climbing, with strong grasping abilities similar to those of *Ptilocercus*, but no gliding or suspensory behaviors (Bloch and Boyer, 2007; Boyer and Bloch, 2008). Following Silcox et al. (2017), seven genera comprise the family: *Paromomys, Phenacolemur, Ignacius, Elwynella, Arcius, Acidomomys,* and *Edworthia*.

In a phylogenetic context, paromomyids were found to be closely related to Picrodontidae and the polyphyletic assemblage "Palaechthonidae", all being placed together under the superfamily Paromomyoidea (Silcox, 2001; Silcox and Gunnell, 2008; Silcox et al., 2017). Whereas, some authors have suggested that paromomyids are more closely related to dermopterans than to primates (Beard, 1989, 1990, 1993a, 1993b; Kay et al., 1990, 1992; Ni et al., 2013), other comprehensive analyses have provided compelling evidence that they are instead stem primates (Krause, 1991; Runestad and Ruff, 1995; Stafford and Thorington, 1998; Hamrick et al., 1999; Silcox, 2001; Sargis,

2002; Bloch and Boyer, 2007; Bloch et al., 2007; Boyer and Bloch, 2008).

Paromomyids are extensively distributed across North America, with records from as far north as Ellesmere Island, and as far south as Texas (Schiebout, 1974; West and Dawson, 1977; McKenna, 1980; Eberle and Greenwood, 2012). Among the furthest westward proposed North American records of the family is material described by Mason (1988, 1990) and Walsh (1991a) from Ventura and San Diego counties (California) that was referred to *Phenacolemur* and compared to the species *Ph. shifrae* Krishtalka 1978, previously identified from late middle Eocene deposits in Wyoming assigned to the Uintan and
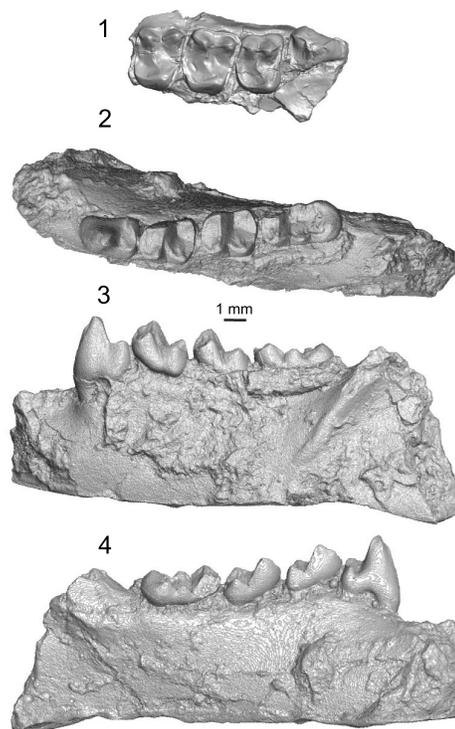

FIGURE 1. The late Wasatchian paromomyid *Phenacolemur citatus*. 1: USGS 6573 (original fossil), right maxilla with P^3-M^2. 2-4: USGS 21712 (cast), left dentary with P_4-M_3 in occlusal (2), buccal (3), and lingual (4) views.

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Duchesnean North American Land Mammals Ages (see Robinson et al., 2004).

However, it is worth noting that there have been some instances of confusion in late occurring samples between paromomyids and another group of early Cenozoic primates, the Omomyoidea. Omomyoids are euprimates (i.e., primates of modern aspect, more closely related to living primates than to plesiadapiforms) that first appear near the Paleocene-Eocene boundary in North America, Europe, and Asia (Ni et al., 2004; Smith et al., 2006; Rose et al., 2011). During the early Paleogene, paromomyid plesiadapiforms and omomyoid primates both diversified at small body sizes, and selected subsets of each clade exhibit very similar dental features (i.e., expanded distolingual basins in upper molars, enlarged sub-horizontal first lower incisors, large hypoconulid lobes on M_3) and may have had similar ecological roles. A late middle Eocene primate from Saskatchewan originally described as a paromomyid (Storer, 1990) was found to be a trogolemurin omomyid, *Trogolemur leonardi* (Beard et al., 1992). Here we follow a restricted concept of Trogolemurini (i.e., only containing two genera: *Trogolemur* and *Sphacorhysis*) as defined by Gunnell and Rose (2002). As so defined, Trogolemurini is a tribe of anaptomorphine omomyoids known from the late early Eocene (late Wasatchian) of Wyoming (Williams and Covert, 1994) and the middle Eocene (Bridgerian to Duchesnean) of Wyoming (Matthew, 1909; Beard et al., 1992; Gunnell, 1995), Nevada (Emry, 1990), and Saskatchewan (Storer, 1990). Trogolemurins are among the smallest known omomyoids. As is true of paromomyid plesiadapiforms, trogolemurins are characterized by having enlarged sub-horizontal central incisors, although they sometimes retain a small I_2. Consequently, they have an anteriorly deep mandible to accommodate this enlarged tooth, like paromomyids do. They retain a small canine and a P_3, unlike most paromomyids. The teeth between I_1 and P_4 are very close together and are inclined mesially. The trogolemurin P_4 is reduced in size, with a very small to absent metaconid, and the M_3 has a short and broad hypoconulid lobe (Gunnell and Rose, 2002; Figure 2), making these teeth quite different from those of most paromomyids, in which the P_4 is expanded and the M_3 hypoconulid more enlarged. The P^4 paracone is much taller than its very small protocone (Gunnell, 1995). Upper molars of trogolemurins have prominent protocones, narrow postprotocingula, and weak conules
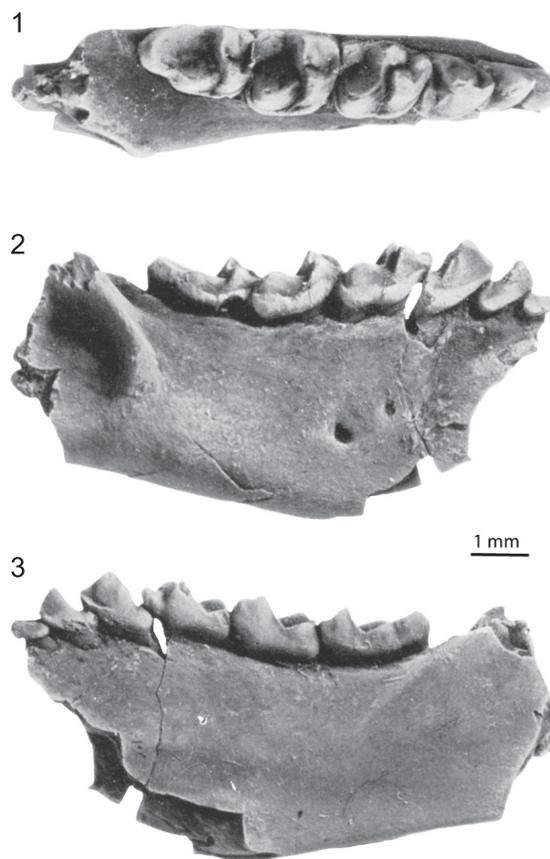

FIGURE 2. Holotype of *Trogolemur myodes*, AMNH 12599 (Matthew, 1909: plate LII, figure 5). Right dentary with P_2-M_3. 1: occlusal view; 2: buccal view; 3: lingual view.

(Gunnell and Rose, 2002), making them more paromomyid-like and generating potential confusion when isolated teeth are found (e.g., Storer, 1990). No trogolemurin postcranial material has been reported.

The first attempt to place a trogolemurin in a cladistic context was done by Williams (1994), and she found that *Tr. myodes* was most closely related to *Anemorhysis*. That was also supported by Williams and Covert (1994). Gunnell (1995) depicted a *Tetonoides-Arapahovius* clade as sister group to Trogolemurini. Although this differs from the results of Williams (1994) and Williams and Covert (1994), this conclusion would still ally trogolemurins with North American anaptomorphins. Later, larger and more comprehensive analyses suggested that *Tr. myodes* is closely related to the European microchoerines *Microchoerus, Necrolemur, Nannopithex,* and *Pseudoloris* (Ross et al., 1998; Ni et al., 2004). However, the analysis by Tornow (2008)

provided support for the previous idea of *Trogolemur myodes* grouping with *Anemorhysis*. There are, therefore, two conflicting interpretations of trogolemurin relationships: they are either related to North American anaptomorphins (Williams, 1994; Williams and Covert, 1994; Gunnell, 1995; Tornow, 2008) or to European microchoerines (Ross et al., 1998; Ni et al., 2004).

In light of the past confusion between specimens of paromomyids and trogolemurins, we formally describe and re-examine the affinities of the southern Californian primate specimens that had been attributed to cf. *Ph. shifrae*, and of similarly aged material from the Uintan and Duchesnean of Wyoming (Robinson, 1968; Krishtalka, 1978). Because these represent some of the youngest reported paromomyids, our study also prompts reconsideration of the larger question of the temporal distribution of paromomyids and, more generally, of the ecological and environmental factors that might have been driving these patterns.

Institutional Abbreviations

AMNH–American Museum of Natural History, New York City, NY, USA; CM–Carnegie Museum of Natural History, Pittsburgh, PA, USA; LACM–Natural History Museum of Los Angeles County, Los Angeles, CA, USA; LACM (CIT)–California Institute of Technology collections, now held by LACM; RSM–Royal Saskatchewan Museum, Regina, SK, Canada; SDSNH–San Diego Society of Natural History, San Diego, CA, USA; SMNH–Saskatchewan Museum of Natural History (now RSM); UCM–University of Colorado Museum, Boulder, CO, USA; UCMP–University of California Museum of Paleontology, Berkeley, CA, USA; UM–University of Michigan, Ann Arbor, MI, USA; USNM–United States National Museum, Washington, DC, USA; YPM VP–Division of Vertebrate Paleontology, Yale Peabody Museum, New Haven, CT, USA.

Historical and Geological Context of Southern Californian Localities

The history of collecting fossil mammals from the Eocene of southern California dates back to the work of Stock (1934a, 1934b, 1935, 1936, 1938, 1948) and Wilson (1935a, 1935b, 1940a, 1940b), when they described the first Eocene insectivores, marsupials, and rodents of the area. Later work recognized several local faunas (Lindsay, 1968; Golz, 1976; Golz and Lillegraven, 1977; Lillegraven, 1979, 1980; Eaton, 1982; Kelly, 1990; Mason, 1988, 1990; Kelly et al., 1991; Theodor, 1999; Wesley and Flynn, 2003; Ludtke and Proth-

ero, 2004; Colbert, 2006; Tomiya, 2013). Of particular note in the current context are the extensive contributions by Walsh (Walsh and Estes, 1985; Walsh, 1987, 1991a, 1991b, 1996, 1997, 1998, 2000; Walsh and Gutzler, 1999), who amassed impressive collections that currently reside at the San Diego Natural History Museum, much of which remains unpublished. However, the primate material from southern California is remarkably scarce. The current study deals specifically with material originally collected by Mason (1988, 1990) and Walsh (1991a) from Ventura and San Diego Counties (California). In the Eocene, fossil localities from these two Californian counties would have had similar latitudinal positions to today but would have lain approximately 2 degrees of latitude to the south and 3 degrees of longitude to the east (see paleoposition reconstruction in Figure 3) due to movement along faults. The western US coastline would have been approximately 10 degrees to the east, having since moved west due to post-Eocene continental and sea-floor spreading movements (see McQuarrie and Wernicke, 2005 for a recent synthesis).
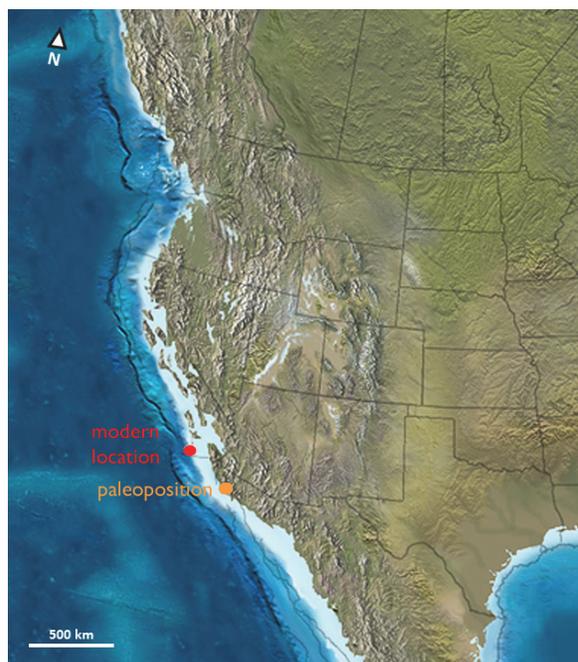

FIGURE 3. Reconstruction of western North America from 40 million years ago. Orange dot indicates the paleoposition of the sites discussed in this paper, whereas the red dot indicates the current relative position of the sites. The map is reproduced with R. Blakey's permission (Colorado Plateau Geosystems, Inc.).

Here we examine specimens from five localities (SDSNH localities 3276, 3426, 4081, 4082, and LACM (CIT) 180), which occur in river-deposited (alluvial) terrestrial sediments. These sediments formed on a coastal plain that would have featured a mix of lagoonal, estuarine, and riverine environments. Westward, the area grades into shelf sediments deposited in forearc basins created by the subduction of the Pacific plate under the North American plate (e.g., Link et al., 1979; Howard and Lowry, 1995; Abbott, 1999; Berry, 1999). The shoreline was never very far to the west, with uplands and mountains with mixed coniferous forests to the east (Frederiksen, 1991). In the Eocene, the climate would have been tropical to subtropical, although researchers differ in their interpretations of forest structure, seasonality, and amount of precipitation in the various formations that have produced mammalian fossils, as discussed below.

The geologic history of San Diego and Ventura counties in southern California is complex, having been affected by significant movement along the San Andreas and related faults, and the literature can be confusing, as some formation names as well as age interpretations have changed. Here we summarize the geology and collecting history of five localities that have produced primate fossil specimens (SDSNH localities 3276, 3426, 4081, 4082, and LACM (CIT) 180), provide data relevant to determining their age and paleoenvironment, and refer the reader to other reviews that can provide more in-depth background on alternate interpretations or older data.

Mission Valley Formation, southwest San Diego County (SDSNH localities 3426 and 4020). SDSNH locality 3426, Collwood South, is a 2 m thick light brown sandy mudstone bed that occurs within the restricted concept of the Mission Valley Formation (see discussion in Walsh et al., 1996). According to the SDSNH records, ~1150 kg of sediment were processed for microvertebrates. The fauna of SDSNH locality 3426 is united with that of other nearby localities as the Cloud 9 local fauna, and is considered late Uintan in age (Walsh, 1991a, 1996).

Walsh et al. (1996) reported a single-crystal $^{40}Ar/^{39}Ar$ age of 42.83 ± 0.24 Ma from a pink bentonite of normal magnetism in the Mission Valley Formation. Measured sections of the Mission Valley Formation in San Diego span both normal and reversed polarity intervals (Bottjer et al., 1991; Walsh et al., 1996). Bottjer et al. (1991) interpreted it as Chron 18r and thought that Chron 19r was

likely missing in the local area (or represented by an unsampled formation), but additional sampling and correlation of local sections led to interpretation as Chrons 20n and 19r (Walsh et al., 1996; Prothero, 2001a), an assignment consistent with the radiometric age.

Peterson and Abbott (1979) reviewed the geologic evidence for immaturity in the development of clay minerals combined with the common development of caliche horizons in the Mission Valley Formation and the slightly older Friars Formation to suggest that the climate was warm (18-20 ºC mean annual temperature) with low average annual rainfall (ca. 63 cm^3). Additional lines of evidence include pollen documenting the presence of palms and a diversity of paratropical to tropical tree taxa (Frederiksen, 1991). Additionally, an analysis of the mammalian diversity (Novacek and Lillegraven, 1979) suggested similarities to complex, modern eastern African habitats with a mix of riparian habitats grading into gallery forests and/or savanna, a slightly wider range of warm temperatures (20-22 ºC), and possible annual rainfall of 50-100 cm^3. Based on land snails from Mission Valley and Friars formations in San Diego, and locality LACM (CIT) 180 in the Sespe Formation, Roth (1988) inferred the presence of dry tropical forest throughout the region.

SDSNH locality 4020 (SR 125 North [Unit I] Grossmont Summit) has previously been assigned to the late Uintan Cloud 9 local fauna (Walsh, 1996), and Penkrot and Zack (2016) have reported on erinaceomorph lipotyphlan tarsals from this site. SDSNH 4020 is in the Mission Valley Formation in the city of El Cajon. Fossils occurred in a ~0.6-1.5 m thick massive, brown, medium-grained, silty sandstone with some calcareous concretions from which thousands of fossils, including articulated skeletons, were recovered. The presence of pulmonate (terrestrial) snails led the site to be informally called "the snail beds". Approximately 3265 kg of sediment were screenwashed.

Member C of Santiago Formation, northwest San Diego County (SDSNH localities 3276, 4081, 4082, and 4925). The only paleoenvironmental interpretation based exclusively on specimens from the Santiago Formation is a study of land snails from SDSNH locality 3276 (Jeff's Discovery, Santiago Formation, Member C, Oceanside, San Diego County, CA), which found the distribution of shell sizes and shapes to be consistent with interpretations of subtropical to tropical conditions and paleotemperatures in excess of 25 ºC (Roth, 1991).

Prothero (2001b) found the strata of Member C of the Santiago Formation at the Jeff's Discovery locality to be entirely reversed and suggested it correlated with Chron C19r (42.5 Ma-41.5 Ma), because correlative rocks with similar fossils from the upper Mission Valley Formation in southern San Diego County probably also correlate with this magnetic chron (Walsh et al., 1996).

SDSNH localities 4081 and 4082 (Emerald Ridge Sites 1 and 2) and 4925 (Kelly Ranch Core – Mammal and Coprolite Site) have not previously been reported in the literature or assigned to a local fauna. All are from Member C of the Santiago Formation and were found during the course of construction projects for the named housing developments in the city of Carlsbad. SDNSH 4081 (Emerald Ridge Site 1) is a 0.3-0.6 m thick weakly-cemented sandstone channel with mudstone and siltstone clasts. A total of ~1995 kg of matrix were collected and washed through 24 mesh (0.7 mm) screens (SDSNH records). SDSNH 4082 (Emerald Ridge Site 2) is lithologically similar to SDSNH 4081 and may be the same bed but is separated from it by faulting. A total of ~1815 kg of matrix were collected and processed (SDSNH records). SDSNH 4925 is a ~0.6 m thick, gray-green, fine grained sandy siltstone from which approximately ~2900 kg of sediment were hand quarried and screenwashed (SDNSH records).

Sespe Formation, Simi Valley, Ventura County (LACM (CIT) 180). Kelly (1990) placed the taxa from the Dry Canyon localities, including LACM (CIT) 180, as part of the Tapo Canyon local fauna, where it co-occurs with the omomyoid *Dyseolemur pacificus* in the late Uintan part of the middle member of the Sespe Formation, the oldest part of the middle Eocene sequences in the Simi Valley area. Locality LACM (CIT) 180 is situated 389 m above the base of the Sespe Formation and was assigned a late Uintan age (Mason, 1990).

Prothero et al. (1996) placed these rocks in the lower half of Chron 18r, but Walsh (1996) expressed skepticism about this younger age assignment. Based on biostratigraphy, Robinson et al. (2004) assigned the Tapo Canyon local fauna to Ui3. Most recently, Kelly et al. (2012) proposed a correlation to Chron 19r based on a new interpretation of the correlation between the southern California middle Eocene record and that of the Uinta and Duchesne River formations in Utah, and this correlation was also found to be most consistent with the ranges of carnivoramorphs (Tomiya, 2013).

As inferred for the Mission Valley Formation, Roth (1988) used the record of land snails and concluded that dry tropical forest was present in the Sespe Formation.

In sum, biostratigraphic, magnetostratigraphic, and radiometric evidence most strongly suggest that all these southern Californian sites are similar in age, likely assignable to the Ui3 subzone of the Uintan North American Land Mammal Age, fall within Chron 19r, i.e., are 42.301 Ma-41.390 Ma in age (Ogg, 2012), and are within the latest part of the Lutetian Standard Stage. Alternative interpretations that suggest the Ventura County localities are younger, or that all the sites are older (see Tomiya, 2013 for a review), are not well supported.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder HAPLORHINI Pocock, 1918
Superfamily OMOMYOIDEA Trouessart, 1879
Family OMOMYIDAE Trouessart, 1879
Subfamily ANAPTOMORPHINAE Cope, 1883
Tribe TROGOLEMURINI Szalay, 1976
Genus *WALSHINA* gen. nov.
Figures 4.1-4.4, 5.1-5.11, 6.1-6.19

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1968	*Phenacolemur* (Matthew, 1915); Robinson, p. 324
1976	*Ignacius* (Matthew and Granger, 1921); Bown and Rose, p. 112 (in part)
1978	*Phenacolemur* (Matthew, 1915); Krishtalka, p. 338, fig. 2-4
1990	*Phenacolemur* (Matthew, 1915); Mason, p. 2, fig. 2
1991a	cf. *Phenacolemur* (Matthew, 1915); Walsh, p. 166, table 1
1996	*Phenacolemur* (Matthew, 1915); Walsh, p. 85, table 2

Type species. *Walshina esmaraldensis* gen. et sp. nov.

Included species. Type species, *Walshina mcgrewi* comb. nov. (= *I. mcgrewi* Robinson, 1968), and *Walshina shifrae* comb. nov. (= *Ph. shifrae* Krishtalka, 1978).

Distribution. Uintan and Duchesnean of Wyoming, and Uintan of California.

Etymology. In memory of Stephen L. Walsh of the San Diego Museum of Natural History, in recognition of his work on the San Diego County faunas.

Diagnosis. Paracristid of M_1 relatively long as in *Trogolemur* and *Sphacorhysis*, but paraconid less clearly distinct from the paracristid. Differs from
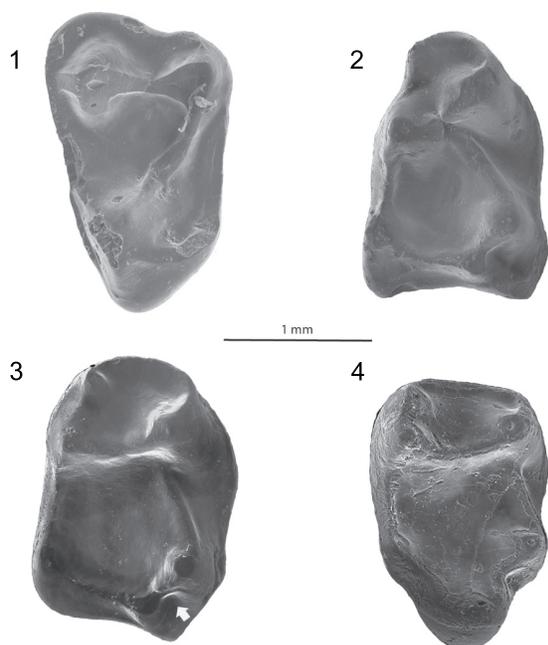
FIGURE 4. Environmental SEM images of four teeth of *Walshina esmaraldensis* gen. et sp. nov. 1: left M^3, SDSNH 76276; 2: right M$_1$, SDSNH 76337; 3: right M$_2$, SDSNH 76338; 4: right M$_3$, SDSNH 72583. All teeth are in occlusal view. Arrow indicates the location of the fovea.

Sphacorhysis (but not *Trogolemur*) in having lower molar talonid basins that are relatively deep with smooth enamel. Differs from *Trogolemur* (but not *Sphacorhysis*) in that the cristid obliqua of M$_1$ contacts the postvallid distal to the protoconid rather than between the protoconid and metaconid. Unlike the other trogolemurins, M$_1$ and M$_2$ of *Walshina* gen. nov. have strong hypoconulids with distinct foveae located below and buccal to the hypoconulid. As in *Sphacorhysis*, the distal aspect of M$_1$ and M$_2$ is convex, whereas in *Trogolemur* it is concave. M$_3$ hypoconulid narrower than in other trogolemurins. M$_3$ trigonid significantly taller than in *Sphacorhysis* (but not *Trogolemur*). Like *Sphacorhysis*, lower molar entocristids form a rounded contour (i.e., forming a U-shaped entocristid) in lingual view, in contrast to the V-shaped entocristid in *Trogolemur*. Further differs from *Trogolemur* and *Sphacorhysis* in having much weaker buccal cingulids. Notably stronger precingulum on M^2 than in *Trogolemur*. Protocone lingual expansion on the upper molars not as pronounced as in *Trogolemur*. Compared to *Trogolemur*, mesial aspect of M^3 straighter, and the lingual border of that tooth much shorter mesiodistally relative to its buccal border.

Discussion. All trogolemurins share a distally expanded distolingual basin of the upper molars (particularly marked in *W. mcgrewi* comb. nov.), which is quite similar to that observed in paromomyid plesiadapiforms. This similarity is likely one reason why some members of *Walshina* gen. nov. have previously been considered paromomyids. However, in other ways the morphology of trogolemurins is inconsistent with that of paromomyids, including the presence of paraconids on M$_3$. *Walshina* gen. nov. remains quite poorly known, with the only record being isolated upper and lower molars. One likely reason for this limited record is that the genus includes the smallest North American omomyoids (see below).

Walshina esmaraldensis gen. et sp. nov.
Figures 4.1-4.4, 5.2, 5.5, 6.1-6.19

Phenacolemur cf. *shifrae* Mason, 1990; Walsh, 1996.

Holotype. LACM 40198, left M^1.

Hypodigm. M^2: SDSNH 42268, 62850, 87336, 87337; M^3: SDSNH 76267; M$_1$: SDSNH 76337, 87331; M$_2$: SDSNH 76338, 87332, 87333; M$_3$: SDSNH 72583, 76266, 76339, 87334, 87335.

Type locality. LACM (CIT) 180, north of Simi Valley, Ventura County, California, USA. Late Uintan (Ui3).

Etymology. In reference to the localities of Emerald Ridge (Vulgar Latin: *esmaraldus*).

Diagnosis. Intermediate in size between *W. mcgrewi* comb. nov. and *W. shifrae* comb. nov. Differs from *W. mcgrewi* comb. nov. in having a hypoconulid closer to the hypoconid than to the entoconid on M$_2$, similar to *W. shifrae* comb. nov. Very large hypoconulids on M$_1$ and M$_2$, whereas they are weakly developed in *W. mcgrewi* comb. nov. and *W. shifrae* comb. nov. M$_2$ trigonid and talonid of similar width, whereas *W. mcgrewi* comb. nov. and *W. shifrae* comb. nov. have significantly wider M$_2$ talonid bases relative to the trigonid base. M$_3$ with larger paraconid and taller metaconid relative to the protoconid than in *W. shifrae* comb. nov. Hypoconulid lobe of M$_3$ not expanded as far distally from the apex of the hypoconulid as in *W. shifrae* comb. nov. Differs from *W. mcgrewi* comb. nov. (but not *W. shifrae* comb. nov.) in having upper molars with smaller distolingual basins. In mesial view, M^1 with a less clearly delineated preprotocrista, like *W. mcgrewi* comb. nov. M^2 with a much more lingually expanded protocone lobe than
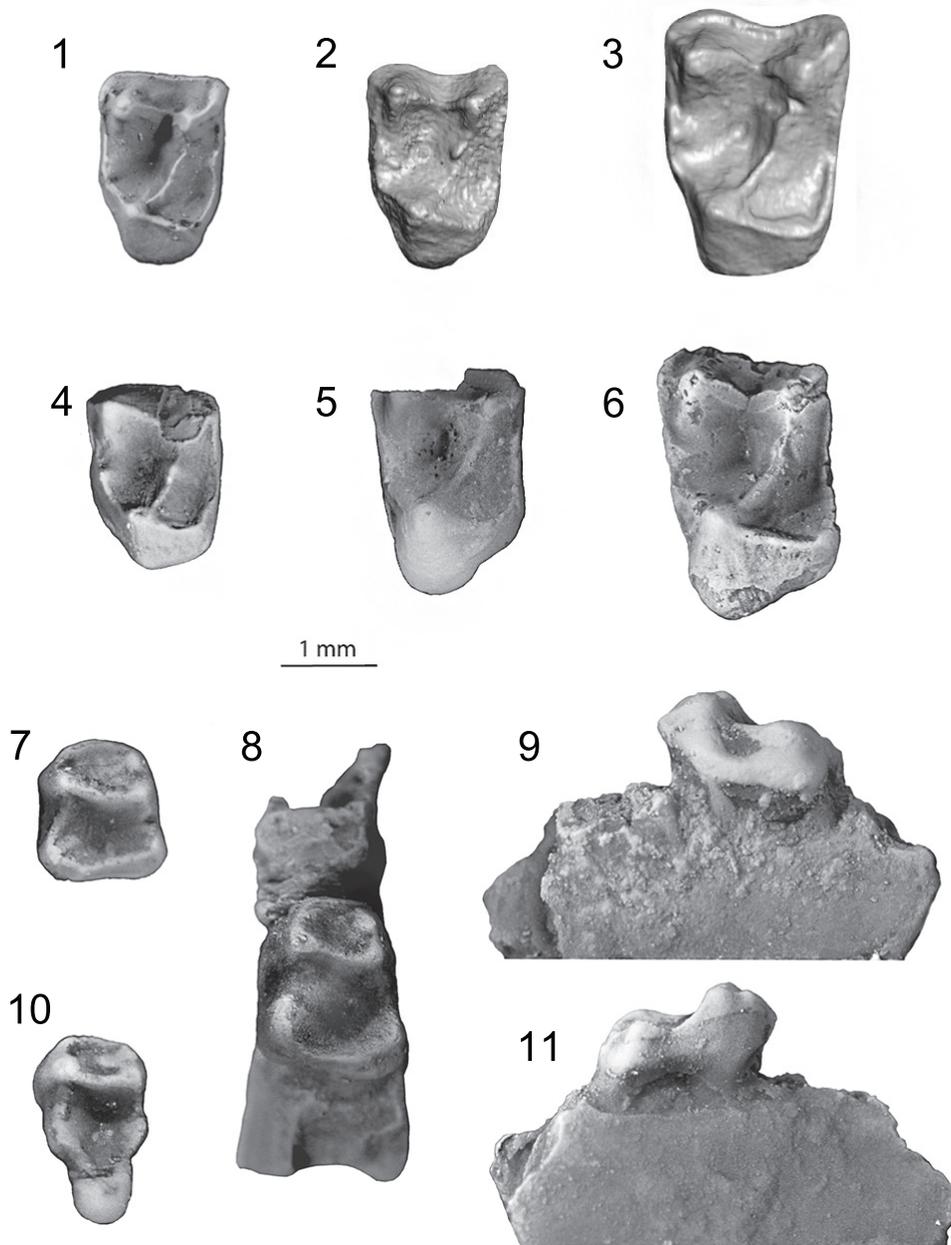
FIGURE 5. Photographs taken with digital camera (1, 4-11) and Micro-CT scan reconstructions generated using Avizo 7 (2, 3). *Walshina shifrae* comb. nov. (1, 4, 7, 10) – 1: right M^1, CM 15797 (holotype; mirrored), in occlusal view; 4: left M^2, CM 15103, in occlusal view; 7: left M_2, CM 21637, in occlusal view; 10: left M_3; CM 15726, in occlusal view. *Walshina esmaraldensis* gen. et sp. nov. (2, 5) – 2: left M^1, LACM 40198 (holotype), in occlusal view; 5: left M^2, SDSNH 62850, in occlusal view. *Walshina mcgrewi* comb. nov. (3, 6, 8, 9, 11) – 3: left M^1, CM 15635 (holotype), in occlusal view; 6: left M^2, CM15794, in occlusal view; 8, 9, 11: left mandibular fragment with M_2, CM 29005, in occlusal (8), buccal (9), and lingual (11) views.

in *W. shifrae* comb. nov. (but not in *W. mcgrewi* comb. nov.).

DESCRIPTION AND COMPARISONS

The only known M^1 of *W. esmaraldensis* gen. et sp. nov. comes from LACM (CIT) 180 from Simi Valley, Ventura County, California, and was described by Mason (1990). It differs from all other
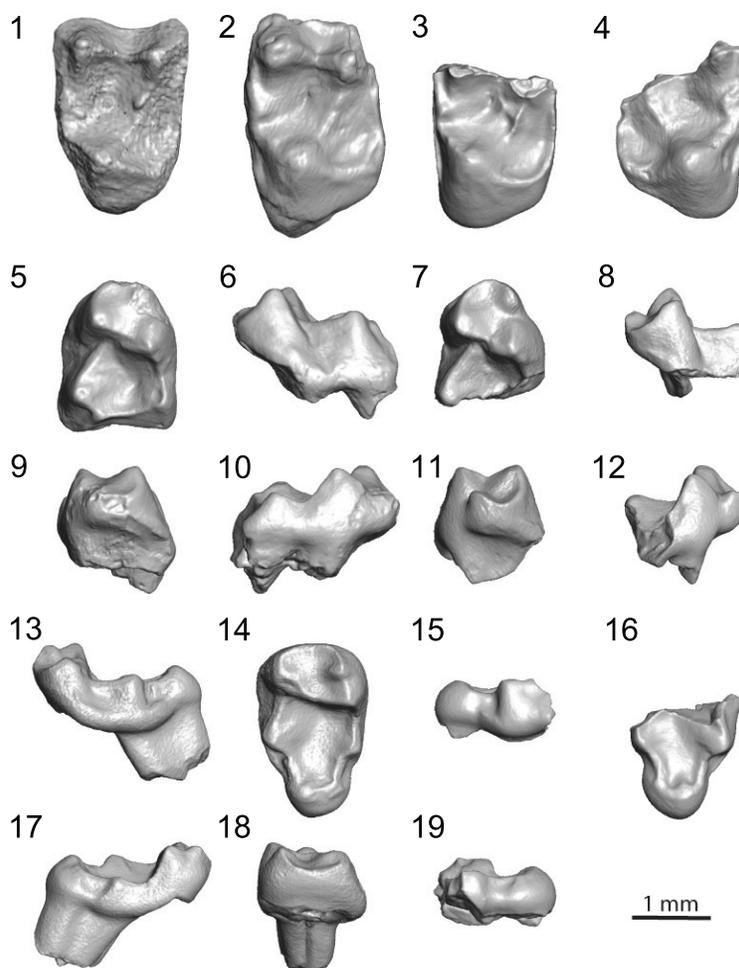
FIGURE 6. Micro-CT scan reconstructions of specimens of *Walshina esmaraldensis* gen. et sp. nov. generated using Avizo 7: 1: left M^1, LACM 40198 (holotype), in occlusal view; 2: left M^2, SDSNH 87336, in occlusal view; 3: lingual fragment of a left M^2, SDSNH 87337, in occlusal view; 4: lingual fragment of a right M^2, SDSNH 42268, in occlusal view; 5, 6, 9, 10: left M_2, SDSNH 87332, in occlusal (5), buccal (6), mesial (9) and lingual (10) views; 7, 8, 11, 12: mesial fragment of a left M_1, SDSNH 87331, in occlusal (7), buccal (8), mesial (11) and lingual (12) views; 13, 14, 17, 18: left M_3, SDSNH 87334, in buccal (13), occlusal (14), lingual (17) and mesial (18) views; 15, 16, 19: distal fragment of a right M_3, SDSNH 87335, in buccal (15), occlusal (16) and lingual (19) views.

upper molars of *W. esmaraldensis* gen. et sp. nov. in having a less expanded distolingual basin, and a metastylar lobe that extends buccally to a similar degree as the parastylar lobe, which is a typical difference between M^1s and M^2s in many early primate taxa. Mason (1990) attributed LACM 40198 to *Ph.* sp. cf. *Ph. shifrae*, and stated that the sole diagnostic character to differentiate *W. mcgrewi* comb. nov. from *W. shifrae* comb. nov. was size. Although size is a useful diagnostic character in *Walshina* gen. nov., there are a number of other distinguishing features (i.e., position of the hypoconulid of M_2, size of the hypoconulid on M_{1-2}, trigo-

nid-talonid width proportion on M_2, size of paraconid on M_3, height of metaconid on M_3, size of hypoconulid lobe on M_3, expansion of distolingual basins on upper molars, expression of the preprotocrista on M^1, expansion of the protocone lobe on M^2) that can be used to differentiate among the species. Nonetheless, Mason (1990) provides an adequate description of this tooth.

Both specimens of M^2 have an oblique buccal border due to a reduced metacone relative to the paracone and a more expanded distolingual basin than M^1. On the M^2, the postprotocingulum runs

straight mesiodistally, creating a sharper angle with the postcingulum than seen on the M^1, where the postprotocingulum and postcingulum are more buccally oblique. The outline of M^2 is rectangular rather than squared, with a longer buccolingual distance. The distolingual basin is deep, with a straight distal aspect of the tooth, instead of concave. The paracone and metacone are well separated. The trigon basin is also deep. The parastylar region is damaged in all M^2 specimens, so it is impossible to determine the presence of a parastyle or the true degree of expansion of the parastylar region. There is no metastyle. Only one conule is present, a minute paraconule, with an associated preparaconule crista, but no postparaconule crista. The paraconule is closer to the paracone than to the protocone. The protocone is slightly skewed mesiolingually. The protocone lobe of *W. esmaraldensis* gen. et sp. nov. is very lingually expanded; more so than in *W. shifrae* comb. nov. but less so than in *Trogolemur*. However, none of the other trogolemurins have a distolingual basin as expanded as that of the M^2 of *W. mcgrewi* comb. nov., which is so expanded that the postcingulum curves distally beyond the plane of the metacone in the lingual aspect of the tooth. In contrast, the distolingual basin in *W. esmaraldensis* gen. et sp. nov. does not extend further distally than the metacone.

The only M^3 known for the genus *Walshina* gen. nov. belongs to *W. esmaraldensis* gen. et sp. nov. The paracone and metacone of this tooth (SDSNH 76267) are very worn. The metacone is significantly smaller than the paracone. No conules are present. There is a strong postprotocrista, but the preprotocrista is completely absent. The lingual half of the M^3 is markedly shorter mesiodistally than the buccal half, so that the tooth has a quite triangular outline.

On the M$_1$, the breadth of the talonid near the apices of the cusps is greater than the breadth of the trigonid. The paraconid is present on a well-developed paracristid that extends well beyond the paraconid and metaconid, making the front of the tooth very long and narrow. On the M$_1$, the paracristid can be as tall as the tip of the paraconid, making that cusp poorly defined; whereas on the M$_2$, the paracristid is lower and the paraconid is more distinct from this crest. On the M$_1$, the metaconid is distally displaced relative to the protoconid and the postvallid is stepped (sensu Silcox, 2001). The crests on the lower molars are all well delineated, in association with the teeth being fairly high

crowned (much more so, for example, than in *Sphacorhysis*). On both M$_1$ and M$_2$, the distal slopes of the entoconid and the hypoconid are expanded beyond the apices of these cusps, giving the distal border of the tooth a convex aspect. There is a fovea on the distal aspect of the tooth between the hypoconulid and the hypoconid. The hypoconulid is well defined and shifted far buccally, being close to the hypoconid.

The M$_3$ paraconid is large. The trigonid has a steep distal aspect of the metaconid. The hypoconulid is enlarged into a lobe. The M$_3$ is narrower at the hypoconulid than at the level of the tip of the hypoconid and the tip of the entoconid (i.e., low hypoconulid lobe/mid tooth ratio). The only other known M$_3$ of *Walshina* gen. nov. belongs to *W. shifrae* comb. nov. Whereas there is a clear difference in size, the two species also differ in the relative proportions of the hypoconulid lobe. The buccolingual width of the hypoconulid lobe in *W. shifrae* comb. nov. is smaller than in *W. esmaraldensis* gen. et sp. nov. relative to the distance between the hypoconid and the entoconid, making this part of the tooth appear narrower. The hypoconulid lobe of *W. shifrae* comb. nov. also has a longer distal slope than in *W. esmaraldensis* gen. et sp. nov., so that the hypoconulid lobe extends further from the tip of the hypoconulid.

Body mass estimates using equations by Gingerich et al. (1982) and the prosimian equation by Conroy (1987) are shown for all species of trogolemurins in Table 1. Measurements used for calculating body mass estimates are shown in Appendix 1. The equation by Conroy (1987) would be expected to provide more relevant estimates, because it is based on the subset of living primates most likely to be comparable to the fossil taxa. However, he only provided an equation for the M$_1$, which is problematic in this case because that tooth locus is unknown in several species of trogolemurins. In particular, although the smallest estimated body mass is 58 g for *Tr. myodes* using the equation by Conroy (1987), if an M$_1$ was known for *W. shifrae* comb. nov., its estimated body mass would certainly be lower. This is because the estimates based on teeth known for both species using the Gingerich et al. (1982) equations are consistently much lower for *W. shifrae* comb. nov. than for *Tr. myodes* (e.g., estimate based on M$_2$ is 142 g for *Tr. myodes* compared to 109 g for *W. shifrae* comb. nov.). This would make *W. shifrae* comb. nov. the smallest of the trogolemurins, and smaller than all other North American omomyoids (based on com-

TABLE 1. Estimated body masses (in g) of all species of Trogolemurini.

	Gingerich et al.'s (1982) equations					Conroy's (1987) M_1 equation
	M_1	M_2	M_3	M^1	M^2	
Walshina esmaraldensis gen. sp. nov.	154	197	254	117	230	72
Walshina mcgrewi comb. nov.	237	275	-	245	315	115
Walshina shifrae comb. nov.	-	109	199	65	108	-
Trogolemur myodes	125	142	263	125	231	58
Trogolemur amplior	-	290	-	-	-	-
Trogolemur fragilis	-	-	227	-	-	-
Trogolemur leonardi	-	-	-	278	-	-
Sphacorhysis burntforkensis	166	270	268	-	-	78

parison to body mass estimates in Jones et al., 2014).

PHYLOGENETIC RELATIONSHIPS OF *WALSHINA GEN. NOV.*

In order to assess the phylogenetic position of *Walshina* gen. nov. among Omomyoidea, we conducted a cladistic analysis based on the study by Ni et al. (2004), as modified by Holroyd and Strait (2008), who revised the coding for two species (*Purgatorius janisae* and *An. savagei*), and added new data for species of *Loveina*. We chose this particular matrix rather than more recent studies (e.g., Ni et al., 2013, 2016) because it includes a trogolemurin, *Tr. myodes*. Having coding from a member of this family available in the original matrix was important to ensure that we were assessing characters in the same way as the original authors. The analysis also includes representative tarsioids, anthropoids, adapoids, crown strepsirrhines, and plesiadapiforms. Scandentia was used as an outgroup to Primates. The rest of the trogolemurin primates were added to the matrix of Holroyd and Strait (2008): *Tr. amplior, Tr. fragilis, Tr. leonardi, Sphacorhysis burntforkensis, W. esmaraldensis* gen. et sp. nov., *W. mcgrewi* comb. nov., and *W. shifrae* comb. nov. The microchoerine *Melaneremia bryanti* (Hooker, 2007), and the anaptomorphins *An. sublettensis* (Gazin, 1952, 1958), *An. wortmani* (Bown and Rose, 1984), and *An. natronensis* (Beard et al., 1992) were added as well. The coding for *Tr. myodes* was partially reassessed, as was the one for *Nannopithex* sp. (to include generic variation seen in *Na. zuccolae* [Hooker, 2007]), and Scandentia was re-coded for character 13. A total of 303 characters (194 dental, 49 craniomandibular, 56 postcranial, and 4 soft tis-

sue and physiological [only coded for extant taxa] characters) were scored for a total of 66 taxa (matrix available on publication from www.morpho-bank.org under project number P3264).

A parsimony analysis was performed using TNT v. 1.5 (Goboloff and Catalano, 2016) with all characters equally weighted and ordered, following the original analysis (Ni et al., 2004; Holroyd and Strait, 2008). Multiple character states were set to be interpreted as polymorphisms, instead of uncertainties. A traditional search was implemented with 1000 repetitions. The tree-bisection-reconnection (TBR) algorithm was used for branch swapping, with 1000 trees to save per replication.

Results of the Phylogenetic Analysis

The cladistic analysis yielded 90 equally parsimonious trees. A strict consensus tree was generated in TNT v. 1.5 from these trees (Figure 7, see also Appendix 2). In the strict consensus tree, *Walshina* gen. nov. is found to be monophyletic, although the relationships among species of *Walshina* gen. nov. remain unclear. The tribe Trogolemurini was also recovered as monophyletic.

The inclusion of the rest of trogolemurins and the four additional species of omomyoids, along with the revisions made by Holroyd and Strait (2008) and in the present paper, caused a few changes to the tree with respect to the topology found by Ni et al. (2004). The position of *Purgatorius* is resolved in our tree, being the sister group to the rest of Primates sensu lato. The rest of Plesiadapiformes (excluding *Purgatorius*) form one clade, sister group of *Altanius orlovi*, as in Ni et al. (2004). However, phylogenetic analyses of plesiadapiforms with greater taxon sampling for that group support the interpretation that this group of primates is paraphyletic and excludes *An. orlovi*,
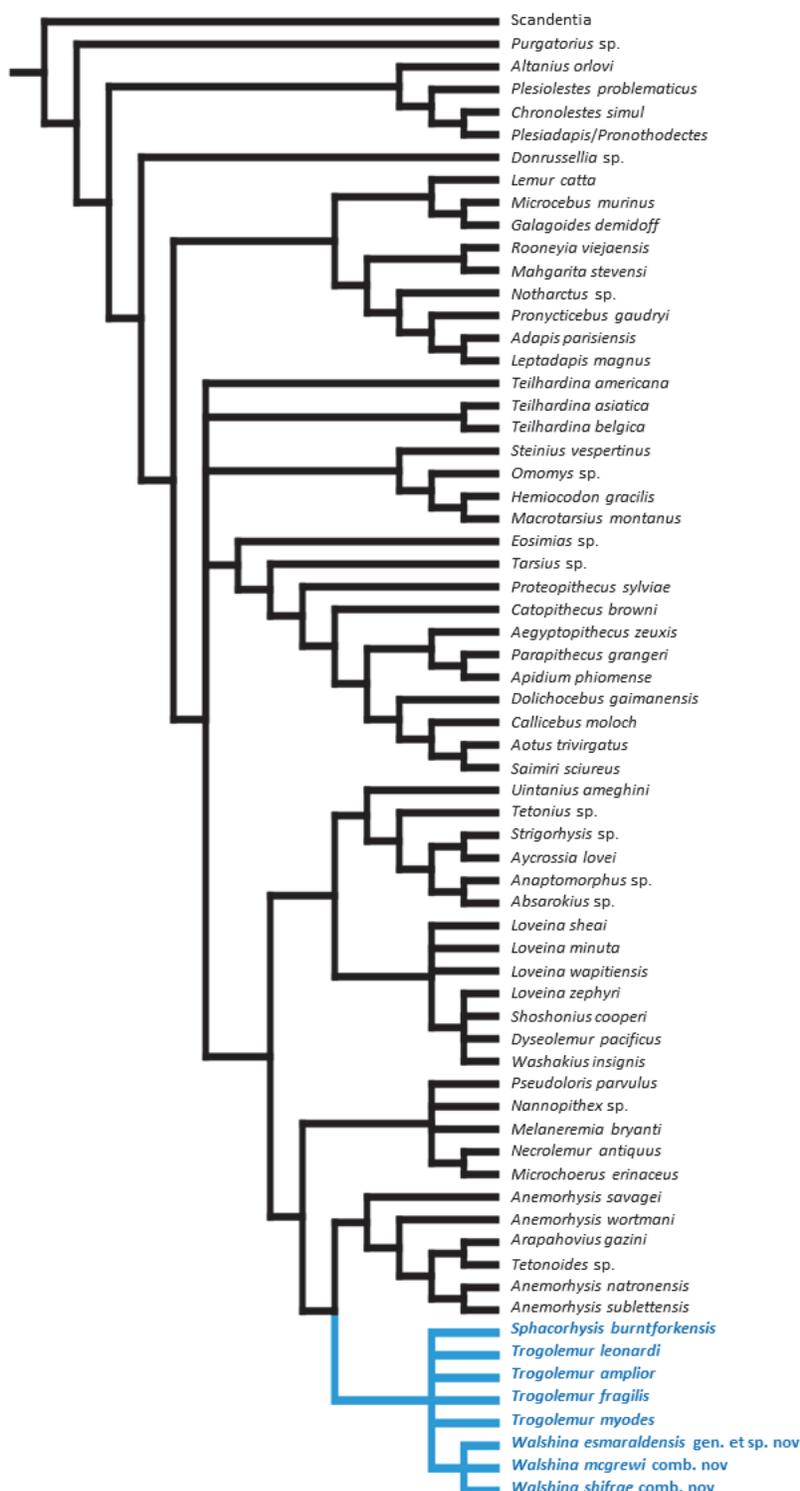
FIGURE 7. Hypothesis of relationships of *Walshina* gen. nov. in the context of the Order Primates. Strict consensus cladogram based on data modified from Holroyd and Strait (2008), including the addition of seven newly-coded trogolemurins (*Trogolemur amplior*, *Tr. fragilis*, *Tr. leonardi*, *Sphacorhysis burntforkensis*, *Walshina esmaraldensis* gen. et sp. nov., *W. mcgrewi* comb. nov., and *W. shifrae* comb. nov.), a microchoerine (*Melaneremia bryanti*), and three anaptomorphins (*Anemorhysis sublettensis*, *An. wortmani*, and *An. natronensis*). Trogolemurins are marked in blue.

which is interpreted as a euprimate (Silcox, 2001; Bloch and Boyer, 2002; Bloch et al., 2007, Silcox et al., 2010; Chester and Bloch, 2013; Chester et al., 2015; Ni et al. 2016). The tree differs from the results obtained by Ni et al. (2004) in resolving the position of *Donrussellia* as the sister taxon to the rest of Euprimates (except for *Altanius*). Our tree also resolves *Mahgarita* and *Rooneyia* as sister taxa. Although *Rooneyia* has been considered an omomyoid, it appears as being part of the strepsirrhine radiation, as it did in Ni et al. (2004). All species of *Teilhardina* appear as basal haplorrhines, with unclear relationships among them. *Eosimias* appears in our tree as the sister taxon of crown haplorrhines (=Anthropoidea + *Tarsius*). Washakiins are monophyletic, although *Loveina* was found to be paraphyletic (consistent with the results of Holroyd and Strait, 2008). Our tree also resolves a clade that includes omomyins and macrotarsiins, in which omomyins are paraphyletic. Washakiins are resolved as the sister group to a subgroup of anaptomorphins, which include *Uintanius, Tetonius, Strigorhysis, Aycrossia, Anaptomorphus,* and *Absarokius*. The rest of anaptomorphins (*Anemorhysis, Tetonoides,* and *Arapahovius*) form another clade that is the sister group of trogolemurins. However, *Anemorhysis* does not appear to be monophyletic. The sister group to the clade (Trogolemurini + *Anemorhysis* + *Tetonoides* + *Arapahovius*) is the Microchoerinae from Europe. The position of trogolemurins is, therefore, in contrast with their position in the tree found by Ni et al. (2004), in which *Trogolemur* clustered together with the European microchoerines. Finding trogolemurins to be more closely related to North American anaptomorphins, rather than to European microchoerids is more biogeographically parsimonious, reducing the number of implied dispersal events between North America and Europe.

DISCUSSION

Trogolemurins have many dental features that converge on those of paromomyids, resulting in taxonomic confusion in the related literature: large hypoconulid lobes on M_3, procumbent lower incisors, upper molars with a well-developed postprotocingulum and a fairly expanded distolingual basin. The most diagnostic tooth for paromomyids is the P_4, which is enlarged with a tall, pointed, upright protoconid, and is very different from a trogolemurin P_4, which is proportionally smaller with a mesially inclined trigonid. However, trogolemurin material has classically been scarce and incom-

plete, often missing the diagnostic P_4 (Robinson, 1968; Krishtalka, 1978; Mason, 1990; Storer, 1990; Walsh, 1991a; Beard et al., 1992) or the upper dentition (Matthew, 1909; Beard et al., 1992), and in many cases taxa are known only from unassociated isolated teeth (Robinson, 1968; Krishtalka, 1978; Mason, 1990; Storer, 1990; Walsh, 1991a). Trogolemurin P_4s are only known for *Trogolemur* and *Sphacorhysis* (Matthew, 1909; Emry, 1990; Gunnell, 1995), but not for *Walshina* gen. nov. It was not until work by Emry (1990) that the first upper molars ascribed to a trogolemurin were described, and not until work by Gunnell (1995) that the first upper dentition of *Trogolemur* in a tooth row (including the first P^4 known for a trogolemurin) was described. This lack of knowledge about the form of the upper molars in trogolemurins led Storer (1990) to describe two complete and other fragmentary isolated upper molars as a new species of paromomyid, *Ph. leonardi*, from the late middle Eocene (Duchesnean) of Saskatchewan. Beard et al. (1992) transferred *Ph. leonardi* to the euprimate genus *Trogolemur* and were the first authors to recognize the similarities between these two groups.

It is now clear that in addition to the differences in the morphology of the P_4, there are important differences in upper and lower molar morphology. Paromomyids have a more quadrangular outline of the upper molars. Although both paromomyids and trogolemurins have expanded distolingual basins, the degree of expansion in trogolemurins is most comparable to the oldest paromomyids with plesiomorphic morphologies (i.e., *Paromomys*), which are millions of years older than the oldest trogolemurins: the oldest paromomyids are from the earliest Torrejonian, approximately 63 Ma (Clemens and Wilson, 2009) whereas the oldest trogolemurins are from the latest Wasatchian, approximately 51 Ma (Williams and Covert, 1994). Trogolemurins are further characterized by having a large lingual expansion of the protocone lobe on the upper molars, which is not seen in any paromomyids.

The M_1 of trogolemurins differs from that tooth in paromomyids in having a very oblique, stepped postvallid, produced by a metaconid that is located well distal to the protoconid. The M_1 also has a very tall, strong paracristid, which is never so expanded in paromomyids. The hypoconulid on the M_1 and M_2 of trogolemurins is also better developed and more distinct, whereas paromomyids show weak to absent hypoconulids on these teeth.

The talonid of the M_2 is shorter in trogolemurins relative to the length of the trigonid, making the trigonid and talonid closer in length in trogolemurins.

In sum, it is clear that in spite of the similarities between trogolemurins and paromomyids, there are numerous characters that distinguish them from one another. An additional element to the argument that the material previously ascribed to *I. mcgrewi* and *Ph. shifrae* does not belong in Paromomyidae is that it demonstrates morphology that would not be expected in paromomyids from so late in the family's evolutionary history. In particular, paromomyids generally exhibit increases in the degree of expansion of the upper molar distolingual basin through time, and yet the upper molars known for the Uintan and Duchesnean purported paromomyids are most comparable to those of the earliest paromomyids.

Re-classifying *I. mcgrewi* and *Ph. shifrae* as members of the new trogolemurin genus *Walshina* gen. nov. reframes our understanding of the timing of the demise of paromomyid diversity. *Ignacius mcgrewi* and *Ph. shifrae* were the only members of the family identified from the Uintan and the Duchesnean, so transferring them to Omomyoidea eliminates the entire Uintan and Duchesnean record of Paromomyidae. It is worth noting, however, that even when they were considered paromomyids, there was a marked discontinuity in the record of the family between the supposed Uintan forms and the next oldest material. The first record of a paromomyid comes from the Torrejonian of Montana, specifically the Torrejonian 1 biozone (Clemens and Wilson, 2009), and from that point there is a continuous presence of this family until the latest Wasatchian (Silcox et al., 2008). Then, the next occurrence of a paromomyid is in the middle Bridgerian (Br2; Gunnell et al., 2009). The absence of paromomyids from the very large samples of mammal specimens from later in the Bridgerian (Matthew, 1909; West, 1976; Emry, 1990; Gunnell and Bartels, 1999; Gunnell et al., 2009) made the apparent reappearance of the group in the late Uintan somewhat surprising. Re-classifying the Uintan and Duchesnean material as Trogolemurini makes it clear that paromomyids were much reduced in richness after the early Bridgerian in North America. The only remaining post-Bridgerian record of a paromomyid is an isolated P^4 from the Chadronian of North Dakota, tentatively ascribed by Kihm and Tornow (2014) to the genus *Ignacius*, which is separated from the next youngest specimen by some of the Bridgerian, and the entire Uintan and Duchesnean, indicating a very long ghost lineage that extends over a period of approximately 12 million years (middle Eocene boundary at 49 Ma, Clyde et al., 2001; Duchesnean-Chadronian boundary at 37 Ma, Prothero and Emry, 2004). The North Dakotan specimen shows clear features that ties it to paromomyids, and in particular to the genus *Ignacius*. The outline of the tooth is squared, instead of rectangular (as seen in *Trogolemur*, Gunnell, 1995), the cusps and styles are blunter, the parastylar lobe is very broad, and the postparacone and premetacone cristae meet obliquely, making a V shape in occlusal view, a trait observed in *Ignacius*.

Regardless of the apparent existence of this one surviving lineage of geographically isolated paromomyids, this family of plesiadapiforms follows a clear trend of declining biodiversity after the end of the early Eocene in North America (late Wasatchian-early Bridgerian), which is clarified by the re-classification of the Uintan and Duchesnean material. Paromomyids reached their highest peak of biodiversity during the Wasatchian 4 (Wa4) biozone, whereas only one species is found in the middle Bridgerian, *Elwynella oreas* (Rose and Bown, 1982; Gunnell et al., 2009). The drop in biodiversity of paromomyids could therefore be correlated with the Early Eocene Climatic Optimum (EECO), the warmest sustained period of the entire Cenozoic (Clyde et al., 2001; Zachos et al., 2008; Hyland and Sheldon, 2013; Chew, 2015). Paromomyids are also extremely rare during the Paleocene-Eocene Thermal Maximum, only known from a lower molar of *I. graybullianus* and an upper molar and an edentulous jaw of *Ph. praecox* (Gingerich, 1989; Rose et al., 2012). The drop in paromomyid biodiversity during the Wasatchian 5 biozone also coincides with the warming period that precedes the EECO (including at least one hyperthermal; Chew and Oheim, 2013). In contrast, the highest peak of paromomyid biodiversity (Wa4) occurs during a cooling period between Biohorizon A and Biohorizon B (Chew and Oheim, 2013). And although the material has yet to be described in detail, paromomyids are also the only primates known from the early-middle Eocene of Ellesmere Island in the Canadian High Arctic (West and Dawson, 1977; McKenna, 1980). That part of the world is interpreted to have been much milder in the Eocene than today, but winter temperatures are still inferred to have been near freezing (Eberle and Greenwood, 2012), making this a chilly environment for primates. These various lines of evidence suggest that, as a family, paromomyids preferred cooler temperatures, and that the near

extinction of the family in North America after the Wasatchian-Bridgerian boundary could potentially be ascribed to increasing global temperatures.

Late Paromomyids from Europe

Although the reinterpretation of most of the latest occurring purported paromomyid material from North America makes it clear that the family was largely extinct on that continent after the early Bridgerian, there are some later occurring specimens from Europe that have been attributed to the family, which could signal a longer persistence on that continent. The only known genus of paromomyid from Europe is *Arcius* (Russell et al., 1967; Godinot, 1984; Estravís, 2000; Marigó et al., 2012). Interestingly, the occurrence of paromomyid species in Europe through time shows some similarities to what has been observed in North America. *Arcius* first appears in Europe during the earliest Eocene (Mammal Paleogene zone 7 [MP7], Neustrian: Estravís, 2000), followed by a continuous presence of this family until the Grauvian (MP10; early-middle Eocene; Godinot, 2015). After that, no paromomyids are found during MP11 or MP12. It is not until MP13 (Geiseltalian) that a few teeth are reported to belong to Paromomyidae (Sudre, 1978; Rémy et al., 1997). A second lower molar of *Arcius* sp. from Saint-Maximin (France) is illustrated and reported in a faunal list by Rémy et al. (1997), and two third lower molars (one of them illustrated in Aumont, 2003) from Bouxwiller (France) appear in a faunal list in Sudre (1978). However, this scarce material, comprised of three isolated molars from the middle Eocene of Europe, might not be paromomyids.

The tooth from Saint-Maximin, identified here as an M_2 (and as either an M_1 or an M_2 by Rémy et al., 1997), is strikingly different from that tooth in any *Arcius* species. It has a prominent paraconid, which is not consistent with what it is observed in a typical *Arcius* M_2. Also, the trigonid area is significantly larger in relation to the talonid than in any species of *Arcius*. We suggest that it could be a diminutive adapoid, and tentatively ascribe it to cf. *Anchomomys* sp., based on the presence of this genus at that site. The M_3s from Bouxwiller were identified as *Arcius lapparenti* by Aumont (2003). However, they are very flat and significantly shorter mesiodistally than those of *Ar. lapparenti*. The trigonid is shorter mesiodistally in relation to its width than in *Ar. lapparenti*, and the buccolingual dimension from the hypoconid to the entoconid is significantly greater than in any species of *Arcius*. Also, the hypoconulid lobe, although expanded, is signifi-

cantly smaller than the ones seen in any Eocene paromomyids. Therefore, we suggest that it could potentially be a microchoerid omomyoid, and tentatively ascribe these teeth to cf. *Nannopithex* sp., based on the presence of this genus at that site. The fact that the Geiseltalian material likely belongs to diminutive euprimates rather than to the Paromomyidae is consistent with the near extinction of paromomyids after the early middle Eocene observed in North America.

CONCLUSIONS

The material from southern California previously ascribed to *Phenacolemur* by Mason (1990) and Walsh (1991a) are not paromomyids. They represent a new species of trogolemurin omomyoid, *W. esmaraldensis* gen. et sp. nov. The Californian sample of *Walshina* gen. nov. adds to our knowledge of the variability and diversity of omomyoids, particularly trogolemurins, and significantly changes our understanding of the temporal distribution of the plesidapiform family Paromomyidae. The former paromomyids *I. mcgrewi* and *Ph. shifrae* from the Uintan and Duchesnean of Wyoming are transferred to the genus *Walshina* gen. nov., eliminating any record of paromomyids from the Uintan and the Duchesnean. The nearly complete lack of paromomyids after the onset of the Bridgerian could be correlated with the warmest sustained period of the Cenozoic, the EECO. This pattern is consistent with the disappearance of paromomyids after the Grauvian in Europe, making this a generalized trend of extinction or near extinction of this group worldwide in the middle Eocene.

Trogolemurin omomyoids and paromomyid plesiadapiforms converge in general dental morphology, suggesting that they might have been eating similar foods. It is notable that omomyoids with this morphology appear only after the near extinction of paromomyids in North America, suggesting that perhaps the marked decline in paromomyids left niche space available for omomyoids. The sole remaining late occurrence of a paromomyid, from the Chadronian of North Dakota, has been interpreted as being part of a relictual fauna surviving in the Great Plains, distinct from the Rocky Mountain province (Kihm and Tornow, 2014). Perhaps survival of a paromomyid in that context was made possible by its isolation from ecologically similar trogolemurin omomyoids.

Finally, our phylogenetic analysis shows that *Walshina* gen. nov. is monophyletic, nested inside Trogolemurini. The most closely related group to trogolemurins is a clade of anaptomorphins com-

posed by *Anemorhysis, Tetonoides,* and *Arapahovius*. Therefore, our phylogenetic analysis is consistent with the previously inferred close relationship of trogolemurins to *Anemorhysis* (Williams, 1994; Williams and Covert, 1994; Tornow, 2008) and to *Tetonoides* and *Arapahovius* (Gunnell, 1995). Although the most recent definition of Trogolemurini by Gunnell and Rose (2002) is fairly constricted in number of genera, our phylogenetic results are consistent with a broader definition of Trogolemurini suggested by Beard et al. (1992), in which *Anemorhysis, Tetonoides,* and *Arapahovius* might also be included.

ACKNOWLEDGMENTS

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APPENDIX 1.

APPENDIX TABLE 1. Measurements (in mm) for upper molars of Trogolemurini.

Specimen	Species	M1L	M1W	M2L	M2W	M3L	M3W	Locality	Reference	Notes
CM 14598	*Walshina shifrae* comb. nov.	-	-	1.24	1.81	-	-	5(A?), Badwater Creek, Natrona Co, WY, USA	Robinson (1968)	Identified as *Ignacius mcgrewi* in Robinson (1986)
CM 15103	*Walshina shifrae* comb. nov.	-	-	1.40	2.00	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
CM 15635	*Walshina mcgrewi* comb. nov.	2.00	2.78	-	-	-	-	5-front, Badwater Creek, Natrona Co, WY, USA	Robinson (1968)	Holotype
CM 15794	*Walshina mcgrewi* comb. nov.	-	-	1.80	2.90	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
CM 15795	*Walshina mcgrewi* comb. nov.	2.00	-	-	-	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
CM 15796	*Walshina mcgrewi* comb. nov.	2.00	-	-	-	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
CM 15797	*Walshina shifrae* comb. nov.	1.30	2.00	-	-	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	Holotype
CM 15798	*Walshina shifrae* comb. nov.	-	-	1.40	-	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
CM 15799	*Walshina shifrae* comb. nov.	1.20	1.90	-	-	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
LACM 40198	*Walshina esmaraldensis* gen. et sp. nov.	1.60	2.20	-	-	-	-	LACM (CIT) 180, north of Simi Valley, Ventura Co, CA, USA	This paper	Holotype
SDNHM 42268	*Walshina esmaraldensis* gen. et sp. nov.	-	-	1.66	-	-	-	SDNHM loc. 3426, Collwood South, San Diego Co, CA, USA	This paper	
SDNHM 62850	*Walshina esmaraldensis* gen. et sp. nov.	-	-	1.64	2.39	-	-	SDNHM loc. 4020, State Route 125, San Diego Co, CA, USA	This paper	
SDNHM 76267	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	1.31	2.05	SDNHM loc. 4082 (Emerald Ridge 2), northwest San Diego Co, CA, USA	This paper	
SDNHM 87336	*Walshina esmaraldensis* gen. et sp. nov.	-	-	1.76	2.48	-	-	SDNHM loc. 4925, Kelly Ranch Core, San Diego Co, CA, USA	This paper	
SDNHM 87337	*Walshina esmaraldensis* gen. et sp. nov.	-	-	1.54	-	-	-	SDNHM loc. 4925, Kelly Ranch Core, San Diego Co, CA, USA	This paper	
SMNH P1899.1007	*Trogolemur leonardi*	1.90	3.17	-	-	-	-	SMNH loc. 72J04-0006, east side of Lac Pelletier, SK, Canada	Storer (1990)	
SMNH P1899.1016	*Trogolemur leonardi*	-	-	-	-	1.58	2.57	SMNH loc. 72J04-0006, east side of Lac Pelletier, SK, Canada	Storer (1990)	Identified as M2 in Storer (1990)

Specimen	Species	M1L	M1W	M2L	M2W	M3L	M3W	Locality	Reference	Notes
UCM 25049	*Walshina shifrae* comb. nov.	-	-	1.24	1.67	-	-	5A, Badwater Creek, Natrona Co, WY, USA	Robinson (1968)	Identified as *Ignacius mcgrewi* in Robinson (1986)
USNM 417390	*Trogolemur myodes*	-	-	1.60	2.60	-	-	Elderberry Canyon Quarry, White Pine Co, NE, USA	Emry (1990)	
USNM 417391	*Trogolemur myodes*	-	-	-	-	1.30	2.20	Elderberry Canyon Quarry, White Pine Co, NE, USA	Emry (1990)	Incorrectly listed as a lower m3 in Emry (1990)
USNM 417396	*Trogolemur myodes*	1.60	2.30	-	-	-	-	Elderberry Canyon Quarry, White Pine Co, NE, USA	Emry (1990)	Identified as M2 in Emry (1990)

APPENDIX TABLE 2. Measurements (in mm) for lower dentition of Trogolemurini.

Specimen	Species	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	Locality	Reference	Notes
AMNH 12599	*Trogolemur myodes*	1.05	0.78	1.33	1.14	1.66	1.23	1.60	1.44	2.07	1.27	Granger S 6, Uinta Co, WY, USA	This paper	Holotype
CM 15793	*Walshina mcgrewi* comb. nov.	-	-	-	-	-	-	2.00	1.80	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
CM 21637	*Walshina shifrae* comb. nov.	-	-	-	-	-	-	1.50	1.30	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
CM 40069	*Trogolemur amplior*	-	-	-	-	2.20	1.85	1.95	1.95	-	-	CM loc. 34, Wind River Basin, Natrona Co, WY, USA	Beard et al. (1992)	
CM 41152	*Trogolemur fragilis*	-	-	-	-	-	-	-	-	1.95	1.20	CM loc. 34, Wind River Basin, Natrona Co, WY, USA	Beard et al. (1992)	
SDNHM 72583	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	-	-	-	-	1.80	1.18	SDNHM loc. 4081 (Emerald Ridge 1), northwest San Diego Co, CA, USA	This paper	
SDNHM 76266	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	-	-	-	-	2.07	1.26	SDNHM loc. 4082 (Emerald Ridge 2), northwest San Diego Co, CA, USA	This paper	
SDNHM 76337	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	1.83	1.48	-	-	-	-	SDNHM loc. 4082 (Emerald Ridge 2), northwest San Diego Co, CA, USA	This paper	
SDNHM 76338	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	-	-	1.90	1.61	-	-		This paper	
SDNHM 76339	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	-	-	-	-	-	1.19	SDNHM loc. 4082 (Emerald Ridge 2), northwest San Diego Co, CA, USA	This paper	
SDNHM 87332	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	-	-	1.79	1.46	-	-	SDNHM loc. 4925, Kelly Ranch Core, San Diego Co, CA, USA	This paper	
SDNHM 87333	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	-	-	1.79	1.57	-	-	SDNHM loc. 4925, Kelly Ranch Core, San Diego Co, CA, USA	This paper	

Specimen	Species	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	Locality	Reference	Notes
SDNHM 87334	*Walshina esmaraldensis* gen. et sp. nov.	-	-	-	-	-	-	-	-	2.17	1.38	SDNHM loc. 4925, Kelly Ranch Core, San Diego Co, CA, USA	This paper	
UCM 25175	*Walshina shifrae* comb. nov.	-	-	-	-	-	-	1.50	1.33	-	-	5A, Badwater Creek, Natrona Co, WY, USA	Robinson (1968)	Identified as *Ignacius mcgrewi* in Robinson (1986)
UCM 26012	*Walshina mcgrewi* comb. nov.	-	-	-	-	2.06	1.76	-	-	-	-	5A, Badwater Creek, Natrona Co, WY, USA	Robinson (1968)	
UCM 26432	*Walshina shifrae* comb. nov.	-	-	-	-	-	-	1.25	1.06	-	-	5A, Badwater Creek, Natrona Co, WY, USA	Robinson (1968)	Identified as *Ignacius mcgrewi* in Robinson (1986)
UCM 29005	*Walshina mcgrewi* comb. nov.	-	-	-	-	-	-	2.00	1.85	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
UCM 38323	*Walshina shifrae* comb. nov.	-	-	-	-	-	-	1.40	1.30	-	-	Badwater Creek, Natrona Co, WY, USA	Krishtalka (1978)	
UCM 46602	*Trogolemur amplior*	1.20	0.95	-	-	-	-	-	-	-	-	UCM loc. 80062, Wind River Basin, Natrona Co, WY, USA	Beard et al. (1992)	
UM 30966	*Sphacorhysis burntforkensis*	-	-	1.40	1.30	1.90	1.50	2.00	1.80	1.80	1.50	UM loc. BRW-264, sec. 22, T.13N., R.113W., Uinta Co, WY, USA	Gunnell (1995)	
USNM 417355	*Trogolemur myodes*	1.00	0.80	1.20	1.20	1.70	1.50	1.40	1.60	2.00	1.30	Elderberry Canyon Quarry, White Pine Co, NE, USA	Emry (1990)	
USNM 417356	*Trogolemur myodes*	1.00	0.90	1.10	1.25	1.50	1.50	1.40	1.60	2.10	1.40	Elderberry Canyon Quarry, White Pine Co, NE, USA	Emry (1990)	
USNM 417389	*Trogolemur myodes*	-	-	-	-	1.70	1.50	-	-	-	-	Elderberry Canyon Quarry, White Pine Co, NE, USA	Emry (1990)	
YPM VP 13523	*Trogolemur myodes*	-	-	-	-	-	-	1.41	1.43	1.96	1.15	Sweetwater Co, WY, USA	This paper	

APPENDIX 2.

Newick format for tree from Figure 7.

(Scandentia,(Purgatorius_spp,((Altanius_orlovi,(Plesiolestes_problematicus,('Plesiadapis/Pro-nothodectes',Chronolestes_simul))),(Donrussellia_sp.,(((Lemur_catta,(Galagoides_demidoff,Microcebus_murinus)),((Mahgarita_stevensi,Rooneyia_viejaensis),(Notharctus_sp.,(Pronycticebus_gaudryi,(Adapis_parisiensis,Leptadapis_magnus))))),(Teilhardina_americana,(Teilhardina_belgica,Teilhardina_asiatica),(Steinius_vespertinus,(Omomys_sp.,(Hemiacodon_gracilis,Macrotarsius_montanus))),(Eosimias_sp.,(Tarsius_sp.,(Proteopithecus_sylviae,(Catopithecus_browni,((Aegyptopithecus_zeuxis,(Apidium_phiomense,Parapithecus_grangeri)),(Dolichocebus_gaimanensis,(Callicebus_moloch,(Aotus_trivirgatus,Saimiri_sciureus))))))))),(((Uintanius_ameghini,(Tetonius_sp.,((Absarokius_sp.,Anaptomorphus_sp.),(Aycrossia_lovei,Strigorhysis_sp.)))),(Loveina_sheai,Loveina_minuta,Loveina_wapitiensis,(Dyseolemur_pacificus,Washakius_insignis,Loveina_zephyri,Shoshonius_cooperi))),((Nannopithex_sp.,Melaneremia_bryanti,Pseudoloris_parvulus,(Microchoerus_erinaceus,Necrolemur_antiquus)),((Anemorhysis_savagei,(Anemorhysis_wortmani,((Anemorhysis_sublettensis,Anemorhysis_natronensis),(Arapahovius_gazini,Tetonoides_sp.)))),(Trogolemur_myodes,Trogolemur_amplior,Trogolemur_fragilis,Trogolemur_leonardi,Sphacorhysis_burntforkensis,(Walshina_esmaraldensis,Walshina_mcgrewi,Walshina_shifrae)))))))))));