The Paromomyidae (Primates, Mammalia): Systematics, Evolution, and Ecology

by

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A thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy
Department of Anthropology
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Abstract

Plesiadapiforms represent the first radiation of Primates, appearing near the Cretaceous-Paleogene boundary. Eleven families of plesiadapiforms are recognized, including the Paromomyidae. Questions surrounding this family explored in this thesis include its pattern of extinction, its phylogeny and migration, and its dietary ecology.

Firstly, there is a record of misclassifying small-sized omomyoid euprimates as late-occurring paromomyid plesiadapiforms. Here, a new omomyoid from the Uintan of California is described. This material was previously thought to pertain to a paromomyid, similar to previously named supposed paromomyids *Phenacolemur shifrae* and *Ignacius mcgrewi*. The new Californian species, *Ph. shifrae*, and *I. mcgrewi* are transferred to Trogolemurini, a tribe of omomyoids. The implications of this taxonomic change are that no paromomyids are found between the early Bridgerian and the Chadronian, suggesting that the group suffered near-extinction during a period of particularly warm climate.

Secondly, migration of paromomyids between North America and Europe is poorly understood. The European material (genus *Arcius*) is taxonomically reassessed, including emended diagnoses for all four previously named species, and description of two new *Arcius* species. A cladistic
analysis of the European paromomyids resolves *Arcius* as monophyletic, implying that the European radiation of paromomyids was a product of a single migration event from North America.

Finally, paromomyid diet has only been assessed qualitatively in previous literature. Dental topographic metrics are used to assess diet in paromomyids and observe patterns of evolutionary change in the P4. The results for P4 are consistent with previous literature for inferences about changes within given lineages, but comparisons across different lineages is challenging. The results for M2 suggest a more varied diet that previously thought for paromomyids. The results presented here show a general trend from more insect intake in primitive members to a more frugivorous diet in more derived and/or later occurring members of various lineages.
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Chapter 1
Introduction
1 Introduction

Plesiadapiforms were a group of small, arboreal, archaic mammals widespread during the Paleocene and the Eocene, between 65 and 37 million years ago (Silcox et al., accepted). It was a very diverse group, including more than 140 named species in 11 families (Silcox et al., accepted; Silcox and López-Torres, accepted), and its broad range of adaptations resulted in an evolutionary diversification that allowed them to colonize North America, Europe, and Asia (Silcox and Gunnell, 2008; Silcox et al., accepted).

Plesiadapiforms have received special attention in the last couple of decades, mainly due to their hypothesized phylogenetic relations with primates. The group was initially included in the order Primates, based on dental characteristics (Gidley, 1923; Jepsen, 1930; Simpson, 1935; Kelly and Wood, 1954; Szalay, 1968; Gingerich, 1975, 1976; Szalay and Delson, 1979). However, some authors prefer to restrict Primates to forms that exhibit a collection of traits seen in all living primates, such as the postorbital bar, thus ruling Plesiadapiformes out of the Order (Martin, 1968; Cartmill, 1992; Soligo and Martin 2006, 2007).

Further debate arises on the phylogenetic relationship of plesiadapiforms to primates due to the description of some cranial (Beard, 1990, 1993a, b) and postcranial specimens (Kay et al., 1990, 1992) of paromomyid plesiadapiforms. These studies interpreted paromomyids to show a closer relationship to the Order Dermoptera than to Primates, giving rise to the mitten gliding hypothesis. As discussed below, discovery of more complete postcranial material has eroded the cases for both a relationship to Dermoptera, and for mitten-gliding behaviour (Bloch and Boyer, 2007; Bloch et al., 2007; Boyer and Bloch, 2008). Other authors have documented a lack of synapomorphies between paromomyids and dermopterans in the cranium (Stafford and Szalay, 2000; Bloch and Silcox, 2001, 2006; Silcox, 2001, 2003; Bloch et al., 2007). Most
comprehensive morphological analyses support a monophyletic group that includes Plesiadapiformes and Euprimates to the exclusion of Dermoptera (Silcox, 2001, 2008; Bloch and Boyer, 2002; Bloch et al., 2007; Silcox et al., 2010), although Ni et al. (2010, 2013, 2016) group together dermopterans and (some) plesiadapiforms.

It has not been determined yet which is the sister taxon of primates among the euarchontan groups, since flying lemurs (Janečka et al., 2007; Mason et al., 2016), treeshrews (Liu et al., 2009), and also the combined group of flying lemurs and treeshrews (Sundatheria; Bloch et al., 2007; Springer et al., 2007; Nie et al., 2008; O’Leary et al., 2013), have all been proposed (Figure 1.1). To date, molecular data cannot resolve this enigma. Plesiadapiforms, as the best sampled group of fossil euarchontans, have the potential to help resolve this debate.

Present taxonomic conceptions of Plesiadapiformes include eleven different families (following Silcox et al., accepted). One of these families is the focus of the present research: the Paromomyidae. Paromomyids are dentally characterized by sub-horizontal incisors; P4 with a tall, pointed, broad-based protoconid; low crowned molars; and a large hypoconulid lobe on M3 (Silcox and Gunnell, 2008; Silcox et al., accepted). Cranially, paromomyids have a long snout, small and widely spaced orbits, absence of postorbital bar, wide zygomatic arches, and auditory bullae ossified from the entotympanic and inflated (Silcox and Gunnell, 2008; Silcox et al., accepted). The postcranial skeleton of Paromomyidae suggests arborealism and vertical climbing, with strong grasping abilities, but not gliding or suspensory behaviours (Bloch and Boyer, 2007; Boyer and Bloch, 2008).

Paromomyids’ relatively low-crowned molars and small body mass (~ 42 - 596 g; Silcox et al., accepted) would be indicative of most likely mixed-feeding dietary behaviour, with a greater reliance on fruit (Gingerich, 1974). Other authors have also proposed that paromomyids might
**Figure 1.1** Hypotheses for sister taxon of Primates. Hypothesis 1: Dermoptera (flying lemurs) is the sister taxon of primates (Janečka et al., 2007). Hypothesis 2: Scandentia (treeshrews) is the sister taxon of primates (Liu et al., 2009). Hypothesis 3: Sundatheria (flying lemurs and treeshrews) is the sister taxon of primates (Bloch et al., 2007; Springer et al., 2007; Nie et al., 2008; O’Leary et al., 2013).
have been insectivores (Godinot, 1984), or fed on tree exudates (Beard, 1990, 1991; Boyer and Bloch, 2008) based on the enlargement of their lower incisor. Living gummivores, such as the phalangeroid marsupial *Petaurus breviceps*, use their similarly enlarged lower incisors to access gum (Fleay 1947; Smith 1982). However, Rosenberger (2010) has criticized this latter notion. The diet of paromomyids will be further explored in Chapter 4.

Paromomyidae is critical to resolving the relationships of plesiadapiforms to other euarchontans because they have been at the centre of the taxonomic controversy (e.g., Beard, 1990, 1993a,b; Kay et al., 1990, 1992; Bloch & Silcox, 2001; Bloch et al., 2007; Boyer & Bloch, 2008). Therefore, understanding their evolution is very relevant to the larger question of euarchontan relationships. In particular, the intra-group relationships amongst paromomyids are understudied, with just a single study performed at the genus-level (Bloch et al., 2002), in which only a handful of exclusively North American taxa were included. Even though North America stands out for a diverse radiation of this group of plesiadapiforms, four species of paromomyid have been described from Europe (Russell et al., 1967; Godinot, 1984; Estravís, 1992; 2000), and there is also at least one Asian species (Tong and Wang, 1998). Therefore, the broad geographic distribution and the fact that the paromomyid record extends from the Paleocene to the Eocene in three different continents make a good test case for future stratocladistic and biogeographic analyses.

### 1.1 Present record of paromomyids

The present record of paromomyid material includes over 1130 specimens, most of which comprise dental and gnathic specimens. This includes 25 species (but see Chapter 2 and Chapter 3) and 7 genera. Paromomyids are geographically distributed across North America, Europe, and
Asia, with reported discoveries from Canada, China, France, Portugal, Spain, the United Kingdom, and the United States, and their biogeographic distribution extending as far north as Ellesmere Island (Figure 1.2).

Cranial material has been reported for four species of paromomyids: *Phenacolemur jepseni* (Szalay, 1972; Bloch and Silcox, 2001), *Ignacius graybullianus* (Rose and Gingerich, 1976; MacPhee et al., 1983, Kay et al., 1990, 1992; Bloch and Silcox, 2001), *Ignacius clarkforkensis* (Bloch et al., 2007; Boyer and Bloch, 2008), and *Acidomomys hebeticus* (Boyer and Bloch, 2008). The cranium of *P. jepseni* (AMNH 48005) was the first reported paromomyid cranium, and was interpreted in comparison to *Plesiadapis tricuspidens* (Szalay, 1972). The more numerous and better-preserved specimens of *I. graybullianus* (UM 68006, UM 65569, USNM 421608, UM 108210 and USNM 482353) have permitted a better understanding of the internal cranial anatomy of paromomyids. Internal cranial anatomy, such as the pattern seen in cranial arteries, is commonly used for determining phylogenetic patterns (Coleman and Boyer, 2011). It has been suggested that paromomyids likely had a small and probably non-functional promontorial branch of the internal carotid artery, a lateral route for the internal carotid nerves crossing the promontorium, a ring-like ectotympanic bone with an annular bridge, and no stapedial artery (Bloch and Silcox, 2001; Silcox, 2003; Coleman and Boyer, 2011). Whereas having a non-functional promontorial branch of the internal carotid artery is a shared trait with dermopterans, the rest of these characteristics link paromomyids to primates rather than to dermopterans (Bloch and Silcox, 2001). The study of the inner ear can predict some elements of the locomotor behaviour. Silcox et al. (2009a) suggest that the small semicircular canals found in *I. graybullianus* is indicative of less agile locomotion than fossil euprimates, which is consistent with plesiadapiforms not being specialized leapers. *Ignacius graybullianus* has also been used to recreate the only virtual brain endocasts known from paromomyids (Silcox et al., 2009b; Boyer
Figure 1.2 Main areas where paromomyids have been unearthed.
et al., 2011), and is reported to have a degree of neocortical development similar to that of other plesiadapiforms (i.e. *Plesiadapis tricuspidentis* and *Microsyops annectens*) and other archaic mammals (Long et al., 2015).

Fragmentary postcranial material was attributed to several paromomyid species by Beard (1989, 1990, 1993a,b): *Ignacius graybullianus*, *Phenacolemur jepseni*, *Phenacolemur praecox*, and *Phenacolemur simonsi*. Much more complete and semi-articulated skeletons are known for *Ignacius clarkforkensis* (Bloch et al., 2007; Boyer and Bloch, 2008) and *Acidomomys hebeticus* (Bloch et al., 2002; Boyer and Bloch, 2008). Beard (1989, 1990, 1993a,b) performed an extensive morphological analysis of the postcranial anatomy and locomotor adaptations of the paromomyids known from the postcranium at the time. He suggested that paromomyids pertained to the Order Dermoptera, based on purported digital proportions that were consistent with gliding behavior (mitten-gliding hypothesis). The inferred close relationship to dermopterans was also supported by the studies of Kay et al. (1990, 1992). The mitten-gliding hypothesis has been challenged by a series of authors (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), who suggested that paromomyids would instead be stem primates. Dermopterans have very long manual intermediate phalanges relative to the proximal manual phalanges, argued by Beard (1989, 1990, 1993a,b) to be related to gliding, and also to be true of paromomyids. Krause (1991) initially pointed out that this inference was not necessarily true for paromomyids, and later Bloch and Boyer (2007; Boyer and Bloch, 2008) showed, based on semi-articulated specimens, that paromomyids have long intermediate foot phalanges, suggesting that the bones that Beard (1989) interpreted as manual intermediate phalanges were likely pedal intermediate phalanges. This would imply that paromomyids did not have demopteran-like hand proportions. This and other lines of evidence
were used to refute the gliding hypothesis for paromomyids (Boyer and Bloch, 2008). Instead, paromomyids are reconstructed as claw-climbing arborealists, with a more active locomotor repertoire than other plesiadapiforms, making frequent use of pronograde bounding (Bloch and Boyer, 2007; Bloch et al., 2007; Boyer and Bloch, 2008).

1.2 Historical record of paromomyids

The first record of a paromomyid was published by Matthew (1915), when he described *Phenacolemur praecox* and *Phenacolemur citatus*, from the early Eocene of the Clark’s Fork and Bighorn Basins (Wyoming, U.S.), respectively. However, these two species were included in the family Apatemyidae, which Matthew (1915) considered then to belong to either Insectivora or Primates. Modern conceptions of Apatemyidae exclude it from Primates and consider them sufficiently different from other mammals to be placed in their own order, Apatotheria (Silcox et al., 2010).

Later, Matthew and Granger (1921) described *Ignacius frugivorus* from the Tiffany beds of Colorado, considering it possibly a plesiadapid, inside the order Menotyphla. Menotyphla was a taxon proposed by Haeckel (1866) that comprised those insectivorans that had a caecum, contrasted with Lipotyphla, which had no caecum. Unfortunately, this diagnosis is certainly problematic when it comes to the ascription of fossil taxa to Menotyphla. The order initially included elephant shrews, treeshrews, and flying lemurs. However, evidence against Menotyphla as a natural group accumulated and the three families within this cluster would later be elevated to the ordinal levels: Dermoptera (Simpson, 1945), Macroscelidea (Butler, 1956), and Scandentia (Butler, 1972), and the concept of Menotyphla abandoned.
Soon after, Gidley (1923) described *Paromomys maturus* and *Paromomys depressidens* and ascribed them to the family Tarsiidae (Mammalia, Primates), this being the first time that a paromomyid was suggested to be clearly related to primates. The ascription to Primates was due to the similarity that Gidley (1923) observed in the enlarged hypoconulid lobes of the M3 of *Paromomys* to the ones in the euprimates *Northarctus* and *Pelycodus*. Then, Jepsen (1930) described *Phenacomlemur pagei*, moving the genus *Phenacomlemur* from Apatemyidae to the family Plesiadapidae (?Primates). The affinities of the pleisadapids had long been disputed. Previously, they had been referred to Insectivora and Rodentia, and by the early 1930’s, it was widely believed that pleisadapids were closely related to the euprimate *Daubentonia*. Later, it was suggested that there was no valid evidence of a particular relationship between pleisadapids and *Daubentonia*, but that pleisadapids were probably an offshoot of a lemuroid that did not clearly lead to any later form (Simpson, 1940).

Simpson (1940) first attempted to group several Paleocene and Eocene primate species under the subfamily Paromomyinae, which was included in the family Anaptomorphidae. This subfamily incorporated the genera *Paromomys*, *Palaechthon*, *Plesiolestes*, and *Palenochtha*. *Phenacomlemur* was not placed in this subfamily, and stayed as Primates *incertae sedis*, mainly due to the poor sample of this genus known at the time (Simpson, 1940). Later, Simpson (1940, 1955) recognized the relationship of *Phenacomlemur* to *Paromomys*, considering *Paromomys* ancestral to *Phenacomlemur*. In light of the evidence of a phylogenetic relationship between these two genera, he proposed a new family, the Phenacomlemuridae (Prosimii, Primates). Ironically, because Simpson himself provided a subfamily level name for this grouping in 1940 (Paromomyinae), Phenacomlemuridae is a junior synonym of Paromomyidae (Simpson, 1940). This new taxon included the genera *Palaechthon*, *Paromomys*, and *Phenacomlemur*. Simpson (1955) considered the genus *Phenacomlemur* a highly distinctive group, and the Torrejonian genus
*Paromomys* was tentatively placed in the same family in light of its resemblance to *Phenacolemur*. The Torrejonian *Palaechthon* was even more tentatively placed in the family Phenacolemuridae, since its resemblance was considered closer to *Paromomys* than to *Phenacolemur*. He also described the new species of “phenacolemurid” *Phenacolemur jepseni*, and suggested that *Phenacolemur praecox* and *Phenacolemur citatus* did not differ enough to be considered two distinct species. The two taxa were regrouped under a single species, *Phenacolemur praecox*, as different subspecies: *Ph. praecox praecox* and *Ph. praecox citatus*. However, these two subspecies would later be re-classified as distinct species by Bown and Rose (1976).

Following Szalay (1968), the subfamily Paromomyinae proposed by Simpson (1940) was elevated to the category of family (Paromomyidae) in place of Phenacolemuridae. The new family Paromomyidae was divided into two tribes, the Paromomyini and the Palaechthonini. The Paromomyini included the genera *Paromomys* and *Phenacolemur*, and the Palaechthonini included the genera *Palaechthon*, *Palenochtha*, and *Plesiolestes*. The genus *Purgatorius* was tentatively ascribed to the Paromomyidae, under the subfamily Purgatoriinae.

However, Bown and Rose (1976) argued that Szalay’s (1968) conception of Paromomyidae obscured the many distinct specializations of this family of stem primates. They removed several species from the Paromomyidae, restricting the family to only *Paromomys* and its probable descendants *Ignacius* and *Phenacolemur*, finally defining the current conception of the Paromomyidae. This new concept of the family resulted in a smaller but more clearly unified group. The rest of the taxa previously thought to be paromomyids (*Palaechthon*, *Plesiolestes*, and *Palenochtha*) are now included in the family “Palaechthonidae” (Gunnell, 1989), with the exception of *Purgatorius*, the most dentally primitive plesiadapiform known, which is classified
under its own family Purgatoriidae (Gunnell, 1989). Since the latest definition of the Paromomyidae (Bown and Rose, 1976), several genera exhibiting similarities to *Ignacius* and *Phenacolemur* have been added to the group: *Elwynella* (Rose and Bown, 1982), *Arcius* (Godinot, 1984), *Acidomomys* (Bloch et al., 2002), and *Edworthia* (Fox et al., 2010).

Table 1.1 provides a complete listing of the members of Paromomyidae under this latest definition, with the publications in which they were named. Two species attributed to the family are particularly worthy of note: *Ignacius mcgrewi* (Robinson, 1968) and *Phenacolemur shifrae* (Krishtalka, 1978). These two species appear in the Uintan and Duchesnean of Wyoming, after a sizeable temporal gap (from the middle Bridgerian). They are also characterized by their uncommonly small size compared to older paromomyids, and the presence of features more similar to primitive paromomyids (such as very reduced distolingual basins) than to late Eocene members of the family. The relevance of these traits in a phylogenetic context is assessed in detail in Chapter 2.

The latest occurring paromomyid is one instance of a P4 of *Ignacius* from the Chadronian of North Dakota (Kihm and Tornow, 2014). This specimen is not included in Table 1.1 since it has not been assigned to a species, but the record is important with respect to the temporal limits of the group.
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<tr>
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<tr>
<td><em>Phenacolemur</em></td>
<td><em>Ph. praecox</em></td>
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<td><em>Ph. citatus</em></td>
<td>Matthew, 1915</td>
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<td></td>
<td><em>Ph. fortior</em></td>
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</tr>
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<td><em>Ph. willwoodensis</em></td>
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<td><em>Ignacius</em></td>
<td><em>I. frugivorus</em></td>
<td>Matthew and Granger, 1921</td>
</tr>
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<td></td>
<td><em>I. mcgrewi</em></td>
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<td><em>I. clarkforkensis</em></td>
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<td><em>Ar. zbyszewskii</em></td>
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<td><em>Acidomomys</em></td>
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<td>Bloch, Boyer, Gingerich and Gunnell, 2002</td>
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<td><em>Edworthia</em></td>
<td><em>Ed. lerbekmoi</em></td>
<td>Fox, Scott and Rankin, 2010</td>
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1.3 Phylogenetic relationships among paromomyids

Gunnell (1989) divided the family Paromomyidae into two distinct subfamilies: the Paromomyinae and the Phenacolemurinae. Basically, Gunnell (1989) argues that paromomyines differ from phenacolemurines by the retention of more primitive characters. These characters include a 2.1.3.3 dental formula, a double-rooted P₂, a large double-rooted P₃, absent or weak metacone in P₄, presence of paraconid in M₁, and the M₃ talonid only slightly expanded by the hypoconulid. Modern systematics does not use primitive characters to group taxa (Hennig, 1965); therefore, reassessment of the subfamilies is mandatory.

Robinson and Ivy (1994) went even further and divided the phenacolemurines into two tribes: the Phenacolemurini and the Simpsonlemurini. They also described three new genera of paromomyids: “Simpsonlemur”, “Dillerlemur”, and “Pulverflumen” from the lower Eocene rocks of the Powder River Basin, Wyoming, currently not recognized as valid taxa (Silcox and Gunnell, 2008). According to Robinson and Ivy (1994), the difference between the two tribes of phenacolemurins is based on the incisor morphology and how gracile the jaw looks, with Simpsonlemurini having more gracile jaws. Simpsonlemurins included two genera, “Simpsonlemur” and Elwynella. The genus “Simpsonlemur” included two species previously attributed to Phenacolemur (“Simpsonlemur” citatus and “Simpsonlemur” jepseni) and two other unnamed species (Species A and Species B). On the other side, phenacolemurins included the genera Phenacolemur, “Dillerlemur”, “Pulverflumen”, Ignacius and the European paromomyid Arcius (although the authors stated that Arcius fuscus and Arcius lapparenti might belong to Simpsonlemurini). They also described a new species of Phenacolemur, Ph. fortior, and two other unnamed species of that same genus (Species C and Species D). The new genus “Dillerlemur” included Phenacolemur pagei (“Dillerlemur” pagei) and the new species
“Dillerlemur robinettei”. The new genus “Pulverflumen” included a single species, “Pu. magnificum”. All three new genera proposed by Robinson and Ivy (1994) have been considered taxonomic synonyms of *Phenacolemur*, and the distinction between the two tribes has not been recognized by subsequent authors (e.g., Silcox and Gunnell, 2008). However, these authors did not evaluate this hypothesis through a comprehensive comparative analysis, so this hypothesis of relationships merits further consideration.

At an ordinal level, Simpson (1955) recognized the ancestral relationship of *Paromomys* in respect to *Phenacolemur*, thus establishing the first phylogenetic ties between the Paleocene and Eocene primates. The primitive traits observed in *Paromomys* also led other authors to suggest that *Ignacius* (Bown and Rose, 1976), and *Acidomomys* (Bloch et al., 2002) could have been derived from a *Paromomys*-like form. Torrejonian *Paromomys* has a primitive lower dental formula of 2.1.3.3, while both *Phenacolemur* and *Ignacius* have lost the I2, and *Phenacolemur* has lost the P3 as well (Bloch et al., 2002). At a specific level, Bown and Rose (1976) suggested that *Paromomys depressidens* is closer in dental morphology to *Ignacius*, while *Paromomys maturus* is more similar to *Phenacolemur*. The distinctively oblique postparacone and premetacone cristae of the upper molars in *Ignacius* are foreshadowed in *Pa. depressidens*, but absent in *Pa. maturus* (Bown and Rose, 1976). In contrast, Rigby (1980) supports *Pa. depressidens* evolving into *Phenacolemur* instead.

According to Bloch et al. (2002), *Acidomomys*, with a dental formula of 2.0.2.3, could have easily been derived from *Paromomys*, and the dental formula alone likely precludes derivation of *Acidomomys* from any known species of *Phenacolemur* (which have all lost I2 and P3) or *Ignacius* (which have all lost I2) (Figure 1.3). Bloch et al. (2002) propose that *Acidomomys* represents a ghost lineage of paromomyids that extends from the middle Clarkforkian back to at
least the late Torrejonian of North America. *Paromomys farrandi* appears to closely resemble *Pa. depressidens* in the lower dentition, but its upper dentition shows a mixture of primitive and derived characters (Clemens and Wilson, 2009). It is unclear what the precise nature of their relationship is, since it has never been formally assessed.

Silcox et al. (2008) suggested that *Phenacolemur praecox* evolved into the similarly sized but morphologically distinct *Phenacolemur fortior*, supported by the faunal succession documented in the southern Bighorn Basin, Wyoming (see Silcox et al., 2008). With respect to *Ignacius*, Bloch et al. (2007) proposed that *Ignacius clarkforkensis* might be a morphologically and temporally intermediate form between earlier *I. frugivorus* and later *I. graybullianus*. This is based on the observation that the upper dentition of the Clarkforkian *I. clarkforkensis* differs from the Wasatchian *I. graybullianus* in having a P2, similarly to the Tiffanian *I. frugivorus*, but differs from the latter in having a single-rooted P2. The hypotheses for both the *Phenacolemur* and *Ignacius* successions need to be assessed in a broader phylogenetic context.

*Elwynella* is the only Eocene paromomyid known to possess P3, which is otherwise present in only the earliest species of Paleocene paromomyids. Rose and Bown (1982) hypothesized that the presence of P3 in a species with such a derived molar and incisor morphology suggests that *Elwynella* represents a separate lineage, evolving in parallel with *Phenacolemur* and derived from an ancestor (in common with *Phenacolemur*) that had not yet lost P3. According to Bown and Rose (1982), *Elwynella* would have diverged from other paromomyids during the Tiffanian.
Figure 1.3 Hypothesis of phylogenetic relationship among four genera of North American paromomyids. Based on 12 dental characters. Modified from Bloch et al. (2002; Fig. 7).
However, Bloch et al. (2002) suggested that it might have been derived from an Acidomomys-like form during the Clarkforkian-Wasatchian. Although it is possible that Elwynella and Acidomomys belong to the same lineage, this argument is only supported by a single symplesiomorphy (shared retention of p3; Silcox and Gunnell, 2008). Also, Silcox and Gunnell (2008) suggest a common ancestor for Phenacolemur, Ignacius, Acidomomys, and Elwynella that is more recent than Paromomys, since they all share derived traits missing from all known species of Paromomys.

Among all the described paromomyids, Edworthia has been argued to represent a distinct primitive lineage (Fox et al., 2010), which contrasts with the idea of Paromomys being the ancestral paromomyid. The retention of P2 is in Edworthia is a primitive feature in paromomyids, otherwise only retained in Paromomys, but Edworthia is more derived than Paromomys in that the P2 is single-rooted, the P4 has a shallow hypoflexid, and the molar protocristid notch is infilled (Fox et al., 2010). Contrarily, Edworthia seems more primitive than Paromomys in that the P4 has a weaker paracristid and weaker postvallid crests, the molar crowns are not swollen, the major cusps are acute, the paraconid on the molars is more distinct from the paracristid and is not connate with the metaconid, and the ectocingulid is less robust and is limited to the trigonid (Fox et al., 2010). This raises the question of whether Edworthia should be considered a paromomyid or to belong to a separate evolutionary branch.

In regard to the European paromomyids, at the time of the description of the first two species of Arcius (Ar. fuscus and Ar. lapparenti), Russell et al. (1967) noted a strong similarity between Ar. fuscus and the North American paromomyid Phenacolemur. Hence, these two species were originally ascribed to the genus Phenacolemur. They also suggested a divergence between the North American and European forms that would have taken place in the late Paleocene/early
Eocene. Both the species named by Russell et al. (1967) were later transferred to the genus *Arcius* when it was erected by Godinot (1984) on the basis that it had an elevated area of the mandible at the point of insertion of P₄, higher cusps than in *Ignacius*, a distinct paraconid on lower molars, and less expanded distolinguinal basins than *Phenacolemur*. Godinot (1984) suggested that *Ar. rougeri* could represent an ancestral stage of the European line of paromomyids. However, he emphasized that it was too early to distinguish between two European lineages without having more complete material of *Ar. rougieri*. Then, Estravís (2000) stated that *Ar. zbyszewskii* was more similar to *Ar. rougieri* than to any other *Arcius*. Since *Ar. zbyszewskii* shows a mosaic of primitive and derived characters, Estravís (2000) did not consider it ancestral to *Ar. fuscus* and *Ar. lapparenti*, but belonging to a different, very primitive lineage. Marigó et al. (2012) attributed a strong resemblance of the *Arcius* sp. found in Masia de l’Hereuet (Spain) to *Ar. lapparenti*, as in size and general morphology. However, the Spanish specimens were not ascribed to a new species by those authors. The relationships among European paromomyids will be further explored in Chapter 3.

An unexpected area that has yielded paromomyid material is the Eureka Formation from Ellesmere Island, in the Canadian Arctic (West and Dawson, 1977; McKenna, 1980; Eberle and Greenwood, 2012), making paromomyids the northernmost non-human primate in the evolutionary history of the Order. This opens up questions about the kind of adaptations these stem primates possessed to allow this geographic distribution. During the Eocene, the Canadian Arctic had warmer temperatures than in present times, but Arctic paromomyids would still have experienced temperatures that went down to freezing during winter. Also, they would have been exposed to long periods of darkness throughout the year, which suggests that Arctic paromomyids either had very flexible diets or were able to hibernate, as it is seen in some modern-day primates (Silcox et al., accepted). However, a detailed description of the Ellesmere
paromomyid material has not been published. The relevance of Arctic paromomyids would be basic to our understanding of the relationships between North American and European paromomyids, because the Arctic acted as a land bridge between these two continents around the Paleocene-Eocene boundary (Hooker, 2015).

Finally, just one occurrence of a paromomyid from Asia has been reported (Tong and Wang, 1998). Material from the Wutu fauna, from the Shandong Province, in China, has been identified as a member of the genus *Ignacius*. Unfortunately, this material has not yet been published in any detail.

### 1.4 Conclusion

Paromomyidae represent a key group to understand the link between Primates and the other Euarchonta, and further understand the evolutionary origin of primates. Their controversial taxonomic position has put this group in the centre of the debate, and the enigma around which group is more likely to be the sister group to primates cannot be resolved without fully understanding paromomyid phylogenetics. However, their phylogenetic relationships have not been studied in depth. In particular, the European paromomyids are poorly understood, and there is uncertainty about the migration patterns of paromomyids between North America and Europe.

Also, the validity of several taxa requires reassessment. This is the case of the later occurring paromomyids during the Uintan of North America (Robinson, 1968; Kristhtalka, 1978). The taxonomic classification of a species initially described as a small-sized, later-occurring paromomyid from Saskatchewan, Canada, has already been challenged by Beard et al. (1992), and this question needs to be further explored for similar material.
Finally, the literature on paromomyid diet is particularly scarce, and morphological aspects of the dentition related to diet in this family of stem primates has never been quantified. The opposing views of many authors on this particular topic based solely on the qualitative assessment of dental morphology (Gingerich, 1976; Godinot, 1984; Beard, 1990, 1991; Boyer and Bloch, 2008; Rosenberger, 2010), makes it necessary to explore this question using quantitative (i.e. dental topographic) methods.

1.5 References


Chapter 2
New Omomyoid (Euprimates, Mammalia) from the late Uintan of Southern California and the Question of the Extinction of the Paromomyidae (Plesiadapiformes, Primates)

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

2.1 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 California specimens also exhibit several dental features that are atypical for paromomyids, such as a strong paraconid on the third lower molar, and differ from earlier species of *Phenacolemur* in lacking a distally expanded distolingual basin on the upper molars. This combination of traits is more typical of earlier and more primitive paromomyids (e.g., *Paromomys*) and as such is inconsistent with the late age of these specimens. The similarly aged purported paromomyids *P. shifrae* and *Ignacius mcgrewi* 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, a group of similar size. We argue that the Southern California material, along with *P. 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.
2.2 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; López-Torres and Silcox, submitted), and the early Eocene of Asia (Tong and Wang, 1998). Paromomyids have been characterized dentally as possessing enlarged sub-horizontal incisors; P4 with a tall, pointed, broad-based protoconid; low crowned molars; and a large hypoconulid lobe on M3 (Silcox and Gunnell, 2008, Silcox et al., accepted; Figure 2.1). Cranially, paromomyids have a long snout, small and widely spaced orbits, absence of postorbital bar, wide zygomatic arches, and auditory bullae ossified from the entotympanic and inflated (Silcox and Gunnell, 2008). The postcranial skeleton of Paromomyidae suggests arborealism and vertical climbing, with strong grasping abilities, but not gliding or suspensory behaviors (Bloch and Boyer, 2007; Boyer and Bloch, 2008). Following Silcox et al. (accepted), seven genera comprise the family: *Paromomys, Phenacolemur, Ignacius, Elwynella, Arcius, Acidomomys*, and *Edworthia*.

In a phylogenetic context, paromomyids are 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., accepted). Whereas, in the past, paromomyids had been at the center of taxonomic controversy regarding their evolutionary relationships to dermopterans (Beard, 1989, 1990, 1993a, 1993b; Kay et al., 1990, 1992), comprehensive analyses have provided compelling evidence that they are instead stem
Figure 2.1 The late Wasatchian paromomyid *Phenacolemur citatus*. A: USGS 6573 (original fossil), right maxilla with $P^3$-$M^2$. B-D: USGS 21712 (cast), left mandible with $P_4$-$M_3$ in occlusal (B), buccal (C), and lingual (D) views.
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 (1991b) from Ventura and San Diego counties (California) that was referred to *Phenacolemur* and compared to the species, *Phenacolemur shifrae* Krishtalka 1978, previously identified from late middle Eocene deposits in Wyoming assigned to the Uintan and 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 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 omomyid primates both diversified at small body size, 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 M₃) 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). The 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 a paromomyid. They retain a small canine and a P$_3$, unlike most paromomyids. The teeth between I$_1$ and P$_4$ are inserted into the mandible very close together and inclined mesially. The trogolemurin P$_4$ is fairly 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 2.2), making these teeth quite different from most paromomyids, in which the P$_4$ is expanded and the M$_3$ hypoconulid more enlarged. The P$_4$ has a paracone much taller than its very small protocone (Gunnell, 1995). Upper molars have prominent protocones, narrow postprotocingula, and weak conules (Gunnell and Rose, 2002), making them more paromomyid-like, however, generating potential confusion when isolated teeth are found (e.g., Storer, 1990). No trogolemurin postcranial material has been reported. Only two genera belong to this tribe: *Trogolemur* and *Sphacorhysis* (following Gunnell and Rose, 2002).

The first attempt to place a trogolemurin in a cladistic context was done by Williams (1994), and she found that *Trogolemur myodes* was most closely related to *Anemorhysis*. That was also supported by Williams and Covert (1994). Gunnell’s (1995) cladogram depicted a *Tetonoides-Arapahovius* clade as sister group to Trogolemurini. Although this differs from the results of Williams (1994; Williams and Covert, 1994), this conclusion would still ally trogolemurins with North American anaptomorphines. Later, in larger, more comprehensive analyses, *Trogolemur*
Figure 2.2 Holotype of *Trogolemur myodes*, AMNH 12599
(Matthew, 1909: plate LII, figure 5). Right mandible with P$_2$–M$_3$.
A: occlusal view; B: buccal view; C: lingual view.
myodes was suggested to be closely related to the European microchoerines Microchoerus, Necrolemur, Nannopithecus, and Pseudoloris (Ross et al., 1998; Ni et al., 2004). However, Tornow’s (2008) analysis 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 anaptomorphines (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 decided to formally describe and re-examine the affinities of the southern Californian primate specimens that had been attributed to cf. Phenacolemur shifrae, and of similarly aged material from the Uintan and Duchesnean of Wyoming (Robinson, 1968; Krishtalka, 1978). Since 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.

2.2.1 Historical and geological context of southern California 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; Lillegraven, 1976, 1980; Golz and Lillegraven, 1977; Eaton, 1982; Kelly, 1990; Mason, 1988, 1990; Kelly et al., 1991; Theodor, 1999; Wesley and Flynn, 2003; Ludtke and Prothero, 2004; Colbert, 2006; Tomiya, 2013). Of particular note in the current context are the extensive contributions by Walsh (1987,
1991a, 1991b, 1996, 1997, 1998, 2000; Walsh and Estes, 1985; 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 coming from southern California is remarkably scarce. The current study deals specifically with material originally collected by Mason (1988; 1990) and Walsh (1991b) 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 14 degrees of longitude to the east (see paleoposition reconstruction in Figure 2.3).

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 (see 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.
**Figure 2.3** Reconstruction of western North America from 40 million years ago. Orange dot indicates the paleoposition of the sites discussed in this paper, while the red dot indicates the current latitude and longitude of the sites. The map is reproduced with R. Blakey’s permission (Colorado Plateau Geosystems, Inc.).
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.

2.2.1.1 Mission Valley Formation, southwest San Diego County (SDSNH locality 3426)

SDSNH locality 3426, Collwood South, is a two meter thick light brown sandy mudstone bed that occurs within the restricted concept of the Mission Valley Formation (see Walsh et al., 1996 for discussion). According to the SDSNH records, 2550 pounds (~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, 1991b, 1996).

Walsh et al. (1996) reported a single-crystal $^{40}$Ar-$^{39}$Ar age of 42.83 ± 0.24 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, 2001b), 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 and (slightly older) Friars formations to suggest that the climate was warm (18-20 °C mean annual temperature) with low average annual rainfall (ca. 63 cm). 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 East African habitats with a mix of riparian habitats grading into gallery forests and/or savanna, a slightly wider range of warm temperatures (20-22 °C), and possible annual rainfall of 50-100 cm. 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.

2.2.1.2 Member C of Santiago Formation, northwest San Diego County (SDSNH localities 4020, 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 consistent with interpretations of subtropical to tropical conditions and paleotemperatures in excess of 25 °C (Roth, 1991).
Prothero (2001a) 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 (41.5-42.5 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).

SDNSH 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. SDNSH 4020 is in the Mission Valley Formation in the city of El Cajon. Fossils occurred in a 2-5 foot thick (~0.6-1.5 m) massive, brown, medium-grained, silty sandstone with some calcareous concretions from which thousands of fossils, including articulated skeletons, were recovered. The presence of pulmonated (terrestrial) snails led the site to be informally called “the snail beds”. Approximately 7200 pounds (3265 kg) of sediment were screenwashed.

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. SDSNH 4081 (Emerald Ridge Site 1) is a 1-2 foot thick weakly-cemented sandstone channel with mudstone and siltstone clasts. A total of 4400 pounds (~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 4000 pounds (~1815 kg) of matrix were collected and processed (SDSNH records). SDSNH 4925 is a foot (~0.6 m) thick, gray-green, fine grained sandy siltstone from
which approximately 6,400 pounds (~2900 kg) of sediment were hand quarried and screenwashed (SDNSH records).

2.2.1.3 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 meters above the base of the Sespe Formation and is 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. Biostratigraphically, Robinson et al. (2004) assigned the Tapo Canyon local fauna to Ui3. Most recently, Kelly et al. (2012) have 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 and Friars Formations, 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 suggests 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 41.390-42.301 Ma in age (Ogg, 2012) and 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 yet older (see Tomiya, 2013 for a review) are not well supported.

2.3 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 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 Natural History Museum, San Diego, CA, USA; SDSNH–San Diego Society of Natural History locality; 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.

2.4 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 2.4a-d, 2.5a-k, 2.6a-s

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

1991b 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.


**Distribution** – Uintan and Duchesnean of Wyoming, and Uintan of California.
Figure 2.4 Environmental SEM images of four teeth of *Walshina esmaraldensis*, gen et sp. nov. A: left M³, SDSNH 76276; B: right M₁, SDSNH 76337; C: right M₂, SDSNH 76338; D: right M₃, SDSNH 72583. All teeth are in occlusal view. Arrow indicates the location of the fovea.
Figure 2.5 Photographs taken with digital camera (A, D-K) and Micro-CT scan reconstructions generated using Avizo 7 (B, C). *Walshina shifrae* (A, D, G, J) – A: right M\(^1\), CM 15797 (holotype; mirrored), in occlusal view; D: left M\(^2\), CM 15103, in occlusal view; G: left M\(_2\), CM 21637, in occlusal view; J: left M\(_3\), CM 15726, in occlusal view. *Walshina esmaraldensis*, gen. et sp. nov. (B, E) – B: left M\(_1\), LACM 40198 (holotype), in occlusal view; E: left M\(_2\), SDSNH 62850, in occlusal view. *Walshina mcgrewi* (C, F, H, I, K) – C: left M\(_1\), CM 15635 (holotype), in occlusal view; F: left M\(_2\), CM 15794, in occlusal view; H, I, K: left mandibular fragment with M\(_2\), CM 29005, in occlusal (H), buccal (I), and lingual (K) views.
Figure 2.6 Micro-CT scan reconstructions of specimens of *Walshina esmaraldensis* generated using Avizo 7: A: left M¹, LACM 40198 (holotype), in occlusal view; B: left M², SDSNH 87336, in occlusal view; C: lingual fragment of a left M², SDSNH 87337, in occlusal view; D: lingual fragment of a right M², SDSNH 42268, in occlusal view; E, F, I, J: left M₂, SDSNH 87332, in occlusal (E), buccal (F), mesial (I) and lingual (J) views; G, H, K, L: mesial fragment of a left M₁, SDSNH 87331, in occlusal (G), buccal (H), mesial (K) and lingual (L) views; M, N, Q, R: left M₃, SDSNH 87334, in buccal (M), occlusal (N), lingual (Q) and mesial (R) views; O, P, S: distal fragment of a right M₃, SDSNH 87335, in buccal (O), occlusal (P) and lingual (S).
**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 *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* 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 is much shorter mesiodistally relative to its buccal border.

**Discussion**—All trogolemurins share a distally expanded distolingual basin of the upper molars (particularly marked in *Walshina mcgrewi*), which is quite similar to that observed in paromomyid plesiadapiforms. This similarity is likely one reason why some members of *Walshina* 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* 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 n. sp.

Figures 2.4a-d, 2.5b,e, 2.6a-s

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

Holotype – LACM 40198, left M1.

Paratypes – M2: SDSNH 62850; M3: SDSNH 76267; M1: SDSNH 76337; M2: SDSNH 87332; M3: SDSNH 87334

Hypodigm – M2: SDSNH 42268, 87336, 87337; M1: SDSNH 87331; M2: SDSNH 76338, 87333; M3: SDSNH 72583, 76266, 76339, 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 Walshina mcgrewi and W. shifrae. Differs from W. mcgrewi in having a hypoconulid closer to the hypoconid than to the entoconid on M2, similar to W. shifrae. Very large hypoconulids on M1 and M2, while they are weakly developed in W. mcgrewi and W. shifrae. Trigonid and talonid of M2 of similar width, whereas W. mcgrewi and W. shifrae have significantly wider M2 talonid bases relative to the trigonid base. M3 with stronger paraconid and taller metaconid relative to the protoconid than in W. shifrae.
Hypoconulid lobe of M₃ not expanded as far distally from the apex of the hypoconulid as in W. shifrae. Differs from W. mcgrewi (but not W. shifrae) in having upper molars with much less expanded distolingual basins. In mesial view, M¹ with a less clearly delineated preprotocrista, like W. mcgrewi. M² with a much more lingually expanded protocone lobe than in W. shifrae (but not W. mcgrewi).

2.5 Descriptions and comparisons

The only known M¹ of Walshina esmaraldensis comes from LACM (CIT) 180 from Simi Valley, Ventura County, California, and was described by Mason (1990). It differs from all other upper molars of W. esmaraldensis in having a less expanded distolingual basin, and a metastylar lobe that extends buccally to a similar degree as the parastylar lobe, which is typical of M¹ s compared to M² s in many early primate taxa. Mason (1990) attributed LACM 40198 to Phenacolemur cf. shifrae, and stated that the sole diagnostic character to differentiate W. mcgrewi from W. shifrae was size. Although size is a useful diagnostic character in Walshina, there are a number of other distinguishing features that can be used to differentiate among the species. Nonetheless, Mason (1990) provides an adequate description of this tooth.

Both specimens of M² have a sloping buccal border due to a reduced metacone relative to the paracone and a more expanded distolingual basin than M¹. On the M², the postprotocingulum runs straight mesiodistally, creating a sharper angle with the postcingulum than seen on the M¹, where the postprotocingulum and postcingulum are more buccally oblique. The outline of M² is rectangular rather than squared. The distolingual basin is deep, with a straight distal aspect of the tooth. The paracone and metacone are well separated. The trigon basin is also deep. The parastylar region is damaged in all M² 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* is very
lingually expanded; more so than in *W. shifrae* but less so than in *Trogolemur*. However, none of
the other trogolemurins have a distolingual basin as expanded as that of *W. mcgrewi*’s M$_2$, in
which it is so expanded that the postcingululum curves distally beyond the plane of the metacone
in the lingual aspect of the tooth. In contrast, the distolingual basin in *W. esmaraldensis* does not
extend further distally than the metacone.

The only M$_3$ known for the genus *Walshina* belongs to *W. esmaraldensis*. The paracone and
metacone of 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.

With respect to M$_1$, the breadth of the talonid near the apices of the cusps is wider than the
breadth of the trigonid. The paraconid is present on a paracristid that is very strong and 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 height 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 in relation to the position of 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 M₃ paraconid is present and very strong. The trigonid is not strongly inclined, with a steep distal aspect of the metaconid. The hypoconulid is enlarged so that it forms a lobe. The hypoconulid is narrower than the transverse dimension between the hypoconid and the entoconid. The only other known M₃ of *Walshina* belongs to *W. shifrae*. 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* is smaller than in *W. esmaraldensis* relative to the distance between the hypoconid and the entoconid, making this part of the tooth appear narrower. The hypoconulid lobe of *W. shifrae* also has a longer distal slope than in *W. esmaraldensis*, so that it extends further from the apex of this cusp.

Body mass estimates using Gingerich et al.’s (1982) and Conroy’s (1987; prosimian) equations are shown for all species of trogolemurins in Table 2.1. Measurements used for calculating body mass estimates are shown in Appendix 2.2. Conroy’s (1987) equation would be expected to provide more relevant estimates, since 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 M₁, which is problematic in this case since that tooth locus is not yet known in several species of trogolemurins. In particular, although the smallest estimated body mass is 58g for *Trogolemur myodes* using Conroy’s (1987) equation, if an M₁ were known for *Walshina shifrae*, its estimated body mass would certainly be lower, as the estimates based on teeth known for both species using the Gingerich et al. (1982) equations are consistently much lower for *W. shifrae* than for *T.*
"myodes (e.g., estimate based on $M_2$ 142g for *T. myodes* compared to 109g for *W. shifrae*). This would make *W. shifrae* the smallest of all of the trogolemurins, and smaller than all other North American omomyoids (based on comparison to body mass estimates in Fleagle, 2013).
Table 2.1 Estimated body masses of all species of Trogolemurini.

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<tr>
<td></td>
<td>( M_1 )</td>
<td>( M_2 )</td>
</tr>
<tr>
<td><em>Walshina esmaraldensis</em></td>
<td>154g</td>
<td>197g</td>
</tr>
<tr>
<td><em>Walshina mcgrewi</em></td>
<td>237g</td>
<td>275g</td>
</tr>
<tr>
<td><em>Walshina shifrae</em></td>
<td>-</td>
<td>109g</td>
</tr>
<tr>
<td><em>Trogolemur myodes</em></td>
<td>125g</td>
<td>142g</td>
</tr>
<tr>
<td><em>Trogolemur amplior</em></td>
<td>-</td>
<td>290g</td>
</tr>
<tr>
<td><em>Trogolemur fragilis</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Trogolemur leonardi</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Sphacorhysis burntforkensis</em></td>
<td>166g</td>
<td>270g</td>
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2.6 Phylogenetic relationships of *Walshina*

In order to assess the phylogenetic position of *Walshina* among Omomyoidea, we conducted a cladistic analysis based on Ni et al.’s (2004) study, as modified by Holroyd and Strait (2008), who revised the codings for two species (*Purgatorius janisae* and *Anemorhysis 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, *Trogolemur myodes*. Having codings from a member of this family available in the original matrix was important to ensure that we were assessing characters in the same way. 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 Holroyd and Strait’s (2008) matrix: *Trogolemur amplior, T. fragilis, T. leonardi, Sphacorhysis burntforkensis, Walshina esmaraldensis, W. mcgrewi*, and *W. shifrae*. The codings for *T. myodes* were partially reassessed, and Scandentia was re-coded for character 13. A total of 303 characters (194 dental, 49 cranial, 56 postcranial, and 4 soft tissue and physiological [only coded for extant taxa] characters) were scored for a total of 62 taxa (matrix available on publication from www.morphobank.org).

A parsimony analysis was performed using PAUP* 4.0 (Swofford, 2003) with all characters equally weighted and ordered, following the original analysis (Ni et al., 2004). Multiple character states were set to be interpreted as polymorphisms, instead of uncertainties. A heuristic search was implemented with 1000 repetitions, automatically increasing the maximum number of trees (MAXTREES) to be saved.
2.6.1 Results of the phylogenetic analysis

The cladistic analysis yielded 150 equally parsimonious trees. An Adams consensus tree was generated in PAUP* 4.0 from these trees (Figure 2.7). This type of consensus tree was chosen because it minimizes the impact of “wildcard” taxa by collapsing them to the highest resolved node (Kearney and Clark, 2003). In the Adams consensus tree, *Walshina* is found to be monophyletic, with *W. esmaraldensis* being closely related to *W. shifrae*. The tribe Trogolemurini was not recovered as a monophyletic clade due to the unresolved position of *Trogolemur leonardi*. This is likely caused by a sampling problem, since *T. leonardi* is only known from upper molars. The M₁ and M₃ were the only teeth that could be confidently coded in the character matrix for that species. Poorly sampled species inevitably reduce the number of characters available for coding, causing stem-ward slippage (Sansom et al., 2010; Pattinson et al., 2015). With the exception of this poorly sampled taxon, Trogolemurini is otherwise recovered as monophyletic, suggesting that it may be a valid group, with *Sphacorhysis* as potentially the most primitive member of the tribe. Although *Trogolemur* appears to be paraphyletic (Figure 2.7), this topology results from a lack of resolution in the phylogenetic positions of *T. fragilis*, *T. myodes*, and *T. leonardi*.

The inclusion of the rest of trogolemurins, along with the revisions made by Holroyd and Strait (2008), caused some changes to the tree with respect to Ni et al.’s (2004) phylogeny. 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, with *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 *A. orlovi*, 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.
Figure 2.7 Hypothesis of relationships of *Walshina* in the context of the Order Primates.

Adams consensus cladogram based on data modified from Holroyd and Strait (2008), including the addition of seven newly-coded trogolemurins (*Trogolemur amplior, T. fragilis, T. leonardi, Sphacorhysis burntforkensis, Walshina esmaraldensis, W. mcgrewi, and W. shifrae*). Trogolemurins are marked in blue.
2016). The tree differs from Ni et al.’s (2004) result in resolving the position of *Mahgarita* and *Pronycticebus* within Adapoidea. *Donrussellia* moves from the basal stem strepsirrhine position in Ni et al. (2004) to group together with the rest of adapoids, making Adapoidea monophyletic (although including *Rooneyia*, a taxon often thought to be an omomyoid). *Eosimias* appears in our tree as the sister taxon of crown haplorhines (=Anthropoidea + *Tarsius*). The sister group to Crown Haplorhini + *Eosimias* is the omomyoid tribe Washakiini (following Gunnell and Rose, 2002), implying that Omomyoidea is not monophyletic unless anthropoids and tarsiers are included. Washakiins are monophyletic, although *Loveina* was found to be paraphyletic (consistent with the results of Holroyd and Strait, 2008).

The position of the clade *Teilhardina belgica* + *Teilhardina asiatica* changes significantly from that recovered by Ni et al. (2004). While in their analysis this clade appears as stem haplorhines, our tree places them as the sister group to Adapoidea. Although we do not necessarily support this result, it does highlight the instability of this analysis, which was supposedly designed to place *T. asiatica* phylogenetically. It is somewhat surprising that adding species many nodes removed (i.e., trogolemurins) would destabilize nodes as deep as those associated with *Teilhardina*.

The sister group to trogolemurins (excluding *Troglemur leonardi*) is the European omomyoid family Microchoeridae (following Fleagle, 2013). This is consistent with the results of Ni et al.’s (2004) analysis, in which *Troglemur* clustered together with microchoerids. Finding these two groups as sister clades is surprising given the fact that trogolemurins are an exclusively North American taxon, whereas microchoerids are only known from the early to late Eocene of Europe, with the exception of the Asian *Indusomys* (Gunnell et al., 2008, 2012). This inferred relationship would imply a complex scenario regarding the biogeographic migratory patterns of
omomyoids at the end of the early Eocene. It is known that rapid geographic dispersal occurred in omomyoids during the earliest Eocene across North America, Europe, and Asia (Smith et al., 2006), and therefore perhaps it could happen later, but the routes that would allow such a migration are unknown at the end of the early Eocene. Alternatively, it suggests the possible presence of a ghost lineage of more basal trogolemurins in North America during part of the early Eocene, an idea that is maybe consistent with their relative rarity and small body size.

2.7 Discussion

Taxonomic confusion in the literature stems from the fact that trogolemurins have many dental features that converge on those of paromomyids: large hypoconulid lobes on M₃, procumbent lower incisors, upper molars with a well-developed postprotocingulum, and a fairly expanded distolingual basin. However, the most diagnostic tooth for paromomyids, the P₄, which is enlarged with a tall, pointed, upright protoconid, is very different from a trogolemurin P₄, which is proportionally smaller with a mesially inclined trigonid. However, trogolemurin material has classically been scarce and incomplete, often missing the diagnostic P₄ (Robinson, 1968; Krishtalka, 1978; Mason, 1990; Storer, 1990; Walsh, 1991b; Beard et al., 1992) or the upper dentition (Matthew, 1909; Beard et al., 1992), and in many cases taxa are only known from unassociated isolated teeth (Robinson, 1968; Krishtalka, 1978; Mason, 1990; Storer, 1990; Walsh, 1991b). Trogolemurin P₄s are only known for Trogolemur and Sphacorhysis (Matthew, 1909; Emry, 1990; Gunnell, 1995), but not for Walshina. It was not until Emry’s (1990) work that the first upper molars ascribed to a trogolemurin were described, and not until Gunnell’s (1995) work that the first upper dentition of Trogolemur in a tooth row (including the first P₄ 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, *Phenacolemur leonardi*, from the late middle Eocene (Duchesnean) of Saskatchewan. Beard et al. (1992) transferred *P. 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 P₄, 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 and most primitive paromomyids (i.e., *Paromomys*), which are millions of years older than the oldest trogolemurins (oldest paromomyids from the earliest Torrejonian, Clemens and Wilson, 2009, approximately 63 Ma; oldest trogolemurins from the latest Wasatchian, Williams and Covert, 1994, approximately 51 Ma). 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 M₁ of trogolemurins differs from that tooth in paromomyids in having a very oblique stepped postvallid, produced by a metaconid that is located well distal of the protoconid. The M₁ also has a very tall, strong paracristid, which is never so expanded in paromomyids. The hypoconulid on the M₁ and M₂ of trogolemurins is also better developed and more distinct, whereas paromomyids show weak to absent hypoconulids. The talonid of the M₂ is shorter in trogolemurins relative to the length of the trigonid, making trogolemurins have a trigonid and talonid closer in length.
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 ascribed to *Ignacius mcgrewi* and *Phenacolemur 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 history. In particular, paromomyids generally exhibit increases to the degree of expansion of the 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 *Ignacius mcgrewi* and *Phenacolemur shifrae* as members of the trogolemurin genus *Walshina* prompts consideration of the timing of the extinction of paromomyids. *Ignacius mcgrewi* and *P. 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 up 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 (see Matthew, 1909; West, 1976; Emry, 1990; Gunnell and Bartels, 1999; Gunnell et al., 2009) made the reappearance of the group in the late Uintan somewhat surprising. Re-classifying the Uintan and Duchesnean material to the Trogolemurini makes it clear that paromomyids were close to extinction after the early Bridgerian in North America. The only remaining post-Bridgerian record of a paromomyid is an
isolated $P^1$ 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, creating a very long ghost lineage that extends over a period of approximately 12 million years (middle Eocene boundary at 49 m.y.a., Clyde et al., 2001; Duchesnean-Chadronian boundary at 37 m.y.a., Prothero and Emry, 2004).

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 supposed Uintan and Duchesnean material. Paromomyids reached their highest peak of biodiversity during the Wasatchian 4 (Wa4) biozone, while 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 *Ignacius graybullianus* and an upper molar and an edentulous jaw of *Phenacolemur 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 (West and Dawson, 1977; McKenna, 1980) from the Canadian High Arctic (Ellesmere Island). 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 can potentially be ascribed to increasing global temperatures.

2.7.1 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 that have been attributed to the family from Europe that 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; López-Torres and Silcox, submitted). 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 up 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 from Bouxwiller (France) appear in a faunal list in Sudre (1978; one of them illustrated in Aumont, 2003). However, this scarce material, comprised of three isolated molars from the middle Eocene of Europe, may not be attributable to the Paromomyidae.
The tooth from Saint-Maximin, identified here as an M\textsubscript{2} (and as either an M\textsubscript{1} or an M\textsubscript{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\textsubscript{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 *Anchomomys* sp., based on the presence of this genus at that site. The M\textsubscript{3}s from Bouxwiller were identified as *Arcius lapparenti* by Aumont (2003). However, they are very flat, and significantly shorter mesiodistally than those of *A. lapparenti*. The trigonid is shorter mesiodistally in relation to its width than in *A. 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 significantly 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 *Nannopithecus* 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.

2.8 Conclusions

The material from southern California previously ascribed to *Phenacolemur* by Mason (1990) and Walsh (1991b) are not paromomyids. They represent a new species of trogolemurin omomyoid, *Walshina esmaraldensis*. The Californian sample of *Walshina* adds to our knowledge of the variability and diversity of omomyoids, particularly trogolemurins, and changes significantly our understanding of the temporal distribution of the plesiadapiform family.
Paromomyidae. The former paromomyids *Ignacius mcgrewi* and *Phenacolemur shifrae* from the Uintan and Duchesnean of Wyoming are transferred to the genus *Walshina*, 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 only appear after the near extinction of paromomyids in North America, suggesting that perhaps the marked decline in paromomyids left niche space available for omomyoids to invade. 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* is a monophyletic clade, nested inside Trogolemurini. The most closely related group to trogolemurins is inferred to be Microchoeridae, suggesting cross-continental dispersal may have happened in more than one lineage of omomyoids in the early Eocene.
2.9 Acknowledgments

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Chapter 3
The European Paromomyidae (Primates, Mammalia): taxonomy, phylogeny, and biogeographic implications

Author contributions: S. López-Torres (University of Toronto Scarborough) and M.T. Silcox (University of Toronto Scarborough) contributed to conception and design of the study, and interpreted the data. S. López-Torres drafted the article. S. López-Torres and M.T. Silcox gave final approval before submission to the thesis committee.
3  The European Paromomyidae (Primates, Mammalia): taxonomy, phylogeny, and biogeographic implications

3.1  Abstract

Plesiadapiforms represent the first radiation of Primates, appearing near the Cretaceous-Paleogene boundary. Eleven families of plesiadapiforms are recognized, including the Paromomyidae. Four species of paromomyids have been reported from Europe: *Arcius fuscus*, *Arcius lapparenti*, and *Arcius rougieri* from France, and *Arcius zbyszewskii* from Portugal. Other specimens of *Arcius* are also known from Masia de l’Hereuet in Spain, Abbey Wood in England, and Sotteville-sur-Mer in Normandy (France).

A cladistic analysis of the European paromomyids has never been published. Existing conceptions of the relationships between species of *Arcius* suggest that *A. rougieri* represents a more primitive stage than *A. fuscus* and *A. lapparenti*. *Arcius zbyszewskii* was suggested to be the most primitive species of the genus, closely related to *A. rougieri*. The Spanish specimens were suggested to be closely related to *A. lapparenti*; the English specimen has been most recently ascribed to *A. lapparenti*; and the Normandy specimen has been tentatively compared to *A. zbyszewskii*.

A total of 53 dental characters were analyzed for the four species of *Arcius* and the *Arcius* specimens from Spain, England, and Normandy. Parsimony based cladistic analysis using TNT yielded a single-most parsimonious cladogram rooted with *Purgatorius coracis*.

The results agree with *A. zbyszewskii* belonging to the most primitive lineage of the genus. *Arcius rougieri* is positioned as the sister taxon of *A. fuscus* and *A. lapparenti*. The English
material pertains to a quite primitive lineage, instead of being closely related to *A. lapparenti*. The phylogenetic relationships of the Spanish material remain unresolved, but it clusters together with the three French species. The results suggest that the Normandy material in fact belongs to *A. zbyszewskii*. In a biogeographic sense, monophyly of the group is consistent with a single migration event from North America to Europe potentially around the earliest Eocene though the Greenland land bridge.

### 3.2 Introduction

Paromomyidae is a family of extinct stem primates known from North America (Silcox and Gunnell, 2008; Silcox et al., 2008), Europe (Russell et al., 1967; Godinot, 1984; Estravís, 2000; Aumont, 2003; Marigó et al., 2012, 2014), and Asia (Tong and Wang, 1998). The oldest paromomyid is *Paromomys farrandi* (Clemens and Wilson, 2009), which is reported from the early Paleocene (Torrejonian 1 North American Land Mammal Age [NALMA]) of northeastern Montana, and thus this family is thought to have had its origins in North America. The Asian paromomyids (Tong and Wang, 1998) have never been formally described, which complicates the study of dispersals between North America and Asia. On the other hand, the European paromomyids have received more attention in the literature (Russell et al., 1967; Godinot, 1981, 1984; Marandat, 1991; Estravís, 2000; Aumont, 2003, 2004; Hooker, 2010; Smith et al., 2011; Marigó et al., 2012), and the dispersal of these primates from North America to Europe is better understood. Recently, Hooker (2015) formulated a model to account for mammalian dispersal patterns during the Paleocene-Eocene transition. According to his model, there were two major dispersal events between North America, Europe, and Europe. The first (Phase 1) occurred during the latest Paleocene, and brought to Europe euprimates, artiodactyls, and perissodactyls
from Asia; rodents, pantodons, oxyaenids, herpetotheriids, apatemyids, palaeanodonts, condylarths, neoplagiaulacids, viverravids, tillodonts from North America, and hyaenodontids from Africa. The second wave of migrant species (Phase 2) to Europe from North America was possible due to increased temperatures during the Paleocene-Eocene Thermal Maximum (PETM) that allowed high latitude dispersal. The second dispersal included the marsupial *Peradectes*, the mesonychid *Pachyaena*, and is also thought to have included paromomyids (Hooker, 2015; but see below).

All paromomyids from Europe have been hypothesized to belong to a single genus, *Arcius* (Godinot, 1984).

A full analysis of the phylogenetic relationships of the European paromomyids has never been published, although some ideas about possible relationships have been expressed. Russell et al. (1967) suggested that the European paromomyids were closely related to *Phenacolemur*; Godinot (1984) proposed *A. rougieri* as a potential ancestor to *A. fuscus* and *A. lapparenti*, and also that *Arcius* would be more closely related to *Ignacius*; and Estravís (2000) advocated that *A. zbyszewskii* was the most basal species of *Arcius*. The only cladistic analysis of the European paromomyids was included by Aumont (2003) in her unpublished dissertation. She found that *A. fuscus* and *A. lapparenti* formed a clade, with *A. zbyszewskii* as its sister taxon, and *A. rougieri* being the most primitive lineage of the genus. The sister taxon for *Arcius* was the North American paromomyid *Acidomomys hebecus*.

The current paper has three aims: 1) to revisit the alpha taxonomy of the European Paromomyidae, 2) to analyze the phylogenetic relationships among European paromomyids and their relationships to other members of the family using a dataset that samples both characters and taxa more comprehensively than Aumont (2003), and 3) to discuss the biogeographic implications of the phylogenetic analysis.

### 3.3 Institutional abbreviations

Montpellier, Montpellier, France; FNR–Fournes collection, Université de Montpellier, Montpellier, France; IPS–Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain; MAM–Mammal collection, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; MU–Mutigny collection, Muséum Nationale d’Histoire Naturelle, Paris, France; PAT–Palette collection, Université de Montpellier, Montpellier, France; RI–Rians collection, Muséum Nationale d’Histoire Naturelle, Paris, France; SV–Silveirinha collection, Universidade Nova de Lisboa, Lisbon, Portugal; UALVP–University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, AB, Canada; UCMP–University of California Museum of Paleontology, Berkeley, CA, USA; UM–University of Michigan Museum of Paleontology, Ann Arbor, MI, USA; USGS–United States Geological Survey collection, Smithsonian Institution, DC, USA; USNM–United States National Museum, Smithsonian Institution, Washington, DC, USA; YPM–PU–Princeton University collection, Yale Peabody Museum, New Haven, CT, USA.

3.4 Systematic paleontology

Order **PRIMATES** Linnaeus, 1758

Superfamily **PAROMOMYOIDEA** (Simpson, 1940)

Family **PAROMOMYIDAE** Simpson, 1940

*Arcius* Godinot, 1984


**Type species:** *Arcius rougieri*

**Included species:** *A. rougieri, A. fuscus, A. lapparenti, A. zbyszewskii, Arcius hookeri* n. sp. *Arcius ilerdensis* n.sp.

**Etymology:** Named after the Valley of Arc, in southern France, where the type species was originally found.

**Distribution:** Neustrian (early Eocene) of France, United Kingdom, Portugal, and Spain; Grauvian (middle Eocene) of France.

**Emended diagnosis** (modified from Godinot, 1984): Lower incisor with a lingual and a buccal crest. Occlusal area of P<sub>3</sub> close to that of M<sub>1</sub>. Lower molar cusps relatively taller than those of *Ignacius*. Lower molar trigonids not as mesially inclined as in any other paromomyid genus. Large third molar hypoconulid with a simple rounded lobe, in contrast to *Phenacolemur,* *Ignacius,* *Acidomomys* and some species of *Paromomys*, which exhibit a central invagination (evident from a distal view) which runs mesiodistally across the hypoconulid lobe. Presence of a molariform P<sup>4</sup> (i.e. metacone approaching the size of paracone, expanded distolingual basin). Upper molars with distolingual basins less expanded distally than in *Phenacolemur.*
Discussion: Following the ascription of material from Condé-en-Brie to the genus *Phenacolemur* by Louis (1966), Russell et al. (1967) subsequently described new material from Mutigny and Avenay as pertaining to that genus based on its resemblance to some of the North American representatives known at that time, such as *Phenacolemur jepseni, Phenacolemur praecox* and *Phenacolemur citatus*. Russell et al. (1967) referred to the development of the hypoconulid in M3 in the European forms as reminiscent of that in *P. citatus* and *P. jepseni*, and the lack of ectocingulum in upper molars as similar to *P. jepseni*. However, Russell et al. (1967) also mentioned that the P4 in the European specimens is smaller in size than the M1, a trait that is characteristic of *Ignacius* rather than *Phenacolemur*.

Following this line of reasoning, Godinot (1984) in his paper naming the genus *Arcius*, would suggest that it was closely related to *Ignacius* instead, specifically to *Ignacius graybullianus* from the early Eocene of Wyoming. One of the characters that Godinot (1984) highlighted as diagnostic of the genus was that the mandible reaches its highest point in the area of P4 and M1 alveoli, but at that time, the only mandible known was that of *Arcius rougieri*. Still today, *Arcius* gnathic remains are extremely rare, with the only ones reported being the mandible and maxillary fragments of *A. rougieri* (PAT1, PAT1 bis, and PAT2), two mandibles of *A. lapparenti* from Condé-en-Brie (CBX1-ph and an uncatalogued specimen [for the uncatalogued specimen, see Aumont, 2003, Appendix G, Plate 3, Fig. 3]), a maxilla and a mandible of *Arcius* sp. from Fournes (FNR43 and FNR54), an uncatalogued mandible of *Arcius* sp. from Le Quesnoy (see Aumont, 2003, Appendix G, Plate 3, Fig. 4), and a mandible with M2-3 from Abbey Wood. The only lower jaw specimen known to exhibit the character described by Godinot (1984) is PAT1 (*Arcius rougieri*), and it is not present in other species (see Aumont 2003, Appendix G, Plate 3, Fig. 3 and 4). Therefore, this character is an autapomorphy of *A. rougieri*,
and should not be considered diagnostic of the genus, but rather solely diagnostic of *A. rougieri* (see below).

Later, Robinson and Ivy (1994) suggested that *Arcius* was not monophyletic and included this genus in the subfamily “Phenacolemurinae”. According to Robinson and Ivy (1994), this subfamily contained the genera *Phenacolemur*, *Ignacius*, and *Elwynella*, along with their proposed genera “Simpsonlemur”, “Pulverflumen”, and “Dillerlemur” whose validity has been a source of debate (Silcox and Gunnell, 2008; López-Torres and Silcox in prep.). In contrast, Aumont (2003) recovered a monophyletic *Arcius* in her cladistic analysis, with the North American *Acidomomys* as its sister taxon.

Diagnostic characters for *Arcius* included here that have not been discussed previously in the literature include the simple enlarged hypoconulid lobe, the molariform P^4, and the weak mesial inflection of the molar trigonids. With the exception of primitive representatives of the paromomyid clade (i.e. *Paromomys farrandi*), a markedly enlarged M^3 hypoconulid lobe is very typical of paromomyids. There are, however, two types of morphology of these lobes: simple and divided. Simple lobes, as observed in all species of *Arcius*, have a rounded shape in distal view, with a concave outline. Divided lobes, as observed in *Phenacolemur*, *Ignacius*, *Acidomomys*, *Edworthia*, and some species of *Paromomys*, exhibit an invagination of the occlusal surface that runs mesiodistally through the center of the lobe (Figure 3.1). This gives the lobe a heart-shaped appearance in distal view. *Arcius* is also characterized by having a P^4 that resembles a molar, more so than in other genera. Although the P^4 metacone is smaller than the paracone, it approaches the size of the paracone. This, combined with the similarity in size of P^4 to M^1 makes the premolar very molar-like. The similarity between the adult P^4 to the M^1 in *Arcius* parallels the resemblance in morphologies between the deciduous P^4 and the M^1 observed
Figure 3.1 Distal view of the M$_3$ of various species of North American and European paromomyids. A) *Phenacolemur citatus*, USGS 21712, right; B) *Paromomys depressidens*, USNM 9677; C) *Edworthia lerbekmoi*, UALVP 50990, right; D) *Ignacius frugivorus*, YPM-PU 20690, left; E) *Acidomomys hebeticus*, UM 108206, left; F) *Arcius fuscus*, MU 6507, left; G) *Arcius lapparenti*, AV 5849, left; H) *Arcius zbyszewskii*, SV3-47, left; I) *Arcius hookeri* n. sp., BMNH.M 44945, right. The paromomyids on the top row (A-E) have an invagination at the top central area of the hypoconulid lobe, while all *Arcius* species lack this feature (F-I).
in other paromomyids, such as *Phenacolemur* (Rose, 1981; Silcox et al., 2008) and *Acidomomys* (Bloch et al., 2002). This might suggest that *Arcius* underwent a process of retention of juvenile characters (paedomorphism), one of them being the retention of a deciduous P₄. *Arcius rougieri*, in particular, shows another paedomorphic character: the retention of a juvenile-like upper central incisor (see below).

Based on the two most complete specimens that belong to the genus *Arcius*, PAT1 and PAT2, the dental formula for this genus would be $\frac{2.1.2.3}{1.0.1.3}$. See also Table 3.1 for estimated body masses for all the species in the genus.
Table 3.1 Estimated average body masses of all species of *Arcius* based on data from Aumont (2003) and the current study (for *A. hookeri* and *A. ilerdensis*). The regression equation used for Conroy’s estimates was the prosimian one.

<table>
<thead>
<tr>
<th>Species</th>
<th>Gingerich et al.’s (1982)</th>
<th>Conroy’s (1987) equation (M₁)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M₁</td>
<td>M₂</td>
</tr>
<tr>
<td><em>A. rougeri</em></td>
<td>201g</td>
<td>143g</td>
</tr>
<tr>
<td><em>A. fuscus</em></td>
<td>194g</td>
<td>205g</td>
</tr>
<tr>
<td><em>A. lapparenti</em></td>
<td>313g</td>
<td>327g</td>
</tr>
<tr>
<td><em>A. zbyszewskii</em></td>
<td>130g</td>
<td>-</td>
</tr>
<tr>
<td><em>A. hookeri</em></td>
<td>-</td>
<td>284g</td>
</tr>
<tr>
<td><em>A. ilerdensis</em></td>
<td>-</td>
<td>247g</td>
</tr>
</tbody>
</table>
Arcius rougieri Godinot, 1984

Figure 3.2 and 3.3

Arcius cf. fuscus Godinot, 1981


Holotype: PAT 1, partial maxilla with right I₁-C and left I₁-M₁.

Paratypes: PAT 2, mandible with right I₁-M₁; PAT 3, left M₃; PAT 5, right M₂.

Horizon and locality: Palette (type locality, PE II, see Biostratigraphy below), Bouches-du-Rhône, France; Fordones (PE II, see Biostratigraphy below), Aude, France; Rians (PE II; Marandat et al., 2012), Var, France.

Etymology: Named after M. Rougier.

Emended diagnosis (modified from Godinot, 1984): Smaller in size than Arcius lapparenti, A. hookeri n. sp., and A. ilerdensis n. sp., but larger than A. zbyszewskii. Highest cusp of the upper central incisor is the anterocone, with a significantly smaller mediocone and posterocone, and laterocone proximally shifted relative to the anterocone compared to A. fuscus and A. lapparenti. No paraconule on P₄. Buccal extension of the parastylar region on M₁. M₃ with distolingual basin not distally expanded and mesiobuccally expanded parastylar area. Differs from A. fuscus in having two crests on the P₄ postvallid. Paraconid of M₁ is smaller than in A. fuscus and A. lapparenti, but larger than in A. zbyszewskii. Mesial inflection of M₁ and M₂ trigonids weaker than in A. ilerdensis n. sp., but stronger than in the other known species of Arcius. Presence of a
Figure 3.2 The mandible of *Arcius rougieri* (PAT 2) in occlusal (A), buccal (B), and lingual (C) views.
Figure 3.3 *Arctos rougieri*. Maxilla (PAT 1, holotype) in occlusal (A), oblique occlusal (B), and oblique frontal (C) views; PAT 5, right M$_2$ (D); and PAT 3, left M$_3$ (E).
stepped postvallid on M₁ and M₂. Presence of a cingulid on the buccal half of the distal aspect of M₁ and M₂ that runs up to the hypoconulid. Highest point of the mandible between P₄ and M₁.

**Biostratigraphy:** There is some disagreement as to the age of Palette and Fordones. Marandat et al. (2012) assigned Palette and Fordones to Paleocene-Eocene biozone I (PE I), and considered them intermediate in age between Silveirinha (older) and Rians/Fournes (younger). However, there seems to be a consensus that Silveirinha is very close in age to Sotteville-sur-Mer, probably slightly younger (Smith et al., 2011; Marandat et al., 2012; Hooker, 2105), and Hooker (2015) assigned Sotteville-sur-Mer to PE II, close to the onset of the Carbon Isotope Excursion (CIE). Rians and Fournes have been calibrated to be of similar age to the site of Meudon (Marandat et al., 2012), and Hooker (2015) suggested PE II as the age for Meudon as well. Therefore, based on the correlations suggested by Hooker (2015), Palette and Fordones would be considered to be PE II in age.

**Discussion:** In this paper, all diagnoses for the six species of *Arcius* include diagnostic features of the paratypes along with the holotype. The reason behind this decision is that the holotypes for *A. fuscus* and *A. lapparenti* are M₃s (Russell et al., 1967), and this tooth position is probably the most variable in paromomyids. This would make the diagnosis for these species solely based on M₃ morphology very limited and not very diagnostic. In order to be consistent throughout the paper, the paratypes have been included in the diagnosis for all species of *Arcius*.

The holotype of *Arcius rougieri*, along with PAT1 bis and PAT2, represent the first described gnathic material with associated teeth in a European paromomyid. The I¹ of *A. rougieri* differs greatly from those of *A. fuscus* and *A. lapparenti* (Rose et al., 1993), and is more similar to the deciduous I¹ of *A. fuscus* and *A. lapparenti*, in that the anterocone is the tallest cusp rather than the mediocone (tallest in adult specimens attributed to *A. fuscus* and *A. lapparenti*). Also, the
laterocone is more proximally located to the mediocone in juveniles of A. fuscus and A. lapparenti than in adult representatives of the tooth, as is observed in the adult form of A. rougieri. There are some differences, however, between the I\(^1\) of A. rougieri and the deciduous I\(^1\) of A. fuscus and A. lapparenti, in that the mediocone is better developed in juveniles of A. fuscus and A. lapparenti while the posterocone is less so, although the posterocone is still poorly expressed in A. rougieri compared to the condition in most adult paromomyid I\(^1\)s. PAT1 is inferred to pertain to an adult because the complete set of teeth is erupted. The second upper incisor and the forth upper premolar erupt after I\(^1\) in the North American paromomyid Acidomomys (Bloch et al., 2002), and both teeth are fully erupted in PAT1. Although it is possible that the dental eruption sequence varied in Arcius from that observed in Acidomomys, it would be surprising for it to vary so much as for I\(^1\) to erupt after all the adult teeth, particularly since no primate species is known to have I\(^1\) as the last tooth to erupt. Indeed, I\(^1\) is usually one of the first teeth to erupt (see López-Torres et al., 2015: table 1). Therefore, it seems that the upper central incisors of A. rougieri retain paedomorphic characters when compared to juveniles of closely related species. Interestingly, as noted above, the genus Arcius also generally has an adult P\(^4\) that resembles a deciduous P\(^4\) (or an adult molar).

Previous to the description of Arcius, Godinot (1981) described a paromomyid M\(_1\) from Rians (RI225) that he tentatively ascribed to Phenacolemur cf. fuscus. Godinot (1981) highlights some differences between the Rians specimen and the specimens from Mutigny (type locality of Arcius fuscus), such as the Rians specimen having a paraconid closer to metaconid, a paracristid curved downwards, and a greater mesiodistal length of the whole tooth. Godinot (1981) admits that a potentially high intraspecific variability for A. fuscus could allow this tooth to be attributed to that species, but suggests that new fossils could shed light on “l’espèce de Rians” (“the species of Rians”; Godinot, 1981, p. 78). The paraconid in RI225 is weak, which contrasts with
the fairly strong paraconids on the M₁ of *A. fuscus* and *A. lapparenti*. The only *Arcius* species with poorly expressed paraconids on M₁ and a size comparable to *A. fuscus* is *A. rougieri*. Therefore, we suggest that the RI225 belongs to *A. rougieri*.

Marandat (1991) tentatively ascribed to *A. rougieri* material found in the locality of Fordones. The Fordones material includes the only known M₃ for this species (FDN28). This specimen is missing the hypoconulid lobe, which is particularly relevant in determining what species of *Arcius* it belongs to. Aumont (2003) suggests that the only way to know the correct ascription of FDN28 is to find an M₃ from the type locality for *A. rougieri* (Palette), but the size, the metric proportions, and the fact that other *A. rougieri* material has been found in Fordones support the inference that FDN28 is the first M₃ known of *A. rougieri* (Marandat, 1991; Aumont, 2003).

**Arcius fuscus** Russell, Louis and Savage, 1967

Figures 3.1F, 3.4A-D, 3.4I-J, 3.4M-P, 3.5B, and 3.5E

“Phenacolemuridae” gen. and sp. indet. Louis and Michaux, 1962.

*Phenacolemur* sp., Louis, 1966.

*Phenacolemur fuscus* (in part) Russell et al., 1967

*Phenacolemur cf. fuscus* Godinot, 1981; Marandat, 1991

*Arcius fuscus* Aumont, 2003; 2004

**Holotype:** MU 6507, left M₃.
Paratypes: AV 422-L, left M2; AV 610-BN, left M2; AV 6838, left I1; CB 1914-L, left P4; CB 2560, left P4; MU 6458, right M1; UCMP 71976, left M1; UCMP 71982, left M3.

Horizon and locality: Mutigny (type locality, PE IV; Marandat et al., 2012), Marne, France; Fournes (PE II; Marandat et al., 2012), Hérault, France; Rians (PE II; Marandat et al., 2012), Var, France; Gland (PE V; Aumont, 2003), Aisne, France; Avenay (PE V; Marandat et al., 2012), Marne, France; Sézanne (PE V; Aumont, 2003), Aisne, France; Condé-en-Brie (PE V; Hooker and Russell, 2012), Aisne, France; St. Agnan (MP10; Hooker, 1996), Aisne, France.

Etymology: Dark, in allusion to the large band of lignite at Mutigny quarry.

Emended diagnosis (modified from Russell et al., 1967, and Aumont, 2003): Area of M3 smaller than in Arcius lapparenti, A. hookeri n. sp., and A. ilerdensis n. sp., but larger than in A. rougieri and A. zbyszewskii. The hypoconulid is large and bulbous, but the buccolingual width at the level of the hypoconulid is shorter than the buccolingual width between the entoconid and hypoconid. Differs from A. zbyszewskii in not having a paraconid on M3. Mediocone taller than anterocone on I1. Metacone approaching the size of the paracone on P4. Complete absence of a postprotocrista on P4. Square outline of M1, with distolingual basin not expanded beyond the distal edge of the tooth. Oblique buccal aspect of the M2. Well defined crests on M1 and M2, with deep basins. Expansion of the distolingual basin on M3, but no expansion of the parastylar area. Presence of prehypoflexid cristid on the P4, (see Discussion below). Relative to M1, P4 is significantly smaller than in A. lapparenti and A. rougieri, with an acute protoconid, and a concave mesial border of the tooth in lateral view. Large paraconid present on M1, but absent on M2. Weak mesial inflection of molar trigonids, but stronger than in A. rougieri. Further differs from A. rougieri in not having a stepped postvallid on M1 and M2. Presence of a cingulid on the buccal half of the distal aspect of M1 that runs up to the hypoconulid.
Figure 3.4 *Arcius fuscus* (A-D, I, J, M-P) and *Arcius lapparenti* (E-H, K, L, Q-S). CB 2560, left P₄, occlusal view (A); MU 6458, right M₁, occlusal view (B); AV 422-L, left M₂, occlusal view (C); MU 6507, holotype, left M₃, occlusal view (D); CB 4162, left P₄, occlusal view (E); AV 7716, right M₁, occlusal view (F); AV 7707, right M₂, occlusal view (G); AV 5849, left M₃, holotype, occlusal view (H); AV 6838, left I¹, lingual (I) and mesial (J) views; AV 7714, right I¹, lingual (K) and mesial (L) views; CB 1914-L, left P₄, occlusal view (M); UCMP 71976, left M¹, occlusal view (N); AV 610-BN, left M², occlusal view (O); UCMP 71982, left M³, occlusal view (P); CB 232-BN, left P₄, occlusal view (Q); AV 1306-Ph, right M¹, occlusal view (R); and AV 1092-BN, right M², occlusal view (S).
Discussion: *Arcius fuscus*, along with *A. lapparenti*, is one of the most common species of the genus found in Europe. When it was first described by Russell et al. (1967), *A. fuscus* was thought to come just from its type locality, Mutigny (Marne, France). *Arcius lapparenti* was also described for the first time by Russell et al. (1967), and at that time was thought to come only from its type locality, Avenay (Marne, France). However, Aumont (2003, 2004), argued these two species were sympatric across many sites in France. Aumont (2003) also interpreted the *Arcius fuscus* sample from Russell et al. (1967) to be a mixture of both *A. fuscus* and *A. lapparenti*, and considered the only two P₄s (MU5627 and MU6294) found at Mutigny to belong to *A. lapparenti*, which is significant since P₄ is generally the most diagnostic tooth for paromomyids. Aumont (2003) came to that conclusion after studying the large sample from Condé-en-Brie (Aisne, France), where there are two distinct P₄ sizes and morphs.

Russell et al. (1967) did not choose a P₄ as the holotype for *Arcius fuscus*, but instead selected an M₃. They used differences in the steepness of the M₃ postvallid, and in the degree of lateral projection of the entoconid, to differentiate *A. fuscus* from *A. lapparenti*, but after the study of the large collection from Condé-en-Brie, it seems as though there is too much variability in these characters for them to be considered diagnostic of species of *Arcius*. Although form of the M₃ hypoconulid is diagnostic for the genus, variability in this tooth position implies that distinguishing among species in the genus *Arcius* also requires consideration of characters from the premolars and other molars. Aumont (2003) suggested new diagnoses for *A. fuscus* and *A. lapparenti* based only on size. Although we agree with Aumont (2003) that size is certainly a diagnostic character to differentiate between *A. fuscus* and *A. lapparenti*, we argue that there are
additional diagnostic differences between the two species, as listed in the emended diagnosis above.

There are two genera of paromomyids that have three distinct crests on the postvallid of some species: *Arcius* and *Paromomys*. These crests are interpreted here as a metacristid (this term used in preference to premetacristid or postmetacristid because the absence of a metaconid; in this case metacristid is used for a crest in the metaconid position), a postprotocristid, and a third crest that we are referring to here as a prehypoflexid cristid. These crests can be told apart in the following way: 1) the metacristid runs lingually from the protoconid to the entocristid or to the lingual aspect of the bottom of the postvallid (if no entocristid is present); 2) the postprotocristid runs buccally or centrally from the protoconid to the cristid obliqua; 3) the prehypoflexid cristid runs buccally from the protoconid to the hypoflexid. The main difference between these two taxa is that all three crests are in the same plane in *Arcius fuscus*, but the prehypoflexid cristid is less well defined and more distally located in *Paromomys* (Figure 3.5). Only two crests are visible on the postvallid in all other known paromomyid species.
Figure 3.5 The prehypoflexid cristid (white arrow) as seen on the P₄ of *Paromomys maturus* (A and D) and *Arcius fuscus* (B and E). *Arcius lapparenti* (C and F) is shown as an example of a paromomyid with no prehypoflexid cristid. When the prehypoflexid cristid is present, the postprotocristid (black arrow) is shifted to a central position across the postvallid. The main difference between the prehypoflexid cristid of *P. maturus* and *A. fuscus* is that in *P. maturus* it is located more mesially (D), contrary to *A. fuscus*, in which the three cristids are in the same plane on the postvallid (E).
Arcius lapparenti Russell, Louis, and Savage, 1967

Figures 3.1G, 3.4E-H, 3.4K-L, 3.4Q-S, 3.5C, and 3.5F

Phenacolemur lapparenti Russell et al., 1967

Arcius lapparenti Aumont, 2003; 2004

Holotype: AV 5849, left M3.

Paratypes: AV 1092-BN, right M2; CB 232-BN, left P4; AV 7707, right M2; AV 7714, right P1; AV 7716, right M1; CB 3583, right M3; CB 4162, left P3; CBX 2-Ph, P1; AV 1306-Ph, right M1.

Horizon and locality: Avenay (type locality, PEV; Marandat et al., 2012), Marne, France; Fournes (PE II; Marandat et al., 2012), Hérault, France; Meudon (PE II; Hooker, 2015), Hauts-de-Seine, France; Pourcy (PE III [55.12 mya]; Hooker, 2010), Marne, France; Mutigny (PE IV; Marandat et al., 2012), Marne, France; Gland (PE V; Aumont, 2003), Aisne, France; Sézanne (PE V; Aumont, 2003), Aisne, France; Condé-en-Brie (PE V; Hooker and Russell, 2012), Aisne, France; Venteuil (MP10; Amount, 2003), Marne, France; St. Agnan (MP10; Hooker, 1996), Aisne, France; Prémontré (MP10 [48.4 mya]; Franzen, 2005), Aisne, France.

Etymology: Named after Albert-Félix de Lapparent (1905-1975), palaeontologist, Sulpician priest, and professor at the Institute Catholique de Paris, for his contribution to the geology and paleontology of the Champagne region.

Emended diagnosis (modified from Russell et al., 1967, and Aumont, 2003): Largest species of Arcius. Hypoconulid of the M3 large and bulbous, with a buccolingual distance at the level of the
hypoconulid that is broader than the buccolingual distance between the entoconid and hypoconid. Differs from *A. zbyszewskii* in not having a paraconid on M₃. Medicone taller than anterocone on I¹. Metacone of the P⁴ almost as strongly developed as the paracone. Complete absence of a postprotocrista on P⁴. Square outline of M¹, with distolingual basin not expanded beyond the distal edge of the tooth. Oblique buccal aspect of the M². Well defined crests on M¹ and M², with deep basins. Distolingual basin on M³ more expanded than in *A. rougieri*, but not as expanded as in *A. fuscus*. No expansion of the parastylar area on M³. Absence of a third crest on the P₄ postvallid (prehypoflexid cristid; see above). Largest P₄ relative to M₁ of all species of *Arcius*. Well-developed paraconid on M₁, but proportionally smaller relative to the metaconid than in *A. fuscus*. Paraconid weak to absent on M₂. Weak mesial inflection of the lower molars, but stronger than in *A. rougieri*. Differs from *A. rougieri* in not having a stepped postvallid on M₁ and M₂. Presence of a cingulid on the buccal half of the distal aspect of M₁ that extends up to the hypoconulid.

**Discussion**: Along with *A. fuscus*, *A. lapparenti* is one of the most common species of this European genus. While Russell et al. (1967) described *A. fuscus* as appearing just at Mutigny, *A. lapparenti* was argued by the same authors to have been present just in Avenay, very close geographically to Mutigny.

When Aumont (2003, 2004) suggested the sympatry of these two species, she also reported that the samples from the type localities of both species were a mix of the two of them. Also, the molariform morphology of *Arcius* fourth upper premolars led to misidentification in the original Russell et al. (1967) paper. AV 5775, reported in Russell et al. (1967) as an M¹ of *A. lapparenti*, is interpreted here to be a P⁴, based on its poorly developed postprotocrista, a feature of P⁴ in other species of *Arcius*. These two teeth can be told apart mainly by the lack of a postprotocrista,
and by the slightly convex mesial aspect of the tooth on P4. Whereas relative size of the metacone to the paracone is often used to discriminate between M1 and P4 in primate species, the paracone of the P4 is so close in size to the metacone in A. lapparenti that it is quite challenging to see a size difference between these two cusps.

As previously mentioned in the discussion for A. fuscus, size is a useful character to identify A. lapparenti (as argued by Amount, 2003), but the two species can also be diagnosed based on morphological contrasts in the premolars and other molars.

*Arcius zbyszewskii* Estravís, 2000

Figures 3.1H and 3.6

*Phenacolemur* sp. Antunes, 1981.


*Arcius zbyszewskii* Estravís, 2000

*Arcius* sp. Smith et al., 2011

**Holotype:** SV1-29, right M2.

**Paratypes:** SV2-99, right P4; SV3-47, left M3; SV3-125, right M1; SV3-317, right M1; SV3-565, right M3.

**Horizon and locality:** Silveirinha (type locality, PE II; see Biostratigraphy), Baixo Mondego, Portugal; Sotteville-sur-Mer (PE II; Hooker, 2015), Normandy, France.
Figure 3.6 *Arcius zbyszewskii*. SV2-99, right P₄, occlusal view (A); SV3-125, right M₁ fragment, occlusal view (B); SV1-29, right M₂, holotype, occlusal view (C); SV3-125, right M₁, occlusal view (D); SV3-47, left M₃, occlusal view (E).
**Etymology:** Named after Dr. Georges Zbyszewski of the Serviços Geológicos de Portugal for his extensive work on the paleontology and geology of Portugal.

**Emended diagnosis** (modified from Estravís, 2000): Smallest species of *Arcius*, approaching the size of *A. rougieri*. Molars with lower relief than in *A. rougieri*. Small but patent paraconids on M\(_1\), stronger paraconid on M\(_3\). Very small hypoconulid on M\(_1\). The hypoconulid lobe on M\(_3\) is enlarged, as typical of paromomyids, but is the smallest lobe in proportion to the rest of the tooth relative to any other paromomyid, with the exception of *Paromomys farrandi*. Upper fourth premolar of similar size to upper molars. Shallow upper molar basins, with distolingual basin not much extended. Presence of a lingual cingulum on M\(_1\) and M\(_3\).

**Biostratigraphy:** Silveirinha has been considered to belong to MP 7 (PE I) (Estravís, 1992, López-Martínez et al., 2006; Badiola et al., 2009; Smith et al., 2011; Marandat et al., 2012), but very close in age to Sotteville-sur-Mer, probably slightly younger (Smith et al., 2011; Marandat et al., 2012). Recently, Hooker (2015) assigned Sotteville-sur-Mer to PE II, so Silveirinha is here considered to be PE II in age following his temporal framework.

**Discussion:** Antunes (1981) first reported the presence of paromomyids in Portugal by including *Phenacolemur* in his faunal list of Silveirinha. It was not until Estravis’ work (1992, 2000) that the Portuguese material was included in the genus *Arcius* and assigned to a new species. *Arcius zbyszewskii* was suggested by Estravís (2000) to represent a primitive lineage of European paromomyids due to its mosaic of *Arcius* characters together with primitive paromomyid characters.
Our interpretation of the Portuguese material differs from Estravís (2000) in that SV1-24 is reported as an M₁, instead of an M₂. We argue that the paraconid on SV1-24 is no smaller than that of the other M₁ (SV3-125), which is typical for paromomyids. There is also no difference in the mesiodistal length of the trigonid between the two specimens, while it is a common trait for paromomyids to have a shorter M₂ trigonid.

Smith et al. (2011) described a diminutive upper tooth of a paromomyid from Sotteville-sur-Mer (Normandy, France) that they considered to be a broken M₁. The authors acknowledged the similarities of this tooth to the Portuguese material, but did not ascribe it to any particular species of Arcius. The poor state of preservation of the tooth and the fact that Arcius is characterized by having molariform upper premolars makes it difficult to assign the specimen to a tooth position, but its very weak postprotocrista suggests it is a P₄ rather than an M₁. Arcius zbyszewskii is the only species of the genus in which the P₄ has a very weak postprotocrista instead of it being completely absent. This trait, paired with the similarly small size of the specimen from Sotteville-sur-Mer to the collection from Silverinha, support attribution of the Normandy specimen to A. zbyszewskii. Sotteville-sur-Mer and Silveirinha are considered to be of very similar age (Smith et al., 2011), and are the oldest sites in Europe that yield paromomyid fossils, which would be consistent with grouping the Arcius from both sites under the same species.
Arcius hookeri n. sp.

Figures 3.11 and 3.7

Phenacolemur cf. fuscus Hooker and Insole, 1980

Arcius fuscus Hooker, 1996, 1998

Arcius lapparenti Aumont, 2003; Hooker, 2010

Holotype: BMNH.M 44945; right dentary with M₂-₃.

Horizon and locality: Blackheath Beds from Abbey Wood (type locality, PE III), England, UK.

Etymology: Named after Dr. Jeremy J. Hooker of the British Museum of Natural History for his unparalleled contributions to the study of the mammalian paleontology of England.

Diagnosis: Distal cingulid absent on M₂, unlike A. fuscus, A. lapparenti and A. rougieri. Buccal cingulids present on M₂, but weaker than those found in A. fuscus and A. lapparenti, and not extended onto the talonid. Paraconid present on M₂. Trigonid wider, with a greater difference in height between the metaconid and the protoconid, than in other species of Arcius. Mesial inflection of the trigonid not as pronounced as in species of other paromomyid genera, but not as vertical as in A. rougieri and A. ilderdensis n. sp. Hypoconid taller than entoconid on M₂. Differs from all other species of Arcius, except for A. ilderdensis n. sp., in having a taller metaconid than the protoconid on M₂ and M₃. Differs from A. zbyszewskii in not having a paraconid on M₃. Double entoconid present on M₃, unlike all other species of Arcius.
Figure 3.7 The holotype of *Arcius hookeri* n. sp. (BMNH.M 44945) in occlusal (A), buccal (B), and lingual (C) views.
Discussion: Hooker and Insole (1980) tentatively reported BMNH.M 44945 as pertaining to *Phenacolemur cf. fuscus*, making this specimen the first known representative of *Arcius* outside continental Europe. Since then, the specific ascription of this specimen has been problematic, and has been suggested to pertain to either *A. fuscus* (Hooker, 1996, 1998) or *A. lapparenti* (Aumont, 2003, Hooker, 2010). Hooker (2010) noted that the English specimen has a small sized M₃ that falls within the size range of *A. fuscus* for that tooth. He also noted that the M₂, although not strictly falling within the size range for that tooth reported in Aumont (2003, 2004), is closer in size to that of *A. lapparenti* than to *A. fuscus*. This suggests differences in terms of the relative proportions of these two teeth, but there are no specimens known in which they are preserved in series to assess this possibility. Hooker (2010) also pointed out the presence of two entoconids on the M₃, a trait never seen in paromomyids before. When considered alongside the contrasts newly noted here (listed in the diagnosis), it seems as though the best solution is to consider the English specimen to pertain to a new species.

*Arcius ilerdensis* n. sp.

Figure 3.8

*Arcius* sp. Marigó et al. 2012

**Holotype:** IPS 57510, right M₂.

**Paratypes:** IPS 57508, left M²; IPS 57511, right M₃.

**Horizon and locality:** Masia de l’Hereuet (MP8+9; Marigó et al., 2012), Lleida, Spain.
Figure 3.8 Arcius ilerdensis n. sp. IPS 57508, left M$^2$, occlusal view (A); IPS 57510, right M$^2$, holotype, occlusal view (B); IPS 5751, right M$^3$, occlusal view.
Etymology: From the Latin *Ilerda* (ancient name of the city of Lleida), in allusion to its province of origin.

Diagnosis: Larger than *A. rougieri* and *A. zbyszewskii*, similar in size to *A. hookeri* n. sp., and smaller than *A. lapparenti*. Absence of distal cingulid on M₂, unlike *A. fuscus*, *A. lapparenti*, and *A. rougieri*. Buccal cingulid absent on M₂, contrary to all other species of *Arcius*. Short buccal cingulid present on the M₃ trigonid. Paraconid present on M₂, but very weakly expressed, less so than in *A. hookeri* n. sp. Mesial inflection of the trigonid on M₂ weaker than any other species of *Arcius*, with the trigonid being completely vertical. Differs from all other species of *Arcius*, except *A. hookeri* n. sp., in having a taller metaconid than the protoconid on M₂ and M₃. Differs from *A. zbyszewskii* in not having a paraconid on M₃. Oblique buccal aspect of the M². Well defined crests on M², with deep basins.

Discussion: The Masia de l’Hereuet specimens were described by Marigó et al. (2012) as members of the genus *Arcius*, but those authors did not give them a specific ascription due to the scarcity of the material. Although we agree with Marigó et al. (2012) that more material needs to be recovered from that site, the few fossils that make up the Spanish *Arcius* show enough distinct traits to be discerned from other species.

Lower molars of paromomyid species that do not belong to the genus *Arcius* have trigonids that are strongly mesially inflected, while *Arcius* shows weak levels of inflection. However, *Arcius ilerdensis* has a uniquely vertical trigonid, even relative to other members of the genus. It is also uncommon among *Arcius* that the metaconid is clearly taller than the protoconid in lower molars, a feature also seen in *A. hookeri* n. sp. The lack of a distal cingulid on the buccal half of the distal
aspect of the $M_{1-2}$ also constrasts with the more derived members of the genus ($A. fuscus$, $A. lapparenti$, and $A. rougieri$), suggesting that $A. ilerdensis$ still retains somewhat primitive characters in the $Arcius$ lineage.

### 3.5 Phylogenetic relationships of $Arcius$

In order to assess the phylogenetic relationships of the different species of $Arcius$ and the position of the genus among Paromomyidae, we conducted a cladistic analysis. A character list was created to specifically assess the relationships of $Arcius$ based on character diagnoses from Matthew (1915), Gidley (1923), Russell et al. (1967), Rose and Bown (1982), Godinot (1984), Robinson and Ivy (1994), Estravís (2000), Bloch et al. (2002), Silcox et al. (2008), and Fox et al. (2010) (Table 3.2). Some of the characters that relate to higher level relationships among plesiadapiforms have been taken from Silcox’s (2001) matrix for plesiadapiforms. The primitive purgatoriid $Purgatorius coracis$ was chosen as the outgroup for Paromomyidae. The analysis also includes the oldest and most primitive members of every paromomyid genus: $Paromomys farrandi$, $Edworthia lerbekmoi$, $Phenacolemur archus$, $Acidomomys hebeticus$, and $Ignacius fremontensis$. The genus $Elwynella$, which includes only the species $E. oreas$, was excluded from this analysis because it is the most recent genus of paromomyid to appear in the fossil record and, although it exhibits the primitive character of retention of a p3, it shares many derived molar characters found in the late Wasatchian paromomyid $Phenacolemur jepseni$, which suggests that it may be nested within a higher level grouping of paromomyids (López-Torres and Silcox in prep.). A total of 53 dental characters were scored for 13 taxa (see Table 3.2; matrix available on publication from www.morphobank.org).
### Table 3.2 Brief descriptions of dental characters.

**Upper incisors**

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<tr>
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<th>Description</th>
<th>Codes</th>
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<tr>
<td>1</td>
<td>Presence of posterocone on $I^1$ (<em>ordered</em>)</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>2</td>
<td>Relative height anterocone/mediocone on $I^1$</td>
<td>0: Anterocone taller than medicone; 1: Medicone taller than anterocone</td>
</tr>
</tbody>
</table>

**Upper premolars**

<table>
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<tr>
<th></th>
<th>Description</th>
<th>Codes</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Presence of $P^2$</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>4</td>
<td>Presence of metacone on $P^4$</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>5</td>
<td>Presence of a molariform $P^4$</td>
<td>0: $P^4$ with a metacone significantly smaller than the paracone, and no expanded distolingual basin; 1: $P^4$ with a metacone approaching in size to the paracone and an expanded distolingual basin</td>
</tr>
<tr>
<td>6</td>
<td>Presence of precingulum on $P^4$</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>7</td>
<td>Presence of parastyle on $P^4$</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>8</td>
<td>Shape of $P^4$ (<em>ordered</em>)</td>
<td>0: T-shaped; 1: Triangular; 2: Quadrangular</td>
</tr>
<tr>
<td>9</td>
<td>Mesial parastylar expansion on $P^4$</td>
<td>0: Projecting beyond the mesial border; 1: Not projecting.</td>
</tr>
<tr>
<td>10</td>
<td>Acuteness of $P^4$ cusps</td>
<td>0: Acute; 1: Bulbous</td>
</tr>
<tr>
<td>11</td>
<td>Height of postprotocingulum on $P^4$</td>
<td>0: Low (crest dips closer to the roots); 1: High (crest stays near the tip of the protocone in height)</td>
</tr>
</tbody>
</table>

**Upper molars**

<table>
<thead>
<tr>
<th></th>
<th>Description</th>
<th>Codes</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>Depth of distolingual basin on $M^{1-2}$</td>
<td>0: Shallow; 1: Deep</td>
</tr>
<tr>
<td>13</td>
<td>Presence of conules on $M^{1-2}$ (<em>ordered</em>)</td>
<td>0: Both conules present; 1: Metaconules absent; 2: Both conules absent</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Score</td>
</tr>
<tr>
<td>---</td>
<td>------------------------------------------------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>14</td>
<td>Parastylar expansion on M(^1)(^{-2})</td>
<td>0: No expansion; 2: Expanded</td>
</tr>
<tr>
<td>15</td>
<td>Outline of M(^1)</td>
<td>0: Squared; 1: Rectangular and narrow</td>
</tr>
<tr>
<td>16</td>
<td>Depth of trigon basin on M(^1)(^{-2})</td>
<td>0: Shallow; 1: Deep</td>
</tr>
<tr>
<td>17</td>
<td>Presence of postmetaconule crista on M(^1)(^{-2})</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>18</td>
<td>Expansion of mesiolabial corner on M(^3)</td>
<td>0: Not expanded, buccal border is straight; 1: Expanded</td>
</tr>
</tbody>
</table>

**Lower canine**

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td>19</td>
<td>Presence of C(_1)</td>
<td>0: Present; 1: Absent</td>
</tr>
</tbody>
</table>

**Lower premolars**

<table>
<thead>
<tr>
<th></th>
<th>Description</th>
<th>Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>Presence of P(_2)</td>
<td>0: Present; 1: Absent</td>
</tr>
<tr>
<td>21</td>
<td>Presence of P(_3)</td>
<td>0: Present; 1: Absent</td>
</tr>
<tr>
<td>22</td>
<td>Trigonid/talonid width proportion on P(_4)</td>
<td>0: Talonid as wide or wider than trigonid; 1: Talonid narrower than trigonid</td>
</tr>
<tr>
<td>23</td>
<td>P(_4)/M(_1) width proportion</td>
<td>0: P(_4) narrower than M(_1); 1: P(_4) of approximately the same with as M(_1)</td>
</tr>
<tr>
<td>24</td>
<td>Width at the base of the P(_4) protoconid</td>
<td>0: Narrowly based protoconid; 1: Broadly based protoconid</td>
</tr>
<tr>
<td>25</td>
<td>Presence of a mesial bulge in the base of the P(_4) protoconid</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>26</td>
<td>P(_4)/M(_1) area proportion</td>
<td>0: Small P(_4) area compared to M(_1) area; 1: Similar</td>
</tr>
<tr>
<td>27</td>
<td>Relative mesiodistal length of P(_4) to M(_1)</td>
<td>0: P(_4) shorter than M(_1); 1: P(_4) equal or longer than M(_1)</td>
</tr>
<tr>
<td>28</td>
<td>Morphology of the hypoflexid</td>
<td>0: Distinct, deep; 1: Not distinct, shallow</td>
</tr>
<tr>
<td>29</td>
<td>Presence of paracristid</td>
<td>0: Present; 1: Absent</td>
</tr>
<tr>
<td>30</td>
<td>Relative length of the talonid compared to the length of the tooth</td>
<td>0: Relatively short talonid (less than 26% of the tooth length); 1: Relatively long</td>
</tr>
<tr>
<td>Number</td>
<td>Description</td>
<td>Details</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
<td>---------</td>
</tr>
<tr>
<td>31</td>
<td>Presence of a crest connecting the protoconid and the hypoflexid fold (prehypoflexid cristid)</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>32</td>
<td>Length of trigonid</td>
<td>0: Trigonids become less mesiodistally compressed from M₁ to M₃, or there is no change; 1: Trigonids become more mesiodistally compressed from M₁ to M₃</td>
</tr>
<tr>
<td>33</td>
<td>Shape of the protocristid on M₁</td>
<td>0: V-shaped; 1: Slightly concave</td>
</tr>
<tr>
<td>34</td>
<td>Presence of distal cingulid on M₁ and M₂</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>35</td>
<td>Presence of hypoconulid on M₁ and M₂</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>36</td>
<td>Presence of buccal cingulid on M₁ and M₂ trigonids</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>37</td>
<td>Presence of buccal cingulid on M₁ and M₂ talonids</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>38</td>
<td>Shape of the M₁ trigonid basin</td>
<td>0: Semicircular; 1: Squared; 2: Triangular</td>
</tr>
<tr>
<td>39</td>
<td>Mesial inflection of the M₁ and M₂ trigonids (ordered)</td>
<td>0: Absent/weak; 1: Somewhat pronounced; 2: Very pronounced</td>
</tr>
<tr>
<td>40</td>
<td>Relative height of the hypoconid compared to the entoconid on M₁</td>
<td>0: Hypoconid taller than entoconid; 1: Subequal; 2: Entoconid taller than hypoconid</td>
</tr>
<tr>
<td>41</td>
<td>Relative height of the protoconid compared to the metaconid on M₁</td>
<td>0: Protoconid taller than metaconid; 1: Subequal; 2: Metaconid taller than protoconid</td>
</tr>
<tr>
<td>42</td>
<td>Presence of paraconid on M₂</td>
<td>0: Absent; 1: Present</td>
</tr>
<tr>
<td>43</td>
<td>Distinctiveness of the M₂ paracaonid relative to the M₁ paraconid</td>
<td>0: Comparably distinct to the M₁ paraconid; 1: Less distinct than the M₁ paraconid</td>
</tr>
<tr>
<td>44</td>
<td>Relative height of the paraconid compared to the metaconid on M₂</td>
<td>0: Paraconid lower than metaconid; 1: Paraconid subequal of taller than metconid</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Score 0</td>
</tr>
<tr>
<td>---</td>
<td>------------------------------------------------------------------------------------------------------</td>
<td>------------------------------------------------------------------------</td>
</tr>
<tr>
<td>45</td>
<td>Relative height of the hypoconid compared to the entoconid on M₂</td>
<td>Hypoconid taller than entoconid; Subequal; Entoconid taller than hypoconid</td>
</tr>
<tr>
<td>46</td>
<td>Relative height of the protoconid compared to the metaconid on M₂</td>
<td>Protoconid taller than metaconid; Subequal; Metaconid taller than protoconid</td>
</tr>
<tr>
<td>47</td>
<td>Acuteness of cusps</td>
<td>Relatively acute; Blunter</td>
</tr>
<tr>
<td>48</td>
<td>Molar enamel roughness inside the basin of M₃</td>
<td>Smooth; Crenulated</td>
</tr>
<tr>
<td>49</td>
<td>Presence of M₃ paraconid</td>
<td>Absent; Present</td>
</tr>
<tr>
<td>50</td>
<td>Relative height of the hypoconid compared to the entoconid on M₃</td>
<td>Hypoconid taller than entoconid; Subequal; Entoconid taller than hypoconid</td>
</tr>
<tr>
<td>51</td>
<td>Relative height of the protoconid compared to the metaconid on M₃</td>
<td>Protoconid taller than metaconid; Subequal; Metaconid taller than protoconid</td>
</tr>
<tr>
<td>52</td>
<td>M₃ trigonid basin area</td>
<td>Small basin, straight at the front; Expansive trigonid basin, curved at the front</td>
</tr>
<tr>
<td>53</td>
<td>Morphology of the M₃ hypoconulid lobe</td>
<td>From a distal view, the central occlusal surface is taller than the sides; From a distal view, the medial and later edges are taller than the central occlusal surface</td>
</tr>
</tbody>
</table>
The parsimony analyses were performed using TNT (Goloboff et al., 2008) with all characters equally weighted. Four of the 53 characters (1, 8, 13, and 39) were ordered, and the rest were left unordered. A heuristic search was implemented with 1000 repetitions, with 1000 trees saved per replication. Four cladistics analyses were run: 1) a basic analysis that excluded the poorly sampled taxa from Abbey Wood (UK), Sotteville-sur-Mer (France), and Masia de l’Hereuet (Spain); 2) an analysis that included the *Arcius* from Abbey Wood; 3) an analysis that included the *Arcius* from Sotteville-sur-Mer; and 4) an analysis that included the *Arcius* from Masia de l’Hereuet. Analysis 1 is meant to give a general understanding of the relationships of *Arcius* based on the well-preserved species, whereas analyses 2, 3, and 4 are meant to accurately place the poorly sampled taxa. Analyses 1, 2, and 3 yielded only one unequivocal tree each (Figure 3.9A-C). Analysis 4 yielded 5 equally parsimonious trees. A strict consensus tree was generated in TNT from these trees (Figure 3.9D).

### 3.5.1 Results of the phylogenetic analysis

In the tree from Analysis 1, *Arcius* is found to be monophyletic, with *A. fuscus* and *A. lapparenti* forming a clade. *Arcius rougieri* appears as the sister group to the *A. fuscus-* *A. lapparenti* clade. *Arcius zbyszewskii* is placed as the most basal European paromomyid, which agrees with the prediction by Estravís (2000) that *A. zbyszewskii* is a separate primitive lineage of European
Figure 3.9 Hypotheses of phylogenetic relationship among selected genera of North American and European paromomyids based on cladistic analysis of 53 dental characters (Table 2, Figure S3.1.1, Appendix 3.2). Cladistic analysis yielded a single most parsimonious cladogram for A, B, and C. All cladograms rooted with Puercan *Purgatorius coracis*. All characters were unordered, except for characters 1, 8, 13, and 39. Cladogram D was generated by strict consensus of 5 trees (see Figure S3.1.1).
paromoyids. In terms of the rest of paromomyid relationships, all of the trees from this paper agree with Bloch et al. (2002) and Aumont (2003) that *Phenacolemur* and *Ignacius* are closely related, and that *Paromomys* is a very primitive member of the family. However, the position of *Acidomomys* seems more contentious. Whereas *Acidomomys* makes a clade with *Ignacius* in our trees, Bloch et al. (2002) found *Acidomomys* to be the sister taxon of the clade *Ignacius*+*Phenacolemur*, and Aumont’s (2003) analysis resulted in *Acidomomys* being the sister taxon to *Arcius*. Aumont (2003) states that the two characters that support the *Acidomomys-Arcius* clade are “l’absence de la p3” (absence of p3) and “la presence d’une P3 uniradiculée” (presence of a single-rooted P3) (Aumont, 2003: p.364). However, *A. hebeticus* does have a P3 (Bloch et al., 2002), and therefore that trait seems to be incorrectly coded in Aumont’s (2003) matrix. Also, the other character (presence of a single-rooted P3) seems to be misreported, because P3 is coded in the matrix as being double-rooted for both *Acidomomys hebeticus* and *Arcius rougieri*, and not observable (i.e. question mark) in the rest of *Arcius* species. While it is clear that *A. hebeticus* had a double-rooted P3 (Bloch et al., 2002), as coded, the number of roots for P3 in *Arcius* is difficult to assess. Only a small piece of the distobuccal aspect of the P3 of *A. rougieri* is preserved (Godinot, 1984), and the alveoli for that tooth are not preserved. It is, therefore, impossible to determine how many roots would have been present. In light of these considerations, we would argue that there is no support for an *Acidomomys-Arcius* clade, which Aumont (2003) tentatively named as the tribe Arciini (incorrectly reported in Aumont [2003, p. 364] as “Arciusini”). Also, the fact that *Acidomomys* appears as the sister taxon to *Arcius* might explain why her phylogeny differs from the ones reported here in that *Arcius rougieri* represents
the most primitive lineage of European paromomyids in her analysis, instead of *Arcius zbyszewskii* as found here.

When *Arcius hookeri* is included in the analysis (Analysis 2; Figure 3.9B), it also yields one tree unequivocally. *Arcius hookeri* is placed as the sister taxon of a clade that includes *A. fuscus*, *A. lapparenti*, and *A. rougieri*. This result supports the inference the *Arcius* specimen from England pertains to a separate lineage, and therefore should be named as a distinct species. The clade that includes *A. hookeri*, *A. fuscus*, *A. lapparenti*, and *A. rougieri* is supported by the loss of the paraconid on the m3, which is clearly present in the more primitive *A. zbyszewskii*.

The addition of the paromomyid specimen from Sotteville-sur-Mer (Normandy, France) also results in a single most parsimonious tree (Analysis 3; Figure 3.9C). In this case, the Normandy specimen (MAM 6 STV 2008) forms a clade with *Arcius zbyszewskii*. This result is consistent with the morphological resemblance between the material from Portugal and the one from Normandy, and supports the inference that all these specimens belong to the same species, *A. zbyszewskii*.

When including *Arcius ilerdensis* in the analysis (Analysis 4), the clade *A. fuscus*-*A. lapparenti*-*A. rougieri*, present in the results from Analyses 1-3, collapses (Figure 3.9D). In two of the five trees recovered from this analysis (Figure S3.1.1A,B) *A. ilerdensis* falls as being most closely related to *A. rougieri*. *Arcius ilerdensis* also appears in two other trees as the sister group to the clade *A. fuscus*-*A. lapparenti*-*A. rougieri*, and as most closely related to *A. lapparenti* in a fifth tree.

In terms of the other genera of paromomyids, our results show that the sister group of *Arcius* is not *Acidomomys*, as reported in Aumont (2003), but the clade that includes *Phenacolemur*,
Ignacius, and Acidomomys. The genus Acidomomys is most closely related to Ignacius. Paromomys and Edworthia appear as members of the most primitive lineage of paromomyids. These results also support the idea from Gunnell (1989) that the Family Paromomyidae could be subdivided into two subfamilies: the Paromomyinae and the Phenacolemurinae. According to Gunnell (1989), based on the genera described at that time, paromomyines would only be comprised of the genus Paromomys, and phenacolemurines would include Phenacolemur, Ignacius, and Elwynella. Here, Paromomyinae would be extended to include Paromomys and Edworthia, and Phenacolemurinae would include Phenacolemur, Ignacius, Elwynella, Arcius, and possibly Elwynella. However, to fully assess this question, more North American paromomyid species should be included in the analysis of the family (López-Torres and Silcox, in prep.).

3.5.2 Biogeographic implications

The results of the phylogenetic analyses, which consistently support the monophyly of Arcius, would suggest that there was only one dispersal event of paromomyids between North America and Europe. The dispersal route would have been possible through land bridges between North America and Europe. The volcanic activity and regional uplift in eastern Greenland closed the Denmark Strait between the British Isles and Greenland, making it much narrower during the Paleocene and Eocene (Knox, 1998). Also, the English Channel was bridged, allowing dispersal between the British Isles and continental Europe (in particular, France) (King, 2006).

One of the oldest occurrences of Arcius comes from the site of Sotteville-sur-Mer in Normandy, France. That region of Normandy could have been the entry point to continental Europe from the Greenland land bridge (Figure 3.10), and this is consistent with finding the oldest representative
Figure 3.10 Paleogeography of western Europe, Greenland, and northeastern North America during the early Eocene, and location of some selected paromomyid-bearing sites (modified from Marandat et al., 2012; Hooker, 2015). 1) Eureka Sound, Canada; 2) Abbey Wood, U.K.; 3) Sotteville-sur-mer, France; 4) Paris Basin, France; 5) Provence Region, France; 6) Masia de l’Hereuet, Spain; 7) Silveirinha, Portugal.
of the genus in that area. However, *Arcius zbyszewskii* is also found at Silveirinha, which is inferred to be of nearly equivalent age to Sotteville-sur-Mer (i.e. PE II according to Hooker, 2015), and is quite distant in space. Iberia was isolated from continental Europe by the Carcassonne Strait already by the earliest Eocene (Marandat et al., 2012), and the intercontinental dispersal of paromomyids is argued to have occurred during the PETM (Hooker, 2015), making the dispersal of *A. zbyszewskii* into southwestern Europe rather difficult. However, other sources (see Plaziat, 1981; Badiola et al., 2009) illustrate a land connection between Iberia and continental Europe during the early Eocene, suggesting that faunal dispersal from continental Europe into Iberia might have been possible by the earliest Eocene. In any case, the broad biogeographic range of *Arcius zbyszewskii* across western Europe suggests that this species might have undergone rapid dispersal across the continent in a short period of time.

In terms of the origins of *Arcius*, the phylogenetic results unequivocally support the existence of a long ghost lineage. The oldest member of the *Phenacolemur-Ignacius-Acidomomys* clade is *Ignacius cf. fremontensis* from To2 (Rose, 1981; Silcox and Williamson, 2012). Therefore, the *Arcius* lineage is inferred to have branched off during the early Torrejonian. The absence of *Arcius*-like species in the well-sampled western North American record during the Torrejonian, Tiffanian, and Clarkforkian suggests that the evolution of this lineage might have happened in more northern latitudes, and closer to the land bridges that would later connect North America with Europe. In fact, undescribed *Ignacius*-like paromomyids have been reported from the Eocene of Ellesmere Island, in the Canadian Arctic (West and Dawson, 1977; Eberle and Greenwood, 2012), hinting at the potential of this region and other areas in the Greenland land bridge, such as the east coast of Greenland (Larsen et al., 2001, 2002), to re-write our understanding of paromomyid evolution and biogeography.
3.6 Conclusions

A revision of the paromomyid material from Europe prompts the rediagnosis of the genus *Arcius* based on a significant collection of new material; redefining *Arcius fuscus* and *Arcius lapparenti* after identifying the mix of specimens in the original taxonomic study by Russell et al. (1967); and the description of two new species: *Arcius hookeri* and *Arcius ilerdensis*.

Our phylogenetic analysis shows that *Arcius* is a monophyletic clade. This is consistent with previous work done by Aumont (2003), but differs in the precise relationships among species of *Arcius*. Our tree suggests that *Arcius zbyszewskii* is the most basal species of *Arcius*, in line with Estravís’ (2000) predictions. Our results further differ from Aumont’s (2003) in finding the clade *Phenacolemur-Ignacius-Acidomomys* as the sister clade to the European paromomyids, instead of just *Acidomomys*. When the more fragmentary taxa were added, the results are consistent with the inference that the Normandy specimen belongs to *Arcius zbyszewskii*, and that *Arcius hookeri* belongs to an independent lineage. The phylogenetic relationships of *Arcius ilerdensis* are less clear, but it appears basal to the clade of French species of *Arcius*. Finally, the monophyly of *Arcius* is consistent with a single dispersal for the family Paromomyidae from North America to Europe.

3.7 Acknowledgments

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3.8 References


Chapter 4
Dental topographic analysis of paromomyid (Plesiadapiformes, Primates) cheek teeth: more than 15 million years of changing surfaces and shifting environments

Author contributions: S. López-Torres (University of Toronto Scarborough), K.R. Selig (University of Toronto Scarborough), K.A. Prufrock (Johns Hopkins University) and M.T. Silcox (University of Toronto Scarborough) contributed to conception and design of the study, and interpreted the data. S. López-Torres, K.R. Selig, D. Lin (University of Toronto Scarborough) and M.T. Silcox collected data. S. López-Torres drafted the article. S. López-Torres, K.R. Selig, K.A. Prufrock, D. Lin and M.T. Silcox revised it critically for important intellectual content, and gave approval for publication.

4 Dental topographic analysis of paromomyid (Plesiadapiformes, Primates) cheek teeth: more than 15 million years of changing surfaces and shifting ecologies

4.1 Abstract

Plesiadapiforms, appearing near the Cretaceous-Paleogene boundary, represent the first primate radiation and show a diverse array of tooth morphologies. Dental topographic metrics provide quantitative data on occlusal surface shape. We used three metrics, Dirichlet normal energy, relief index, and 3D orientation patch count rotated, to assess changes in the morphology of lower fourth premolars and lower second molars in a taxonomically broad sample of one family of plesiadapiforms, Paromomyidae, stretching more than 15 million years.

Our results indicate that paromomyids occupied a more diverse range of dietary categories than suspected. Whereas all paromomyids were likely omnivores, some species show higher levels of insectivory, while other taxa are inferred to have been mixed-feeding omnivores with high levels of fruit intake. The results also show that the more primitive members of the different paromomyid lineages were more insectivorous than the derived and more recent members of those lineages. Relief index values also show taxonomic signals that are consistent with ancestor-descendant relationships hypothesized for species of *Phenacolemur*. These results suggest that dental topographic metrics are informative to the study of paromomyids for both dietary categorization and for the distinction of species at a fine taxonomic level.
4.2 Introduction

The Paromomyidae are a family of extinct primates known from the early Paleocene (early Torrejonian) 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 to the 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). The closest relatives to paromomyids are members of the plesiadapiform family Picrodontidae and the polyphyletic assemblage “Palaechthonidae”, all being classified in the superfamily Paromomyoidea (Silcox, 2001, 2008; Bloch et al., 2007; Silcox and Gunnell, 2008; Silcox et al., accepted). Whereas, in the past, paromomyids had been at the center of taxonomic controversy regarding their evolutionary relationships to dermopterans (Beard, 1989, 1990, 1993a, 1993b; Kay et al., 1990, 1992), several lines of evidence have supported the inference that they are instead stem primates (Krause, 1991; Runestad and Ruff, 1995; Stafford and Thorington, 1998; Hamrick et al., 1999; Silcox, 2001, 2008; Sargis, 2002; Bloch and Boyer, 2007; Bloch et al., 2007; Boyer and Bloch, 2008).

In terms of the cranium, paromomyids have a long snout, small and widely spaced orbits, no postorbital bar, wide zygomatic arches, and inflated auditory bullae ossified from the entotympanic (Silcox and Gunnell, 2008). The postcranial evidence suggests that paromomyids had adaptations for arborealism and vertical climbing, with strong grasping abilities, but lacked adaptations for gliding or suspensory behaviours (Bloch and Boyer, 2007; Boyer and Bloch, 2008). Dentally, paromomyids are characterized by enlarged sub-horizontal incisors; P₄s with a tall, pointed, broad-based protoconid; low crowned molars; and a large hypoconulid lobe on M₃ (Silcox and Gunnell, 2008; Silcox et al., accepted). Their relatively flat molars in combination
with their fairly small body mass (~ 42 - 596 g; Silcox et al., accepted), would suggest that paromomyids were probably mixed-feeding omnivores, with diets heavy in fruit (Gingerich, 1974). Because the term ‘omnivore’ has a variety of meanings, it is here defined as a species that feeds on both plant and faunal material. In the case of paromomyids in particular, an omnivore could feed both on fruit and insects. In any case, the dietary inferences for paromomyids have never been tested quantitatively. Other authors have suggested that paromomyids might have fed primarily on insects (Godinot, 1984), or on tree exudates (Beard, 1990, 1991; Boyer and Bloch, 2008) based on the presence of an enlarged lower incisor. Extant gummivores, such as the phalangeroid marsupial *Petaurus breviceps*, use their similarly enlarged lower incisors to access gum (Fleay, 1947; Smith, 1982). However, the inference that paromomyids might have been gummivores has been critiqued by Rosenberger (2010).

With the increasing availability and affordability of X-ray Micro-CT, new techniques in the measurement of surface morphology have begun to appear in the literature. A range of homology-free, high-throughput methods collectively termed dental topographic analysis (DTA) enables quantification of the entire tooth surface based on virtually created three-dimensional models of teeth.

The various DTA methods have proven useful in studying the functional changes affecting teeth as they wear (Ungar and Williamson, 2000; M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Dennis et al., 2004, Pampush et al., 2016a), in addressing questions of evolutionary history (e.g., Boyer et al. 2010, 2012), and have been shown to be effective at quantifying dietary signals in samples that include worn teeth (Bunn et al., 2011). Topographic analyses have also been used in the exploration of dietary ecology (e.g., Berthaume, 2015; Ungar et al., 2016), faunal community changes (e.g., Godfrey et al., 2012), and niche overlap (Prufrock et al., 2016a,b).
Three topographic metrics that are coming to be broadly used in the study of diet are Relief Index ([RFI] M’Kirera and Ungar 2003; Ungar and M’Kirera 2003; Boyer 2008), Orientation Patch Count Rotated ([OPCR] Evans et al. 2007; Evans and Jernvall 2009; Winchester 2016), and Dirichlet Normal Energy ([DNE] Bunn et al. 2011).

Relief Index quantifies the ratio between the three-dimensional area of the occlusal surface of a tooth and its two-dimensional planimetric area or ‘footprint’ (Figure 4.1; M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Boyer, 2008; Bunn et al., 2011). Tall, hypsodont teeth with more crests will have a higher relief index as compared to low-crowned, bunodont teeth (Boyer, 2008; Bunn et al., 2011). Higher RFI values have been shown to correspond to insectivorous and folivorous diets, while lower RFI values correspond to frugivorous diets (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Ulhaas et al., 2004; Boyer, 2008; Ungar and Bunn, 2008; Bunn and Ungar, 2009; Boyer et al., 2010; Bunn et al., 2011; Winchester et al., 2014; Prufrock et al., 2016a,b).

Orientation Patch Count Rotated is a measure of surface complexity calculated as the number of specific regions or patches on the occlusal surface facing the same cardinal direction (Evans and Jernvall, 2009). OPCR is derived from orientation patch count (OPC), which was originally applied to entire rows of teeth (Evans et al., 2007). OPCR differs in that the tooth is rotated a set number of times and an the average OPC value is calculated, which alleviates issues with the orientation of the tooth on the XY plane (Winchester, 2016). Essentially, OPCR is a
Figure 4.1 Comparison of M$_2$s with varying RFI values. A) *Purgatorius janisae* (UCMP 107406, rM$_2$, cast), RFI = 0.569, inferred to be primarily insectivorous; B) *Phenacolemur fortior* (USNM 488331, lM$_2$ reversed), RFI = 0.488, inferred to be omnivorous; C) *Arcius lapparenti* (CB 4162, lM$_2$ reversed, cast), RFI = 0.382, inferred to be primarily frugivorous. Scale bars = 1 mm.
measurement of the “tools” present on a given tooth (Winchester et al., 2014; Prufrock et al., 2016b). Teeth with more tools such as cusps, crests, or crenulations will have a higher OPCR value, which tends to reflect the need for processing physically demanding foods such as insects and leaves (Evans et al., 2007; Bunn et al., 2011; Winchester et al., 2014; Winchester, 2016).

Finally, DNE is a method of calculating occlusal surface curvature (Bunn et al., 2011; Pampush et al., 2016b; Winchester, 2016). Higher DNE values are indicative of greater occlusal curvature and therefore dentition characterized by sharper cusps and greater shearing potential (Figure 4.2). It has proven possible to use DNE values to separate taxa by diet, with the highest DNE values suggesting insectivory followed by folivory, while lower values indicate omnivory and frugivory (Bunn et al., 2011; Winchester et al., 2014; Winchester, 2016).

The aims of this paper are 1) to make a preliminary assessment of the dietary niches for most species of paromomyids by quantifying the three-dimensional morphology of M2 for individual specimens, and 2) to understand the shifting morphology of the most diagnostic tooth of paromomyids, the P4, through a sample that represents more than 15 million years of paromomyid evolution, using the three aforementioned dental topographic metrics. The degree to which the DTA values are consistent with hypotheses about inter-relationships among taxa is
Figure 4.2 Comparison of P₄s with varying DNE values.  A) *Purgatorius janisae* (UCMP 107406, rP₄, cast), DNE = 214.294, implying a highly curved surface; B) *Phenacolemur citatus* (USNM 544792, lP₄ reversed), DNE = 102.209, moderately curved surface; C) *Ignacius clarkforkensis* (UM 108210, rP₄), DNE = 66.535, less curved surface. Scale bars = 1 mm.
also considered, to assess whether or not these metrics might inform our understanding of particular ancestor-descendant relationships in paromomyids.

4.3 Institutional abbreviations


4.4 Materials and methods

The sample in this study includes X-ray micro-CT scans of second lower molars (M₂) and fourth lower premolars (P₄) of representative specimens of 22 paromomyid species (n = 21 for M₂, and n = 23 for P₄). The “palaechthonid” Premnoides douglassi Gunnell 1989 is included as it has been hypothesized to have a special relationship to paromomyids (Gunnell, 1989; Silcox and Gunnell, 2008), and purgatoriids (Purgatorius coracis Fox and Scott 2011 and Purgatorius janisae Van Valen 1994) were included as representatives of the most primitive plesiadapiforms. In most cases, each species is represented by only an M₂ and a P₄. The intention here was to maximize the number of species included in order to get the broadest possible overview of dietary ecology among paromomyids. However, studies on variability within the various species
will certainly be necessary in the future to test the preliminary inferences about ecology and evolution for particular species made here. Together, these specimens represent a broad taxonomic sample of paromomyids and early plesiadapiforms from North America and Europe, spanning from the earliest Paleocene to the middle Eocene. The sample comprises a mixture of fossil specimens (n = 12) and casts (n = 25). The casts were made of epoxy resin (predominantly TAP Plastics Super-Hard Four to One Epoxy Resin), and the bulk of the molds were made of polyvinylsiloxane (Coltene President Jet Microsystem, Light body). All teeth used in this study were either unworn or very lightly worn.

Both fossils and casts were X-ray Micro-CT scanned, and the resulting data were rendered and cropped in Avizo 7.0 (Visualization Sciences Group, 2009–2011). The segmentation protocol followed Prufrock et al. (2016a). Surfaces were generated with no smoothing, and were then cropped along the cervix (or root crown junction) following Boyer (2008) and Prufrock et al. (2016b). Once cropped, the surface files were simplified using the “Simplification Editor” in Avizo to 10,000 faces, oriented occlusally using the “Transformation Editor,” and saved as .ply files. Surfaces were then smoothed one step using Laplacian smoothing with 1D Boundary Smoothing and Contangent weighting in MeshLab (Visual Computing Lab, 2014). Then the files were saved with no additional parameters selected and binary encoding turned off. Smoothing and simplification procedures followed Prufrock et al. (2016a). The resulting files were opened in MorphoTester 1.1.2 (Winchester, 2016). Under the DNE options, outlier removal percentile was set to 99.0 and implicit fair smoothing was enabled with 3 iterations and a step size of 0.1 following Prufrock et al. (2016a) while the minimum patch count was set to 5 under the OPCR options following Winchester (2016).
Previous measurements of OPC and OPCR have treated surface models as two-and-a-half-dimensional data (Evans et al., 2007; Evans and Jernvall, 2009; Prufrock et al., 2016a,b) while MorphoTester assesses OPCR in three dimensions, a metric known as 3D-OPCR (Winchester, 2016). Thus, direct comparison of the values calculated in previous publications using the two-and-a-half-dimensional methods is not possible due to the fact that the numbers they generate are fundamentally not comparable. In addition, some past calculations of RFI have treated the metric as a simple ratio between the three-dimensional surface area of the crown and the two-dimensional footprint of the tooth (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Ulhaas et al., 2004). MorphoTester also calculates RFI in this same way:

\[ RFI = \frac{\text{3D crown area}}{\text{2D crown area}} \]

RFI was re-calculated here (Tables 4.1-4.4) following Boyer (2008) for the sake of comparability to other more recent studies as:

\[ RFI = \ln\left(\frac{\text{3D crown area}}{\text{2D crown area}}\right)^{1/2} \]

### 4.5 Results

The DTA results are detailed first in terms of broad-scale, overall patterns, and then within the context of four clusters. These clusters include 1) the most primitive taxa (i.e., non-paromomyids and paromomyids that are inferred to be near the base of the clade [Paromomys, Edworthia]); and each of the three most speciose genera, discussed with their likely close relatives: 2) Arcius, 3) Ignacius (considered with Acidomomys), and 4) Phenacolemur (considered with Elwynella).
4.5.1 Overall patterns

The three non-paromomyid taxa (*Purgatorius janisae*, *Pu. coracis*, and *Premnoides douglassi*) had higher RFI values for the M2 than any paromomyids (see Table 4.1). The paromomyid with the highest RFI value for M2 was *Phenacolemur willwoodensis* Silcox, Rose and Bown 2008. This pattern contrasts with the results for the P4, where *Phenacolemur jepseni* Simpson 1955 and *Arcius fuscus* Russell, Louis and Savage 1967 have higher values than non-paromomyid species. The DNE results for M2 show a similar pattern to RFI, but the paromomyid *Arcius rougieri* Godinot 1984 has one of the highest values for M2, just below *Pu. janisae*. *Arcius fuscus* again has one of the highest DNE values for P4, but *Ph. jepseni* has more intermediate values. Although *Ar. fuscus* has the highest P4 3D-OPCR value of any taxon studied, in most other ways the results for this metric do not mirror the results seen in RFI and DNE. In particular, based on their high M2 DNE values it would be expected that the non-paromomyid taxa might also exhibit high M2 3D-OPCR values, but this is not the case (Table 4.1) with *Pu. janisae*, for example, having the highest DNE value, but a lower 3D-OPCR value than many paromomyids.

The lowest RFI values for M2 are observed in *Arcius lapparenti* Russell, Louis and Savage 1967 and *Paromomys farrandi* Clemens and Wilson 2009. The RFI results for P4 are similar in that *Pa. farrandi* is at the bottom of the list for paromomyids, but the P4 of *Ar. lapparenti* shows a more intermediate RFI value for a paromomyid. In the DNE results *Ignacius clarkforkensis* Bloch, Silcox, Boyer and Sargis 2007 has the lowest values for both M2 and P4.

4.5.2 Primitive plesiadapiforms and early members of the Paromomyidae

The highest values of RFI for M2 are observed in members of the genus *Purgatorius*, followed by the “palaechthonid” *Premnoides*. Among primitive paromomyids, *Edworthia lerbekmoi* Fox,
Scott and Rankin 2010 has higher RFI values than members of the genus *Paromomys*, which show varying degrees of occlusal relief. Occlusal relief is variable within *Paromomys*, although the P4 values obtained with RFI parallel the patterns seen in M2 — *Pu. janisae* has the highest RFI values, whereas *Pa. farrandi* has the lowest RFI values among the primitive taxa (0.424 in *Paromomys farrandi* vs. 0.595 in *Paromomys maturus* Gidley 1923; Table 4.1).

The DNE results for M2 exhibit a similar pattern to that observed in RFI, with the exception that *Premnoides* has higher values than *Pu. coracis*. On the other hand, the pattern of the DNE values for P4 differ from that seen in RFI and in DNE for M2. Although *Pu. janisae* still has the highest value among the primitive plesiadapiforms sampled, *Pa. maturus* and *Pa. farrandi* come next, with higher values than the “palaechthonid” *Premnoides*. *Edworthia* follows *Premnoides*, as expected from the RFI and the DNE results for M2. *Paromomys depressidens* Gidley 1923 has the lowest DNE values for P4 among the primitive taxa, while *Pa. farrandi* exhibits the lowest RFI values for P4.

The 3D-OPCR results show that for both M2 and P4, *Pa. farrandi* has the highest values, and *Ed. lerbekmoi* the lowest. These results strongly contrast with the RFI and DNE results. In particular, it is surprising that *Ed. lerbekmoi*, which has a relatively high DNE value (126.396), has such a low 3D-OPCR value (60.000; Table 4.1).
Table 4.1 Relief Index (RFI), Dirichlet Normal Energy (DNE), and 3D Orientation Patch Count Rotated (3D-OPCR) values for species of primitive plesiadapiforms (*Purgatorius*, Purgatoriidae; *Premnoides*, “Palaechthonidae”) and early paromomyids (*Paromomys* and *Edworthia*).  

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen</th>
<th>Tooth</th>
<th>RFI</th>
<th>DNE</th>
<th>3D-OPCR</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Purgatorius coracis</em></td>
<td>UALVP 51012</td>
<td>M₂</td>
<td>0.561</td>
<td>219.727</td>
<td>107.375</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Purgatorius janisae</em></td>
<td>UCMP 107406</td>
<td>M₂</td>
<td>0.569</td>
<td>296.593</td>
<td>98.500</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Premnoides douglassi</em></td>
<td>YPM-PU 19794</td>
<td>M₂</td>
<td>0.558</td>
<td>240.848</td>
<td>134.500</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Paromomys farrandi</em></td>
<td>UWBM 97705</td>
<td>M₂</td>
<td>0.454</td>
<td>165.518</td>
<td>155.750</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Paromomys matures</em></td>
<td>USNM 9542</td>
<td>M₂</td>
<td>0.525</td>
<td>188.589</td>
<td>99.625</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Edworthia lerbekmoi</em></td>
<td>UALVP 50990</td>
<td>M₂</td>
<td>0.534</td>
<td>206.844</td>
<td>75.125</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Purgatorius janisae</em></td>
<td>UCMP 107406</td>
<td>P₄</td>
<td>0.662</td>
<td>214.294</td>
<td>87.375</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Premnoides douglassi</em></td>
<td>YPM-PU 14802</td>
<td>P₄</td>
<td>0.631</td>
<td>136.738</td>
<td>82.625</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Paromomys farrandi</em></td>
<td>UCMP 157702</td>
<td>P₄</td>
<td>0.424</td>
<td>151.016</td>
<td>96.500</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Paromomys matures</em></td>
<td>USNM 9542</td>
<td>P₄</td>
<td>0.595</td>
<td>175.195</td>
<td>85.375</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Paromomys depressidens</em></td>
<td>USNM 9677</td>
<td>P₄</td>
<td>0.433</td>
<td>114.856</td>
<td>96.000</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Edworthia lerbekmoi</em></td>
<td>UALVP 50990</td>
<td>P₄</td>
<td>0.574</td>
<td>126.396</td>
<td>60.000</td>
<td>Fossil</td>
</tr>
</tbody>
</table>
4.5.3 European paromomyids

Among European paromomyids, *Arcius rougieri* shows the highest RFI value for M2, followed by *Ar. fuscus*. *Arcius lapparenti* has the lowest RFI value for both M2 and P4. However, *Ar. fuscus* has a higher RFI value than *Ar. rougieri* for P4. DNE differs from RFI in that *Ar. lapparenti* has a higher M2 value than *Ar. fuscus*, and a higher P4 value than *Ar. rougieri*. It is notable that *Ar. fuscus* has an extremely high DNE value for P4 (399.962), much higher than observed in the other *Arcius* taxa (Table 4.2).

The 3D-OPCR results for M2 contrast with the RFI results. The species with the highest 3D-OPCR values is *Ar. lapparenti*, followed by *Ar. rougieri*, and finally *Ar. fuscus*. The 3D-OPCR results for P4, however, match the pattern seen in RFI in terms of the ordering of the taxa (i.e., the highest value is observed for *Ar. rougieri* and the lowest for *Ar. fuscus*). Like with the DNE results, it is notable that the 3D-OPCR value for *Ar. fuscus* is much higher (148.250) than that observed for the other *Arcius* species (Table 4.2).
Table 4.2 Relief Index (RFI), Dirichlet Normal Energy (DNE), and 3D Orientation Patch Count Rotated (3D-OPCR) values for species of European paromomyids (genus *Arcius*).

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen</th>
<th>Tooth</th>
<th>RFI</th>
<th>DNE</th>
<th>3D-OPCR</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Arcius rougieri</em></td>
<td>PAT 5</td>
<td>M₂</td>
<td>0.508</td>
<td>277.892</td>
<td>104.625</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Arcius fuscus</em></td>
<td>UCMP 71977</td>
<td>M₂</td>
<td>0.466</td>
<td>159.432</td>
<td>92.250</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Arcius lapparenti</em></td>
<td>AV 5824</td>
<td>M₂</td>
<td>0.382</td>
<td>213.938</td>
<td>155.625</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Arcius rougieri</em></td>
<td>PAT 2</td>
<td>P₄</td>
<td>0.654</td>
<td>123.135</td>
<td>86.625</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Arcius fuscus</em></td>
<td>CB 2560</td>
<td>P₄</td>
<td>0.677</td>
<td>399.962</td>
<td>148.250</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Arcius lapparenti</em></td>
<td>CB 4162</td>
<td>P₄</td>
<td>0.616</td>
<td>126.883</td>
<td>45.000</td>
<td>Cast</td>
</tr>
</tbody>
</table>
4.5.4 *Ignacius* and *Acidomomys*

Among the species of *Ignacius*, *Ignacius graybullianus* Bown and Rose 1976 has the highest RFI values for M₂, followed by *Ignacius clarkforkensis*, then *Ignacius fremontensis* Gazin 1971, and finally *Ignacius frugivorus* Matthew and Granger 1921 (Table 4.3). This pattern is also consistent with the P₄ results. *Acidomomys hebeticus* Bloch, Boyer, Gingerich and Gunnell 2002 has a slightly higher value for M₂ than *I. frugivorus*.

The pattern seen in DNE for M₂ is almost the opposite of the RFI results. *Ignacius clarkforkensis* and *I. graybullianus* have the lowest DNE values for M₂, with *I. fremontensis* having the highest DNE value for the genus, and *I. frugivorus* having an intermediate value. The DNE value calculated for the M₂ of *Acidomomys* falls between those calculated for *I. frugivorus* and *I. graybullianus*. The DNE results for P₄ also differ from the RFI results, with *I. fremontensis* having the highest value in the genus, followed by *I. graybullianus*, then *I. frugivorus*, and finally *I. clarkforkensis.*

The 3D-OPCR results are fairly consistent with the DNE results. The only difference is that *I. frugivorus* has a higher 3D-OPCR value than *I. fremontensis* for M₂.
Table 4.3 Relief Index (RFI), Dirichlet Normal Energy (DNE), and 3D Orientation Patch Count Rotated (3D-OPCR) values for species of *Ignacius* and *Acidomomys*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen</th>
<th>Tooth</th>
<th>RFI</th>
<th>DNE</th>
<th>3D-OPCR</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ignacius fremontensis</em></td>
<td>AMNH 88309</td>
<td>M₂</td>
<td>0.494</td>
<td>183.053</td>
<td>117.000</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Ignacius frugivorus</em></td>
<td>UM 77268</td>
<td>M₂</td>
<td>0.467</td>
<td>174.378</td>
<td>125.500</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Ignacius clarkforkensis</em></td>
<td>UM 108210</td>
<td>M₂</td>
<td>0.509</td>
<td>129.505</td>
<td>51.375</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Ignacius graybullianus</em></td>
<td>USNM 493883</td>
<td>M₂</td>
<td>0.513</td>
<td>131.615</td>
<td>79.625</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Acidomomys hebeticus</em></td>
<td>UM 10826</td>
<td>M₂</td>
<td>0.476</td>
<td>167.819</td>
<td>105.875</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Ignacius fremontensis</em></td>
<td>AMNH 88309</td>
<td>P₄</td>
<td>0.624</td>
<td>124.663</td>
<td>94.875</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Ignacius frugivorus</em></td>
<td>UM 77268</td>
<td>P₄</td>
<td>0.616</td>
<td>101.767</td>
<td>84.125</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Ignacius clarkforkensis</em></td>
<td>UM 108210</td>
<td>P₄</td>
<td>0.642</td>
<td>66.535</td>
<td>33.125</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Ignacius graybullianus</em></td>
<td>USGS 27066</td>
<td>P₄</td>
<td>0.650</td>
<td>108.657</td>
<td>88.500</td>
<td>Fossil</td>
</tr>
</tbody>
</table>
4.5.5 *Phenacolemur* and *Elwynella*

The RFI results for both M₂ and P₄ show that the highest values are observed in *Phenacolemur willwoodensis*, *Phenacolemur jepseni*, *Phenacolemur praecox* Matthew 1915, and *Phenacolemur citatus* Matthew 1915 (Table 4.4). The intermediate form between *Phenacolemur praecox* and *Phenacolemur fortior* Robinson and Ivy 1994 (here called *Phenacolemur praecox-fortior*) following Silcox et al. 2008) shows the lowest RFI values for M₂. *Phenacolemur pagei* Jepsen 1930 has the lowest RFI for P₄. *Elwynella oreas* Rose and Bown 1982 has one of the lowest RFI values for M₂.

The DNE results for both M₂ and P₄ put *Ph. willwoodensis* as having the highest value among *Phenacolemur*, and *Ph. fortior* showing the lowest values. DNE differs from RFI in the position of *Elwynella*, where it is placed as the second highest RFI value for M₂.

The 3D-OPCR results are not consistent with the results seen in RFI and DNE. *Phenacolemur pagei* has the highest value for its genus for M₂, and *Ph. fortior* the lowest. *Phenacolemur simonsi* Bown and Rose 1976 has the highest value for P₄, and *Ph. citatus* the lowest.
<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen</th>
<th>Tooth</th>
<th>RFI</th>
<th>DNE</th>
<th>3D-OPCR</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phenacolemur archus</em></td>
<td>UM 77163</td>
<td>M₂</td>
<td>0.483</td>
<td>211.842</td>
<td>130.125</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur pagei</em></td>
<td>YPM-PU 14030</td>
<td>M₂</td>
<td>0.500</td>
<td>206.147</td>
<td>142.000</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur praecox</em></td>
<td>UM 65572</td>
<td>M₂</td>
<td>0.524</td>
<td>192.592</td>
<td>86.125</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur praecox-fortior</em></td>
<td>USGS 12883</td>
<td>M₂</td>
<td>0.477</td>
<td>170.376</td>
<td>85.375</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur fortior</em></td>
<td>USNM 488331</td>
<td>M₂</td>
<td>0.488</td>
<td>148.247</td>
<td>53.500</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur citatus</em></td>
<td>USGS 21712</td>
<td>M₂</td>
<td>0.507</td>
<td>205.113</td>
<td>117.875</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur simonsi</em></td>
<td>USNM 4540232</td>
<td>M₂</td>
<td>0.504</td>
<td>168.123</td>
<td>128.625</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur willwoodensis</em></td>
<td>USNM 511214</td>
<td>M₂</td>
<td>0.553</td>
<td>214.070</td>
<td>124.375</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur jepseni</em></td>
<td>AMNH 48005</td>
<td>M₂</td>
<td>0.552</td>
<td>178.404</td>
<td>121.625</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Elwynella oreas</em></td>
<td>USGS 10403</td>
<td>M₂</td>
<td>0.479</td>
<td>214.018</td>
<td>106.875</td>
<td>Fossil</td>
</tr>
</tbody>
</table>

Table 4.4 Relief Index (RFI), Dirichlet Normal Energy (DNE), and 3D Orientation Patch Count Rotated (3D-OPCR) values for species of *Phenacolemur* and *Elwynella*.
<table>
<thead>
<tr>
<th>Species</th>
<th>Catalog Number</th>
<th>Tooth</th>
<th>Length</th>
<th>Width</th>
<th>Fossil Type</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phenacolemur archus</em></td>
<td>UM 109601</td>
<td>P₄</td>
<td>0.609</td>
<td>89.024</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur pagei</em></td>
<td>YPM-PU 13392</td>
<td>P₄</td>
<td>0.560</td>
<td>89.137</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur praecox</em></td>
<td>UM 65572</td>
<td>P₄</td>
<td>0.648</td>
<td>100.078</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur praecox</em></td>
<td>USNM 538053</td>
<td>P₄</td>
<td>0.595</td>
<td>101.291</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur praecox-fortior</em></td>
<td>USGS 12883</td>
<td>P₄</td>
<td>0.574</td>
<td>104.658</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur forterior</em></td>
<td>USNM 521810</td>
<td>P₄</td>
<td>0.568</td>
<td>82.772</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur citatus</em></td>
<td>USNM 544792</td>
<td>P₄</td>
<td>0.619</td>
<td>102.209</td>
<td>Fossil</td>
</tr>
<tr>
<td><em>Phenacolemur citatus</em></td>
<td>USGS 21712</td>
<td>P₄</td>
<td>0.627</td>
<td>113.536</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur simonsi</em></td>
<td>USNM 493867</td>
<td>P₄</td>
<td>0.578</td>
<td>130.073</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur willwoodensis</em></td>
<td>USNM 511214</td>
<td>P₄</td>
<td>0.650</td>
<td>136.806</td>
<td>Cast</td>
</tr>
<tr>
<td><em>Phenacolemur jepseni</em></td>
<td>AMNH 48005</td>
<td>P₄</td>
<td>0.700</td>
<td>125.613</td>
<td>Cast</td>
</tr>
</tbody>
</table>
4.6 Discussion

Of the three metrics, 3D-OPCR seems to be particularly sensitive to the raw material of the specimen that was scanned, i.e., if the X-ray microCT data come from a cast or a fossil specimen. Fossil specimens in this analysis typically generate lower 3D-OPCR values, whereas casts show higher values. This might be due to the rougher surface of the included casts, which could potentially create more surface complexity (Figure 4.3). Although there may be some cases in which a morphological signal is still coming through in the 3D-OPCR results (e.g., the high values for P₄ of *Ar. fuscus*, which also exhibits some of the highest DNE and RFI values), in other cases the 3D-OPCR values seem to be entirely at odds with indications from the other metrics (e.g., the relatively low number of patches for *Ed. lerbekmoi* for both P₄ and M₂, which would be unexpected given that taxon’s relatively high values for DNE). Therefore, future studies combining data for 3D-OPCR from casts and fossil specimens should take this issue into account. A possible solution to the problem may be to increase the patch size to avoid subtle surface roughness in casts from inflating the calculated values. On the other hand, RFI and DNE appear to be more robust to this effect, with no consistent pattern in terms of casts having especially high or low values.

For RFI and DNE, published data from modern primate taxa of known diet (Bunn et al. 2011) make it possible to reconstruct preliminary dietary categories based on the data for M₂ (Table 4.5; see Figures 4.4 and 4.5). As inferred from Bunn et al.’s (2011: fig. 4) work, RFI values for
Figure 4.3 Comparison of 3D-OPCR maps for a real fossil specimen vs. a cast. A) *Edworthia lerbekmoi* (UALVP 50990, original fossil, rM2) OPCR = 75.125; B) *Paromomys farrandi* (UCMP 157702, cast, IM2 reversed) OPCR = 155.750. Note the much higher number of patches on the *Pa. farrandi* specimen. Although the contrast may represent some differences in the shape of the teeth, the fact that similar areas of the two teeth (e.g., the talonid basin) are divided up so differently suggests that the rougher surface of the cast is introducing some noise to the 3D-OPCR calculation. Scale bars = 1 mm.
M$_2$ between 0.337 and 0.465 are reconstructed as coming from frugivores, values between 0.453 and 0.528 from omnivores, and values between 0.539 and 0.671 from insectivores. With respect to DNE, values between 74.142 and 175.384 are reconstructed as coming from frugivores, values between 139.888 and 221.975 from omnivores, and values between 211.634 and 338.430 from insectivores. Folivory is not considered among paromomyids because, with the exception of the taxonomically controversial “Pulverflumen magnificum” (Robinson and Ivy, 1994; not included in this study), all paromomyids are well below Kay’s (1984) threshold, implying that they were too small to fulfill a significant part of their protein needs from leaves. Assessing gummivory in paromomyids is also beyond the aims of this study, because DTA has not been shown to detect any signal related to gum-eating behaviors.

Relief index values for M$_2$ are consistent with the more primitive members of plesiadapiforms, such as *Purgatorius*, having taller cusps than in most paromomyids (Figure 4.1). RFI values drop in the earliest members of the paromomyids, suggesting a transition to lower-crowned teeth and a more frugivorous diet. The surprisingly low values calculated for *Paromomys farrandi* are probably affected by the relatively high degree of wear observed in the included tooth, reducing the height of the trigonid cusps. DNE values for M$_2$ are consistent with the RFI results in being generally lower in paromomyids than in primitive plesiadapiforms.
Table 4.5 Reconstructed diets for paromomyids and other plesiadapiforms. Diets are reconstructed following Bunn et al. (2011), based on RFI values (RFI column), DNE values (DNE column), and the combination of RFI and DNE (Diet column).

<table>
<thead>
<tr>
<th>Species</th>
<th>RFI</th>
<th>DNE</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acidomomys hebeticus</em></td>
<td>Omnivore</td>
<td>Omnivore-Frugivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td><em>Arcius fuscus</em></td>
<td>Omnivore</td>
<td>Omnivore-Frugivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td><em>Arcius lapparenti</em></td>
<td>Frugivore</td>
<td>Omnivore-Insectivore</td>
<td>Omnivore</td>
</tr>
<tr>
<td><em>Arcius rougieri</em></td>
<td>Omnivore</td>
<td>Insectivore</td>
<td>Omnivore-Insectivore</td>
</tr>
<tr>
<td><em>Edworthia lerbekmoi</em></td>
<td>Omnivore-Insectivore</td>
<td>Omnivore</td>
<td>Omnivore-Insectivore</td>
</tr>
<tr>
<td><em>Elwynella oreas</em></td>
<td>Omnivore</td>
<td>Omnivore-Insectivore</td>
<td>Omnivore-Insectivore</td>
</tr>
<tr>
<td><em>Ignacius clarkforkensis</em></td>
<td>Omnivore</td>
<td>Frugivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td><em>Ignacius fremontensis</em></td>
<td>Omnivore</td>
<td>Omnivore</td>
<td>Omnivore</td>
</tr>
<tr>
<td><em>Ignacius frugivorus</em></td>
<td>Omnivore</td>
<td>Omnivore-Frugivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td><em>Ignacius graybullianus</em></td>
<td>Omnivore</td>
<td>Frugivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td><em>Paromomys farrandi</em></td>
<td>Omnivore-Frugivore</td>
<td>Omnivore-Frugivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td>Species</td>
<td>Diet 1</td>
<td>Diet 2</td>
<td>Diet 3</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----------------------</td>
<td>-----------------------</td>
<td>-----------------------</td>
</tr>
<tr>
<td><em>Paromomys maturus</em></td>
<td>Omnivore</td>
<td>Omnivore</td>
<td>Omnivore</td>
</tr>
<tr>
<td><em>Phenacolemur archus</em></td>
<td>Omnivore</td>
<td>Omnivore-Insectivore</td>
<td>Omnivore-Insectivore</td>
</tr>
<tr>
<td><em>Phenacolemur citatus</em></td>
<td>Omnivore</td>
<td>Omnivore</td>
<td>Omnivore</td>
</tr>
<tr>
<td><em>Phenacolemur fortior</em></td>
<td>Omnivore</td>
<td>Frugivore-Omnivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td><em>Phenacolemur jepseni</em></td>
<td>Insectivore</td>
<td>Omnivore</td>
<td>Omnivore-Insectivore</td>
</tr>
<tr>
<td><em>Phenacolemur pagei</em></td>
<td>Omnivore</td>
<td>Omnivore</td>
<td>Omnivore</td>
</tr>
<tr>
<td><em>Phenacolemur praecox</em></td>
<td>Omnivore</td>
<td>Omnivore</td>
<td>Omnivore</td>
</tr>
<tr>
<td><em>Phenacolemur praecox-fortior</em></td>
<td>Omnivore</td>
<td>Omnivore-Frugivore</td>
<td>Omnivore-Frugivore</td>
</tr>
<tr>
<td><em>Phenacolemur simonsi</em></td>
<td>Omnivore</td>
<td>Omnivore</td>
<td>Omnivore</td>
</tr>
<tr>
<td><em>Phenacolemur willwoodensis</em></td>
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<td>Omnivore-Insectivore</td>
<td>Insectivore-Omnivore</td>
</tr>
<tr>
<td><em>Premnoides douglassi</em></td>
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<td>Insectivore</td>
<td>Insectivore</td>
</tr>
<tr>
<td><em>Purgatorius coracis</em></td>
<td>Insectivore</td>
<td>Omnivore-Insectivore</td>
<td>Insectivore-Omnivore</td>
</tr>
<tr>
<td><em>Purgatorius janisae</em></td>
<td>Insectivore</td>
<td>Insectivore</td>
<td>Insectivore</td>
</tr>
</tbody>
</table>
The RFI and DNE values for M2 of *Pu. janisae* agree with Kay and Cartmill (1977) in supporting the inference of a predominantly insectivorous diet for that genus. It has been suggested that the rounder cusps and broader talonid basins of *Purgatorius*, compared to contemporary specialized insectivores, may be indicative of less specialization for insectivory (Scott et al., 2016; Silcox and López-Torres, accepted; Silcox et al., accepted). The results of this analysis may seem to contradict this inference. However, it is worth noting that, although *Pu. janisae* has high RFI and DNE values within the context of this sample, the absence of non-primates means that its degree of insectivory with respect to contemporary specialized insectivores that it may have been competing with for food resources cannot be assessed. Further, *Pu. coracis*, is reconstructed here as a mixed-feeding omnivore with a high insect intake rather than a strict insectivore.

Although the diet of *Premnoides* has not been discussed in the literature, small-bodied “palaechthonids” are often regarded as insectivores (Kay and Cartmill, 1974; Silcox and López-Torres, accepted; Silcox et al., accepted). Both RFI and DNE results are consistent with this inference. The results suggest that the earliest paromomyids (i.e. *Paromomys* and *Edworthia*) were more omnivorous than *Premnoides* and *Purgatorius*, with *Edworthia* relying more on insects than *Paromomys*. Whereas *Paromomys maturus* is reconstructed as a mixed-feeding omnivore, the results suggest that *Pa. farrandi* would be more frugivorous than *Pa. maturus*, although still an omnivore. However, the wear on the cusps of *Pa. farrandi* might be influencing the inferred dietary signal and exaggerating the difference between these taxa.
Figure 4.4 Temporal ranges of species of the purgatoriids, palaechthonids, and North American paromomyids used in this study, coloured by dietary niches.
**Figure 4.5** Temporal ranges of species of *Arcius* used in this study, coloured by dietary niches.
The P₄s in the non-paromomyid sample have trigonid cusps and cristids that are less well-developed, or even absent in paromomyids (for example, the prominent paraconid in the sampled specimen of *Pu. janisae* (Figure 4.6A) and the long, robust paracristid in the P₄ of *Premnoides*; see Figure 4.6C). The presence of an additional cusp might be expected to lead to a higher RFI value. However, the fact that the RFI value is actually higher in some paromomyids (i.e., *Ph. jepseni, Ar. fuscus*) than observed in *Pu. janisae* suggests that the situation is not that simple. It appears as though RFI is strongly affected by the size of the base (i.e., the footprint) --for example, the footprint of the P₄ is very small in *Ph. jepseni*, and because the footprint area is in the denominator of the RFI equation, it may be the reason why the RFI value for *Ph. jepseni* is so high. This makes RFI more complicated to interpret than originally expected. On the other hand, DNE seems to better reflect the presence or absence, or degree of development, of particular features of the crown. So, for example, the strong paracristid observed in both *Pu. janisae* and *Pa. maturus* contributes to higher DNE values than seen in other relatively primitive taxa sampled (Figure 4.6).

Bown and Rose (1976) pointed out that *Pa. depressidens* was more similar to *Ignacius* than to other species of *Paromomys*, and hypothesized an ancestor-descendant relationship between *Pa. depressidens* and the genus *Ignacius*. Whereas RFI values for the P₄ of *Pa. depressidens* are quite different for those of any species of *Ignacius*, DNE values bring *I. fremontensis*, the oldest
Figure 4.6 Comparison of DNE for relatively primitive P₄s. A) *Purgatorius janisae* (UCMP 107406, rP₄ reversed, cast) DNE = 214.294; B) *Paromomys maturus* (USNM 9542, rP₄ reversed, cast) DNE = 175; C) *Premnoides douglassi* (YPM-PU 14802, rP₄ reversed, cast) DNE = 136.738; D) *Paromomys depressidens* (USNM 9677, rP₄ reversed, cast) DNE = 114.856. *Purgatorius* and *Pa. maturus* both have quite highly curved surfaces, in part as a result of a strong paracristid. *Premnoides douglassi* actually had a P₄ with a lower level of curvature, similar to that seen in some paromomyids, including *Pa. depressidens*. Scale bars = 1 mm.
member of the genus, very close to the DNE value for Pa. depressidens. Although DNE values are consistent with Bown and Rose’s (1976) hypothesis, it does not necessarily imply an ancestor-descendant relationship between Pa. depressidens and Ignacius. A phylogenetic analysis of paromomyids at a species level is needed to further shed light on this question.

Previous work (Godinot, 1984) has suggested that Arcius rougieri might have been ancestral to Ar. fuscus and Ar. lapparenti, although the basis upon these claims were made has been questioned (Hooker, 1998). However, if this inference is correct, then the RFI results for M2 would be consistent with a transition from omnivory to a more frugivorous diet within the European radiation of paromomyids in showing lower values for both Ar. fuscus and Ar. lapparenti than observed in Ar. rougieri (Table 4.2). In contrast to RFI, the DNE values for M2 are quite different for Ar. fuscus when compared to Ar. lapparenti. However, both taxa still have lower M2 DNE values than observed in Ar. rougieri, meaning the results are consistent with a transition from more curved teeth with sharper edges and taller cusps to more bunodont teeth.

All analyzed species of Arcius are inferred to have had a mixed-feeding omnivorous diet (Table 4.5), although with differing degrees of insectivory and frugivory. The RFI and DNE results for M2 suggest that Ar. rougieri relied more on insects than the other two species of Arcius, while Ar. lapparenti relied more on fruit than Ar. fuscus, with the latter being a generalized omnivore. This pattern of dietary niches is consistent with diets heavier in insects in more primitive lineages, and a transition to more frugivory over time.

Arcius fuscus has the highest values for P4 for both RFI and DNE. This is likely due to the presence of an additional crest on the postvallid of the P4 of Ar. fuscus that is not seen in any other European paromomyid, creating additional curves and a higher 3D surface area (Figure 4.7).
**Figure 4.7** Comparison of DNE for *Arcius* P₄s. A) *Arcius rougieri* (PAT 2, rP₄ reversed, cast), DNE = 123.135; B) *Arcius lapparenti* (CB 4162, lP₄, cast), DNE = 126.883; C) *Arcius fuscus* (CB 2560, lP₄, cast), DNE = 399.962. Note that the DNE values for *Ar. rougieri* and *Ar. lapparenti* are very similar, reflecting their fundamentally similar shapes. In contrast, *Ar. fuscus* has a much higher DNE value, likely as a result of the presence of an additional crest on the hypoflexid. Scale bars = 1 mm.
Potential ancestor-descendant relationships have been hypothesized between Ignacius frugivorus and I. clarkforkensis, and I. clarkforkensis and I. graybullianus (Bloch et al., 2007). The DNE results for M₂ show low levels of curvature for the more recent species of Ignacius (i.e. I. graybullianus and I. clarkforkensis), and higher values for the older and presumably more primitive species (I. frugivorus and I. fremontensis), which could suggest that, like Arcius, Ignacius exhibited increasing degrees of frugivory through time. Although the sequence I. frugivorus-I. clarkforkensis-I. graybullianus does not hold in terms of the ordering of the results, the RFI and DNE values for M₂, and the RFI values for P₄ of I. clarkforkensis and I. graybullianus are very similar, which mirrors how close these two species have been inferred to be morphologically (Figure 4.8; Bloch et al., 2007). However, the DNE results for P₄ are not consistent with the other findings, with I. graybullianus having a notably higher DNE score for its P₄ than calculated for I. clarkforkensis. This reflects the fact that the P₄ in the sampled specimen of I. clarkforkensis is an exceptionally simple tooth (Figure 4.8B). Interpreting this apparent contrast would require study of additional specimens of both taxa. Whereas RFI categorizes all species of Ignacius as mixed-feeding omnivores, DNE values suggest more frugivory in I. frugivorus, I. clarkforkensis and I. graybullianus relative to the oldest and most primitive member of the genus, I. fremontensis, which can be inferred to have been a more
Figure 4.8 Comparison of relief maps of $P_4$s for *Ignacius* specimens that differ in RFI. A) *Ignacius frugivorus* (UM 77268; r$P_4$ reversed, cast), RFI = 0.616; B) *Ignacius clarkforkensis* (UM 108210; r$P_4$ reversed), RFI = 0.642; C) *Ignacius graybullianus* (USGS 27066; l$P_4$), RFI = 0.650. Note that *I. clarkforkensis* and *I. graybullianus* have very similar RFI scores, consistent with the inference that they are closely related. The values for RFI for *Ignacius* are generally quite high, likely related to the small footprint of $P_4$s in this genus relative to their height. Scale bars = 1 mm.
generalized omnivore (Figure 4.9). Ironically, *I. frugivorus* is suggested by its RFI values to not have been completely frugivorous, contrary to its hypothesized diet in the early studies of the first known paromomyids by Matthew and Granger (1921).

The generally low DNE values for P₄ reflect the simplicity of the morphology of that tooth in *Ignacius*, especially in *I. clarkforkensis*. *Ignacius fremontensis* has a convex mesial aspect of the P₄, creating more curvature, and therefore showing a higher DNE value. The RFI results contrast with the DNE numbers in showing quite high values for P₄ in all species of *Ignacius* (Table 4.3), which probably at least partly reflects the small footprint of the P₄ in *Ignacius* (Figure 4.8).

*Acidomomys hebeticus* is hypothesized as the sister taxon to *Ignacius* and *Phenacolemur* (Bloch et al., 2002). However, its teeth are very bunodont, similar to those seen in the more derived species of *Ignacius* (i.e., *I. clarkforkensis* and *I. graybullianus*). *Acidomomys* is reconstructed as a mixed-feeding omnivore relying heavily on fruit (Figure 4.9C).

*Phenacolemur* is the most diverse paromomyid genus in terms of values for RFI and DNE. All species of *Phenacolemur* occupy the omnivore space in the analysis of M₂ (Table 4.5), but the omnivory seen in *Ph. fortior* was likely very different to that of *Ph. willwoodensis*. The genus exhibits a broad range of values for both RFI and DNE, suggesting a diversity of modes of omnivory, ranging from a heavy reliance on fruit, to a high intake of insects. Based on DNE values, *Ph. fortior* is inferred to have been the most frugivorous species of *Phenacolemur*, although the transitional form *Ph. praecox-fortior* was already likely relying more on fruit than its ancestor, *Ph. praecox*, a generalized omnivore. Interestingly, the hypothesized descendant species of *Ph. fortior*, *Ph. citatus*, transitioned back to a more omnivorous space, being less reliant on fruit. *Phenacolemur fortior* lived during Wa-4 (Wasatchian North American Land Mammal Age [NALMA]) between two periods of faunal turnover in the Bighorn Basin.
Figure 4.9 Comparison of DNE for *Ignacius* and *Acidomomys* M2s.  
A) *Ignacius fremontensis* (AMNH 88309, lM2 reversed, cast), DNE = 183.053; B) *Ignacius frugivorus* (UM 77268, lM2 reversed, cast), DNE = 174.378; C) *Acidomomys hebeticus* (UM 108206, lM2 reversed, cast), DNE = 167.819; D) *Ignacius clarkforkensis* (UM 108210, lM2 reversed), DNE = 129.505.  Based on these four specimens, three of the taxa (*I. clarkforkensis*, *I. frugivorus*, and *Ac. hebeticus*) are inferred to have been omnivores that heavily relied on fruit, while the more primitive *I. fremontensis* has a DNE value consistent with it having been a generalized omnivore. Scale bars = 1 mm.
(Wyoming), termed Biohorizons A and B (Schankler, 1980; Silcox et al., 2008). The shift in dietary niche might be related to a drop in temperatures that is inferred to have occurred between the two Biohorizons (Chew and Oheim, 2013). Palaeotemperature proxies indicate that the mean annual temperature in the Bighorn Basin during the cool period of the Wasatchian was around 11 °C (Bao et al., 1999; Wing et al., 2000; Chew and Oheim, 2013). Low temperatures could potentially reduce the availability of the types of resources crucial to primates, such as fruit and insects, and drive animals into more restrictive dietary niches.

The results for the primitive *Phenacolemur archus* Secord 2008 suggest that it was an omnivore that relied more on insects than on other food sources. Based on the patterns seen in other paromomyid lineages (discussed above), this might be expected of the oldest member of the genus. However, *Ph. jepseni*, one of the latest species of *Phenacolemur*, is also inferred to have had a diet heavy in insects. This is consistent with its tall, obliquely-oriented cusps. *Phenacolmeur willwoodensis* is inferred to be even more extreme in its degree of insectivory -- indeed, the RFI value for this taxon actually suggests it was predominantly insectivorous (Figure 4.10), while the DNE values put it at the highly insectivorous end of omnivory. Utilizing a more insect-based diet might have been a strategy to avoid competition with the very abundant generalized omnivore *Ph. citatus*, also present in the latest subages of the Wasatchian NALMA.

The highest RFI value for the P₄ in *Phenacolemur* (or any paromomyid sampled) is calculated for *Ph. jepseni* (0.700, Table 4.4). Many derived species of *Phenacolemur* have a mesial bulge at the base of the protoconid that increases the footprint area for the calculation of RFI, and therefore decreases the RFI value. Although *Ph. jepseni* does have this mesial bulge in the protoconid, it is directed downwards, which means that the footprint area is significantly relatively smaller compared to species of *Phenacolemur* in which the bulge is more mesially
Figure 4.10 Comparison of relief maps of $M_2$s for *Phenacolemur* specimens that differ in RFI. A) *Phenacolemur fortior-praecox* intermediate (USGS 12883, $lM_2$), RFI = 0.477; B) *Phenacolemur citatus* (USGS 21712; $lM_2$), RFI = 0.507; C) *Phenacolemur willwoodensis* (USNM 511214; $RM_2$ reversed), RFI = 0.553. The RFI values for *Ph. fortior-praecox* and *Ph. citatus* suggest omnivorous habits, while the higher value for *Ph. willwoodensis* suggests that it was more insectivorous. Scale bars = 1 mm.
oriented, such as *Ph. pagei* or *Ph. fortior* (both with low RFI values). *Phenacolemur willwoodensis* lacks the mesial bulge and is calculated to have had a high RFI value.

Silcox et al. (2008) suggested an ancestor-descendant relationship for *Ph. praecox-Ph. fortior*, with specimens being identified that were both temporally and morphologically intermediate. The RFI results for P₄ support a transition to more premolar bunodonty, with the intermediate form between *Ph. praecox* and *Ph. fortior* falling between the two species (Figure 4.11).

The values for RFI differentiate between the two diminutive species of *Phenacolemur* from the late Wasatchian: *Phenacolemur simonsi* and *Ph. willwoodensis*. Whereas DNE gives similar results in terms of the curvature of the P₄ for these two species, RFI gives very different results, most probably driven by the presence of a mesial bulge at the base of the protoconid of the P₄ of *Ph. simonsi*. This distinct contrast supports the inference that there were indeed two small species of *Phenacolemur* in the Wasatchian of the Bighorn Basin (Silcox et al., 2008).

Although this study does not attempt to examine the degree of intraspecific variability present within paromomyid taxa, the two P₄ specimens for both *Ph. praecox* and *Ph. citatus* provide some very preliminary indications of variation within those taxa. The two *Ph. citatus* specimens have both DNE and RFI values that are quite similar to one another, and the DNE scores for the two specimens of *Ph. praecox* are also very similar (Table 4.4). However, the two specimens of *Ph. praecox* are separated by 0.052 from one another in terms of RFI. This means that the range of intraspecific variation observed for RFI in even this small sample of *Ph. praecox* encompasses the variation among multiple taxa, including *Ph. archus* and *Ph. citatus*. Although outside the scope of this paper, a study on intraspecific variation is clearly needed to fully understand patterns of evolution within the family, the degree to which they can be quantified using various
Figure 4.11 Comparison of relief maps of P₄s for *Phenacolemur* specimens that differ in RFI. A) *Phenacolemur praecox* (USNM 538053, lP₄ reversed) RFI = 0.595; B) *Phenacolemur fortior-praecox* intermediate (USGS 12883, lP₄ reversed), RFI = 0.574; C) *Phenacolemur fortior* (USNM 521810, rP₄) RFI = 0.568. The decreasing RFI values from *Ph. praecox* to *Ph. fortior* reflects the shift from a taller, more pointed form of the P₄ to a lower more bulbous tooth, with the inferred intermediate having an intermediate RFI value. Scale bars = 1 mm.
DTA metrics, and the extent to which the conclusions of this paper are borne out with a larger sample.

*Elwynella oreas* has been described as resembling *Ph. jepseni* in terms of dental morphology, although it is characterized by the presence of a P3 alveolus, a tooth position lacking in *Ph. jepseni* (Rose and Bown, 1982). However, values of both RFI and DNE for M2 are quite different for the two species. Nevertheless, in terms of diet, *El. oreas* falls into the omnivore-insectivore space, as does *Ph. jepseni* (Table 4.5).

### 4.7 Conclusions

Dental topographic analysis provides a powerful tool for understanding evolutionary patterns in plesiadapiforms and teasing apart differences among dietary niches. Our results show that values for 3D-OPCR are particularly sensitive to inflation in casts relative to original fossils. This observation may require some re-thinking of the standard protocols for calculating 3D-OPCR, particularly for mixed samples of small taxa.

The other two metrics considered, RFI and DNE, seem to quantify somewhat different aspects of dental morphology and can potentially tell rather different stories. In some cases, relative values of RFI and DNE are consistent--this is true, for example, of the high RFI and DNE values for the P3 of *Arcius fuscus* and *Phenacolemur willwoodensis*. However, when RFI is calculated for tall paromomyid P4s, the results are very sensitive to the size of the footprint. Many derived species of paromomyids (i.e., *Phenacolemur*) have large mesial bulges at the base of the P4 protoconids, which increase the footprint size, and therefore reduce the RFI values. This complicates the interpretation of the data for P4 across the range of taxa included here.
In general, our results show that paromomyids occupied a more diverse range of dietary niches than previously thought (Gingerich, 1974; Godinot, 1984; Beard, 1990, 1991; Boyer and Bloch, 2008; Rosenberger, 2010), moving into a more fruit-based type of omnivory in relation to earlier plesiadapiforms. Although all paromomyids were likely omnivores, there are strong indications of higher levels of insectivory in some taxa, particularly in *Phenacolemur willwoodensis*, and to a lesser degree in *Ph. archus, Ph. jepseni, Elwynella oreas, Arcius rougieri*, and *Edworthia lerbekmoi*. Contrary to expectations that the apparently low-crowned molar teeth of *Ignacius* would reflect a clear signal for strict frugivory, all *Ignacius* species are inferred to have been mixed-feeding omnivores, although likely with high levels of fruit intake.

The use of dental topographic metrics also sheds light on broader evolutionary scenarios. Our results show that in all lineages, the more primitive and older members seem to have exhibited high degrees of insectivory, inherited from even more primitive plesiadapiforms, with parallel shifts in some derived members of *Arcius, Ignacius* and *Phenacolemur* towards higher levels of frugivory. Future work with larger specific samples will be needed to test this inferred pattern.

### 4.8 Acknowledgments

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4.9 References


*Evolutionary Monographs*, 15:1-79.


Chapter 5
Conclusions
5 Conclusions

Throughout the research work presented in this thesis, important aspects of the evolution and ecology of paromomyids have been explored.

5.1 Chapter 2

Chapter 2 describes a new species of omomyoid euprimate from the Uintan of southern California, specifically from the Ventura and San Diego counties. The southern California material was previously thought to pertain to a late occurring species of paromomyid (Mason, 1990; Walsh, 1996), morphologically similar to the Uintan-Duschesnean paromomyid species *Phenacolemur shifrae* and *Ignacius mcgrewi* from Wyoming (Robinson, 1968; Krishtalka, 1978). The new species from California, together with *Ph. shifrae* and *I. mcgrewi*, is transferred to the new trogolemurin genus *Walshina*. The implications of this taxonomic change are that no paromomyids are found between the early Bridgerian and the Chadronian, suggesting that a climatic event, such as the Early Eocene Climatic Optimum, might have been detrimental for the survival of paromomyids.

5.2 Chapter 3

Chapter 3 is a taxonomic reassessment of the European paromomyid material. All of this material has been referred to the genus *Arctius* (Godinot, 1984). In over 50 years of collecting of paromomyid fossils in France, England, Portugal, and Spain a significant sample for this group of stem primates has been amassed (Louis and Michaux, 1962; Louis, 1966, 1970; Russell et al., 1967, 1988, 1990; Hooker and Insole, 1980; Antunes, 1981; Godinot, 1981, 1984; Louis and
Laurain, 1983; Dégremont et al., 1985; Marandat, 1986, 1991; Estravís, 2000; Aumont, 2003; Smith et al., 2011; Marigó et al., 2012). This chapter presents emended diagnoses for all four previously known species of *Arcius* (Russell et al., 1967; Godinot, 1984; Estravís, 2000), and describes two new *Arcius* species from material previously collected in England (Hooker and Insole, 1980) and Spain (Marigó et al., 2012). A cladistic analysis of the European paromomyids resolves *Arcius* as monophyletic, supporting the referral of all European paromomyid species to that genus, and implying that the European radiation of paromomyids was a product of a single migration event from North America through the Greenland land bridge.

5.3 Chapter 4

Chapter 4 uses dental topographic metrics to assess diet in paromomyids and observe patterns of evolutionary change of this family’s most diagnostic tooth, the P4. The dental topographic analysis results for P4 change are consistent with previous literature for inferences about changes within the *Phenacolemur praecox-fortior* lineage. However, comparisons of the degree of morphological change across different paromomyid lineages is challenging. The results for M2 suggest a more varied diet that previously thought for paromomyids, which were categorized as either omnivores that relied heavily on fruit (Gingerich, 1974), insectivores (Godinot, 1984), or gummivores (Beard, 1990, 1991; Boyer and Bloch, 2008). The results presented here show a general trend from more insect intake in primitive members of several paromomyid lineages to a more frugivorous diet in more derived and/or later occurring members of the lineage.
5.4 Discussion and future directions

These three pieces of research surrounding the evolution, systematics, and ecology of paromomyids have expanded our current knowledge of this group of early primates in several ways. The diet of paromomyids has been explored using methods that allow for the quantification of three-dimensional dental morphology in Chapter 4. The results of this study show that paromomyids had a more flexible diet than was previously articulated in the literature, which just took into account qualitative variables of tooth morphology and/or aspects of their arboreal behaviour (Gingerich, 1974; Godinot, 1984; Beard, 1990, 1991; Boyer and Bloch, 2008; Rosenberger, 2010). Paromomyid dietary reconstruction suggests varying degrees of insect and fruit intake within the realm of omnivory, ranging from highly insectivorous omnivores to complete frugivores. This plasticity in the dietary niches of this group is consistent with their broad biogeographic range, and success as a group during the Paleocene and early Eocene. Indeed, the presence of paromomyids in regions as different as the Canadian Arctic, southern United States, or east Asia could have been made possible through the diverse range of dietary adaptations. However, an important limitation on this study was the small sample sizes per species. Certainly future studies will need to assess these conclusions using a larger sample for each species.

Paromomyids seem to have been well adapted to a fairly broad range of temperatures as well, being able to survive both in the almost freezing temperatures of the Eocene winter of Ellesmere Island (Eberle and Greenwood, 2012) but also living in much warmer conditions, such as the southern United States (Schiebout, 1974). However, Chapter 2 hypothesizes that paromoymids might have had a slim tolerance to unusually high temperatures, such as those reported for the Early Eocene Climatic Optimum. This sustained warm period could have been the cause of the
drop in paromomyid biodiversity after the Wasatchian. Only one species is known from the Bridgerian (*Elwynella oreas*, Rose and Bown, 1982) and subsequent to that there is but a single specimen from an undescribed species of *Ignacius* from the Chadronian (Kihm and Tornow, 2014).

Chapter 2 redefined the history of the group in both North America and Europe by reconsidering various of the later-occurring purported records of the family. In North America, the paromomyid record in the Uintan and the Duchesnean is non-existent. Paromomyids are present in the fossil record from the Torrejonian until the middle Bridgerian, being especially rich in biodiversity in the early Paleocene and the middle Wasatchian. Similarly, the European record of paromomyids seems to end after the Neustrian (early Eocene), mirroring the drop in biodiversity seen in North America as well. This is based on the recognition that all ascribed post-Neustrian specimens to Paromomyidae are non-diagnostic or questionable in their attribution. Therefore, the Early Eocene Climatic Optimum seems to have affected paromomyid populations worldwide.

Independently of the phylogenetic position of the Ellesmere Island paromomyid (which still remains unknown), the presence of paromomyids in the Arctic demonstrates that members of this family were able to live in early Eocene Arctic conditions, and therefore this observation is consistent with the idea of a migratory route of paromomyids going from North America to Europe through a Greenland land bridge. Chapter 3 resolves European paromomyids as monophyletic, suggesting that the migration from North America to Europe was product of one single migratory event. This is consistent with a hypothesized migration of this group around the Paleocene-Eocene boundary (Hooker, 2015).

However, some important questions still remain unanswered to fully understand the patterns of migration and evolution of paromomyids. The cladogram that presented in Chapter 3 showed the
Phenacolemur-Ignacius-Acidomomys clade as the sister taxon of the European paromomyids. Among all species of Phenacolemur, Ignacius, and Acidomomys, the oldest record belongs to Ignacius fremontensis, which is reported to come from as early as Torrejonian 2 (Gazin, 1971; Silcox and Williamson, 2012). This would imply that a North American Arcius-like ghost lineage must have existed from the Torrejonian to the early Eocene, for which there is no fossil evidence. Whether or not this scenario is correct needs to be assessed in a species level analysis of the North American paromomyids, in particular with respect to species close to the basal node of Paromomyidae. Therefore, it is of utmost importance that the phylogenetic relationships of North American paromomyids be resolved to better understand the time-line for intercontinental migrations.

Also, in order to understand intercontinental migration, it is very relevant to further explore bridging areas (i.e., Greenland; Larsen et al., 2001, 2002) and describe the material that comes from adjacent areas in transit to the bridging landmasses (i.e., Ellesmere Island; West and Dawson, 1971; McKenna, 1980; Eberle and Greenwood, 2012). In particular, the description of the paromomyid found in Ellesmere Island could shed light on what kind of adaptations paromomyids would have in an environment that is close to freezing temperatures in winter and is dark or low levels of sunlight for long periods of the year.

Besides the Ellesmere paromomyid, another specimen vital for the understanding of paromomyid biogeography is the one from the Wutu fauna in China (Tong and Wang, 1998). The Asian record of paromomyids is extremely poor (indeed, as far as we know it is just one specimen) and not at all understood. Tong and Wang (1998) reported the specimen to be similar morphologically to Ignacius. Therefore, Asia opens up the possibility for more paromomyid
discoveries that might help us understand when and how they dispersed between North America and Asia; a question that has not yet been explored.

Finally, the resolution of phylogenetic relationships among members of the family Paromomyidae not only provides a context for explaining the biogeography of the family, but also can illuminate the question of which living Order is more closely related to Primates. As discussed in the Introduction, Scandentia, Dermoptera, and Sundatheria (Dermoptera + Scandentia) have all been suggested as possible sister groups to Primates in various morphological and genetic studies (Bloch et al., 2007; Janečka et al., 2007; Springer et al., 2007; Nie et al., 2008; Liu et al., 2009; O’Leary et al., 2013). Resolving the relationships of the deepest nodes in the primate tree can bring us closer to a definitive answer, because characterizing the primitive condition in primates is necessary for determining meaningful directions of evolutionary change.

5.5 References


Appendices

**Appendix 2.1** Newick format for tree from Figure 2.5.

(Scandentia,((((((Tarsius_sp.,(Proteopithecus_sylviae,(Catopithecus_browni,((Aegyptopithecus_zeuxis,(Parapithecus_grangeri,Apidium_phiomense)),(Dolichocebus_gaimanensis,((Aotus_trivirgatus,Saimiri_scireus),Callicebus_moloch))))),Eosimias_sp.),((((Dyseolemur_pacificus,Washakius_insignis),Shoshonius_cooperi),Loveina_zephyri),((Loveina_sheai,Loveina_minuta,Loveina_wapitiensis)),(((Absarokius_sp.,Anaptomorphus_sp.),(Aycrossia_lovei,Strigorhysis_sp.)),Tetonius_sp.),Uintanius_ameghini),Trogolemur_leonardi,(((Sphacorhysis_burntforkensis,(Trogolemur_fragilis,Trogolemur_myodes,(Trogolemur_amplior,((Walshina_mcgrewi,(Walshina_shifrae,Walshina_esmaraldensis)))),Anemorhysis_savagei),(Arapahovius_gazini,Tetonoides_sp.)),((Hemiacodon_gracilis,Macrotarsius_montanus),Omomys_sp.),Steinius_vespertinus)),Teilhardina_american)),((Lemur_catta,(Microcebus_murinus,Galagoides_demidoff)),((Teilhardina_belgica,Teilhardina_asiatica),(Donrussellia_sp.,(Notharctus_sp.,(Rooneyia_viejaensis,(Mahgarita_stevensi,(Pronycticebus_gaudryi,(Adapis_parisiensis,Leptadapis_magnus))))))),Purgatorius_sp.));
### Appendix 2.2 Dental measurements of Trogolemurini.

#### Table S2.2.1 Measurements for upper molars of Trogolemurini.

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**Table S2.2.2** Measurements for lower dentition of Trogolemurini.

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Identified as *Ignacius mcgrewi* in Robinson (1986).
| UCM 26432 | Walshina shifrae | - | - | - | - | - | - | 1.25 | 1.06 | - | - | 5A, Badwater Creek, Natrona Co, WY, USA | Robinson (1968) |
| UCM 29005 | Walshina mcgrewi | - | - | - | - | - | - | 2.00 | 1.85 | - | - | Badwater Creek, Natrona Co, WY, USA | Krishtalka (1978) |
| UCM 38323 | Walshina shifrae | - | - | - | - | - | - | 1.40 | 1.30 | - | - | Badwater Creek, Natrona Co, WY, USA | Krishtalka (1978) |
| UCM 46602 | Trogolemur amplior | 1.20 | 0.95 | - | - | - | - | - | - | - | UCMB 17262, 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 3.1 Hypotheses of relationships among species of *Arcius*.

Figure S3.1.1 Five most parsimonious trees once *Arcius ilerdensis* n. sp. is included. The strict consensus for these five trees is shown in Figure 9D.
Appendix 3.2 Newick format for trees from Figures 9 and S3.1.1A-E.

Fig. 3.9A:

(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,(Arcius_rougieri,(Arcius_lapparenti,Arcius_fuscus))))));

Fig. 3.9B:

(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,(Arcius_hookeri,(Arcius_rougieri,(Arcius_lapparenti,Arcius_fuscus))))));

Fig. 3.9C:

(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),((Arcius_zbyszewskii,Arcius_Normandy),(Arcius_rougieri,(Arcius_lapparenti,Arcius_fuscus)))));

Fig. 3.9D:

(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,(Arcius_ilerdensis,Arcius_rougieri,Arcius_lapparenti,Arcius_fuscus)))));
Fig. S3.1.1A:
(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,((Arcius_rougieri,Arcius_ilerdensis),(Arcius_lapparenti,Arcius_fuscus))))));

Fig. S3.1.1B:
(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,(((Arcius_rougieri,Arcius_ilerdensis),Arcius_lapparenti),Arcius_fuscus)))));

Fig. S3.1.1C:
(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,((Arcius_rougieri,(Arcius_ilerdensis,Arcius_lapparenti)),Arcius_fuscus)))));

Fig. S3.1.1D:
(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,(((Arcius_rougieri,Arcius_fuscus),Arcius_lapparenti),Arcius_ilerdensis)))));

Fig. S3.1.1E:
(Purgatorius_coracis,((Paromomys_farrandi,Edworthia_lerbekmoi),((Phenacolemur_archus,(Ignacius_fremontensis,Acidomomys_hebeticus)),(Arcius_zbyszewskii,((Arcius_rougieri,(Arcius_lapparenti,Arcius_fuscus)),Arcius_ilerdensis)))));
References


