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

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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. Four species of paromomyids from the early Eocene have been reported from Europe: *Arcius fuscus* Russell et al., 1967, *Arcius lapparenti* Russell et al., 1967, and *Arcius rougieri* Godinot, 1984 from France and *Arcius zbyszewskii* Estravís, 2000 from Portugal. Other *Arcius* specimens from the early Eocene are known from Masia de l'Hereuet (Spain), Abbey Wood (England), and Sotteville-sur-Mer (Normandy, France). A cladistic analysis of the European paromomyids has never previously been published. A total of 53 dental characters were analyzed for the four *Arcius* species and the specimens from Spain, England, and Normandy. The results of a parsimony analysis using TNT agree with previous conceptions of *A. zbyszewskii* as the most primitive member of the genus. Consistent with existing hypotheses, *Arcius rougieri* is positioned as the sister taxon of *A. fuscus* and *A. lapparenti*, and the results suggest that the fossil from Normandy is *A. zbyszewskii*. However, the English fossil pertains to a primitive lineage, rather than grouping with *A. lapparenti* as had been suggested; as such it is recognized here as a distinct species (*Arcius hookeri* new species). The Spanish fossils cluster together with the French species but do not show the previously proposed special relationship with *A. lapparenti* and are sufficiently distinct to be placed in a new species (*Arcius ilerdensis*). *Arcius* is recovered as monophyletic, which is consistent with a single migration event from North America to Europe around the earliest Eocene through the Greenland land bridge.

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Introduction

Paromomyidae Simpson, 1940 is a family of plesiadapiforms 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). Plesiadapiforms are herein considered stem primates (following Simpson, 1955; Van Valen and Sloan, 1965; Szalay, 1968, 1975a, 1975b; Gazin, 1971; Szalay et al., 1975, 1987; Bown and Rose, 1976; Radinsky, 1982; Rose and Bown, 1982; Silcox, 2001, 2007, 2008, 2017; Bloch and Boyer, 2002, 2007; Sargis, 2002; Bloch and Silcox, 2006; Bloch et al., 2007; Boyer and Bloch, 2008; Silcox et al., 2010, 2015, 2017; Silcox and López-Torres, 2017). We acknowledge that some authors consider plesiadapiforms to be more distantly related to primates, with some or all taxa sharing a closer relationship to dermopterans (e.g., Beard, 1989, 1990, 1991, 1993a, 1993b; Kay et al., 1990, 1992; Ni et al., 2013, 2016). The debate over the broader relationships of plesiadapiforms does not impact the current study as it deals with relationships internal to Paromomyidae. 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. The early age of this species, coupled with the fact that all of the most likely ancestors of paromomyids (i.e., members of the plesiadapiform families Purgatoriidae and Palaechthonidae) are also known from North America, is consistent with the hypothesis that this family had its origins on that continent. However, the paromomyids from Asia (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 two-phase model to account for mammalian dispersal patterns during the Paleocene-Eocene transition. The first (Phase 1) occurred during the latest Paleocene and brought to Europe euprimates, artiodactyls, and perissodactyls from Asia; rodents, pantodonts, oxyaenids, herpetotheriids, apatemyids, palaeanodonts, condylarths, neoplagiaulacids, viverravids, tillodonts from North America; and hyaenodontids from Africa. However, Beard et al. (2010) pointed out that direct migration

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between Asia and Europe would have been rather difficult because the Turgai Strait would have posed a significant marine barrier to terrestrial mammals. The second wave of immigrant 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* Matthew and Granger, 1921 and the mesonychid *Pachyaena* Cope 1874 and is thought to have included paromomyids (Hooker, 2015; but see the following).

European paromomyids were first reported from Pourcy, France (Paleocene-Eocene Mammal Zone [PE] III), by Louis and Michaux (1962) in a faunal list as an indeterminate species and genus of the 'Phenacolemuridae,' a family name now considered a junior synonym to Paromomyidae (Simpson, 1955). They were later ascribed to the North American paromomyid genus *Phenacolemur* Matthew, 1915 by Louis (1966), but no species level identification was given. Soon after, Russell et al. (1967) wrote the first comprehensive taxonomic study of European paromomyids in which they described two species from France: *Phenacolemur fuscus* from Mutigny, and *Phenacolemur lapparenti* from Avenay (PE V). Later, Godinot (1984) described a new species, *Arcius rougieri*, from Palette (PE II), France. In that paper, Godinot (1984) transferred the other two known species of European paromomyid into the newly named genus *Arcius*. Paromomyids have also been described from multiple early Eocene sites in France (Azillanet [Marandat, 1986], Condé-en-Brie [Louis, 1966; Aumont, 2003, 2004], Fordones [Marandat, 1991], Fournes [Marandat, 1991], Gland [Aumont, 2003], Grauves [Louis, 1970], Meudon [Russell et al., 1988, 1990], Prémontré [Dégremont et al., 1985], Rians [Godinot, 1981], Sézanne [Louis, 1970], Sotteville-sur-Mer [Smith et al., 2011], St. Agnan [Louis and Laurain, 1983], Venteuil [Aumont, 2003]), the United Kingdom (Abbey Wood [Hooker and Insole, 1980; Hooker, 1991, 1996, 1998]), Portugal (Silveirinha [Antunes, 1981; Estravís, 1992, 2000; Antunes et al., 1997]), and Spain (Masia de l'Hereuet [Marigó et al., 2012]). Godinot (1984) hypothesized that all paromomyids from Europe belong to a single genus, *Arcius*.

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 *Arcius fuscus* Russell et al., 1967 and *Arcius lapparenti* Russell et al., 1967 and that *Arcius* would be more closely related to *Ignacius* Matthew and Granger, 1921; Estravís (2000) advocated that *A. zbyszewskii* Estravís, 2000 was the most basal species of *Arcius*. The only cladistic analysis of the European paromomyids was included by Aumont (2003) in her unpublished dissertation, using 12 taxa and 35 dental characters. 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 hebeticus* Bloch et al., 2002.

This 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 data set that samples both characters and taxa more comprehensively than Aumont (2003), and (3) to discuss the biogeographic implications of the phylogenetic analysis.

Repositories and institutional abbreviations.—British Museum of Natural History (BMNH), London, UK; Institut Català de Paleontologia Miquel Crusafont (IPS), Sabadell, Spain; Muséum National d'Histoire Naturelle (Avenay collection, AV; Condé-en-Brie collection, CB; Mutigny collection, MU; Rians collection, RI), Paris, France; Royal Belgian Institute of Natural Sciences (Mammal collection, MAM), Brussels, Belgium; Universidade Nova de Lisboa (Silveirinha collection, SV), Lisbon, Portugal; Université de Montpellier (Fondones collection, FDN; Fournes collection, FRN; Palette collection, PAT), Montpellier, France; University of Alberta Laboratory of Vertebrate Paleontology (UALVP), Edmonton, Canada; University of California Museum of Paleontology (UCMP), Berkeley, USA; University of Michigan Museum of Paleontology (UM), Ann Arbor, USA; United States Geological Survey collection (USGS), Washington, USA; United States National Museum (USNM) Washington, USA; Yale Peabody Museum (Princeton University collection, YPM-PU), New Haven, USA.

Systematic paleontology

Order Primates Linnaeus, 1758
Superfamily Paromomyoidea (Simpson, 1940)
Family Paromomyidae Simpson, 1940
Arcius Godinot, 1984

1962	'Phenacolemuridae' gen. indet. Louis and Michaux, p. 171.
1966	*Phenacolemur* Louis, p. 51.
1967	*Phenacolemur*; Russell et al., p. 8, 12.
1970	*Phenacolemur*; Louis, p. 114.
1980	*Phenacolemur*; Hooker and Insole, p. 38.
1981	*Phenacolemur*; Antunes, p. 257.
1981	*Phenacolemur*; Antunes and Russell, p. 1101.
1981	*Phenacolemur*; Godinot, p. 77.
1983	*Phenacolemur*; Louis and Laurain, p. 9.
1984	*Arcius* Godinot, p. 85.
1985	*Phenacolemur*; Dégremont et al., p. 16.
1986	*Arcius*; Marandat, p. 88.
1988	*Arcius*; Russell et al., p. 432.
1991	*Arcius*; Marandat, p. 92.
1996	*Arcius*; Hooker, p. 209.
1998	*Arcius*; Hooker, p. 449.
2000	*Arcius*; Estravís, p. 283.
2003	*Arcius*; Aumont, pl. 1–24.
2004	*Arcius*; Aumont, fig. 3.
2010	*Arcius*; Hooker, p. 48.
2011	*Arcius*; Smith et al., fig. 19A, B.
2012	*Arcius*; Marigó et al., p. 430.

Type species.—*Arcius rougieri.*

Other species.—*A. fuscus*, *A. lapparenti*, *A. zbyszewskii*, *Arcius hookeri* n. sp., *Arcius ilerdensis* n. sp. (see descriptions below).

Emended diagnosis (modified from Godinot, 1984).—Presence of a molariform P^4 (i.e., metacone approaching the size of paracone, expanded distolingual basin), not observed in any other paromomyid. Upper molars with distolingual basins less expanded distally than in *Phenacolemur*. Incisor with a lingual and a buccal crest, in contrast to *Ignacius*. The computed two-dimensional (2-D) area (max length × width of the crown in occlusal view) of P_4 is similar to that of M_1, in contrast to *Ignacius*. Lower molar cusps relatively taller relative to the base of the crown than those of *Ignacius*. Lower molar trigonids not as mesially inclined relative to the level of the base of the talonid basin 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) that runs mesio-distally on the hypoconulid lobe.

Occurrence.—Neustrian (early Eocene) of France, United Kingdom, Portugal, and Spain; Grauvian (middle Eocene) of France.

Remarks.—Following the classification of fossils from Condé-en-Brie to the genus *Phenacolemur* by Louis (1966), Russell et al. (1967) subsequently described new fossils from Mutigny and Avenay and classified them under that genus based on their resemblance to some of the North American representatives known at that time, such as *Phenacolemur jepseni* Simpson, 1955; *Phenacolemur praecox* Matthew, 1915; and *Phenacolemur citatus* Matthew, 1915. Russell et al. (1967) referred to the development of the hypoconulid in M_3 in the European forms as reminiscent of that in *Phenacolemur citatus* and *Phenacolemur jepseni*, and the lack of ectocingulum in upper molars as similar to *Phenacolemur jepseni*. However, Russell et al. (1967) also mentioned that the P_4 in the European specimens is smaller in size than the M_1, a trait that is characteristic of *Ignacius* rather than *Phenacolemur*.

Following this line of reasoning, Godinot (1984), in his paper naming the genus *Arcius*, suggested that it was closely related to *Ignacius* instead, specifically to *Ignacius graybullianus* Bown and Rose, 1976 from the early Eocene of Wyoming. One of the characters that Godinot (1984) highlighted as diagnostic of the genus was that the mandible (or, more appropriately, the alveolar ridge) reaches its highest point in the area of P_4 and M_1 alveoli, but at that time, the only mandible known was that of *Arcius rougieri* (Fig. 1). Still today, *Arcius* gnathic fossils 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, pl. 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 (Aumont, 2003, appendix G, pl. 3, fig. 4), and a mandible with M_{2-3} from Abbey Wood. The only lower jaw specimen known to exhibit the character described by Godinot (1984) is PAT2 (Fig. 1; *Arcius rougieri*), and it is not present in other species (Aumont, 2003, appendix G, pl. 3, figs. 3 and 4). Therefore, this character is an autapomorphy of *A. rougieri*, and
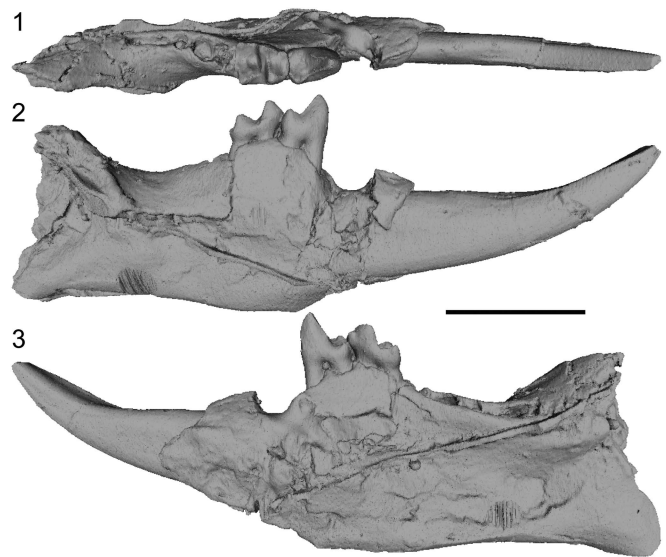

Figure 1. Micro-CT scan images of a cast of the mandible of *Arcius rougieri* Godinot, 1984 (PAT2) (**1**) in occlusal, (**2**) buccal, and (**3**) lingual views. Note that the strong line cutting through the mandible is a feature of the cast, not on the original specimen. Scale bar = 0.5 cm.

should not be considered diagnostic of the genus, but rather solely diagnostic of *A. rougieri* (see the following).

Later, Robinson and Ivy (1994) suggested that *Arcius* was not monophyletic and classified this genus in the subfamily 'Phenacolemurinae.' According to Robinson and Ivy (1994), this subfamily contained the genera *Phenacolemur*, *Ignacius*, and *Elwynella* Rose and Bown, 1982, along with their proposed genera 'Simpsonlemur,' 'Pulverflumen,' and 'Dillerlemur,' whose validity has been a source of debate (Silcox and Gunnell, 2008). By contrast, Aumont (2003) recovered a monophyletic *Arcius* in her cladistic analysis, with the North American *Acidomomys* Bloch et al., 2002 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 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 (Fig. 2.6–2.9). Divided lobes, as observed in *Phenacolemur*, *Ignacius*, *Edworthia* Fox et al., 2010, some species of *Paromomys* Gidley, 1923, and to a lesser extent, *Acidomomys*, exhibit an invagination of the occlusal surface that runs mesiodistally through the center of the lobe (Fig. 2.1–2.5). 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 (Figs. 3.13, 3.17, 4.1). 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 in other paromomyids, such as *Phenacolemur*
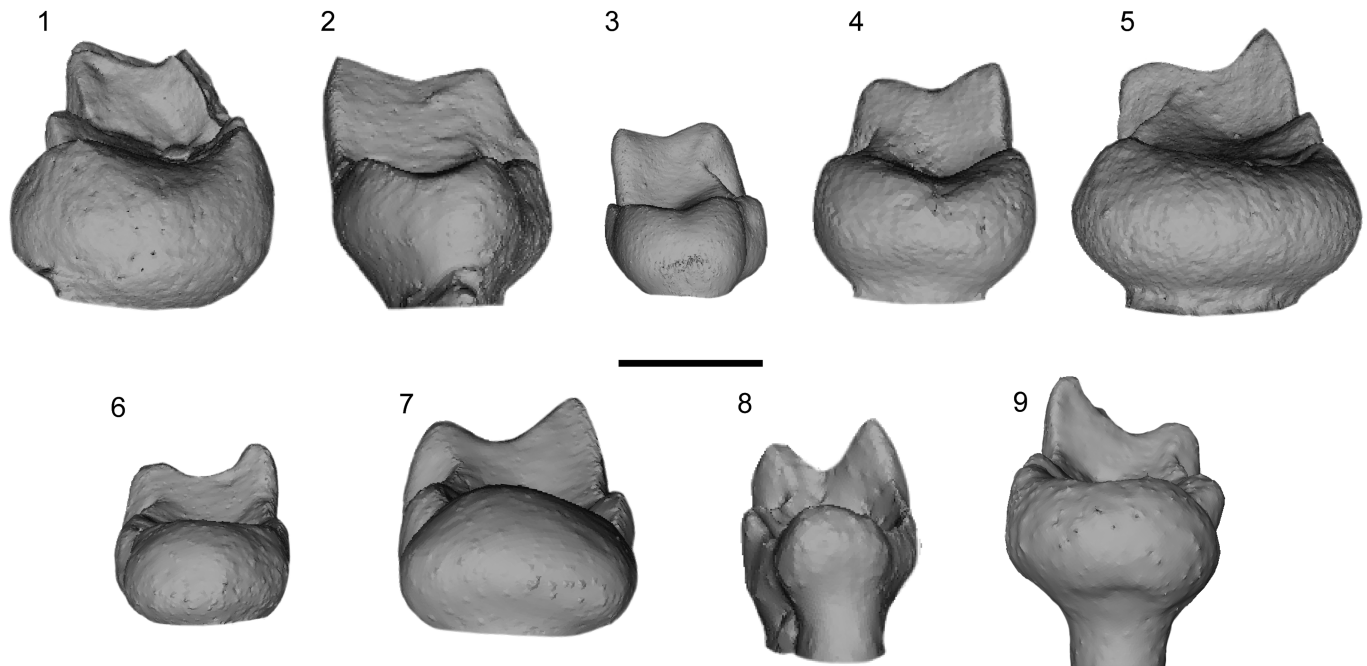
Figure 2. Distal view of micro-CT scan images of the M_3 of various species of North American and European paromomyids. (**1**) *Phenacolemur citatus* Matthew, 1915, USGS 21712, right; (**2**) *Paromomys depressidens* Gidley, 1923, USNM 9677; (**3**) *Edworthia lerbekmoi* Fox et al., 2010, UALVP 50990, right; (**4**) *Ignacius frugivorus* Matthew and Granger, 1921, YPM-PU 20690, left; (**5**) *Acidomomys hebeticus* Bloch et al., 2002, UM 108206, left; (**6**) *Arcius fuscus* Russell et al., 1967, MU 6507, left; (**7**) *Arcius lapparenti* Russell et al., 1967, AV 5849, left; (**8**) *Arcius zbyszewskii* Estravís, 2000, SV3-47, left; (**9**) *Arcius hookeri* n. sp., BMNH.M 44945, right. The paromomyids on the top row (**1–5**) have an invagination at the top central area of the hypoconulid lobe; all *Arcius* species (**6–9**) lack this feature. Scale bar = 1 mm.

(Rose, 1981; Silcox et al., 2008) and *Acidomomys* (Bloch et al., 2002). This might suggest that *Arcius* underwent a process of retention of a deciduous P^4. *Arcius rougieri* shows a possible retention of the deciduous upper central incisor (see the following).

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 1 for estimated body masses for all the species in the genus.

Arcius rougieri Godinot, 1984
Figures 1, 5

1981   *Arcius* cf. *A. fuscus* Godinot, 1981, p. 77.
1984   *Arcius rougieri* Godinot, 1984, p. 85.
1991   ?*Arcius rougieri*; Marandat, 1991, p. 92.
2003   *Arcius rougieri*; Aumont, 2003, pl. 3, fig. 5, pl. 6, fig, 5, 6. Pl. 18, fig. 1, pl. 19, 23.

Holotype.—PAT1, partial maxilla with right I^1–C and left I^1–M^1.

Emended diagnosis (modified from Godinot, 1984).—Smaller M_2 than *Arcius lapparenti*, *A. hookeri* n. sp., and *A. ilerdensis* n. sp., but larger M_1 than *A. zbyszewskii*. Further differs from *A. fuscus* and *A. lapparenti* in having a more apically extended (taller) anterocone than mediocone on I^1, with a significantly smaller posterocone, and laterocone proximally shifted relative to the anterocone. Further differs from all other species of *Arcius* in having a more buccally extended parastylar region on M^1 and a stepped postvallid on M_1 and M_2. Further differs from *A. fuscus* in having a more distally expanded distolingual basin

on M^3. Further differs from *A. fuscus* in having two crests, instead of three, on the P_4 postvallid. Paraconid of M_1 is smaller than in *A. fuscus* and *A. lapparenti* but larger than in *A. zbyszewskii*. Mesial inflection of M_1 and M_2 trigonids weaker than in *A. ilerdensis* n. sp. but stronger than in the other known species of *Arcius*. Further differs from *A. zbyszewskii* and *A. ilerdensis* n. sp. in having a cingulid on the buccal half of the distal aspect of M_1 that runs up to the hypoconulid. Highest point of the alveolar ridge between P_4 and M_1; this has not been observed in any other species of *Arcius*.

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

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, 2015), 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.
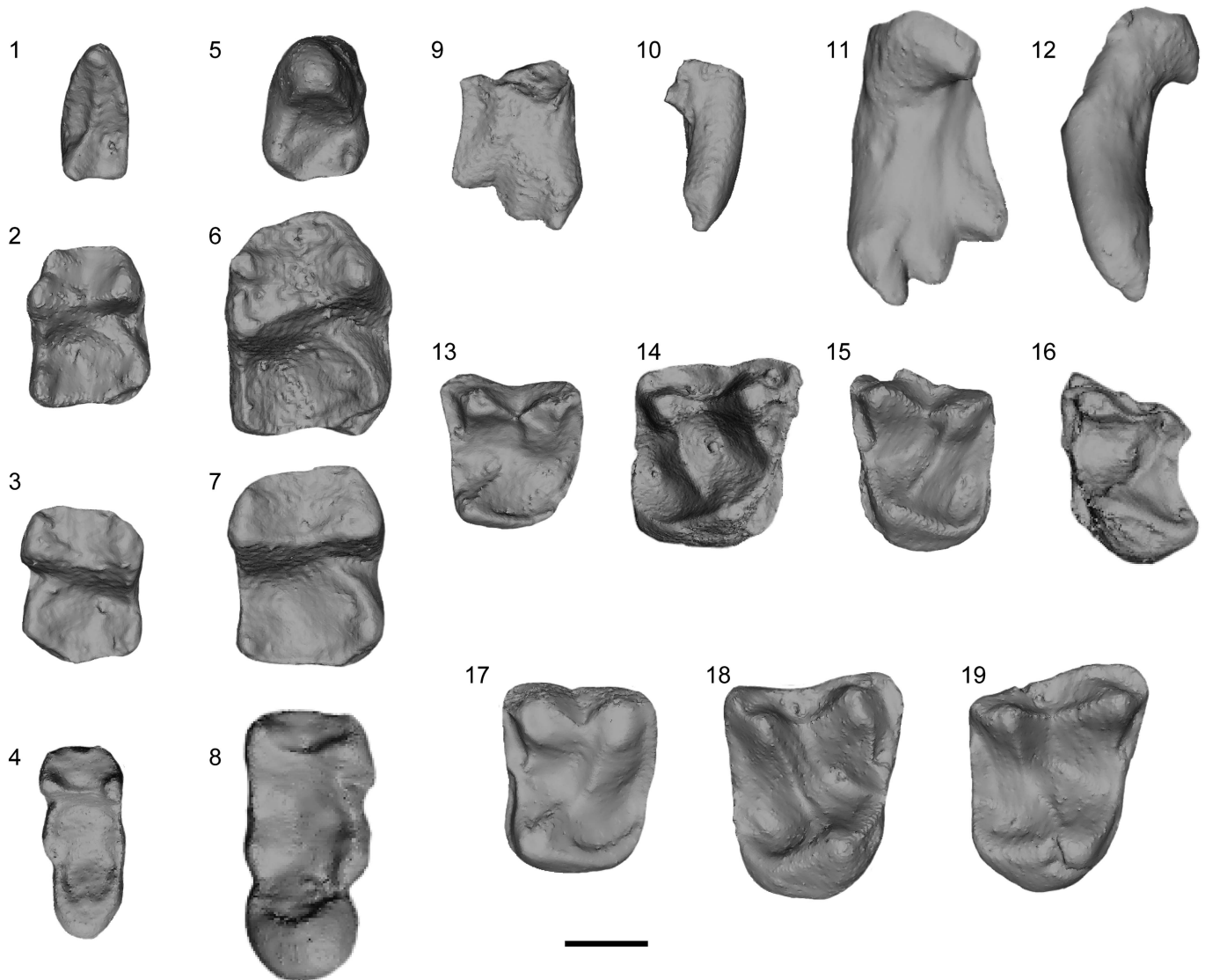
Figure 3. Micro-CT scan images; (**1–4, 9, 10, 13–16**) *Arcius fuscus* Russell et al., 1967; (**5–8, 11, 12, 17–19**) *Arcius lapparenti* Russell et al., 1967. (**1**) CB 2560, left P_4, occlusal view; (**2**) MU 6458, right M_1, occlusal view; (**3**) AV 422-L, left M_2, occlusal view; (**4**) MU 6507, holotype, left M_3, occlusal view; (**5**) CB 4162, left P_4, occlusal view; (**6**) AV 7716, right M_1, occlusal view; (**7**) AV 7707, right M_2, occlusal view; (**8**) AV 5849, left M_3, holotype, occlusal view; (**9, 10**) AV 6838, left I^1, (**9**) lingual view, (**10**) mesial view; (**11, 12**) AV 7714, right I^1, (**11**) lingual view, (**12**) mesial view; (**13**) CB 1914-L, left P^4, occlusal view; (**14**) UCMP 71976, left M^1, occlusal view; (**15**) AV 610-BN, left M^2, occlusal view; (**16**) UCMP 71982, left M^3, occlusal view; (**17**) CB 232-BN, left P^4, occlusal view; (**18**) AV 1306-Ph, right M^1, occlusal view; (**19**) AV 1092-BN, right M^2, occlusal view. Scale bar = 1 mm.

Materials.—PAT2, mandible with right I_1–M_1; PAT3, left M^3; PAT5, right M_2.

Remarks.—In this paper, all diagnoses for the six species of *Arcius* include diagnostic features of the referred material along with the holotype. The reason behind this decision is that the holotypes for *A. fuscus* and *A. lapparenti* are M_3 specimens (Russell et al., 1967), and this tooth position is probably the most variable in paromomyids, in particular with respect to the relative proportions of the hypoconulid lobe with the rest of the tooth. This would make the diagnosis for these species solely based on M_3 morphology very limited and not very diagnostic.

The holotype of *Arcius rougieri*, along with PAT1 bis and PAT2, represent the first described gnathic fossils with associated teeth in a European paromomyid. The I^1 of

A. rougieri differs greatly from those of *A. fuscus* and *A. lapparenti* (Rose et al., 1993) and is more similar to the deciduous I^1 of *A. fuscus* and *A. lapparenti* (Fig. 6) in that the anterocone is the tallest cusp rather than the mediocone (tallest in adult specimens attributed to *A. fuscus* and *A. lapparenti*). In addition, 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^1s. PAT1 is inferred to pertain to an adult because all of its
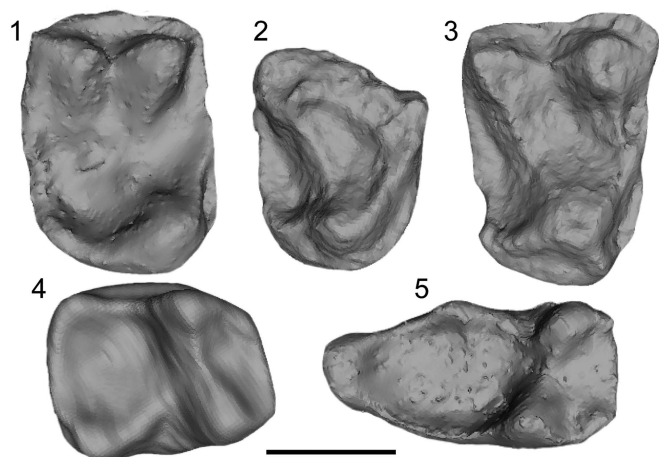
Figure 4. Micro-CT scan images of *Arcius zbyszewskii* Estravís, 2000. (**1**) SV2-99, right P^4, occlusal view; (**2**) SV3-125, right M^1 fragment, occlusal view; (**3**) SV1-29, right M^2, holotype, occlusal view; (**4**) SV3-317, right M_1, occlusal view; (**5**) SV3-47, left M_3, occlusal view. Scale bar = 1 mm.

Table 1. Estimated average body masses of all species of *Arcius* Godinot, 1984 based on data from Aumont (2003) and the current study (for *A. hookeri* n. sp. and *A. ilerdensis* n. sp.). The regression equation used for Conroy's (1987) estimates was the one based on the prosimian sample.

	Gingerich and colleagues' (1982) equations				Conroy's (1987) equation (M_1)
	M_1	M_2	M^1	M^2	
A. rougeri	164 g	201 g	143 g	—	78 g
A. fuscus	194 g	205 g	119 g	119 g	93 g
A. lapparenti	313 g	327 g	264 g	264 g	156 g
A. zbyszewskii	130 g	—	—	116 g	60 g
A. hookeri	—	284 g	—	—	—
A. ilerdensis	—	247 g	—	316 g	—

adult teeth have erupted. The second upper incisor and the fourth 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 that I^1 would 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 (López-Torres et al., 2015, table 1). Therefore, it seems that the upper central incisors of *A. rougieri* were retained. Interestingly, as noted, the genus *Arcius* also 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. *P. 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 downward, and a greater mesiodistal length of the whole tooth. Godinot (1981) admits that 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 on RI225 is weak, which contrasts with the fairly strong paraconids on the M_1 of *A. fuscus* and *A. lapparenti*. The only *Arcius* species with poorly
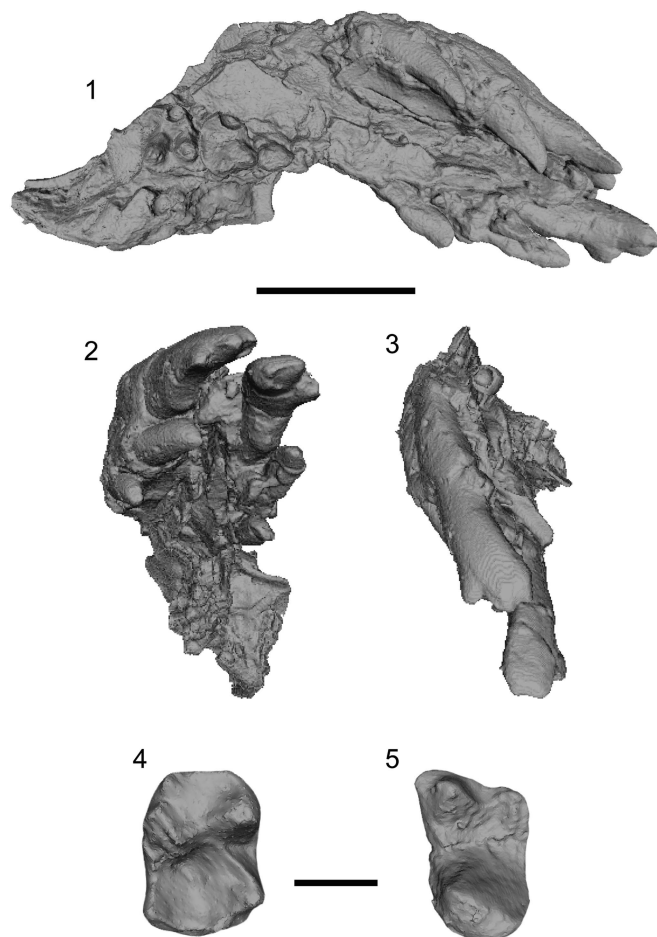

Figure 5. Micro-CT scan images of *Arcius rougieri* Godinot, 1984. Maxilla (PAT1, holotype) in (**1**) occlusal, (**2**) oblique occlusal, (**3**) oblique frontal views; (4) PAT5, right M_2, occlusal view; (**5**) PAT3, left M^3, occlusal view. (**1–3**) Scale bar = 0.5 cm; (**4, 5**) scale bar = 1 mm.
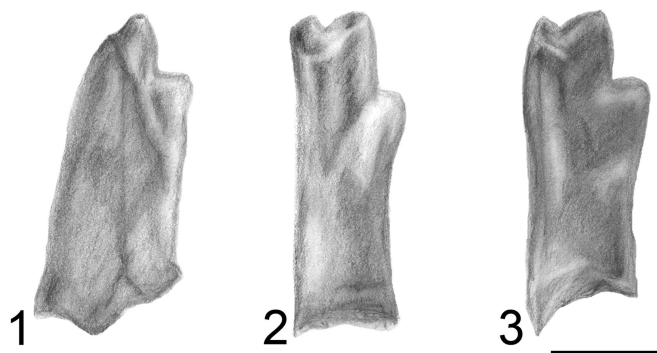

Figure 6. Drawing of a decidious upper central incisor of *Arcius lapparenti* Russell et al., 1967 (GR10029) in (**1**) medial view, (**2**) lingual view, (**3**) oblique (mediolingual) view. Original photograph in Aumont (2003, appendix G, pl. 9, fig. 8). Scale bar = 1 mm. Drawing by V. Bodo.

expressed paraconids on M_1 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* fossils found in the locality of Fordones. The Fordones fossils include the only known M_3 for this species (FDN28). This specimen is

missing the hypoconulid lobe, which is particularly relevant in determining which species of *Arcius* it belongs to. Aumont (2003) suggested that the only way to know the correct ascription of FDN28 is to find an M_3 from the type locality for *A. rougieri* (Palette), but the size, the metric proportions, and the fact that other *A. rougieri* fossils have been found in Fordones support the inference that FDN28 is the first M_3 known of *A. rougieri* (Marandat, 1991; Aumont, 2003).

Arcius fuscus Russell, Louis, and Savage, 1967
Figures 2.6, 3.1–3.4, 3.9, 3.10, 3.13–3.16, 7.2, 7.5

1962   'Phenacolemuridae' gen. indet. sp. indet. Louis and Michaux, p. 171.

1966   *Phenacolemur* sp. Louis, p. 51.

1967   *Phenacolemur fuscus* (in part) Russell et al., figs. 2a–j, l, 3d, g.

1981   *Phenacolemur* cf. *P. fuscus* Godinot, p. 77.

1984   *Arcius fuscus* Godinot, fig. 2b.

1991   *Phenacolemur* cf. *P. fuscus* Marandat, p. 92.

2003   *Arcius fuscus*; Aumont, pl. 1, figs. 3, 4, 8, pl. 2, figs. 9–12, pl. 4, figs. 4, 5, pl. 5, figs. 5, 6, 10, pl. 7, figs. 8–15, pl. 8, figs. 3, 8, 9, 13, 14, pl. 10, figs. 6–8, pl. 11, fig. 2, pl. 12, figs. 4, 6, pl. 13, figs. 3–5, 10, pl. 14, fig. 3.

2004   *Arcius fuscus*; Aumont, fig. 3.5–3.9, 3.14–3.16.

Holotype.—MU 6507, left M_3.

Emended diagnosis (modified from Russell et al., 1967 and Aumont, 2003).—Smaller M_2 than those of *Arcius lapparenti*, *A. hookeri* n. sp., and *A. ilerdensis* n. sp. but larger M_1 than those of *A. rougieri* and *A. zbyszewskii*. Further differs from *A. rougieri* in having a more apically extended (taller) mediocone than anterocone on I^1, no expansion of the parastylar area of M^3, presence of 'prehypoflexid cristid' on the P_4, a concave mesial border of P_4 in lateral view, stronger mesial inflection of molar trigonids, and lacking a stepped postvallid on M_1. Further differs from *A. zbyszewskii* and *A. ilerdensis* n. sp. in having a cingulid on the buccal half of the distal aspect of M_1 that runs up to the hypoconulid. Further differs from *A. zbyszewskii* in not having a paraconid on M_3.

Occurrence.—Mutigny (type locality, PE IV; Marandat et al., 2012), Marne, France; Fournes (PE II; Marandat et al., 2012), Hérault, France; 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.

Materials.—AV 422-L, left M_2; AV 610-BN, left M^2; AV 6838, left I^1; CB 1914-L, left P^4; CB 2560, left P_4; MU 6458, right M_1; UCMP 71976, left M^1; UCMP 71982, left M^3.

Remarks.—*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 P_4 specimens (MU5627 and MU6294) found at Mutigny to belong to *A. lapparenti*, which is significant since P_4 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 P_4 sizes and morphs.

Russell et al. (1967) did not choose a P_4 as the holotype for *Arcius fuscus* but instead selected an M_3. They used differences in the inclination of the M_3 postvallid, and in the degree of lateral projection of the entoconid, to differentiate *A. fuscus* from *A. lapparenti*. However, 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 M_3 hypoconulid is diagnostic for the genus as a whole, 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.

There are two genera of paromomyids that have three distinct crests on the postvallid of the P_4 of some species: *Arcius* and *Paromomys*. These crests are interpreted here as a metacristid (this term used in preference to premetacristid or postmetacristid because of 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 distinguished 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; and (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* (Fig. 7). Only two crests are visible on the postvallid in all other known paromomyid species.

Arcius lapparenti Russell, Louis, and Savage, 1967
Figures 2.7, 3.5–3.8, 3.11, 3.12, 3.17–3.19, 6, 7.3, 7.6

1967   *Phenacolemur lapparenti* (in part) Russell et al., figs. 2k, 3a–c, e, f.

1984   *Arcius lapparenti* Godinot, fig. 2c–f.

2003   *Arcius lapparenti*; Aumont, pl. 1, figs. 1, 2, 5–7, pl. 2, figs. 1–8, pl. 3, figs. 1–3, pl. 4, figs. 1–3, 6–8, pl. 5, figs. 1, 2, 7–9, pl. 6, figs. 1–4, pl. 7, figs. 1–7, pl. 8, figs. 1, 2, pl. 9, pl. 10, figs. 1–5, pl. 11, figs. 1, 9, pl. 12, figs. 1–3, 5, 7–12, pl. 13, figs. 1, 2, 6–9, 11–13, pl. 14, figs. 1, 2, 4–8, pl. 15, figs. 1, 2, pl. 16, 17, pl. 18, figs. 3, 4.

2004   *Arcius lapparenti*; Aumont, fig. 3.1–3.4, 3.10–3.13.

Holotype.—AV 5849, left M_3.
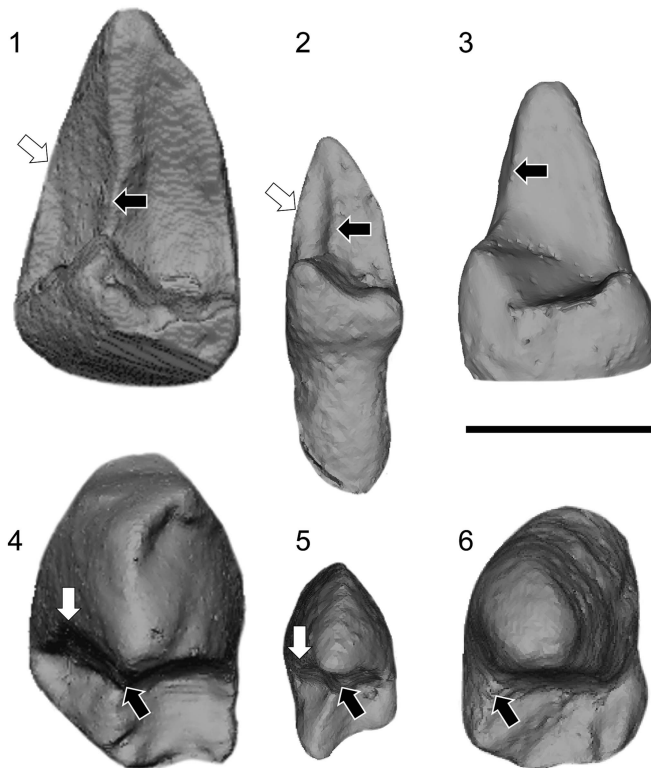
Figure 7. Micro-CT scan images of three paromomyid P_4s. (**1, 2, 4, 5**) The 'prehypoflexid cristid' (white arrow) as seen on the P_4 of (**1, 4**) *Paromomys maturus* Gidley, 1923 and (**2, 5**) *Arcius fuscus* Russell et al., 1967. (**3, 6**) *Arcius lapparenti* Russell et al., 1967 is shown as an 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 *Paromomys maturus* and that of *A. fuscus* is that in (**4**) *Paromomys maturus* it is located more mesially, contrary to (**5**) *A. fuscus*, in which the three cristids are in the same plane on the postvallid. Scale bar = 1 mm.

Emended diagnosis (modified from Russell et al., 1967 and Aumont, 2003).—Largest species of *Arcius*. Further differs from *A. rougieri* in having a more apically extended (taller) mediocone than anterocone on I^1, no expansion of the parastylar area of M^3, and stronger mesial inflection of molar trigonids and lacking a stepped postvallid on M_1. Further differs from *A. fuscus* in lacking a 'prehypoflexid cristid.' Well-developed paraconid on M_1, but proportionally smaller relative to the metaconid than in *A. fuscus*. Further differs from *A. zbyszewskii* and *A. ilerdensis* n. sp. in having a cingulid on the buccal half of the distal aspect of M_1 that runs up to the hypoconulid. Further differs from *A. zbyszewskii* in not having a paraconid on M_3.

Occurrence.—Avenay (type locality, PE V; 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; Aumont, 2003), Marne, France; St. Agnan (MP10; Hooker, 1996), Aisne, France; Prémontré (MP10 [48.4 mya]; Franzen, 2005), Aisne, France.

Materials.—AV 1092-BN, right M^2; CB 232-BN, left P^4; AV 7707, right M_2; AV 7714, right I^1; AV 7716, right M_1; CB 3583, right M^3; CB 4162, left P_4; CBX 2-Ph, I_1; AV 1306-Ph, right M^1.

Remarks.—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 at Mutigny, *A. lapparenti* was argued by the same authors to have been present 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 mixed. In addition, 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 M^1 of *A. lapparenti*, is interpreted here to be a P^4 based on its poorly developed postprotocrista, a feature of P^4 in other species of *Arcius*. These two teeth can be distinguished mainly by the lack of a postprotocrista and by the slightly convex mesial aspect of the tooth on P^4. Whereas relative size of the metacone to the paracone is often used to discriminate between M^1 and P^4 in primate species, the paracone of the P^4 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.

Arcius zbyszewskii Estravís, 2000
Figures 2.8, 4

1981 *Phenacolemur* sp. Antunes, p. 257.
1981 *Phenacolemur* cf. *P. fuscus* Antunes and Russell, p. 1101.
2000 *Arcius zbyszewskii* Estravís, p. 283.
2003 *Arcius zbyszewskii*; Aumont, pl. 24.
2011 *Arcius* sp.; Smith et al., fig. 19A, B.

Holotype.—SV1-29, right M^2.

Emended diagnosis (modified from Estravís, 2000).—Smallest species of *Arcius*, approaching the size of *A. rougieri*. Distolingual basin of M^3 somewhat expanded distally, more than in *A. rougieri* but less than in *A. fuscus*. Small but patent paraconid on M_1, stronger paraconid on M_3 than in other species of *Arcius*. 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*.

Horizon and locality.—~~.~~Silveirinha (type locality, PE II; see Biostratigraphy), Baixo Mondego, Portugal; Sotteville-sur-Mer (PE II; Hooker, 2015), Normandy, France.

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 also to be 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.

Material.—SV2-99, right P^4; SV3-47, left M_3; SV3-125, right M_1; SV3-317, right M^1; SV3-565, right M^3.

Remarks.—Antunes (1981) first reported the presence of paromomyids in Portugal by including *Phenacolemur* in his faunal list of Silveirinha. It was not until Estravís's work (1992, 2000) that the Portuguese fossils were 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 fossils differs from Estravís (2000) in that SV1-24 is interpreted as an M_1, instead of an M_2. We argue that the paraconid on SV1-24 is no smaller than that of the other M_1 (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 M_2 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 M^1. The authors acknowledged the similarities of this tooth to the Portuguese fossils 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 P^4 rather than an M^1. *Arcius zbyszewskii* is the only species of the genus in which the P^4 has a very weak postprotocrista instead of it being completely absent. This trait, paired with the similarity in the small size of the specimen from Sotteville-sur-Mer compared to the collection from Silverinha, supports 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.

<div align="center">

Arcius hookeri new species
Figures 2.9, 8

</div>

1980 *Phenacolemur* cf. *P. fuscus* Hooker and Insole, p. 38.
1996 *Arcius fuscus* Hooker, p. 209.
1998 *Arcius fuscus* Hooker, p. 449.
2003 *Arcius lapparenti* (in part) Aumont, appendix A, tables 3, 4.
2010 *Arcius lapparenti* Hooker, p. 48.

Holotype.—BMNH.M 44945, right dentary with M_2–M_3.

Diagnosis.—Buccal cingulids present on M_2, but weaker than those found in *A. fuscus* and *A. lapparenti* and not extended onto the talonid. 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. ilerdensis* n. sp. Differs from all other species of *Arcius*, except for *A. ilerdensis* n. sp., in having a taller
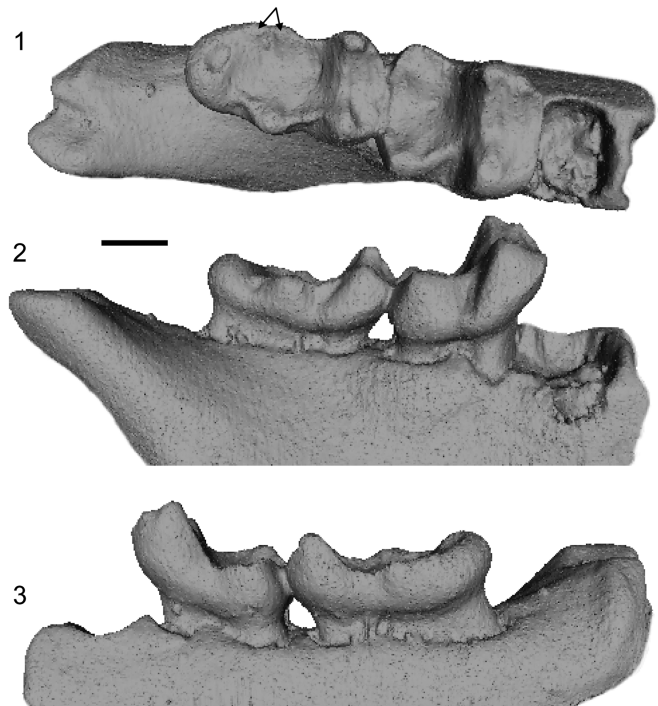

Figure 8. Micro-CT scan images of the holotype of *Arcius hookeri* n. sp. (BMNH.M 44945) in (**1**) occlusal, (**2**) buccal, (**3**) lingual views. Arrows indicate the presence of a double entoconid. Scale bar = 1 mm.

metaconid than the protoconid on M_2 and M_3. Differs from *A. zbyszewskii* in not having a paraconid on M_3. Double entoconid present on M_3, unlike all other species of *Arcius*.

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

Biostratigraphy.—Abbey Wood is a reference locality for PE III using mammalian biostratigraphy (Hooker, 1996).

Description.—BMNH.M 44945 is the only specimen known of this species. It is composed of a partial dentary with an associated M_2 and M_3 in place. The complete distal alveolus of M_1 is preserved, as well as the distal aspect of the mesial alveolus of M_1. The mandibular ramus is partially preserved, and it retains the anterior edge of the masseteric fossa (Hooker, 2010). *Arcius hookeri* n. sp. shows typical paromomyid characteristics such as reduced paraconids, a protoconid-metaconid notch that is obscured by a fold of enamel, and an expanded hypoconulid on M_3 that forms an additional lobe (Silcox and Gunnell, 2008). It shares with other *Arcius* species features such as taller cusps than in *Ignacius*, trigonids not as inclined as in other paromomyid genera, and the presence of a simple rounded hypoconulid lobe on M_3 (instead of the bilobed hypoconulid lobe seen in other paromomyids; Fig. 2).

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.

Remarks.—The record of paromomyids from England is very limited, with BMNH.M 44945 being the only specimen of a

paromomyid to have ever been found in northwestern Europe. Hooker and Insole (1980) tentatively reported BMNH.M 44945 as pertaining to *Phenacolemur* cf. *P. fuscus*, making this specimen the first known representative of *Arcius* outside continental Europe. Since then, the specific classification of this specimen has been problematic; it 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 M_3 that falls within the size range of *A. fuscus* for that tooth. He also noted that the M_2, although not strictly falling within the size range for that tooth reported by Aumont (2003, 2004), is closer in size to that of *A. lapparenti* than to that of *A. fuscus*. This suggests differences in terms of the relative proportions of these two teeth, but there are no specimens known for either *A. lapparenti* or *A. fuscus* in which the M_2 and M_3 are preserved in series to assess this possibility. Hooker (2010) also pointed out the presence of two entoconids on the M_3, 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. See also Table 2 for diagnostic comparisons.

Arcius ilerdensis new species
Figure 9

2012   *Arcius* sp. Marigó et al.

Holotype.—IPS 57510, right M_2.

Diagnosis.—Larger M_2 than *A. rougieri*, larger M^2 than *A. zbyszewskii*, similar areas of M_2 to *A. hookeri* n. sp., and smaller M_2 than *A. lapparenti*. Absence of distal cingulid on M_2, unlike *A. fuscus*, *A. lapparenti*, and *A. rougieri*. Differs from all other species of *Arcius* in lacking a buccal cingulid on M_2 and having a short buccal cingulid on the M_3 trigonid. Paraconid present on M_2, but weakly expressed. Mesial inflection of the trigonid on M_2 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 M_2 and M_3. Further differs from *A. zbyszewskii* in not having a paraconid on M_3.

Horizon and locality.—Masia de l'Hereuet (MP10?), Lleida, Spain.

Biostratigraphy.—Marigó et al. (2012) described this site as MP8 + 9, but most genera found in Masia de l'Hereuet usually appear in younger deposits (e.g., *Eogliravus*, MP10-13 [Escarguel, 1999]; *Lophiodon*, MP 10 and later [Cuesta, 1994], although it is present but rare in MP8 + 9 [Checa, 1997]).

Description.—*Arcius ilerdensis* n. sp. is represented only by four isolated teeth: two left M^2 (one of which is damaged; IPS57509), a right M_2, a right M_3. It shares with other *Arcius* species features such as taller cusps than in *Ignacius*, trigonids not as inclined as in other paromomyid genera, and the presence of a simple, rounded hypoconulid lobe on M_3 (instead of the bilobed hypoconulid lobe seen in other paromomyids; Fig. 2). The M^2 (IPS57508) has a strong postparacrista and premetacrista, with deep basins. A very small paraconule and metaconule are present, typical of paromomyids (Silcox and Gunnell, 2008). The distal margin of the tooth is straight, with a distolingual basin that is fairly expanded, but less so than in *Phenacolemur*, a typical *Arcius* trait. The buccal cingulum is broad. The parastylar region is expanded, forming a parastyle, but no metastyle is present. A precingulum is present, but short (Marigó et al., 2012). The M_2 (IPS57510) exhibits a trigonid and talonid of similar width and a concave postvallid on the trigonid. The protoconid is lower than the metaconid, and the paraconid is reduced, as is typical of paromomyids (Silcox and Gunnell, 2008). On the talonid, the hypoconulid and the entoconid are poorly distinguishable (Marigó et al., 2012). The M_3 (IPS57511) has a more buccally positioned cristid obliqua than on the M_2, with more clearly demarcated entoconid and hypoconid (Marigó et al., 2012). It lacks a paraconid and has a very broad hypoconulid lobe, which are typical features of paromomyids (Silcox and Gunnell, 2008).

Table 2. Diagnostic characters for *Arcius* Godinot, 1984 species. Question marks indicate nonobservable characters.

|	*A. rougieri*	*A. fuscus*	*A. lapparenti*	*A. zbyszewskii*	*A. hookeri*	*A. ilerdensis*
Highest cusp on I^1	Anterocone	Mediocone	Mediocone	?	?	?
Parastylar region on M^1	Expanded buccally	Not expanded	Not expanded	?	?	?
Parastylar region on M^3	Expanded buccally	Not expanded	Not expanded	?	?	?
Distolingual basin on M^3	Not expanded	Expanded	Somewhat expanded	Somewhat expanded	?	?
Number of crests on the P_4 postvallid	2	3	2	?	?	?
Mesial border of the P_4 protoconid	Slightly concave	Concave	Mostly straight	?	?	?
Size of M_1 paraconid	Medium	Large	Large	Small	?	?
Stepped postvallid on M_1	Present	Absent	Absent	Absent	?	?
Cingulid on the buccodistal aspect of M_{1-2}	Present	Present	Present	Absent	Absent	Absent
Metaconid/protoconid on M_2	?	Protoconid taller than metaconid	Protoconid taller than metaconid	?	Metaconid taller than protoconid	Metaconid taller than protoconid
Paraconid on M_3	?	Absent	Absent	Present	Absent	Absent
Entoconid on M_3	?	Simple	Simple	Simple	Double	Simple
Mesial inflection of lower molars	Weak	Somewhat weak	Somewhat weak	Somewhat weak	Somewhat weak	Very weak
Highest point of the alveolar ridge	Between P_4 and M_1	?	Flat	?	Flat	?
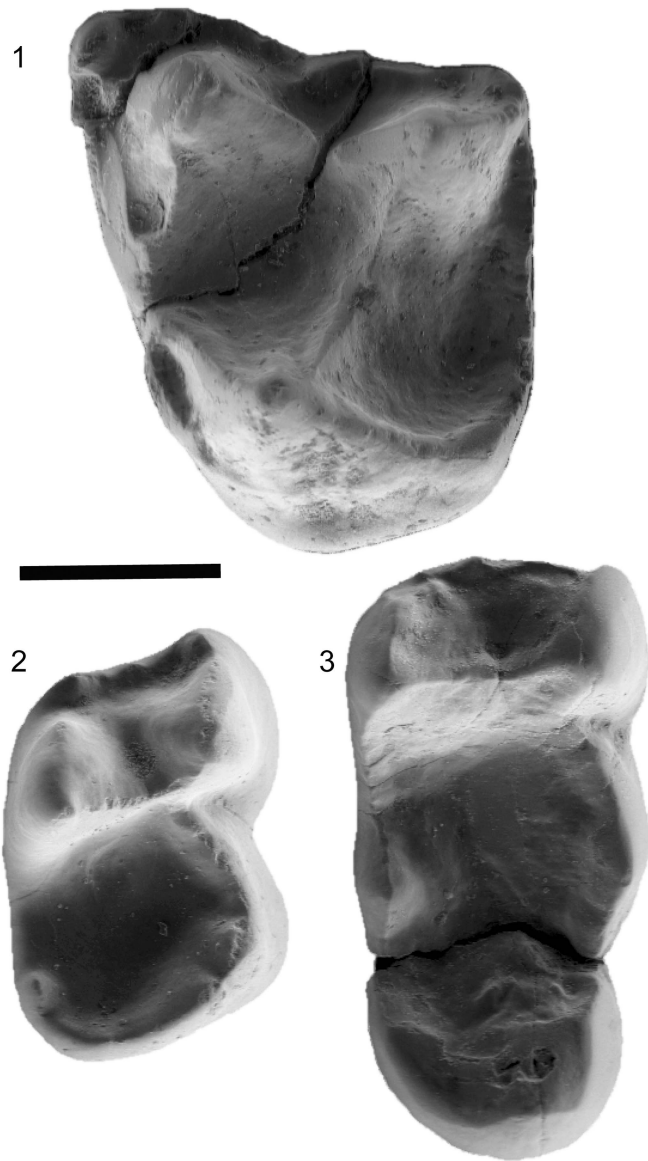
Figure 9. Micro-CT scan images of *Arcius ilerdensis* n. sp. (**1**) IPS 57508, left M^2, occlusal view; (**2**) IPS 57510, lower right M$_2$, holotype, occlusal view; (**3**) IPS 57511, right M$_3$, occlusal view. Scale bar = 1 mm..

Etymology.—From the Latin *Ilerda* (ancient name of the city of Lleida), in allusion to its province of origin.

Materials.—IPS 57508, left M^2; IPS 57511, right M$_3$.

Remarks.—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 it would be beneficial for more fossils to be recovered from that site, the few fossils known show enough distinctive 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 contrasts 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.

Phylogenetic relationships of *Arcius*

To assess the phylogenetic relationships among the different species of *Arcius*, and the position of the genus among Paromomyidae, we conducted a cladistic analysis. A character list was created to assess specifically 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). Some of the characters that relate to higher-level relationships among plesiadapiforms were taken from Silcox's (2001) matrix for plesiadapiforms. The primitive purgatoriid *Purgatorius coracis* Fox and Scott, 2011 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* Fox et al., 2010, *Phenacolemur archus* Secord, 2008, *Acidomomys hebeticus*, and *Ignacius fremontensis* Gazin, 1971. The genus *Elwynella*, which includes only the species *Elwynella oreas* Rose and Bown, 1982, 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 P$_3$, 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. A total of 53 dental characters were scored for 13 taxa (Table 3; matrix available on publication from the Dryad Digital Repository; see also Supplemental Data 2).

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 1,000 repetitions, with 1,000 trees saved per replication. Five 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; (4) an analysis that included the *Arcius* from Masia de l'Hereuet; and (5) an analysis that included all European paromomyid taxa. 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. Analysis 5 is also meant to give a general understanding of the relationships of the genus but including all taxa (both well and poorly sampled). Analyses 1, 2, and 3 yielded only one unequivocal tree each (Fig. 10.1–10.3). Analysis 4 yielded 6 equally parsimonious trees. A strict consensus tree was generated in TNT from these trees (Fig. 10.4). Analysis 5 also yielded 6 equally parsimonious trees, and a strict consensus tree was generated in TNT (Fig. 11).

Table 3. Descriptions of dental characters.

	Upper incisors	
1	Presence of posterocone on I^1 (ordered)	0: Absent; 1: Present
2	Relative height anterocone/mediocone on I^1	0: Anterocone taller than mediocone; 1: Mediocone taller than anterocone
	Upper premolars	
3	Presence of P^2	0: Absent; 1: Present
4	Presence of metacone on P^4	0: Absent; 1: Present
5	Presence of a molariform P^4	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
6	Presence of precingulum on P^4	0: Absent; 1: Present
7	Presence of parastyle on P^4	0: Absent; 1: Present
8	Shape of P^4 (ordered)	0: T-shaped; 1: Triangular; 2: Quadrangular
9	Mesial parastylar expansion on P^4	0: Projecting beyond the mesial border; 1: Not projecting.
10	Acuteness of P^4 cusps	0: Acute; 1: Bulbous
11	Height of postprotocingulum on P^4	0: Low (crest dips closer to the roots); 1: High (crest stays near the tip of the protocone in height)
	Upper molars	
12	Depth of distolingual basin on M^{1-2}	0: Shallow; 1: Deep
13	Presence of conules on M^{1-2} (ordered)	0: Both conules present; 1: Metaconules absent; 2: Both conules absent
14	Parastylar expansion on M^{1-2}	0: No expansion; 2: Expanded
15	Outline of M^1	0: Squared; 1: Rectangular and narrow
16	Depth of trigon basin on M^{1-2}	0: Shallow; 1: Deep
17	Presence of postmetaconule crista on M^{1-2}	0: Absent; 1: Present
18	Expansion of mesiolabial corner on M^3	0: Not expanded, buccal border is straight; 1: Expanded
	Lower canine	
19	Presence of C_1	0: Present; 1: Absent
	Lower premolars	
20	Presence of P_2	0: Present; 1: Absent
21	Presence of P_3	0: Present; 1: Absent
22	Trigonid/talonid width proportion on P_4	0: Talonid as wide as or wider than trigonid; 1: Talonid narrower than trigonid
23	P_4/M_1 width proportion	0: P_4 narrower than M_1; 1: P_4 of approximately the same with as M_1
24	Width at the base of the P_4 protoconid	0: Narrowly based protoconid; 1: Broadly based protoconid
25	Presence of a mesial bulge in the base of the P_4 protoconid	0: Absent; 1: Present
26	P_4/M_1 area proportion	0: Small P_4 area compared to M_1 area; 1: Similar
27	Relative mesiodistal length of P_4 to M_1	0: P_4 shorter than M_1; 1: P_4 equal or longer than M_1
28	Morphology of the hypoflexid	0: Distinct, deep; 1: Not distinct, shallow
29	Presence of paracristid	0: Present; 1: Absent
30	Relative length of the talonid compared to the length of the tooth	0: Relatively short talonid (less than 26% of the tooth length); 1: Relatively long talonid (more than 26% of the tooth length)
31	Presence of a crest connecting the protoconid and the hypoflexid fold (prehypoflexid cristid)	0: Absent; 1: Present
	Lower molars	
32	Length of trigonid	0: Trigonids become less mesiodistally compressed from M_1 to M_3, or there is no change; 1: Trigonids become more mesiodistally compressed from M_1 to M_3
33	Shape of the protocristid on M_1	0: V-shaped; 1: Slightly concave
34	Presence of distal cingulid on M_1 and M_2	0: Absent; 1: Present
35	Presence of hypoconulid on M_1 and M_2	0: Absent; 1: Present
36	Presence of buccal cingulid on M_1 and M_2 trigonids	0: Absent; 1: Present
37	Presence of buccal cingulid on M_1 and M_2 talonids	0: Absent; 1: Present
38	Shape of the M_1 trigonid basin	0: Semicircular; 1: Squared; 2: Triangular
39	Mesial inflection of the M_1 and M_2 trigonids (ordered)	0: Absent/weak; 1: Somewhat pronounced; 2: Very pronounced
40	Relative height of the hypoconid compared to the entoconid on M_1	0: Hypoconid taller than entoconid; 1: Subequal; 2: Entoconid taller than hypoconid
41	Relative height of the protoconid compared to the metaconid on M_1	0: Protoconid taller than metaconid; 1: Subequal; 2: Metaconid taller than protoconid
42	Presence of paraconid on M_2	0: Absent; 1: Present
43	Distinctiveness of the M_2 paraconid relative to the M_1 paraconid	0: Comparably distinct to the M_1 paraconid; 1: Less distinct than the M_1 paraconid
44	Relative height of the paraconid compared to the metaconid on M_2	0: Paraconid lower than metaconid; 1: Paraconid subequal of taller than metaconid
45	Relative height of the hypoconid compared to the entoconid on M_2	0: Hypoconid taller than entoconid; 1: Subequal; 2: Entoconid taller than hypoconid
46	Relative height of the protoconid compared to the metaconid on M_2	0: Protoconid taller than metaconid; 1: Subequal; 2: Metaconid taller than protoconid
47	Acuteness of cusps	0: Relatively acute; 1: Blunter
48	Molar enamel roughness inside the basin of M_3	0: Smooth; 1: Crenulated
49	Presence of M_3 paraconid	0: Absent; 1: Present
50	Relative height of the hypoconid compared to the entoconid on M_3	0: Hypoconid taller than entoconid; 1: Subequal; 2: Entoconid taller than hypoconid
51	Relative height of the protoconid compared to the metaconid on M_3	0: Protoconid taller than metaconid; 1: Subequal; 2: Metaconid taller than protoconid
52	M_3 trigonid basin area	0: Small basin, straight at the front; 1: Expansive trigonid basin, curved at the front
53	Morphology of the M_3 hypoconulid lobe	0: From a distal view, the central occlusal surface is taller than the sides; 1: from a distal view, the medial and later edges are taller than the central occlusal surface

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 inference by Estravís (2000) that *A. zbyszewskii* is a
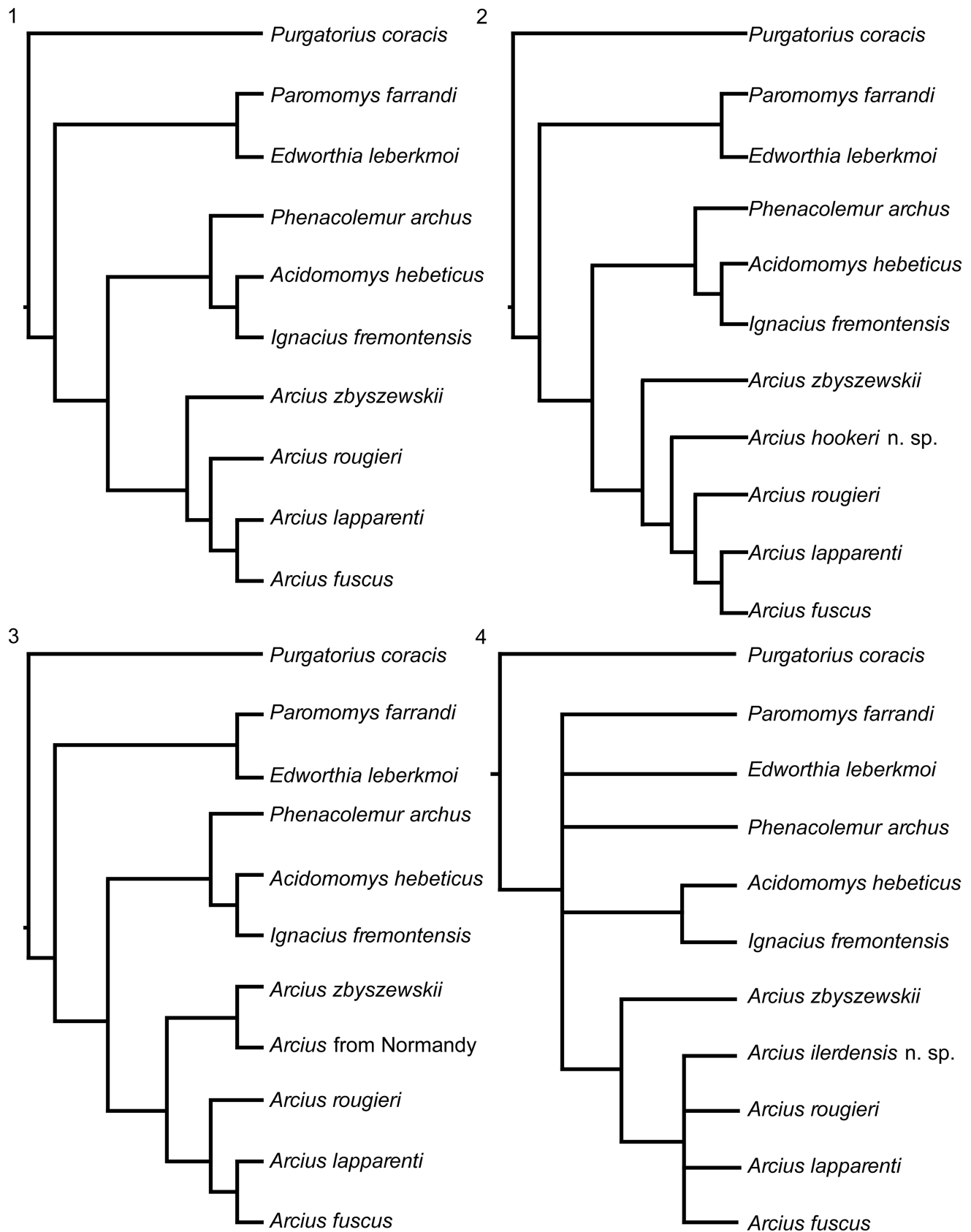
Figure 10. Hypotheses of phylogenetic relationship among selected genera of North American and European paromomyids based on cladistic analysis of 53 dental characters (Table 3, Supplemental Data 1, Figure S1). Cladistic analysis yielded a single most parsimonious cladogram for (**1**), (**2**), and (**3**). All cladograms rooted with Puercan *Purgatorius coracis* Fox and Scott, 2011. All characters were unordered, except for characters 1, 8, 13, and 39. Cladogram (**4**) was generated by strict consensus of six trees (Figure S1).

Purgatorius coracis

Paromomys farrandi

Edworthia leberkmoi

Phenacolemur archus

Acidomomys hebeticus

Ignacius fremontensis

Arcius zbyszewskii

Arcius rougieri

Arcius hookeri

Arcius ilerdensis

Arcius from Normandy

Arcius lapparenti

Arcius fuscus
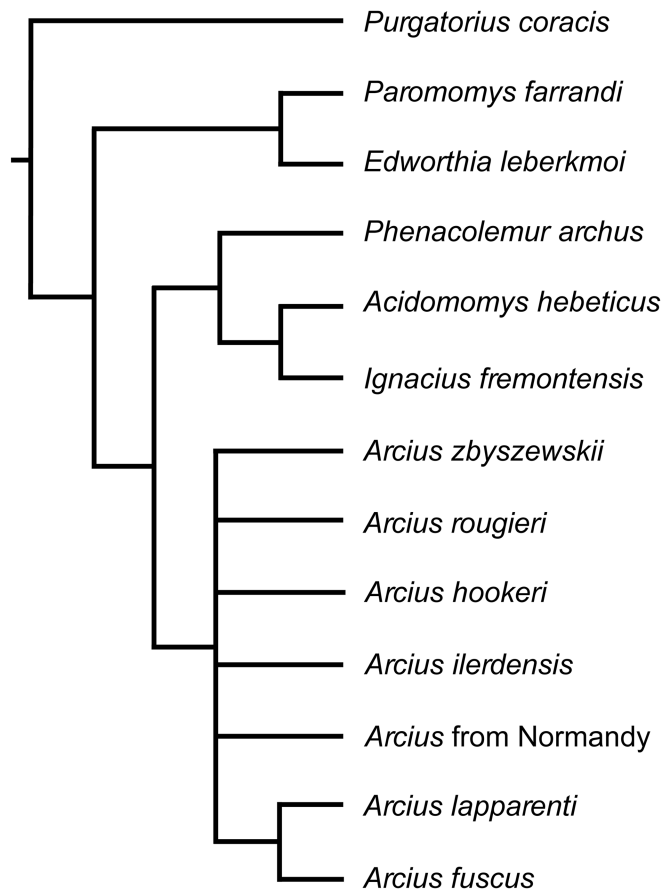
Figure 11. Cladogram generated by strict consensus of six trees. All European paromomyid taxa were included in this tree.

primitive lineage of European paromomyids, opening up the possibility of it being an ancestral species to all European paromomyids. 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) stated that the two characters that support the *Acidomomys-Arcius* clade are "l'absence de la p3" (absence of P_3) and "la presence d'une P3 uniradiculée" (presence of a single-rooted P^3) (Aumont, 2003, p. 364). However, *Acidomomys hebeticus* does have a P_3 (Bloch et al., 2002), and therefore that trait seems to be incorrectly coded in Aumont's (2003) matrix. In addition, the other character (presence of a single-rooted P^3) seems to be misreported because P^3 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 *Acidomomys hebeticus* had a double-rooted P^3 (Bloch et al., 2002), as coded, the number of roots for P^3 in *Arcius* is difficult to assess. Only a small piece of the distobuccal aspect of the P^3 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 by Aumont [2003, p. 364] as 'Arciusini'). In addition, the fact that *Acidomomys* appears as the sister taxon to *Arcius* might explain why Aumont's phylogeny differs from those 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* n. sp. is included in the analysis (Analysis 2; Fig. 10.2), 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 that 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 M_3, 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; Fig. 10.3). 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 fossils 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* n. sp. in the analysis (Analysis 4), the clade *A. fuscus-A. lapparenti-A. rougieri*, present in the results from Analyses 1–3, collapses (Fig. 10.4). In three of the six trees recovered from this analysis (Fig. S1.1, S1.2, S1.6), *A. ilerdensis* falls out as being most closely related to *A. rougieri*. *Arcius ilerdensis* also appears in two other trees (Fig. S1.4, S1.5) as the sister group to the clade *A. fuscus-A. lapparenti-A. rougieri*, and as most closely related to *A. lapparenti* in another tree (Fig. S1.3).

When all species are included in the analysis (Analysis 5; Fig. 11), most *Arcius* lineages collapse, likely because of the large amounts of missing data for several taxa. However, it is important to note that the clade including *A. fuscus* and *A. lapparenti* still holds in this cladogram.

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 composed 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*, *Arcius*, and possibly *Elwynella*.
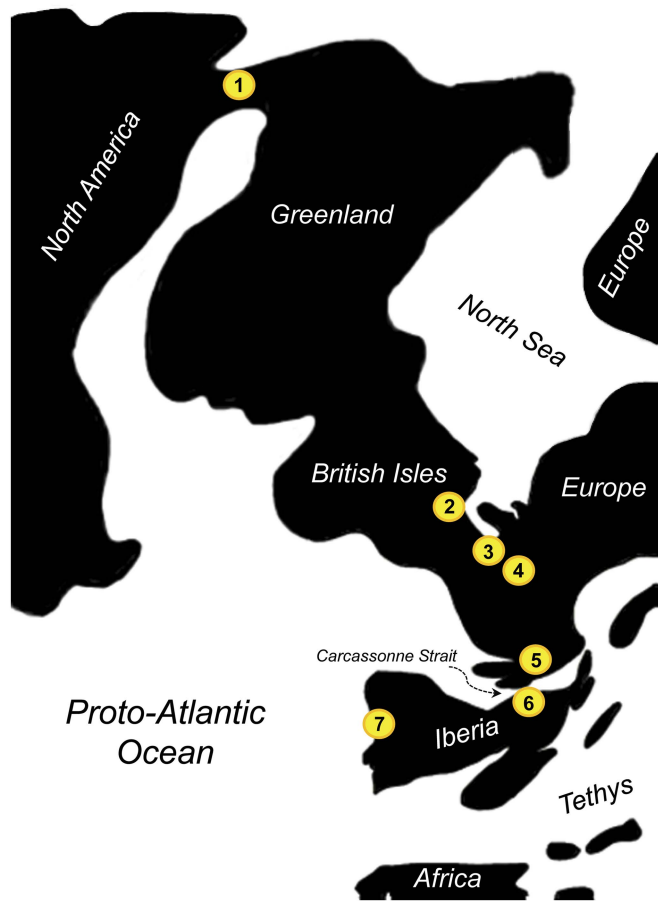
Figure 12. Paleogeography of Western Europe and Greenland during the earliest Eocene and location of some selected paromomyid-bearing locations (modified from Eberle and Greenwood, 2012, fig. 3; Marandat et al., 2012, fig. 1; and Hooker, 2015, fig. 8). (**1**) Eureka Sound Group, Canada; (**2**) Abbey Wood, UK; (**3**) Sotteville-sur-mer, France; (**4**) Paris Basin, France; (**5**) Palette, France; (**6**) Masia de l'Hereuet, Spain; (**7**) Silveirinha, Portugal.

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 (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. Even if the fossils from Silveirinha and Normandy did not belong to the same species, it would be one of the first cases of finding similar species in northern and southern Europe, which goes against the strong trend of north–south regionalism in this continent (Marandat, 1997).

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. *I. fremontensis* from Torrejonian 2 (To2; Rose, 1981; Silcox and Williamson, 2012). Therefore, the *Arcius* lineage is inferred to have branched off prior to To2. 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 of other areas in the Greenland land bridge (e.g., the east coast of Greenland; Larsen et al., 2001, 2002), to rewrite our understanding of paromomyid evolution and biogeography.

Conclusions

A new revision of the paromomyids from Europe (after Aumont, 2004) prompts the rediagnosis of the genus *Arcius* based on a significant collection of previously unpublished 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* n. sp. and *Arcius ilerdensis* n. sp.

Our phylogenetic analysis shows that *Arcius* is monophyletic. This is consistent with previous work done by Aumont (2003) but differs from her results 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's (2000) inferences. 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 to the phylogenetic analysis, 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

However, to assess this question more fully, additional North American paromomyid species should be included in the analysis of the family.

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. This dispersal would have been possible through land bridges between North America and Europe. The volcanic activity and regional uplift in eastern Greenland closed the Greenland Strait (or Denmark Strait) between Europe and Greenland, making it much narrower during the Paleocene and Eocene (Knox, 1998). In addition, the English Channel was bridged, allowing dispersal between the British Isles and continental Europe, and in particular with 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 (Fig. 12), which would be consistent with finding the oldest representative of the genus in that area. However, *Arcius zbyszewskii* is also found at Silveirinha,

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.

Acknowledgments

Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.873c4

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