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## PLESIADAPID MAMMALS FROM THE LATEST PALEOCENE OF FRANCE OFFER NEW INSIGHTS ON THE EVOLUTION OF *PLESIADAPIS* DURING THE PALEOCENE-EOCENE TRANSITION

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**ABSTRACT**—Plesiadapidae are among the most successful mammal families of the Paleocene, but in North America they disappear abruptly around the Paleocene-Eocene boundary. In contrast, in Europe, they survive a few million years into the Eocene, although only as the genus *Platychoerops*. The latest Paleocene deposits of Petit-Pâtis (Paris Basin, France) have produced three new plesiadapid species, one of each genus known in Europe: *Plesiadapis ploegi*, sp. nov., *Platychoerops boyeri*, sp. nov., and *Chiromyoides mauberti*, sp. nov. Each of these new species is represented by the very characteristic upper incisor, thus ascertaining their concomitant presence and in particular the spatial and temporal coexistence of *Plesiadapis* and *Platychoerops*. *Plesiadapis ploegi*, sp. nov., is morphologically intermediate between *Plesiadapis tricuspis* and *Platychoerops russelli*, with a tricuspid I1 typical of *Plesiadapis* and a semimolariform p4 closer to *Platychoerops*. Its relatively high morphological variability is illustrated. *Platychoerops boyeri*, sp. nov., has the simple derived I1 of all *Platychoerops* and a p4 slightly more molariform than that of *Ples. ploegi*. *Chiromyoides mauberti*, sp. nov., is closest to *Chiromyoides campanicus*, but it is smaller and has a particular I1 with multiple posterocones. The systematic position of ‘*Platychoerops georgei*’ is discussed; this taxon is considered a chimera, and its type I1 belongs to either *Chiromyoides* or *Plesiadapis*. Cladistic analysis highlights the paraphyly or polyphyly of all genera of Plesiadapidae. Finally, there is some indication of morphological convergences between European and North American plesiadapids, which may be the result of similar environmental changes on both continents just before the Paleocene-Eocene boundary.

<http://zoobank.org/urn:lsid:zoobank.org:pub:A73AEFC3-AA93-4EB6-8BD2-E3B15515C6FB>

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

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### INTRODUCTION

Plesiadapidae is a family of ‘plesiadapiforms,’ a verifiably paraphyletic and possibly polyphyletic assemblage of Laurasian primate-like mammals (Bloch et al., 2007; Silcox et al., 2010; Boyer et al., 2012a). ‘Plesiadapiforms’ are traditionally considered to be the closest Paleocene relatives to the extant order Primates (Simons, 1972; Szalay and Delson, 1979). For the last decade, some researchers focusing on relationships between extant Primates and ‘plesiadapiforms’ have been including them in the order Primates as a paraphyletic group excluded from the crown clade, the latter then called Euprimates (e.g., Silcox et al., 2005, 2008, 2017; Bloch et al., 2007, 2016; Chester et al., 2015, 2017). This view is now relatively widespread (e.g., Rose, 2006; Silcox and Gunnell, 2008; Silcox and López-Torres, 2017). However, many recent phylogenetic studies still place at least some of the families of these ‘plesiadapiforms’ outside the order Primates (e.g., Fleagle, 1998; Wible et al., 2007; Gingerich, 2012; Ni

et al., 2013, 2016; Soligo and Smaers, 2016). The most logical (but not necessarily the most widespread) way to proceed would be to call Primates all descendants of the last common ancestor of extant primates (original concept of Primates and crown definition as for all other mammalian orders), thus excluding ‘plesiadapiforms’ in their original sense. One could keep the name Plesiadapiformes for a clade including ‘plesiadapiforms’ (in their original meaning) and Primates (= Euprimates), unlike in its original conception. However, the relationship between Primates and ‘plesiadapiforms’ is still subject to much debate (e.g., comparing results in Ni et al., 2013, 2016, with Ni et al., 2005, Bloch et al., 2007, or Silcox et al., 2017), so we advise against such practice for the time being. In this paper, Primates are considered to be a crown group, whereas the term ‘plesiadapiform’ is used as an informal group in its original conception (Simons, 1972). Whether or not Plesiadapidae are members of the order Primates, they resemble the earliest primates in their molar morphology, particularly early adapiforms such as *Cantius* or *Notharctus* (e.g., Boyer et al., 2012a), implying a similar diet (e.g., Maas et al., 1988). These similarities in diet and ecological needs have been suggested as being a main driving factor for their extinction at the Paleocene-Eocene boundary (PEB) when adapiforms appear (Szalay, 1972), although

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plesiadapids seem to have disappeared shortly before adapiforms appear, at least in North America (Maas et al., 1988).

Unlike what can be observed in North America, European members of the family Plesiadapidae do not disappear abruptly close to the PEB but rather persist a few million years into the Eocene, although represented only by the genus *Platychoerops* (Gingerich, 1976; Hooker, 1994; Boyer et al., 2012a). This genus was restricted to the Eocene until a new species was recently described, based on associated lower cheek teeth from the late Paleocene of Berru (Boyer et al., 2012a). Because of its similarities with *Plesiadapis* and because it only occurred in Eocene localities, where *Plesiadapis* is absent, scientists long believed *Platychoerops* to be a particular lineage of European *Plesiadapis* that underwent rapid evolution from a frugivorous-omnivorous diet towards a mainly folivorous diet near the PEB (Gingerich, 1976; Boyer et al., 2010), likely due to (1) the changes in temperature and environment associated with the Paleocene-Eocene Thermal Maximum (PETM); and (2) the arrival of frugivorous-

omnivorous competitors in the form of rodents and euprimates (Hooker, 1994; Boyer et al., 2012a). Recent work (Boyer et al., 2012b) concluded, as already suggested by Russell (1964) and Gingerich (1976), that the species of *Plesiadapis* most closely related to the *Platychoerops* clade was *Plesiadapis cookei* (Clark-forkian, U.S.A.), thus implying a dispersal from North America to Europe at the PEB, which is perfectly plausible in view of the wide array of Euro-American dispersals documented at the PEB (e.g., Smith et al., 2014; Hooker, 2015). The third European genus of the family Plesiadapidae is *Chiromyoides*, which was described based on European material by Stehlin (1916); over 50 years passed before species from North America were referred to that genus (Gingerich, 1973), which is still poorly known and whose presence in the deposits is rare at best.

The deposits of Petit-Pâtis, in Rivecourt, Paris Basin (Fig. 1), were discovered by French amateurs in 2007 (Gagnaisson et al., 2009), and field work was conducted until 2012. The continental deposits that delivered the mammal fauna are dated latest

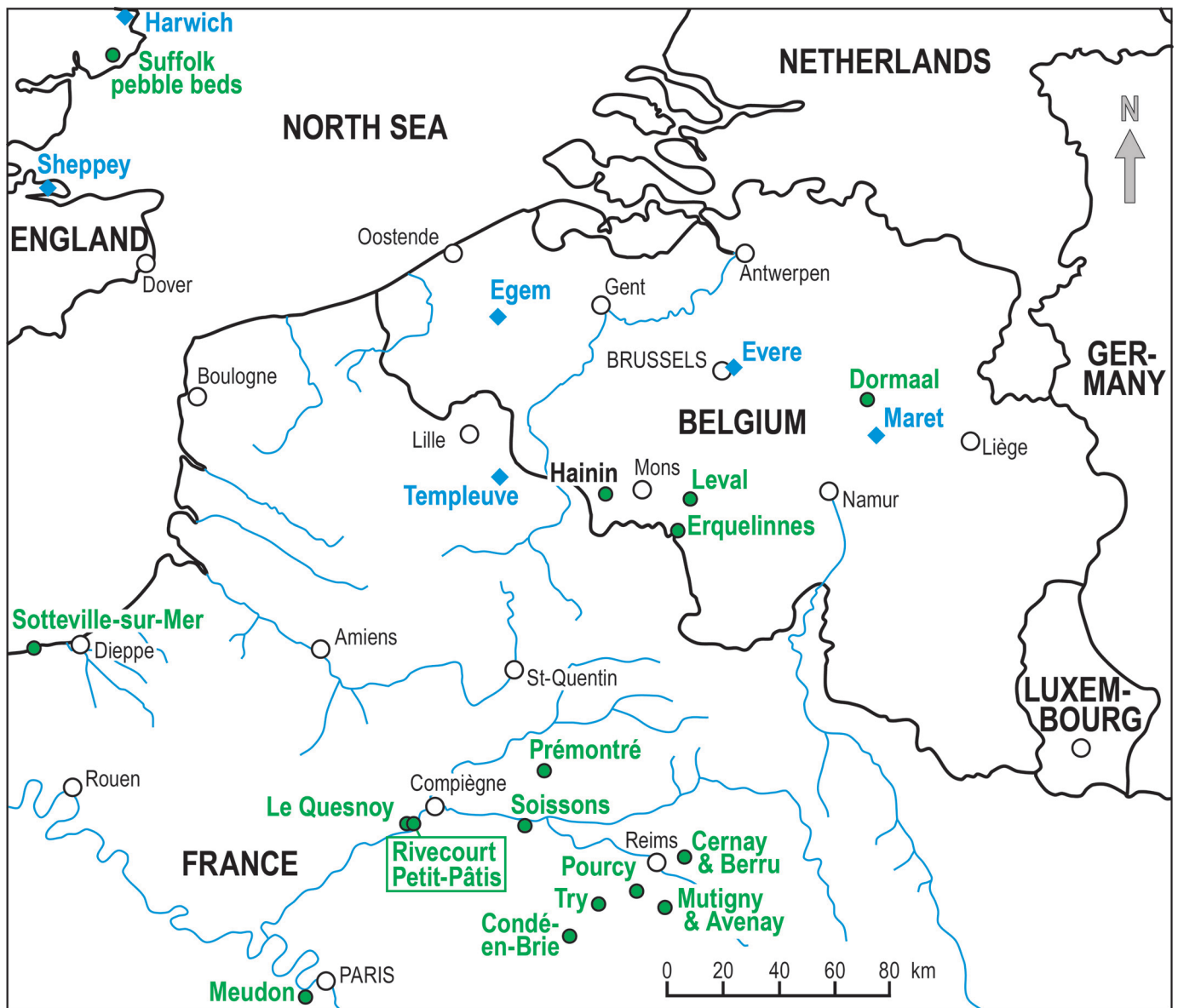


FIGURE 1. Map of the Paris Basin and surrounding areas with the early Paleogene localities having delivered mammal fossils. The Petit-Pâtis quarry of Rivecourt is in the northeastern part of the Paris Basin, an area with a concentration of continental localities of early Paleogene age. Green circles indicate terrestrial localities, whereas blue diamonds indicate marine levels in which terrestrial mammals were discovered.



Thanetian based on palynoflora and  $\delta^{13}\text{C}$ ; the mammal fauna corroborates this age with a mix of taxa typical of MP6a (late Thanetian) and MP7 (earliest Ypresian; see Smith et al., 2014, for an overview).

Here we report one new species of each European plesiadapid genus: *Plesiadapis ploegi*, sp. nov., *Platychoerops boyeri*, sp. nov., and *Chiromyoides mauberti*, sp. nov., all from the same latest Paleocene locality of Petit-Pâtis, and verify their generic attribution with a cladistic analysis. Each of these new species is represented by its most diagnostic upper I1, thus ascertaining the concomitant presence of the three genera, and particularly the coexistence in space and time of *Plesiadapis* and *Platychoerops*. *Platychoerops boyeri* is characterized by a very typical I1, large size, and presence of vestigial laterocone and mediocone. Moreover, although being definitely molariform to the same extent as other species of *Platychoerops*, its p4 displays crests in the place usually occupied by a paraconid, a feature shared only with the derived and markedly younger *Platychoerops daubrei*. *Plesiadapis ploegi* is characterized by a more molariform p4 than those of all other species of *Plesiadapis*, being morphologically intermediate between the most derived species of *Plesiadapis* (i.e., *Ples. cookei*) and the most primitive species of *Platychoerops* (either *Plat. antiquus* or *Plat. russelli*). Its deciduous dentition and morphological variability is illustrated and discussed. Finally, *Chiromyoides mauberti* is characterized by a slightly more primitive morphology than the older *Chiromyoides campanicus* and has a very typical I1 with multiple posterocones.

**Institutional Abbreviations**—**IRSNB**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **MNHN**, National Museum of Natural History, Paris, France; **NMB**, National History Museum of Basel, Basel, Switzerland; **PU**, Princeton University, Princeton, New Jersey, U.S.A.

## MATERIALS AND METHODS

Field work was conducted between 2007 and 2012, by several teams of amateur and professional paleontologists, with the permission and logistic support of the Lafarge Granulats Company (Oise).

The fossil mammal material is stored in the Musée Antoine Vivenel (Compiègne, France) under the collection name RIV.PPV (Rivecourt, Petit-Pâtis, Vertebrates). With the exception of rare large remains, most vertebrate specimens were collected by screen washing fossiliferous sediments in the field on meshes of 5, 2, and 1 mm. Sorting was done under a binocular microscope for the 1-mm fraction. All specimens were treated at IRSNB laboratories with the binder Degalan P24, a polymer based on methylmethacrylate and *n*-butylmethacrylate, in order to consolidate them and stop the natural oxidation processes. Photographs of small specimens were taken with an FEI Quanta 200 environmental scanning electron microscope. Specimens larger than 10 mm were photographed with a digital camera after being covered with  $\text{NH}_4\text{Cl}$  in order to enhance the surface structures, because the fossil material is dark brown to black in color.

Nomenclature for all dental structures follows that presented by Gingerich (1976:5–6). Synonymy lists utilize Richter's signs and follow the modifications of Matthews (1973).

## SYSTEMATIC PALEONTOLOGY

EUTHERIA Huxley, 1880

'PLESIADAPIFORMES' Simons and Tattersall in Simons, 1972  
Superfamily PLESIADAPOIDEA Trouessart, 1897

Family PLESIADAPIDAE Simons, 1972

Genus *PLESIADAPIS* Gervais, 1877

**Type Species**—*Plesiadapis tricuspidens* Gervais, 1877.

**Other Known Species**—*Plesiadapis remensis* Lemoine, 1887; *Plesiadapis dubius* (Matthew, 1915); *Plesiadapis rex* (Gidley,

1923); *Plesiadapis cookei* Jepsen, 1930; *Plesiadapis fodinatus* Jepsen, 1930; *Plesiadapis anceps* Simpson, 1936; *Plesiadapis insignis* (Piton, 1940); *Plesiadapis walbeckensis* Russell, 1964; *Plesiadapis churchilli* Gingerich, 1975; *Plesiadapis praecursor* Gingerich, 1975; *Plesiadapis simonsi* Gingerich, 1975; *Plesiadapis gingerichi* Rose, 1981; *Plesiadapis ploegi*, sp. nov.

**Occurrence**—Middle to late Paleocene of North America (one occurrence in the earliest Eocene; see Rose and Bown, 1982); middle to late Paleocene of Europe.

## *PLESIADAPIS PLOEGI*, sp. nov.

(Figs. 2–5)

- v. 2009 *Plesiadapis tricuspidens* Gervais: Gagnaison et al., 2009: pl. 4, figs. 2–6.
- v. 2014 *Plesiadapis tricuspidens* Gervais: Smith et al., 2014: fig. 6a–e.
- v. 2014 new unidentified 'condylarth': Smith et al., 2014: fig. 6m–o.

**Holotype**—RIV.PPV0544, left p4.

**Referred Material**—RIV.PPV0842, L dentary with m1–m2; RIV.PPV0541, L dentary with m2–m3; RIV.PPV0690, R dentary with m2–m3; RIV.PPV0841, L dentary with m2; RIV.PPV0540, R dentary with m3; RIV.PPV0567, RI1; RIV.PPV0570, LI1; RIV.PPV0571, RI1; RIV.PPV0593, LI1; RIV.PPV0594, LI1; RIV.PPV0843, LI1; RIV.PPV0846, I1; RIV.PPV1045, RI1; RIV.PPV1057, LI1; RIV.PPV1058, RI1; RIV.PPV599, LDI1; RIV.PPV669, RDI1; RIV.PPV1042, RDI1; RIV.PPV0561, RP4; RIV.PPV0613, RP4; RIV.PPV0729, RP4; RIV.PPV0851, RP4; RIV.PPV0885, RP4; RIV.PPV0899, LP4; RIV.PPV0907, RP4; RIV.PPV1033, RP4; RIV.PPV1054, LP3, LP4; RIV.PPV0549, RDP4; RIV.PPV0702, LDP4; RIV.PPV0703, LDP4; RIV.PPV0351, LM1; RIV.PPV0353, RM1; RIV.PPV0563, LM1; RIV.PPV0604, fragmentary RM1; RIV.PPV0608, RM1; RIV.PPV0609, RM1; RIV.PPV0610, RM1; RIV.PPV0611, RM1; RIV.PPV0642, RM1; RIV.PPV0647, LM1; RIV.PPV0901, RM1; RIV.PPV0564, LM2; RIV.PPV0607, RM2; RIV.PPV0350, LM3; RIV.PPV0352, LM3; RIV.PPV0603, RM3; RIV.PPV0653, LM3; RIV.PPV0689, LM3; RIV.PPV0727, LM3; RIV.PPV0900, RM3; RIV.PPV1059, LM3; RIV.PPV1067, LM3; RIV.PPV1111, RM3; RIV.PPV0368, fragmentary M; RIV.PPV0598, fragmentary M; RIV.PPV0605, fragmentary RM; RIV.PPV0728, fragmentary M; RIV.PPV1041, fragmentary M; RIV.PPV0575, Li1; RIV.PPV0576, Li1; RIV.PPV0577, Li1; RIV.PPV0579, Li1; RIV.PPV0597, Li1; RIV.PPV0848, Li1; RIV.PPV0853, i1; RIV.PPV1040, i1; RIV.PPV1064, Ri1; RIV.PPV0569, Ldi1; RIV.PPV0574, Ldi1; RIV.PPV0580, Ldi1; RIV.PPV0581, Ldi1; RIV.PPV0582, Rdi1; RIV.PPV0583, Ldi1; RIV.PPV0584, Ldi1; RIV.PPV0585, Ldi1; RIV.PPV0586, Rdi1; RIV.PPV0587, Ldi1; RIV.PPV0588, Ldi1; RIV.PPV0589, Ldi1; RIV.PPV0590, Ldi1; RIV.PPV0591, Ldi1; RIV.PPV0592, Ldi1; RIV.PPV0595, Rdi1; RIV.PPV0726, Ldi1; RIV.PPV0855, Ldi1; RIV.PPV0906, Ldi1; RIV.PPV1063, Ldi1; RIV.PPV1068, Ldi1; RIV.PPV1109, Ldi1; RIV.PPV0612, p3; RIV.PPV0623, p3; RIV.PPV0730, Lp3; RIV.PPV0883, Lp3; RIV.PPV1052, Rp3; RIV.PPV1055, Lp3; RIV.PPV1056, Rp3; RIV.PPV0354, Rp4; RIV.PPV0620, Rp4; RIV.PPV0621, Lp4; RIV.PPV0622, Lp4; RIV.PPV0722, Lp4; RIV.PPV0539, Ldp4; RIV.PPV0548, Rdp4; RIV.PPV0701, Rdp4; RIV.PPV1035, Rdp4; RIV.PPV0557, Rm1; RIV.PPV0602, Rm1; RIV.PPV0735, Lm1; RIV.PPV0881, Rm1; RIV.PPV1065, Rm1; RIV.PPV1066, Lm1; RIV.PPV0373, Rm1, Rm2; RIV.PPV0566, Rm1, Rm2; RIV.PPV0768, Rm1, Rm2; RIV.PPV0560, RIV.PPV0559, Rm2; Lm2; RIV.PPV0619, Rm2; RIV.PPV0721, Rm2; RIV.PPV0723, Rm2; RIV.PPV0724, Lm2; RIV.PPV0558, Rm3; RIV.PPV0614, Lm3; RIV.PPV0615, Lm3; RIV.PPV0616, Lm3;

RIV.PPV0617, Rm3; RIV.PPV0720, Lm3; RIV.PPV0852, Rm3; RIV.PPV1110, Lm3.

**Occurrence**—Latest Paleocene of Petit-Pâtis quarry, Rivecourt, France.

**Diagnosis**—Molar dentition globally similar to that of *Ples. tricuspidens*; upper molars with more dilambodont centrocrista and larger mesostyle; p4 larger relative to m1 and more molarized, with a distinct metaconid and sometimes a small paraconid; P4 longer and more molarized, with equally sized and reasonably separated paracone and metacone; on average, I1 slightly larger and m3 slightly smaller relative to m1 than in *Ples. tricuspidens*. Differs from all described species of *Platychoerops* by the large laterocone on I1, the smaller and less individualized metaconid of p4, and the smaller paraconid on p4 (except *Plat. boyeri* described further).

**Measurements**—See Table 1.

**Etymology**—In honor of Gaël de Ploëg, who discovered the vertebrate site of Petit-Pâtis and realized its scientific interest.

## Description

**I1**—The I1 (Fig. 3A–C) is morphologically very close to that of *Ples. tricuspidens* from Cernay and Berru, with a large laterocone, small but individualized mediocone, and single, relatively large posterocone. *Plesiadapis ploegi*, nevertheless, differs from *Ples. tricuspidens* by the consistently smaller posterocone.

**D11**—Several small upper incisors (Fig. 4A–C) resemble the tricuspid incisor of *Plesiadapis* spp., although markedly smaller and shorter; they are here interpreted as the D11 of *Ples. ploegi*. These teeth have a laterocone almost as large as the anterocone, a relatively large mediocone connected to the laterocone by a straight crest, and no posterocone.

**P4**—The P4 (Figs. 2J–K, 5P–S) is semimolariform, with paracone and metacone well separated (for a species of *Plesiadapis*) and similarly sized. The preparacrista is directed anteriorly close to the tip of the paracone, before curving slightly labially. The postmetacrista aims straight posteriorly. There are no stylar cusps except for a small parastyle where the preparacrista joins the labial cingulum. There is a small paraconule halfway between the paracone and the protocone, bearing no crest; there is no metaconule. The protocone, occupying as much occlusal space as the two labial cusps combined, has no visible postprotocrista (although see RIV.PPV0899, Fig. 5P), whereas the discrete pre-protocrista runs labially, either to the paraconule or even past it to the parastyle. There is a relatively narrow precingulum at the

anterior base of the protocone, whereas the postcingulum is wider and runs from the lingual margin of the tooth to the postmetacrista but features no trace of even a crestiform hypocone. These pre- and postcingula do not join lingually.

**DP4**—The DP4 (Fig. 4D–G) has an almost rounded outline and is almost as long as it is wide. It is composed of three main cusps of equal dimensions. The paracone and metacone are linked by a dilambodont centrocrista, with a moderate mesostyle. The preparacrista is directed anteriorly and only slightly labially, whereas the postmetacrista points labially and slightly posteriorly. A narrow ectocingulum is present. The protocone is anteroposteriorly situated at the level of the mesostyle; its lingual slope is short. The paraconule is small and placed slightly closer to the paracone than to the protocone. The slightly larger metaconule is situated halfway between the metacone and the protocone. There is a precingulum and a postcingulum, but no visible hypocone. The postcingulum extends beyond the tip of the metacone, almost all the way to the labial margin of the tooth.

**M1**—The dilambodont M1 (Figs. 2H–I, 5T–V) is usually almost as long as wide. The pre- and postparacrista and pre- and postmetacrista curve labially, each pair almost sketching a half circle, joining close to the labial margin on a developed crestiform mesostyle. There is a parastyle, but no metastyle. The paraconule is usually slightly larger than the metaconule; both are equally distant from the protocone, and neither bears marked crests. The protocone is larger and slightly higher than the paracone and metacone. There are relatively narrow pre- and postcingulum joining lingually on some specimens. The pseudohypocone is as large as the paraconule and linked to the protocone by a small crest.

**M2**—The M2 (Figs. 2F–G, 5W–X) is organized similarly to the M1, but it is wider mainly due to a longer slope of the protocone and to an increased distance between the protocone and conules.

**M3**—The M3 (Figs. 2D–E, 5Y–Z) is broadly similar to the M2, with a slightly reduced metastyle region. The tooth is also more asymmetrical due to a posteriorly shifted protocone and a lingually shifted metacone. The hypocone region is not reduced, but the conules are less visible than on M1 and M2: the paraconule is barely visible and close to the base of the paracone (as in M2), whereas the metaconule is so reduced that it is no longer identifiable amongst the crenulations of the enamel.

**Dentary**—The dentary (Fig. 2A–C) is of standard height for a derived *Plesiadapis*, three times as high as the crown of m2 under m2. All lower cheek teeth are biradicate; there was very likely a diastema between i1 and the first next tooth, i.e., p3, but the specimens are too damaged to be certain of this. There is at least one mental foramen, under the posterior root of p4. The symphysis does not extend posteriorly beyond the anterior root of p3.

**i1**—The i1 (Fig. 3D–F) is spade-like, with a marked margocristid but without margoconid.

**di1**—The sediments of Petit-Pâtis delivered abundant isolated lower incisors (Fig. 4H–J) that strongly resemble those of *Plesiadapis*, but are significantly smaller and proportionally somewhat less elongated than the i1 of *Ples. ploegi*, and all missing their root. We interpret these teeth as the di1 (deciduous lower incisor) of *Ples. ploegi*.

**p3**—The p3 (Fig. 2X–Z) is mainly composed of a tall acute protoconid. There is neither a paraconid nor a metaconid. The talonid is wide but short and features two cuspid occupying the places of a hypoconid and an entoconid. Three crests run posteriorly down the trigonid: one on its lingual margin towards the entoconid, one on its labial margin, and one in the middle towards the hypoconid (oblique cristid). The talonid is distinctly wider than the trigonid, and its basin is open lingually.

**p4**—The p4 (Figs. 2U–W, 5A–D) is semimolariform. The metaconid and the protoconid are of comparable heights and

TABLE 1. Measurements (in mm) of the teeth of *Plesiadapis ploegi* from the latest Paleocene of Petit-Pâtis, Rivecourt.

Tooth	n	L	OR	Se	V	W	OR	Se	V
i1	4	8.63	7.7–9.71	0.81	9.43	3.30	2.9–3.65	0.27	8.09
di1	18	5.14	4.44–5.78	0.37	7.11	2.57	2.18–3.00	0.19	7.23
p3	5	3.50	3.28–3.80	0.17	4.93	2.88	2.53–3.11	0.22	7.50
p4	6	3.90	3.51–4.14	0.20	5.03	3.45	3.18–3.72	0.17	4.94
dp4	4	3.54	3.35–3.83	0.19	5.40	2.69	2.55–2.76	0.08	3.06
m1	6	4.40	4.04–4.87	0.32	7.29	3.77	3.46–4.18	0.24	6.31
m2	9	4.98	4.65–5.40	0.25	5.37	4.08	3.82–4.28	0.14	3.48
m3	12	6.81	6.39–7.18	0.29	4.20	3.99	3.74–4.28	0.19	4.68
I1	6	6.50	5.64–7.0	0.46	7.13	3.87	3.55–4.40	0.31	8.01
D11	3	3.79	3.66–3.90	0.10	2.60	2.86	2.83–2.89	0.02	0.87
P4	7	3.28	2.94–3.44	0.18	5.34	4.84	4.11–5.36	0.41	8.45
DP4	2	3.56	3.54–3.57	0.01	0.42	3.70	3.70–3.70	0.00	0.00
M1	9	4.14	3.83–4.32	0.16	3.78	5.36	5.07–5.68	0.20	3.72
M2	2	4.52	4.33–4.70	0.19	4.10	6.28	5.92–6.64	0.36	5.73
M3	8	4.55	4.28–4.85	0.19	4.12	6.44	5.96–6.78	0.23	3.61

**Abbreviations:** L, mean length; n, number of specimens; OR, observed range; Se, standard deviation; V, coefficient of variation ( $V = 100 \times \text{Se}/\text{mean}$ ); W, mean width.

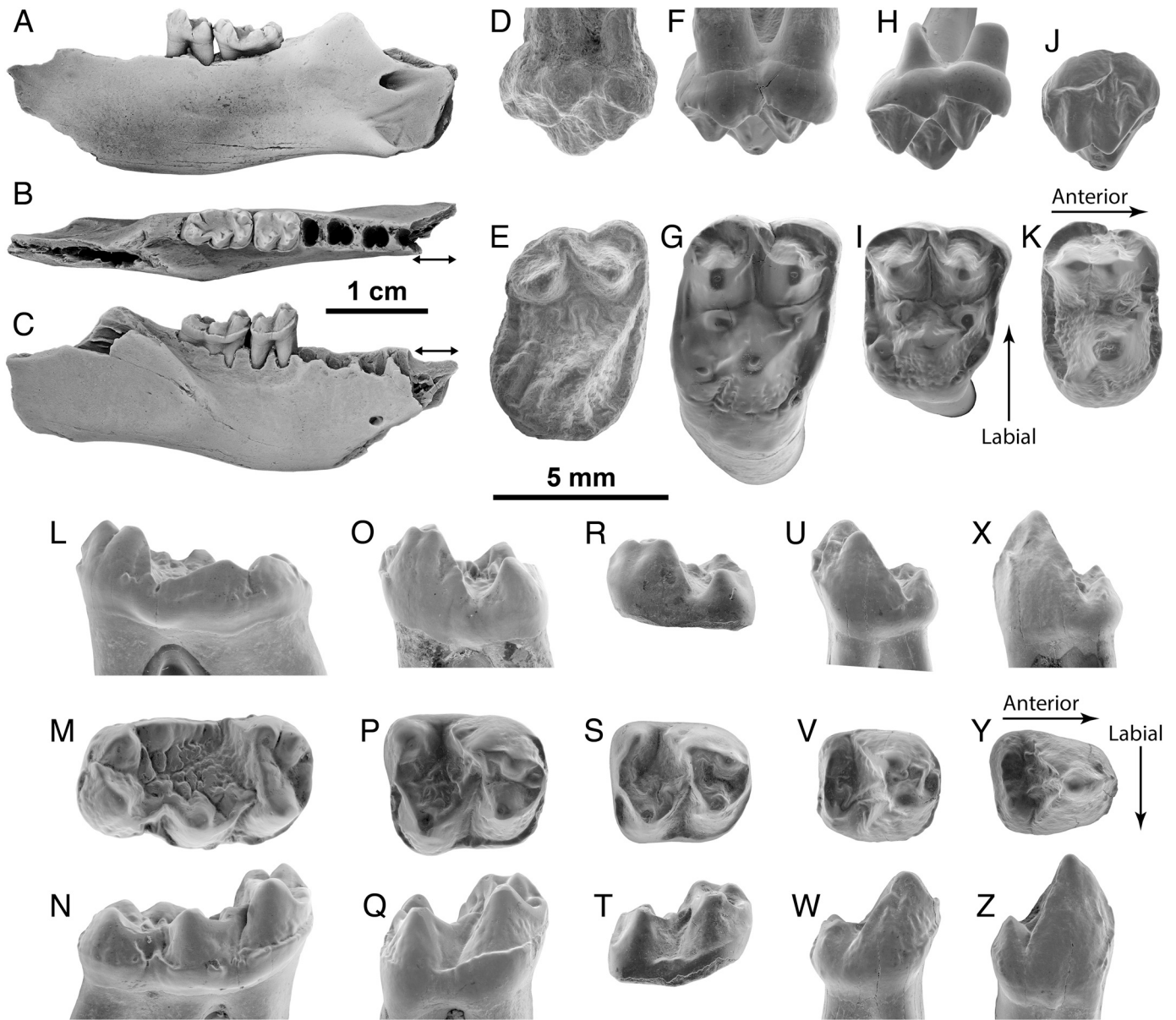


FIGURE 2. Cheek teeth of the plesiadapid *Plesiadapis ploegi* from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A–C**, R dentary with m2–m3, RIV.PPV0690. Double arrows indicate the position of the diastema between the incisor and p3; **D–E**, reversed LM3, RIV.PPV1059; **F–G**, reversed LM2, RIV.PPV0564; **H–I**, RM1, RIV.PPV0642; **J–K**, RP4, RIV.PPV0561; **L–N**, Rm3, RIV.PPV0558; **O–Q**, Rm2, RIV.PPV0721; **R–T**, Rm1, RIV.PPV0602; **U–W**, reversed Lp4, RIV.PPV0544; **X–Z**, reversed Lp3, RIV.PPV0883. Views are labial (C, D, F, H, J, N, Q, T, W, Z), occlusal (B, E, G, I, K, M, P, S, V, Y), and lingual (A, L, O, R, U, X).

sizes and flank a small trigonid basin, particularly well delimited on RIV.PPV0621 (Fig. 5D). The paraconid is small to absent. The metaconid arises more posteriorly than the protoconid. The talonid is as long as the trigonid and often slightly wider. There are two talonid cusps, a hypoconid and an entoconid, linked by a straight crest. As on p3, three crests run from the tip of the protoconid; the oblique cristid runs first towards the entoconid before curving labially to reach the hypoconid. The basin is open lingually. The posterior margin of the p4 is straight, implying a straight anterior margin of m1.

**dp4**—The dp4 (Fig. 4K–M) is characterized by little height difference between the trigonid and the talonid, as on lower molars, and by a triangular trigonid that is rather short for a dp4. The paraconid is large and aligned with the metaconid and

the entoconid. The paraconid is marked and, unlike on m1, only slightly curved. The protoconid and the metaconid are of similar sizes and linked by a relatively marked crest. The talonid is markedly wider than the trigonid. The hypoconid and the entoconid are large and sharp, both bulging laterally. The hypoconulid is very small and much lower than the other talonid cusps; it is placed halfway between the hypoconid and the entoconid. The oblique cristid is very marked and reaches the tip of the metaconid. The wear is particularly strong on the higher part of this oblique cristid. As on lower molars, there is no entocristid and the talonid basin is consequently wide open lingually.

**m1**—The m1 (Figs. 2R–T, 5E–G) talonid is slightly wider than its trigonid. There is a relatively large trigonid basin, flanked by

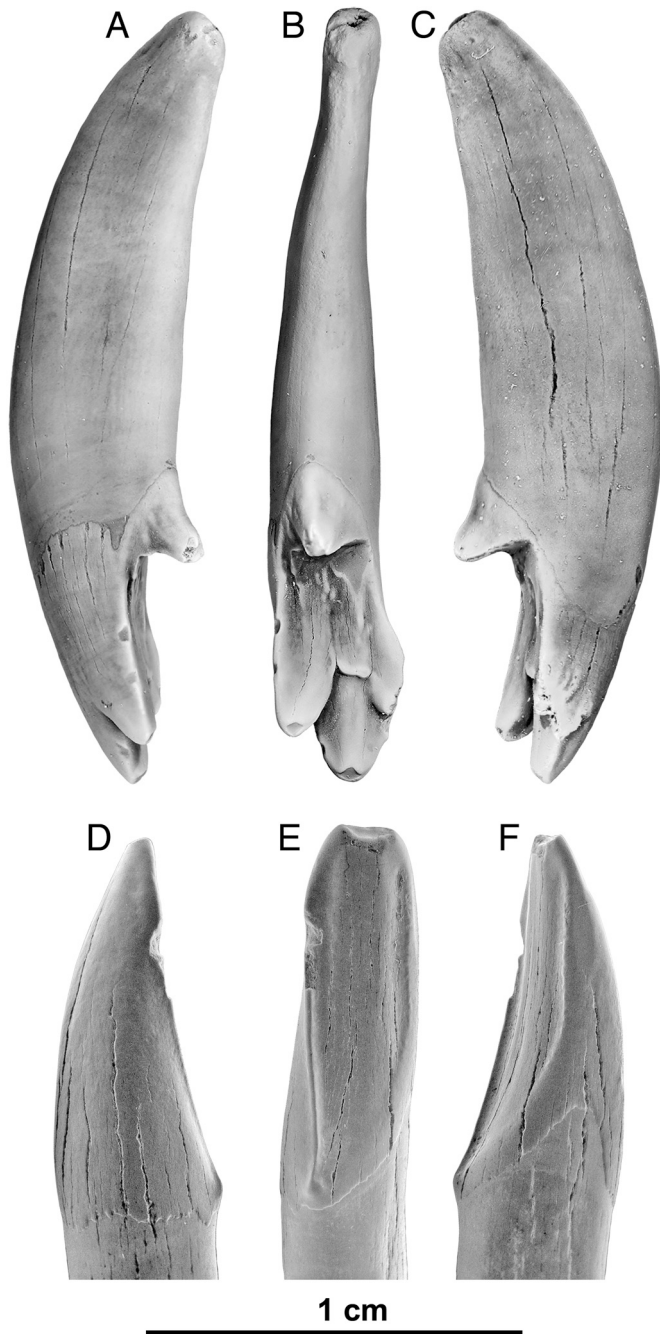


FIGURE 3. Incisors of the plesiadapid *Plesiadapis ploegi* from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A–C**, L11, RIV.PPV0570; **D–F**, Li1, RIV.PPV0575. Views are lateral (A, D), occlusal (B, E), and medial (C, F).

three well-individualized cusps (paraconid, metaconid, and protoconid), extending more anteriorly than the paraconid. The oblique cristid almost reaches the lowest point of the protoconid and is characterized by the presence of a short accessory crest directed towards the middle of the basin. This accessory crest is visible on all unworn specimens. The talonid basin is open lingually due to the absence of an entocristid.

**m2**—The m2 (Figs. 2O–Q, 5H–K) is relatively similar to m1, from which it differs by the paraconid being in closer approximation to the metaconid, by the stronger labial cingulum at the base of the tooth, by the trigonid that is as wide as the talonid, by

the larger size, and by the lower length/width ratio. The metaconid is also lower than the paraconid, although not smaller in occlusal area. A robust spur links the paracristid to the precingulid at the most anterior point of the trigonid; this spur is also visible on m1 and m3, although not as developed. A distinct accessory cusp between the paraconid and the protoconid is visible at the top of this spur, particularly on m2s.

**m3**—The m3 (Figs. 2L–N, 5L–O) trigonid is similar to that of the m2, but proportionally wider. As in all plesiadapids, the m3 is characterized by an elongated talonid, mainly due to a hypoconulid that is especially shifted posteriorly, so that the talonid is more than twice as long as on m2. This hypoconulid is twinned and deeply incised by one or two indentations on its posterolingual side. The enamel is distinctly wrinkled on all cheek teeth, particularly so on the m3.

#### Tooth Association

Apart from the natural association guaranteed by a few dentaries with teeth, *Ples. ploegi* is also by far the most abundant taxon in Petit-Pâtis, thus helping association by relative abundance. Upper and lower molars all display a very typical *Ples. tricuspidentis*-like morphology and correspond in length. The P4, p4, and incisors are also of typical plesiadapid affinities and are associated based on their size and relative abundance.

#### Morphological Comparisons

The most abundant species at Petit-Pâtis is a mid-sized plesiadapid easily recognizable by its long m3 with enlarged hypoconulid lobe, dilambdodont upper molars, and large tricuspid upper incisor (Silcox and Gunnell, 2008). The relatively large size for a plesiadapid, the crenulated enamel, the fissured hypoconulid lobe of m3, the loss of p2, and the developed laterocone on I1 indicate a derived species of the genus *Plesiadapis*. Interestingly, the m1 postvallid is almost not stepped, unlike in most Plesiadapoidea (*Plesiadapidae* + *Carpolestidae*). However, the postvallid of *Platychoerops daubrei* is barely stepped and that of *Platychoerops richardsoni* is similarly not stepped. The specimens from Petit-Pâtis differ from all described species of *Platychoerops*, the closest genus to *Plesiadapis*, by the strong laterocone on I1 and the small to absent paraconid on p4 (Boyer et al., 2012a; but see description of *Plat. boyeri* in this paper for the p4 paraconid). The size and morphology of the upper and lower molars are very close to those of *Plesiadapis tricuspidentis* from Cernay and Berru, so that they were initially confused (Gagnaison et al., 2009; Smith et al., 2014). However, the p4s from Petit-Pâtis (Figs. 5A–D, 10C) are more molariform than those from Cernay and Berru (Fig. 10A), actually more molariform than any other species of *Plesiadapis*, including the most derived *Ples. cookei* (Fig. 10B). The metaconid is larger and better individualized, and the talonid basin is wider and longer. In that regard, the p4s from Petit-Pâtis somewhat resemble those of *Platychoerops antiquus* from Berru (Fig. 10D), from which they differ by the smaller paraconid and metaconid and by the smaller size. Unsurprisingly, the P4s (Fig. 5P–S) are also more molarized, with paracone and metacone better individualized than in *Ples. tricuspidentis*, although the difference is less obvious than for p4s. The paracone and metacone are similarly isolated in *Ples. cookei*, but the latter is more derived in that its P4 centrocrista is slightly dilambdodont. The paraconid and metaconid of m2 (Fig. 5H–K) are closely approximated in *Ples. ploegi*, as in *Ples. tricuspidentis*, *Plat. russelli*, *Plat. boyeri*, and *Plat. richardsoni*. These two cusps are less approximated in *Plat. antiquus* and *Plat. daubrei*. Detailed examination of the molars revealed a few characters that differ slightly though consistently from *Ples. tricuspidentis*. Well-preserved and unworn lower molars of *Ples. ploegi* are all characterized by the presence of a small accessory crest at the lowest point of the oblique cristid, pointing towards

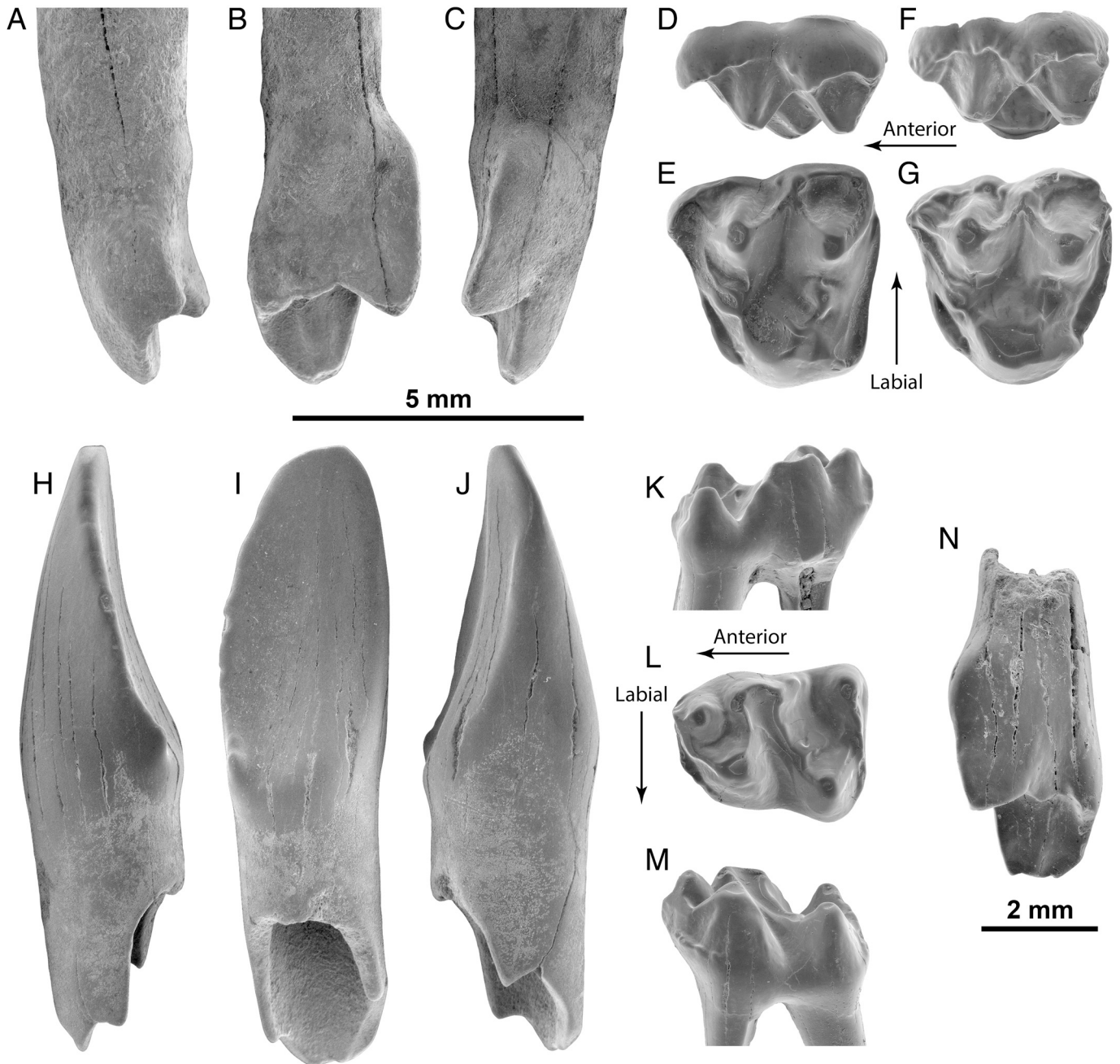


FIGURE 4. Deciduous teeth of *Plesiadapis* spp. from the Paris basin. **A–M**, *Plesiadapis ploegi* from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A–C**, RDI1, RIV.PPV1042; **D–E**, LDP4, RIV.PPV0703; **F–G**, LDP4, RIV.PPV0702; **H–J**, Ldi1, RIV.PPV0580; **K–M**, reversed Rdp4, RIV.PPV0701. **N**, *Plesiadapis tricuspidens* from the late Paleocene of Cernay, France, LDI1, IRSNB M2300. Views are lateral (C, H), occlusal (B, E, G, I, L, N), medial (A, J), labial (D, F, M), and lingual (K).

the talonid basin. In *Plat. antiquus* and *Ples. cookei*, there is a small tubercle at the same place but no crest, in *Ples. dubius* and *Ples. tricuspidens* such a tubercle is visible only in some specimens, whereas species of *Platychoerops* other than *Plat. antiquus* have a more marked crest of such type and other species of *Plesiadapis* no crest at all. Moreover, the dilambdodonty of upper molars is more pronounced in *Ples. ploegi* than in *Ples. tricuspidens* and most species of *Plesiadapis*, but similar to that observed in *Ples. cookei* and *Platychoerops* spp. In *Ples. ploegi*, it is usually pronounced enough that the postparacrista and premetacrista barely meet each other before reaching the labial margin of the

tooth. The upper molars of *Ples. ploegi* also feature a shallow notch on their labial margins, at the anterior base of the mesostyle. All species of *Platychoerops* for which the upper molars are known have a deep indentation at the same place, whereas species of *Plesiadapis* all have a whole labial margin. The presence of such a notch in *Ples. tricuspidens* from Cernay and Berru is variable, although when present it is very shallow. The upper incisors from Petit-Pâtis (Fig. 3A–C) are morphologically very similar to those of *Ples. tricuspidens* from Cernay and Berru, except for the proportionally smaller posterocone and mediocone and a less curved occlusal face, derived characters also

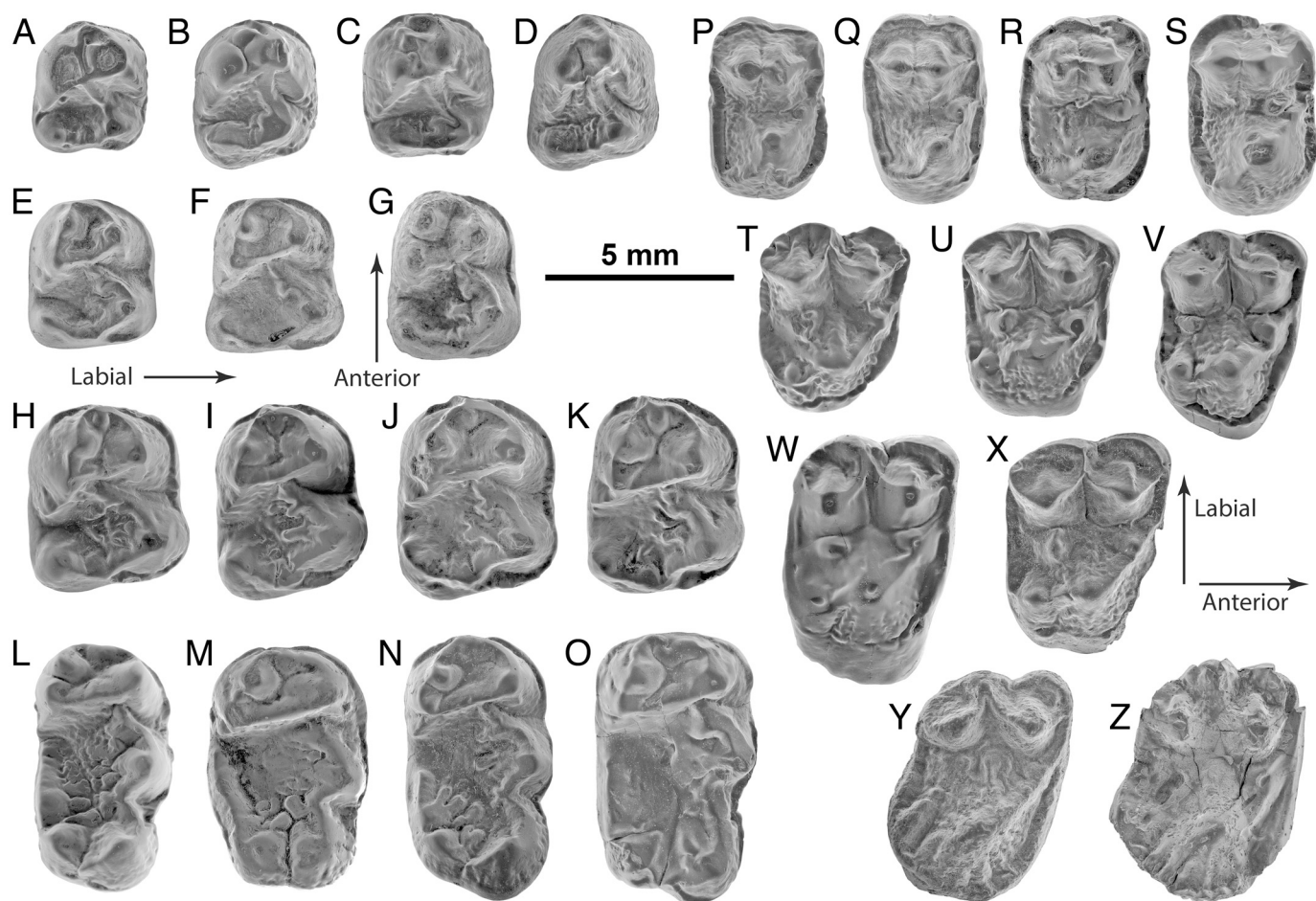


FIGURE 5. Intraspecific variability of cheek teeth of *Plesiadapis ploegi* from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A–D**, p4; **A**, RIV.PPV0354; **B**, RIV.PPV0620; **C**, RIV.PPV0544; **D**, RIV.PPV0621. **E–G**, m1; **E**, RIV.PPV0602; **F**, RIV.PPV1066; **G**, RIV.PPV0557. **H–K**, m2; **H**, RIV.PPV0721; **I**, RIV.PPV0723; **J**, RIV.PPV0559; **K**, RIV.PPV0724. **L–O**, m3; **L**, RIV.PPV0558; **M**, RIV.PPV0720; **N**, RIV.PPV0615; **O**, RIV.PPV0614. **P–S**, P4; **P**, RIV.PPV0899; **Q**, RIV.PPV0885; **R**, RIV.PPV0729; **S**, RIV.PPV0561. **T–V**, M1; **T**, RIV.PPV0609; **U**, RIV.PPV0642; **V**, RIV.PPV0563. **W, X**, M2; **W**, RIV.PPV0607; **X**, RIV.PPV0564. **Y, Z**, M3; **Y**, RIV.PPV1059; **Z**, RIV.PPV0350. All views are occlusal; **C, D, F, K, M, N, O, Q, T, V, W, Z**, left teeth reversed to be figured as right.

observed in *Ples. cookei* and hinting at the simpler morphology of the upper incisors of *Platychoerops*. The i1 is very similar to that of *Ples. tricuspidens*, both differing from i1s of most species of *Plesiadapis* by the absence of a margoconid. The I1 of *Ples. ploegi* is somewhat smaller than that of *Ples. tricuspidens*: the mean size of the specimens from Petit-Pâtis still falls within the documented variation of *Ples. tricuspidens* from Cernay, but not from Berru. The size of the m3 of the specimens from Petit-Pâtis is also similar to that of the specimens from Cernay, but smaller than the average of *Ples. tricuspidens* from Berru. In contrast, the p4 specimens from Petit-Pâtis are larger than those from Cernay and Berru. As a result, the p4/m1 length ratio of the specimens from Petit-Pâtis (p4/m1 length = 0.89) is significantly higher than in the specimens of *Ples. tricuspidens* from Cernay and Berru (p4/m1 length = 0.80 based on the measurements of Russell, 1964, from Cernay and Berru combined; 0.82 based on the measurements of Gingerich, 1976, from Berru alone). The other loci have very similar dimensions in Petit-Pâtis and in Cernay and Berru.

#### Deciduous Dentition

The teeth identified as di1 (Fig. 4H–J) are spade-shaped and have no margoconid, just as the permanent i1 (Fig. 3D–F),

although they are significantly smaller. They match those supposed to belong to *Ples. tricuspidens* (figured by Russell, 1964:pl. 3, fig. 7a) in morphology and in their size relative to i1. These teeth are abundant in the deposits of Petit-Pâtis, more abundant than expected for any species other than *Ples. ploegi*, strengthening the assumption that these teeth are the deciduous incisors of *Plesiadapis*, as first proposed by Schlosser (1921) and followed by Gingerich (1976). They also all lack a complete root. The DI1 (Fig. 4A–C) are characterized by a typical plesiadapid tricuspid morphology and match di1 in size. They are characterized by a laterocone of about the same size as the anterocone, just as the permanent I1. They resemble the tooth from Cernay figured by Russell (1964:pl. 3, fig. 7d) very much, except for a slightly shorter anterocone and a slightly smaller mediocone. The specimen illustrated in Figure 4N, from Cernay, is also very similar, differing mainly by being proportionally narrower.

The first dp4 and DP4 discovered were initially thought to belong to a condylarth (Smith et al., 2014) because these dp4s are unusually short, with a paraconid that is not so developed, thus resembling a somewhat atypical permanent molar, because the relatively square DP4s are markedly dilambdodont, which is unusual for DP4s, and because there are very few figured deciduous premolars of plesiadapids (see Bloch et al., 2002, for a review). The dp4s (Fig. 4K–M) feature the very long oblique



crisid and well-isolated paraconid (although not as anteriorly placed) observed in *Ples. tricuspiciens* and other species of Plesiadapidae (see, e.g., Teilhard de Chardin, 1922; Simpson, 1935). Nevertheless, they differ from that of the similar *Ples. tricuspiciens* by the shorter and wider trigonid, and from that of the younger *Plat. daubrei* by being wider and by the less transverse oblique crisid. The dp4 of the paromomyid *Acidomomys* (Bloch et al., 2002) is also characterized by a proportionally shorter trigonid with less anteriorly developed paraconid and less wide talonid than in other plesiadapids, but it differs from that of *Ples. ploegi* by the oblique crisid that is less ascending the posterior wall of the trigonid and by being proportionally longer. The identified DP4s (Fig. 4D–G) have no root and are approximately as long as wide, both characters suggesting DP4, but are markedly dilambdodont, which is much less frequent in DP4s. This dilambdodonty of DP4 is consistent with the marked dilambdodonty of the upper molars and the particularly long oblique crisid of dp4. The postprotocrista runs all the way down to the postcingulum, which is characteristic of *Plesiadapis*: the term ‘*Nannopithecoid*’ being used by early authors for this structure (see Simpson, 1955:435). These DP4s differ from that referred to *Ples. cookei* (Rose, 1981) by the more marked dilambdodonty (even though the dilambdodonty of permanent upper molars is similar), by the larger conules and more lingual paraconule, and by the transversally shorter precingulum. The DP4s are very similar to those of *Plat. daubrei*, from which they differ by the slightly less marked dilambdodonty (as on dp4) and the smaller precingulum. The DP4s differ more markedly from those of *Acidomomys* (Bloch et al. 2002) by being markedly dilambdodont and by the much smaller postcingulum.

#### Generic Attribution

The attribution of the specimens from Petit-Pâtis to the genus *Plesiadapis* could be questioned based on the more molariform morphology of the p4, because, as shown by Boyer et al. (2012a), it is one of the main differences between *Plesiadapis* and *Platychoerops*. Nevertheless, although the p4 morphology places the Petit-Pâtis specimens more or less intermediate between *Ples. tricuspiciens* and *Plat. antiquus*, upper incisor and general molar morphology place them much closer to *Ples. tricuspiciens* than to *Platychoerops* spp. The medium intensity of the crenulation of the enamel also favors referring this species to *Plesiadapis*, although some specimens are more crenulated than others. Moreover, the presence of a small accessory crest on the oblique crisid, observed only in described species of *Platychoerops*, together with shallow notch in the labial margin of the upper molars at the anterior base of the mesostyle and the robust accessory cusp between the paraconid and the protoconid, would be additional arguments to consider the new species as a primitive *Platychoerops* rather than a derived *Plesiadapis*. *Plesiadapis ploegi* is thus characterized by a mosaic of characters shared with *Plesiadapis* and *Platychoerops*. Given the typical and relatively primitive morphology of its I1 compared with that in *Platychoerops*, a tooth that is very diagnostic and meaningful for the evolutionary position within Plesiadapidae, the species from Petit-Pâtis is considered to belong to the genus *Plesiadapis*.

Genus *PLATYCHOEROPS* Charlesworth, 1855

**Type Species**—*Platychoerops richardsoni* Charlesworth, 1855.

**Other Known Species**—*Platychoerops daubrei* (Lemoine, 1880); *Platychoerops russelli* (Gingerich, 1976); *Platychoerops antiquus* Boyer, Costeur, and Lipman, 2012; *Platychoerops boyeri*, sp. nov.

**Occurrence**—Late Paleocene and early Eocene of Europe.

**Diagnosis**—Emended from Boyer et al. (2012a): differs from other plesiadapid genera in having more molarized premolars

(specifically in having at least an incipient molar-type paraconule on P4; in having p4 with a distinct, molar-type paraconid, a metaconid that is similar in size to the protoconid, and a distinct trigonid basin; in having a p4 that is at least 80% the size of m2 in occlusal area); in having more complex lower molars with greater crown relief and crenulated enamel; in having an I1 with greatly reduced/absent laterocone, a long anterocone (over 40% of total crown length); and in having a deep gash across the whole depth of the tooth crown on the labial margin of upper molars, at the mesial base of the mesostyle.

*PLATYCHOEROPS BOYERI*, sp. nov.

(Figs. 6, 7)

v. 2014 *Platychoerops* sp.: Smith et al., 2014:fig. 6i.

**Holotype**—RIV.PPV0719, RI1.

**Referred Material**—RIV.PPV0707, LI1; RIV.PPV0562, RM2; RIV.PPV1031, LM2; RIV.PPV0691, fragment of L dentary with p3–m1; RIV.PPV0880, Lp4; RIV.PPV0658, Rm2.

**Occurrence**—Latest Paleocene of Petit-Pâtis quarry, Rivecourt, France.

**Diagnosis**—Differs from all other species of *Platychoerops* by the absence of a paraconid on p4, by the longer lingual slope of the protocone of M2, and by the slightly inflated base of the cusps on m2. Differs from all species save *Plat. russelli* by the more approximated paraconid and metaconid on the m2 trigonid. Further differs from *Plat. daubrei* by retaining a large posterocone on I1. Further differs from *Plat. antiquus* by the presence of an accessory crest on the oblique crisid, the more crenulated enamel, and the more fused paraconid and metaconid on m2. Further differs from *Plat. russelli* by the smaller laterocone and medially tilted anterocone of I1, and by the proportionally larger I1 relative to the molars. Further differs from *Plat. richardsoni* by the less crenulated enamel, by the more labiolingually elongated M2, and by the less developed accessory crest on the oblique crisid.

**Measurements**—See Table 2.

**Etymology**—In honor of Dr. Douglas M. Boyer (Duke University), who recently described the first Paleocene species of *Platychoerops*, and in recognition of his work on Plesiadapidae.

#### Description

**I1**—The I1 (Fig. 6A–G) is characterized by a long crown, with a long and acute anterocone. The tooth looks asymmetrical because the tip of the anterocone is shifted laterally. The laterocone is very small and does not form a developed cusp but rather a bulge on the lateral crest of the incisor. The mediocone is relatively small and inserted at the same level as the laterocone. There is no crest joining the laterocone and mediocone, and no centroconule. The posterocone is large, single-cusped, and

TABLE 2. Measurements (in mm) of the teeth of *Platychoerops boyeri* from the latest Paleocene of Petit-Pâtis, Rivecourt.

RIV.PPV	Tooth	L	W
0691	Lp3	3.69	3.32
0880	Lp4	3.76	3.36
0691	Lp4	4.12	3.85
0691	Lm1	4.67	3.92
0658	Rm2	6.39	4.87
0707	LI1	10.9*	5.95
0719	RI1	—	5.87
0562	RM1	5.18	7.88
1031	LM1	5.16	7.60

Abbreviations: **L**, length; **W**, width; \*, estimated measurement.

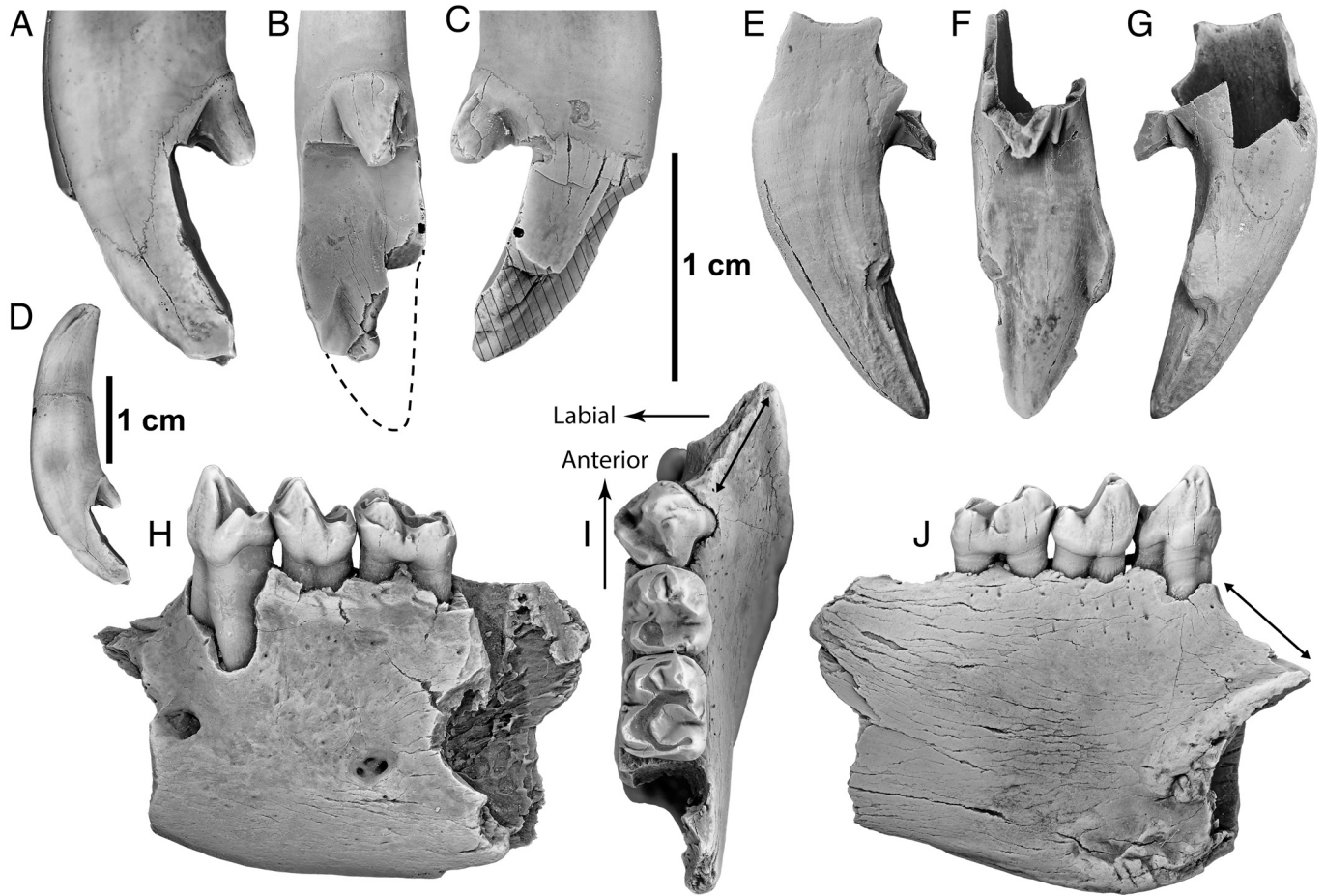


FIGURE 6. The plesiadapid *Platychoerops boyeri*, sp. nov., from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A–D**, LI1, RIV.PPV0707; **E–G**, RI1, RIV.PPV0719 (holotype); **H–J**, fragment of L dentary with p3, p4 and m1, RIV.PPV0691. Double-headed arrows indicate the position of the diastema between the incisor and p3. Dashed line represents a hypothetical reconstruction of the tip of the incisor, and dashed area indicates breakage surface. Views are lateral (A, D, G), occlusal (B, F, I), medial (C, E), labial (H), and lingual (J).

situated on the medial margin of the base of the crown. The root is thick and slightly curved dorsoventrally.

**M2**—The M2 (Fig. 7A–D) is dilambdodont and has crenulated enamel. The paracone and metacone have similar dimensions. There is a marked mesostyle. The labial margin of the tooth forms two distinct, rounded lobes, separated by a deep gash at the anterior base of the mesostyle. The preparacrista is directed anteriorly and slightly labially. The postmetacrista is directed posterolabially. The protocone is larger than the paracone. The conules are very weakly developed. There is a relatively large pseudohypocone, linked to the protocone by a crest. A lingual cingulum around the protocone seems to have been present, although the wear has erased most of it.

**Dentary**—The dentary (Fig. 6H–J) is relatively deep (around four times the height of the crown of m1 under m1 and even deeper under p3). There is a relatively short diastema in front of p3, about the same length as m1, and the alveolus for i1, although broken, indicates that the tooth was particularly large. There are two dental foramina: one under the diastema, between the root of i1 and the anterior root of p3, and one under p4. The symphysis ends posteriorly at the level of the anterior root of p3.

**p3**—The only known p3 (Fig. 7E–G, K–M) is implanted askew in the dentary, so that its morphology may be influenced by this abnormality. It is only slightly smaller than the p4. The trigonid is twice the height of the talonid and is mainly composed of a protoconid, although a small cuspidate metaconid is visible, markedly lower than the protoconid. There is no paraconid, but

an anterior crest running from the tip of the protoconid to a paracingulum. The talonid is composed of two cusps. The oblique cristid runs from the hypoconid up to the tip of the protoconid. There is a postmetaconid cristid but no entocristid, so that the short talonid basin is open lingually.

**p4**—The p4 (Fig. 7E–G, K–M) is semimolariform to molariform. The trigonid is much higher than the talonid, but of similar length. The metaconid and protoconid are similarly sized and relatively well separated. Two crests run anteriorly from the tips of the metaconid and protoconid, respectively, and meet at the position of a paraconid, although no formed cusp is visible. The talonid is slightly wider than the trigonid and bears three cusps, although the hypoconulid is markedly smaller than the hypoconid and entoconid. The oblique cristid is sharp and runs from the hypoconid up to the tip of the protoconid. The entocristid is faint to nonexistent and the talonid basin is therefore open lingually.

**m1**—The only known m1 (Fig. 7E–G) is worn. The trigonid is only slightly higher than the talonid and is composed of three large individualized cusps. The protoconid is almost as anteriorly situated as the paraconid, and there is a marked paracristid. The metaconid is implanted markedly more posteriorly than the protoconid and seems to have been of similar dimensions. There is a marked anterior cingulum circling the trigonid from its anterolingual margin to the hypoflexid, with a small cuspidule in this hypoflexid. The talonid is as long as the trigonid. The hypoconid is the largest of the three talonid cusps, whereas the hypoconulid is the smallest. The oblique cristid reaches the posterior wall of the trigonid halfway

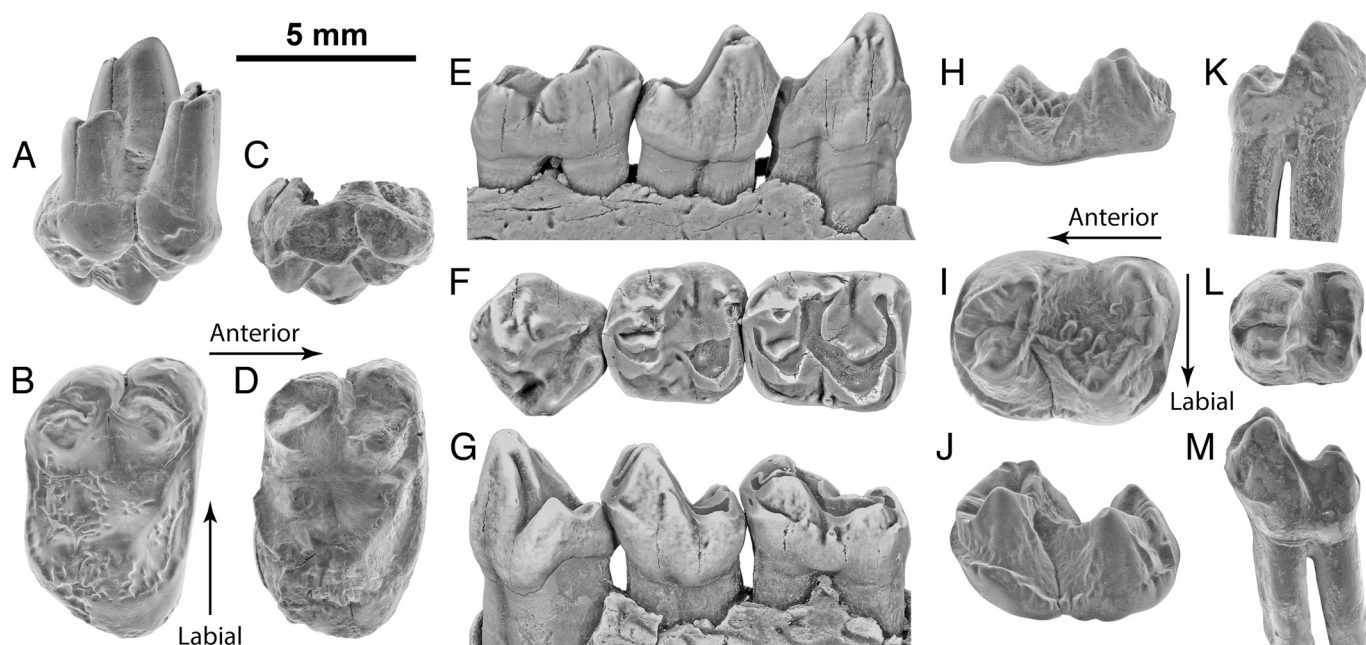


FIGURE 7. The plesiadapid *Platychoerops boyeri*, sp. nov., from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A, B**, RM2, RIV.PPV0562; **C, D**, reversed LM2, RIV.PPV1031; **E–G**, teeth of a fragment of L dentary with p3, p4, and m1, RIV.PPV0691; **H–J**, reversed Rm2, RIV.PPV0658; **K–M**, Lp4, RIV.PPV0880. Views are labial (A, C, G, J, M), occlusal (B, D, F, I, L), and lingual (E, H, K).

between the protoconid and the metaconid. The relatively small talonid basin is wide open lingually due to the absence of an entoconid. The hypoconulid is placed slightly closer to the entoconid than to the hypoconid. The entoconid is inserted posteriorly to the hypoconid. There is a small cingulum at the posterior base of the hypoconid, but not encircling it labially. The enamel seems only lightly crenulated, although the wear could be masking part of it.

**m2**—Unlike the m1, the m2 (Fig. 7H–J) has strongly crenulated enamel and is distinctly larger (35% longer and 25% wider). Further differences or additional characters unobservable on the m1, due to its wear, include the following: The paraconid and metaconid are almost fused together and there is an accessory cuspid at the place usually occupied by the paraconid. Crests link the tips of the trigonid cusps, delimiting a relatively large enclosed basin. The talonid is longer and wider than the trigonid. The sharp oblique cristid ascends the posterior wall of the trigonid up to the notch of the protocristid. There is an accessory crest bifurcating from the oblique cristid at its lowest point and aiming posterolingually; where the two crests meet a small tubercle is visible.

### Morphological Comparisons

The two broken incisors stand apart from other plesiadapid specimens from Petit-Pâtis by their much larger size and were therefore the first specimens to be noticed. The morphology of the best-preserved incisor crown (RIV.PPV0719) differs from that of all species of *Plesiadapis* by the very small laterocone and the medially shifted anterocone, which is also longer—i.e., the length between the tip of the anterocone and the insertion point of the laterocone is similar to that between the insertion point of the laterocone and the base of the posterocone. This morphology is typical of *Platychoerops*, a genus that was until recently believed to be restricted to the Eocene (see Boyer et al., 2012a). Specimen RIV.PPV0719 differs from the incisor of *Plat. russelli* (MP8+9, Meudon, France) by the proportionally shorter crown, by the larger posterocone (primitive character), by the anterocone being slightly more medially tilted (primitive

character), and by the proportionally slightly smaller laterocone (derived character). It differs from that of *Plat. daubrei* (MP8+9, Paris Basin, France) by the less asymmetrical apex, by the presence of a vestigial laterocone (both primitive characters), and by the proportionally slightly longer crown. The posterocone of *Plat. daubrei* is vestigial in the type locality of Mutigny, but specimens referred to *Plat. daubrei* from Pourcy (likely slightly older than Mutigny) do feature a distinctly larger posterocone. Morphologically, the specimen is therefore intermediate between *Plat. daubrei* and *Plat. russelli*. The size is similar to that of *Plat. daubrei* and slightly smaller than that of *Plat. russelli*. Upper incisors of other species of *Platychoerops* are unknown. Both I1s differ from those of all species of *Plesiadapis* by the proportionally smaller posterocone (except in *Ples. cookei*). Moreover, RIV.PPV0719 differs by the very small laterocone, and by the proportionally longer anterocone (less than 35% of the total crown length in all species of *Plesiadapis*, but more than 40% of the crown length for all species of *Platychoerops* whose I1 is known).

The upper molars are referred to *Platychoerops* because of their significantly larger size than those of *Ples. ploegi*, their deeply incised labial margin, and the pseudohypocone that is markedly larger than on all species of *Plesiadapis*. Given their width-to-length ratio, the shape of the posterolingual margin, and their size compared with lower molars, both upper molars are considered to be M2s. Their size and morphology are very similar to those of *Plat. russelli*, thus suggesting an incisor proportionally slightly smaller relative to the molars in *Plat. boyeri*. The only minor differences from *Plat. russelli* are the slightly more developed pseudohypocone and the longer lingual slope of the protocone. The M2 of *Plat. boyeri* differs from that of *Plat. daubrei* by being proportionally wider, which is mainly due to a wider profossa, and by the markedly smaller conules of *Plat. daubrei*. The new species is markedly smaller than *Plat. richardsoni* (MP8+9, Herne Bay, U.K.), from which it further differs by the larger pseudohypocone, longer lingual slope of the protocone, larger conules, and lesser crenulation of the enamel. The upper dentition of *Plat. antiquus* (MP6a, Berru, France) is unknown.

The dentary fragment RIV.PPV0691 (Figs. 6H–J, 7E–G) seems to bear teeth that are slightly too small to match the other specimens of *Plat. boyeri*, especially when comparing the size of its m1 with that of the isolated m2. This isolated m2 also has markedly more crenulated enamel. Nevertheless, the isolated p4 RIV.PPV0880 (Fig. 7K–M) is markedly more molariform than all those referred to *Ples. ploegi* and matches that of the dentary in size and morphology (notably in the absence of paraconid). The absence of visible wrinkles on the enamel of the m1 (Fig. 7F) can easily be explained by the more extensive wear of the teeth, especially because m1 is usually less crenulated than m2 (e.g., in *Plat. richardsoni* and *Ples. ploegi*). The extensive size difference between m1 and m2 is here considered characteristic of *Plat. boyeri*, but additional specimens are needed to statistically confirm this observation.

The isolated p4 referred to the new species is only slightly larger than those of *Ples. ploegi* from Petit-Pâtis, but it differs by being significantly more molariform, with a large talonid basin, by well-separated protoconid and metaconid and larger metaconid, and by the wider and longer trigonid basin. These characters are apomorphies of *Platychoerops* relative to *Plesiadapis* (Boyer et al., 2012a). The p4s of *Plat. boyeri* differ from that of *Plat. antiquus* by the absence of the paraconid, the trigonid that is narrower than the talonid, and the shorter talonid. They differ from those of *Plat. daubrei* by the absence of the paraconid, the smaller trigonid basin, less marked hypoconulid, and less sharp cusps on the whole tooth. *Plat. richardsoni* differs by being larger, markedly more molariform, and by having a large paraconid, much like that of *Plat. daubrei*. The p4s of *Plat. boyeri* are morphologically closest to that of *Platychoerops* sp. from Abbey Wood (Hooker, 2010:fig. 20d–f), from which it differs by the slightly wider talonid and the less oblique oblique cristid. The p4 of *Plat. russelli* is unknown.

The m2 is significantly larger than lower molars of any species of *Plesiadapis*. It seems to be closest to that of *Plat. richardsoni*, from which it differs by the more fused paraconid and metaconid and by being proportionally wider. The paraconid and metaconid of m2 are more approximated (primitive character?) in *Plat. russelli* and *Plat. boyeri*, but less so in *Plat. antiquus*, *Plat. daubrei*, and *Plat. richardsoni*. The m2 of *Plat. boyeri* differs from that of *Plat. russelli* by the slightly more inflated cusps, by being proportionally wider, and by the slightly less developed hypoconid. It differs from that of *Plat. daubrei* by the proportionally shorter trigonid. It differs more strongly from that of *Plat. antiquus*, mainly by the paraconid that is almost fused to the metaconid, by the more crenulated enamel, by the more marked crests, and by the more posterior insertion of the entoconid.

#### Genus *CHIROMYOIDES* Stehlin, 1916

**Type Species**—*Chiromyoides campanicus* Stehlin, 1916.

**Other Known Species**—*Chiromyoides caesor* Gingerich, 1973; *Chiromyoides minor* Gingerich, 1975; *Chiromyoides potior* Gingerich, 1975; *Chiromyoides major* Gingerich, 1975; *Chiromyoides gingerichi* Secord, 2008; *Chiromyoides gigas* Burger and Honey, 2009; *Chiromyoides mauberti*, sp. nov.

**Occurrence**—Late Paleocene of Europe and North America.

#### *CHIROMYOIDES MAUBERTI*, sp. nov.

(Figs. 8, 9)

v. 2014 *Chiromyoides* sp.; Smith et al., 2014:fig. 6h.

**Holotype**—RIV.PPV1102, right dentary with i1 and m1–m2.

**Referred Material**—RIV.PPV0572, R11; RIV.PPV0660, R11; RIV.PPV1044, L11; RIV.PPV0672, Lm2; RIV.PPV0700, LM2; RIV.PPV0631, left dentary with m2–m3; RIV.PPV0682, left

TABLE 3. Measurements (in mm) of the teeth of *Chiromyoides mauberti* from the latest Paleocene of Petit-Pâtis, Rivecourt.

RIV.PPV	Tooth	L	W
372	p4	1.98	2.28
572	I1	4.2*	2.74
573	i1	8.5*	3.47
657	m3	3.75	2.52
660	I1	4.58	3.01
672	m2	2.77	2.69
682	m3	4.34	2.80
700	M2	2.24	2.99
1044	I1	4.33	3.23
1101	m1	2.26	2.07
1101	m2	2.53	2.38
1101	m3	3.87	2.52
1102	i1	7.54	2.72
1102	m1	2.28	2.26
1102	m2	2.59	2.56

Abbreviations: **L**, length; **W**, width; \*, estimated measurement.

dentary fragment with m3; RIV.PPV1101, right dentary with m1–m3 (cast); RIV.PPV0573, L11; RIV.PPV0372, Rp4; RIV.PPV0657, Lm3.

**Occurrence**—Latest Paleocene of Petit-Pâtis quarry, Rivecourt, France.

**Diagnosis**—Differs from all other species of *Chiromyoides* by the I1 bearing several posterocones, the curved margocristid on i1, and the presence of a small metaconid on p4. Differs from *C. campanicus* by its smaller size, shallower dentary, and shorter m3 relative to m1 and m2.

**Measurements**—See Table 3.

**Etymology**—In honor of François Maubert, property manager for the company Lafarge Granulats, for his outstanding logistic support, much appreciated during the field work.

#### Description

A small species of plesiadapid represented by a few lower jaw fragments and several isolated teeth, including upper incisors.

**I1**—The crown of the I1 (Fig. 9A–C) is short anteroposteriorly, and the tip of the anterocone is rounded. The laterocone and mediocone are similarly sized and inserted at nearly the same height on the crown; they are linked by a ‘V’-shaped crest crossing the crown but not developing into a centroconule. The posterocone is relatively small and is flanked medially and laterally by several accessory cusps. These cusps are only slightly smaller than the posterocone and delimit a shelf along the whole width of the tooth.

**M2**—The only other upper tooth identified is an M2 (Fig. 9D–E) based on the shape of the anterior labial cingulum, the length of the lingual slope of the protocone, and the size relative to the lower molars. The crown displays a relatively flat surface, with rather low cusps. The paracone and metacone are equally sized and occupy a similar occlusal space. The centrocrista is ‘T’-shaped, connecting the tips of the paracone and metacone by a straight line, with an accessory crest linking the small mesostyle to the lowest point of the crest linking paracone and metacone. The styler shelf is reduced to a cingulum and accounts for 20% of the width of the tooth. The preparacrista and postmetacrista are marked and straight and aligned anteroposteriorly. The relatively large paraconule is placed at equal distances from the paracone and protocone, and anterior to the paracone. The smaller metaconule is situated close to the base of the metacone and on the straight crest linking the metacone to the paracone. The crests delimiting the basin, especially the postprotocrista, are relatively sharp. The protocone is larger than the paracone and metacone, but not taller. The precingulum is well developed.

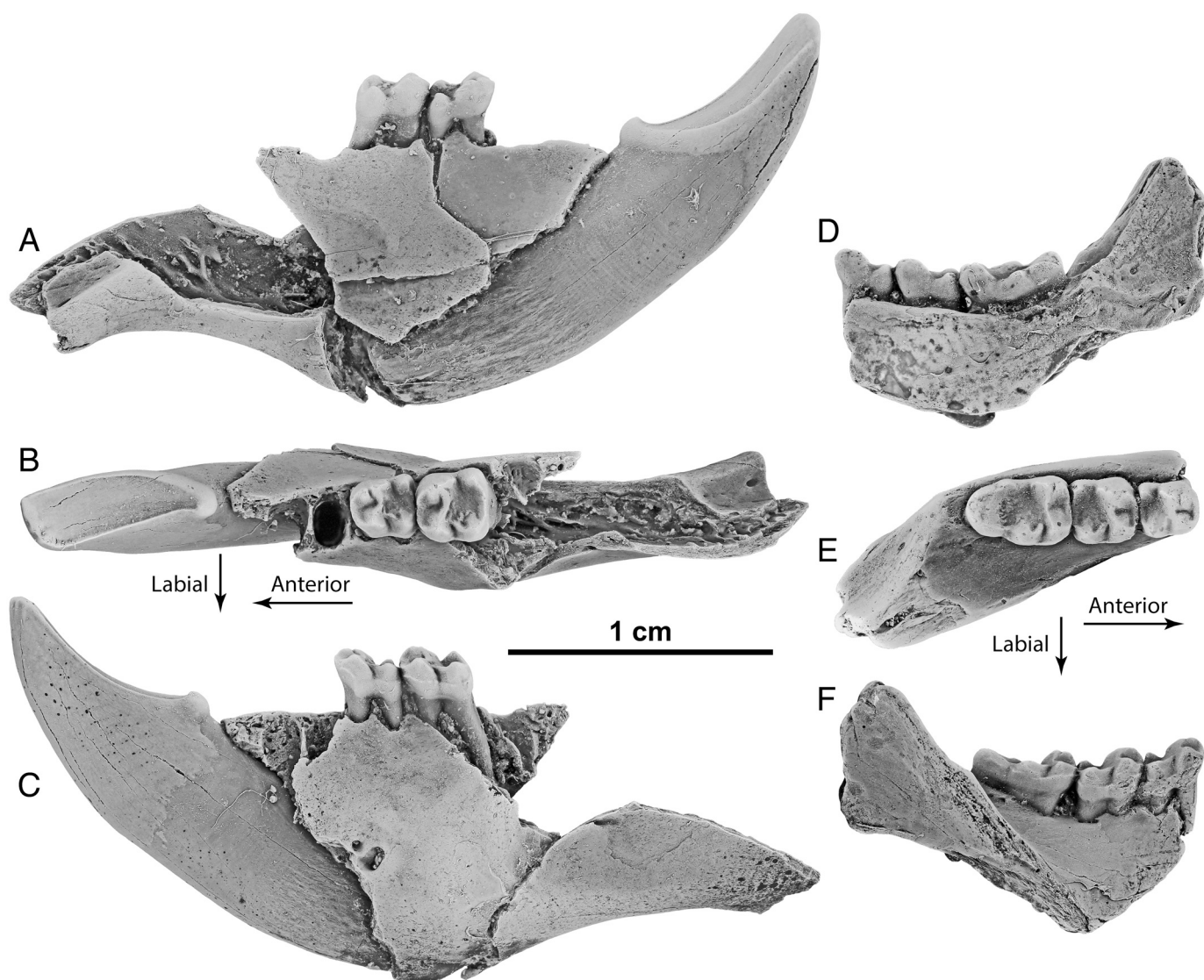


FIGURE 8. The plesiadapid *Chiromyoides mauberti*, sp. nov., from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A–C**, fragment of L dentary with i1 and m1–m2, RIV.PPV1102 (holotype); **D–F**, fragment of R dentary with m1–m3, RIV.PPV1101 (cast). Views are labial (A, D), occlusal (B, E), and lingual (C, F).

The postcingulum is wide and delimited by a crest running posteriorly from the top of the protocone and widely curving labially. There is no formed pseudohypocone. The lingual slope of the protocone is relatively long and only gently curved.

The holotype RIV.PPV1102 (Fig. 8A–C) preserves a good part of the dentary. This dentary is characterized by a very great depth (estimated at six times the height of the crown of m1). Based on the alveoli, p3 and p4 were uniradicate and the diastema between i1 and p3 was very short if present.

**i1**—The i1 (Fig. 8A–C) is preserved in place on one dentary, and an additional isolated i1 was identified. These teeth are both spade-shaped, characterized by the presence of a small, distinct margoconid and a slightly curved margocrisid.

**p4**—The p4 (Fig. 9F–H) has a tall, long trigonid and a very short but wide talonid. Three cusps are discernible on the trigonid, although they are inflated and partly fused. The paraconid is small and labially placed. The metaconid and protoconid have similar heights and occlusal surfaces. No individual cusps are visible on the talonid, which is almost reduced to a cingulum without basin. The posterior margin of the tooth is straight.

**m1**—The trigonid of the m1 (Figs. 8A–F, 9I–K) has a straight anterior margin and is barely taller than the talonid. The paraconid is well developed but in relatively close approximation to the metaconid. A ‘U’-shaped crest links the tips of the paraconid and protoconid by running along the anterior margin of the tooth. The talonid is wider than the trigonid and bears two similarly sized cusps, a hypoconid and an entoconid; however, the hypoconulid is not visible. The oblique cristid is not very oblique, directed towards the tip of the protoconid without reaching it. The entocristid is absent, and the talonid basin is consequently open lingually.

**m2**—The m2 (Figs. 8A–F, 9I–K) is as long as but significantly broader than the m1. The paraconid is completely fused to the protoconid, the trigonid slightly more compressed anteroposteriorly than on m1, and its anterior margin is straighter.

**m3**—The m3 (Figs. 8D–F, 9L–N) is characterized, as in all plesiadapids, by an elongation of the talonid. It differs from the m2 by the trigonid being more compressed anteroposteriorly and the expanded hypoconulid lobe, which is rounded, symmetrical, and not split.

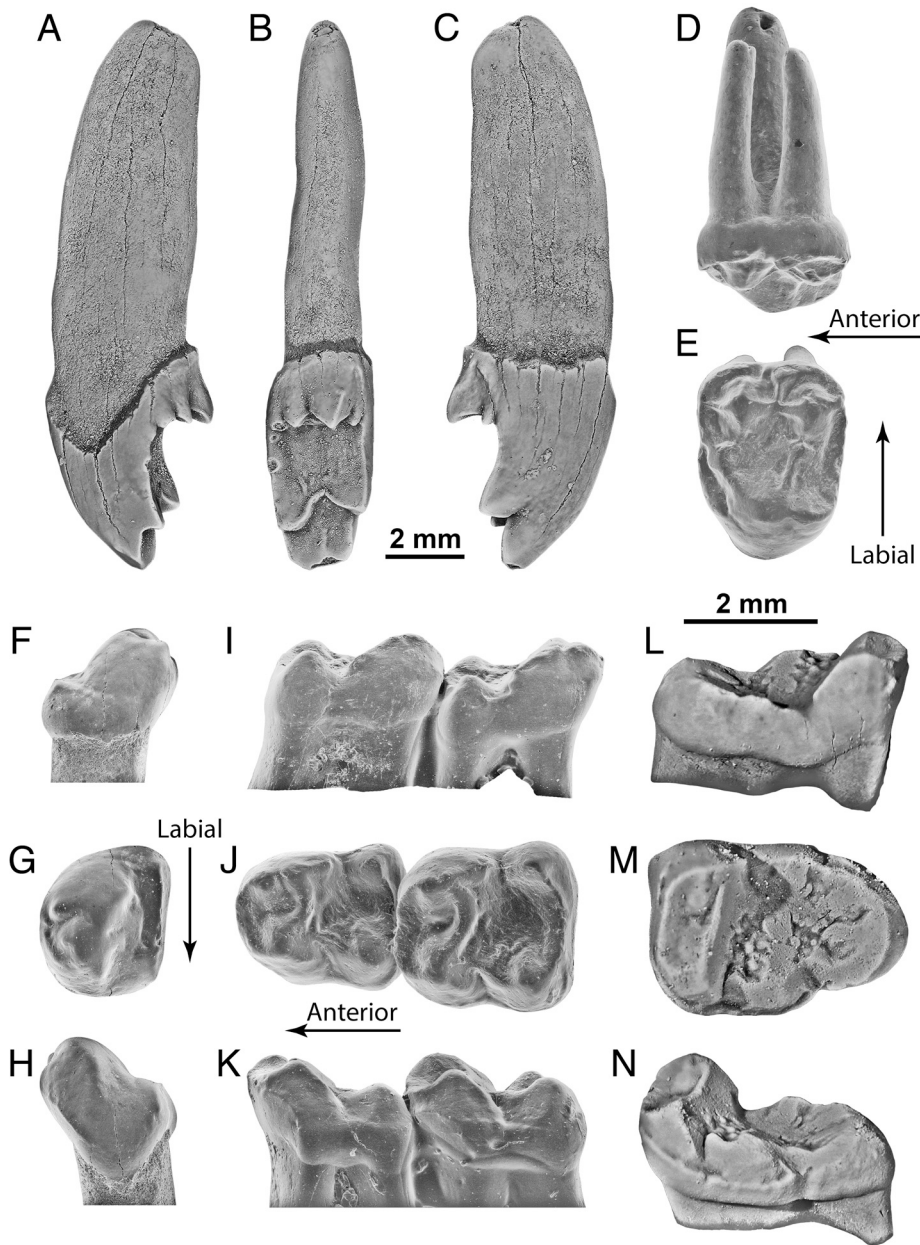


FIGURE 9. The plesiadapid *Chiromyoides mauberti*, sp. nov., from the latest Paleocene of Petit-Pâtis, Rivecourt, France. **A–C**, R11, RIV.PPV0572; **D–E**, LM2, RIV.PPV0700; **F–H**, reversed Rp4, RIV.PPV0372; **I–K**, teeth of a fragment of L dentary with m1–m2, RIV.PPV1102 (holotype); **L–N**, left m3, RIV.PPV0682. Views are lateral (C), occlusal (B, E, G, J, M), labial (A), labial (D, H, K, N), and lingual (F, I, L).

### Morphological Comparisons

The upper incisor has an unusual morphology in being almost symmetrical, bearing several small posterocones linked by a crest and delimiting a small platform, instead of the single, larger posterocone observed on most plesiadapids. The only species that display comparable incisor morphology are *Chiromyoides campanicus*, known from Cernay and Berru (MP6a), and ‘*Platychoerops georgei*, from the earliest Eocene (MP7) of Try, Dormaal, Erquennes, and the Suffolk Pebble Beds (Hooker, 1994). In *C. campanicus*, the posterocone region bears a main cusp and displays a few small accessory cusps along the crests running medially and laterally, whereas in the species from Petit-Pâtis these accessory cusps are larger and more numerous. In both species, the laterocone and mediocone are similarly sized and linked by a marked crest. These two features clearly distinguish *Chiromyoides* from *Plesiadapis* and *Platychoerops*. North American species of

*Chiromyoides* all have a single large posterocone. ‘*Platychoerops georgei*’ is likely a composite species (see discussion in Godinot et al., 1998; Boyer et al., 2012a; this paper). Its holotype upper I1 is somewhat similar to that of *C. campanicus* in that the tooth, despite its incompletely preserved posterocone region, seems to have borne a small shelf at the base of the posterocone. It differs from that of *C. campanicus* and from the specimens from Petit-Pâtis in that the laterocone is markedly larger than the mediocone, a character that is more consistent with the genus *Plesiadapis*. The incisors of ‘*Plat.*’ *georgei* and *C. campanicus* are very similar in size (crown length around 5.5 mm from the tip of the anterocone to the base of the posterocone) and markedly larger than that of *C. mauberti* from Petit-Pâtis (crown length of 4.25 mm).

The upper molar is attributed to *C. mauberti* because it matches the incisor and lower molars in size and because morphologically it is similar to the upper molars of *C. campanicus*. In particular, both species share the ‘T’-shaped centrocrista and the wide and rounded



## DISCUSSION

Variability in Size and Morphology of *Plesiadapis*

crest delimiting the postcingulum. The upper molar from Petit-Pâtis differs from that of *C. campanicus* by the larger precingulum and the smaller size (length 2.23 vs. 2.7 mm). The upper molars of *Chiromyoides caesor* (see Winterfeld, 1982; Secord, 2008) are slightly smaller, have more labially placed paracone and metacone, even lower cusps, a more marked postmetaconule crista but no postparaconule crista, and are overall more asymmetrical. The upper molars referred to '*Plat.* *georgei*' are very different, much closer in morphology to those of species of *Plesiadapis* and *Platychoerops*, with a typical 'V'-shaped centrocrista, strongly crenulated enamel, and small pseudohypocone.

Part of the dentary is preserved on two specimens. It is particularly deep and short, far deeper than on species of *Plesiadapis*, although not as deep as in *C. campanicus*.

The i1 is proportionally slightly shorter than the i1s attributed to *Ples. ploegi*, from which it further differs by the presence of a margoconid, by a curved margocristid, and by having an occlusal surface that is more tilted relative to the axis of the root. The size of the i1 relative to the m1 is very similar to that observed in *C. campanicus*, with a 3:1 ratio, and the occlusal surface is similarly tilted relative to the axis of the root. However, the margoconid of *C. campanicus* is distinctly larger and its margocristid is straight.

The p4 is similar to that of *C. campanicus* in that it is mainly composed of a wide, rounded trigonid with partially fused cusps and a talonid basin reduced to a very wide and short cingulum. It differs from that of *C. campanicus* by being proportionally longer and by retaining a distinct, small metaconid. It differs from that of *C. caesor* also by retaining a slightly distinct metaconid, by a rounded instead of a triangular outline, and by the absence of crests on the posterior wall of the trigonid.

The lower molars are mostly similar to those of *C. campanicus*. They share the relatively straight anterior margin of the trigonid, the extended width, the paraconid visible only on m1 and partially fused to the metaconid, and the indistinct hypoconulid on m1–m2. The differences from the lower molars of *C. campanicus* include the proportionally longer m1 and m2, but shorter m3 with less expanded talonid, the less developed hypoconid, the straighter anterior margin of the trigonids (especially m3), the less oblique posterior wall of the trigonid of m3, and the less square, narrower hypoconulid lobe of m3. The lower molars differ from those of *C. caesor* by the oblique cristid being less oblique, by the wider m1 talonid, by the m2 paraconid being completely fused to the metaconid, and by the shorter m3 talonid with less protruding hypoconid. *Chiromyoides minor* (Tiffanian, Wyoming, U.S.A.) differs from *C. mauberti* by having proportionally shorter trigonids and a wider m3 talonid with twinned hypoconulid (see Gingerich and Dorr, 1979).

All in all, the resemblances to *C. campanicus* are much stronger than to any other plesiadapid, but the differences make *Chiromyoides mauberti* easily recognizable as a distinct species.

At Petit-Pâtis, the dimensions of the species of *Plesiadapis* are overall intermediate between those of *Ples. tricuspidens* from Cernay and *Ples. tricuspidens* from Berru, with the exception of I1s, M2s, and m3s, which are more similar to the dimensions from Cernay than to those from Berru, i.e., smaller, and of p4s that are larger even than those from Berru. On average, the specimens from Petit-Pâtis are proportionally slightly less developed transversally (more visible for m2 and M1). The coefficients of variation of the teeth of *Ples. ploegi* from Petit-Pâtis (see Table 1) are similar to those observed in communities of living and fossil primates (e.g., Gingerich and Schoeninger, 1979), thus arguing for the presence of only one species of *Plesiadapis* in Petit-Pâtis.

Morphological variability is illustrated in Figure 5. The p4 sometimes features a small paraconid, sometimes just crests; the orientation of the posterior margin is either perpendicular to the anteroposterior axis of the tooth or inclined so that the lingual side is extended posteriorly. Lower molars always feature a short accessory crest in the talonid basin. The m1 width, especially its talonid width, is more variable than its length. The enamel of m2s is always more crenulated than that of m1s, and the degree of approximation of the paraconid and metaconid and the relative width of the trigonid vary a little. Unsurprisingly, the m3 is the most variable lower cheek tooth (e.g., Gingerich, 1974), with variability notably in the relative length of the trigonid, the relative and absolute width of the talonid, and the shape of its posterior margin. The P4s differ in their relative width, the degree of separation of the paracone and metacone, and the morphology of the postprotocrista. The upper molars all feature a shallow notch in their labial margin, except the M1 RIV.PPV0642 (Figs. 2H–I, 5U) where this indentation is absent; all upper molars vary in the shape of their labial margin and in the length of the lingual slope of the protocone. On most upper molars, the postparacrista and premetacrista barely join before reaching the labial margin, except in one M2 (Fig. 5X) where the junction is more lingual.

Evolution of the Dentition in *Plesiadapis* and *Platychoerops*

The evolutionary transition between the genera *Plesiadapis* and *Platychoerops* in terms of the morphology of their cheek teeth was recently reviewed (Boyer et al., 2010). The molarization of the p4 (see Fig. 10), associated with the development of crests on lower molars, is considered to be the result of an adaptive shift towards a folivorous diet (Gingerich, 1976; Boyer et al., 2010). Although derived species of *Plesiadapis*, as well as all species of *Platychoerops*, feature semimolariform to molariform p4s, the oldest species of *Platychoerops* (*Plat. antiquus*) features a developed paraconid, whereas the slightly younger *Plat. boyeri* does

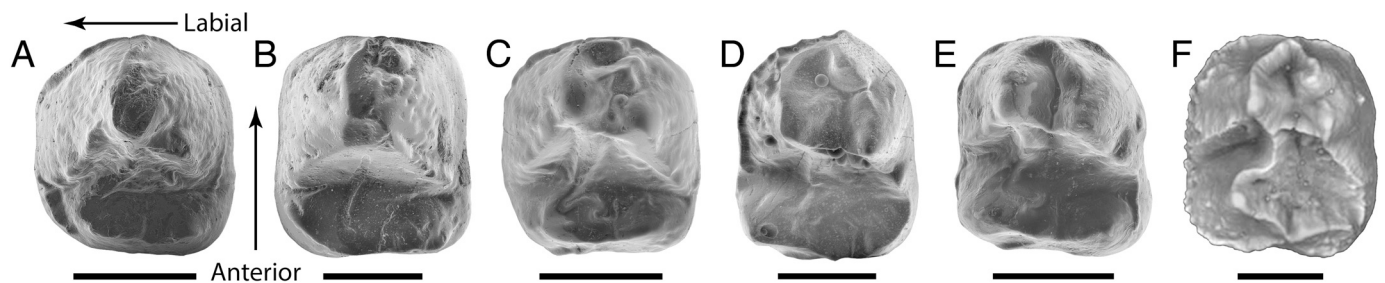


FIGURE 10. Comparison of p4s of *Platychoerops* spp. and derived species of *Plesiadapis*. **A**, *Plesiadapis tricuspidens*, IRSNB M2301 from Berru, France. **B**, *Plesiadapis cookei*, cast of PU13293 from Little Sand Coulee, Wyoming (holotype). **C**, *Plesiadapis ploegi*, sp. nov., RIV.PPV0620 from Petit-Pâtis, France. **D**, *Platychoerops antiquus*, cast of NMB Bru 4 from Berru, France (holotype, reversed). **E**, *Platychoerops boyeri*, sp. nov., RIV.PPV0880 from Petit-Pâtis, France. **F**, *Platychoerops daubrei*, MNHN AL-J from around Reims, France, reversed. All views are occlusal, G from Boyer et al. (2010). Scale bars equal 2 mm.

not; neither do the most derived species of *Plesiadapis*, *Ples. cookei*, and *Ples. ploegi*. The dilambdodonty of upper molars is also more marked in *Platychoerops* and derived species of *Plesiadapis* such as *Ples. cookei* and *Ples. ploegi*. Meanwhile, the I1 has a smaller mediocone but a relatively large laterocone on *Ples. cookei* and *Ples. ploegi*, whereas the laterocone, where observable, is vestigial to absent on all species of *Platychoerops*. Lower molars of all species of *Platychoerops* except *Plat. antiquus* have a marked additional crest in the talonid, branching from the oblique cristid. This crest is adumbrated by a tubercle or very short crest in *Plat. antiquus*, *Ples. cookei*, *Ples. ploegi*, and some specimens of *Ples. fodinatus* and *Ples. tricuspidens*. The upper molars of derived species of *Platychoerops* all feature a deep incision on the labial margin of their upper molars, across the whole depth of the enamel. This character is not obviously linked to an adaptation to folivory, but it characterizes all European plesiadapids of the latest Paleocene to early Eocene: some specimens of *Ples. tricuspidens*, most specimens of *Ples. ploegi*, and all specimens of *Platychoerops* spp. North American species, however, do not display this character; nevertheless, the depth of the indentation is variable across species, within species, and even between tooth positions of the same individual.

As a result, it is plausible that at least two lineages developed these adaptations to folivory convergently: one lineage with an I1 keeping the laterocone and a p4 bearing crests but no paraconid, grouping *Ples. cookei* and *Ples. ploegi*; the other lineage with I1 without laterocone and a p4 with paraconid, grouping *Plat. antiquus*, *Plat. daubrei*, *Plat. russelli*, and *Plat. richardsoni*. *Plat. boyeri* is intermediate between these two putative lineages, having an already derived, *Platychoerops*-style I1, but still no paraconid on p4.

Furthermore, evolution towards folivory—including the simplification of I1, the development of crests on upper and lower molars, and the molarization of p4—possibly occurred in parallel in North America and in Europe. *Ples. cookei* would then be the most specialized North American plesiadapid, whereas *Ples. ploegi* would be the closest relative of the European *Platychoerops* clade instead of *Ples. cookei* as proposed previously (e.g., Russell, 1964; Gingerich, 1976; Boyer et al., 2012b). This hypothesis reduces the need for intercontinental dispersal to explain a relationship between *Ples. cookei* and *Platychoerops* but is not parsimonious in terms of character evolution.

### Identification of the Specimens Belonging to ‘*Platychoerops georgei*’

As first implied by Godinot et al. (1998), and explicitly proposed and convincingly discussed in Boyer et al. (2012a), the species named *Platychoerops georgei* Hooker, 1994, is very likely a chimera. The type specimen of ‘*Plat.*’ *georgei* is an I1 from Try (France). The locality has delivered mammal specimens from at least two different levels: one featuring typical MP6a taxa such as *Pleuraspidotherium aumonieri* and *Orthaspidotherium edwardsi*, whereas the other definitely has Eocene affinities, with the presence of *Coryphodon* and *Cymbalophus cuniculus* (see Louis et al., 1983; Hooker, 1994; Louis, 1996). According to Hooker (1994), the specimens of ‘*Plat.*’ *georgei* likely come from the upper level (i.e., early Eocene) because *Platychoerops* was then known only from the Eocene; however, specimens of *Platychoerops* are now reported from the late Paleocene of Berru (Boyer et al., 2012a) and from the latest Paleocene of Petit-Pâtis (Smith et al., 2014; this paper).

The tricuspid morphology of the type I1 is clearly typical of Plesiadapidae (see Fig. 11) and was considered to be very similar to that of *Chiromyoides* by Hooker (1994) and Boyer et al. (2012a). However, its large laterocone, significantly larger than the mediocone, is consistent in Europe only with the genus *Plesiadapis*. Nevertheless, the posterocone region, although broken, is too large to have borne a single cusp. Only in European *Chiromyoides* (*C.*

*campanicus* and *C. mauberti*) is the posterocone flanked by accessory cusps. Unlike in ‘*Plat.*’ *georgei*, the laterocone and mediocone are of similar sizes in all species of *Chiromyoides*. The I1s of ‘*Plat.*’ *georgei* are characterized by a relatively short crown with rounded apex, which is compatible with *Chiromyoides*: the crown is broader and slightly deeper than in species of *Plesiadapis*, although not as deep as in other species of *Chiromyoides*. Hooker (1994) noted that the crest linking laterocone to mediocone was only observed in *Chiromyoides*, but *Ples. ploegi*, as well as some specimens referred to *Ples. tricuspidens*, also features such a crest, which is, on the other hand, totally absent from other described species of *Platychoerops* (where the tooth is known). It is, moreover, unlike any described I1s of *Platychoerops*, all characterized by a very simplified morphology without developed laterocone. Meanwhile, up to now, *Plesiadapis* and *Chiromyoides* are known only during the Paleocene, whereas ‘*Plat.*’ *georgei* is supposedly from the earliest Eocene. As part of the taxa reported from Try are of typical Paleocene affinities and the exact provenance of the specimens of ‘*Plat.*’ *georgei* is uncertain, it is inferred here that the I1 belongs to a species of *Plesiadapis* or *Chiromyoides*, likely coming from the lower Thanetian beds as originally supposed (Louis et al., 1983).

The M2 from Dormaal and that from Try both feature the derived character of marked dilambdodonty (more marked than in *Ples. tricuspidens*, but similar to *Ples. ploegi*). Moreover, the enamel of the tooth from Dormaal is distinctively wrinkled and its labial margin is deeply incised at the anterior base of the mesostyle, a character that all species of *Platychoerops* share, but that is not present in *Ples. tricuspidens* and barely so in *Ples. ploegi*. As a result, we concur with Gingerich (1976) and Boyer et al. (2012a) in referring this tooth to the genus *Platychoerops*; its specific position remains questionable. The M2 from Try is unfortunately too damaged to ascertain its generic attribution, but from the imperfectly preserved shallow notch at the anterior base of the mesostyle and the less crenulated enamel than on the tooth from Dormaal, it is more likely a derived *Plesiadapis* (as derived as *Ples. ploegi*).

The i1 from Erquelinnes alone does not carry enough morphological characters for specific attribution; it is very likely a Plesiadapidae, but even the generic attribution is doubtful if not based on the fact that only *Platychoerops* is reported from the European Eocene up to now, Erquelinnes being confirmed earliest Eocene (Missiaen et al., 2013).

The p4 from Try is quite typical of *Plesiadapis* (as indicated by Boyer et al., 2012a), being completely premolariform and featuring a very small metaconid and neither paraconid nor trigonid basin. It could be either the only specimen of a less derived species of *Plesiadapis* or the p4 of the species *georgei*, thus adding support to its reattribution to the genus *Plesiadapis*.

The m2 features a few characters that are more consistent with *Platychoerops*, such as the relatively distinct metaconid and paraconid and the presence of an accessory tubercle on the oblique cristid, although the crest associated to this tubercle is very short, similar to that observed in *Ples. ploegi*.

In conclusion, the rich plesiadapid fauna of Petit-Pâtis, in particular the well-preserved upper incisors and co-occurrence of *Plesiadapis*, *Platychoerops*, and *Chiromyoides*, allows reassessment of ‘*Plat.*’ *georgei* from Try. Represented only by its type I1 for the time being, it seems to be a plesiadapid that is none of the other described European species. Nevertheless, due to the fragmentary nature (posterocone region broken and occlusal area slightly worn), to the unsure provenance (Thanetian or Ypresian) of the holotype, and to its being morphologically intermediate between *Plesiadapis* and *Chiromyoides*, its generic attribution is doubtful and could be either of these two genera, but likely not *Platychoerops*. Confirming the validity of the name *georgei* would require additional specimens of the same species; in the meantime, it would be safer to consider the species ‘*Platychoerops georgei*’ a nomen dubium, awaiting more characteristic and especially

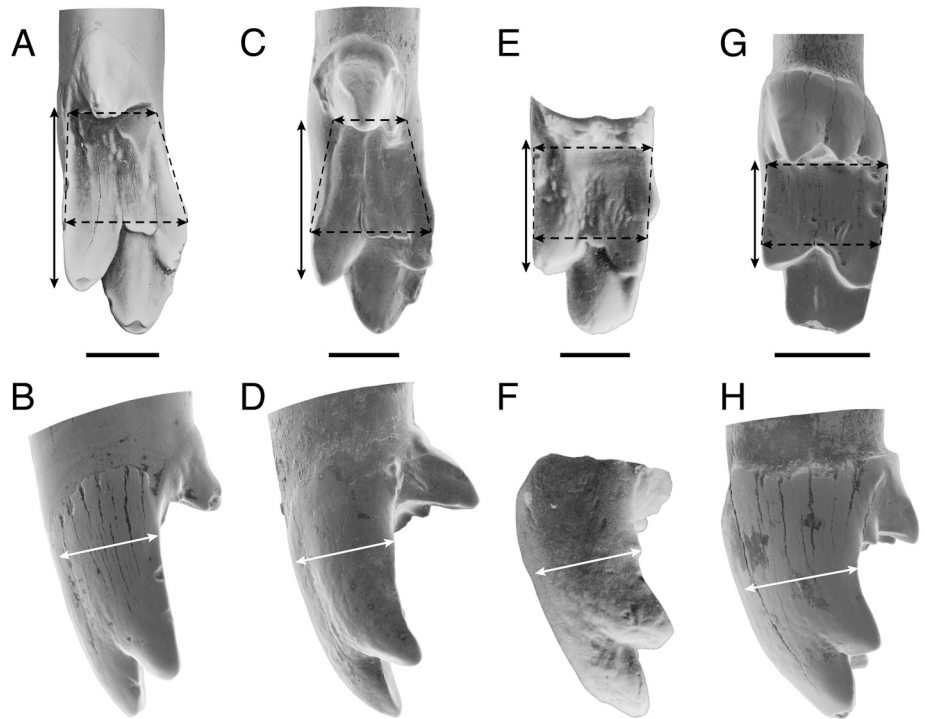


FIGURE 11. Comparison of the upper incisors of ‘*Platychoerops*’ *georgei* and other European plesiadapids from the late Paleocene. **A–B**, RIV.PPV0570, *Plesiadapis ploegi*, LI1; **C–D**, IRSNB M2302, *Plesiadapis tricuspidens*, reversed RI1; **E–F**, MNHN.TRY-18-L, ‘*Platychoerops*’ *georgei*, LI1 (from Hooker, 1994); **G–H**, RIV.PPV0572, *Chiro-myoides mauberti*, reversed RI1. Views are occlusal (A, C, E, G) and lateral (B, D, F, H). Scale bars equal 2 mm.

better-preserved specimens from the type locality of Try to designate a neotype and ascertain its generic attribution.

### Paleobiogeography

Russell (1964:fig. 12) already suggested that *Plat. daubrei* emerged from a *Plesiadapis cookei*-like lineage. This hypothesis was further tested by Boyer et al. (2012a), who reached the same conclusion.

However, the new species of *Plesiadapis* from Petit-Pâtis offers an alternative hypothesis for the emergence of *Platychoerops* in Europe. Indeed, *Ples. ploegi* is morphologically intermediate between the late Paleocene *Ples. tricuspidens* and the early Eocene *Plat. russelli*, and temporally placed between these two taxa, thus providing a morphological intermediate between *Plesiadapis* and *Platychoerops* without requiring intercontinental dispersals from North America to Europe of a *Ples. cookei*-like taxon. Nevertheless, because *Ples. cookei* is restricted to CF2, it is still possible that the dispersal occurred at that time and that the deposits of Petit-Pâtis post-date this dispersal. Still, there is no morphological evidence that *Ples. cookei* occupies an intermediate position between a *Ples. tricuspidens*-like ancestor and *Ples. ploegi*. Moreover, the existence of *Plat. antiquus* in Cernay and Berru means that the divergence between a *Ples. tricuspidens*-like ancestor and *Platychoerops* had already occurred by then; *Ples. ploegi* would thus be similar to a putative morphological intermediate between *Ples. tricuspidens* and *Platychoerops* spp. without being this intermediate taxon. Alternatively, the ecological conditions of the late Paleocene favored the parallel development of folivory in different, closely related species, so that molar complexity of Plesiadapidae increased in several lineages during the late Paleocene, thus rendering phylogenetic relationships much more complex and hard to determine based on the morphology. The genus *Plesiadapis*, present on both continents, would then have developed similar specialization towards folivory close to the PEB, but this specialization was more rapid and more refined in European species of *Plesiadapis*, allowing the family Plesiadapidae to survive for some time into the Eocene despite the arrival of competitors of modern orders. A third possibility would be the

development of two parallel lineages in Europe, developing similar adaptations to folivory. One lineage would be *Ples. tricuspidens*–*Ples. ploegi*–*Plat. russelli*, with early molarization of p4 but I1 keeping a laterocone that dwindles and migrates towards the apex of the tooth (as in *Ples. cookei*), and the other *Plat. antiquus*–*Plat. boyeri*–*Plat. daubrei*, with an I1 becoming asymmetrical and losing its laterocone early in evolution without migrating towards the tip of the crown. However, the molarization of p4 is much more similar in *Plat. antiquus* and *Plat. richardsoni* than in *Plat. boyeri*. In particular, the development of the (large) paraconid is very similar in the two former species, so that it would be strange that *Plat. boyeri*, placed temporally in between the two others, has no paraconid at all.

Meanwhile, the evolution of the genus *Plesiadapis* in Europe and North America is very similar in rate and direction during the Paleocene and has been used to estimate temporal correlation between deposits of Europe and North America (e.g., Gingerich, 1976). This parallel evolution can be explained in two ways: either (1) a dispersal route between Europe and North America was regularly open during the late Paleocene, although open only to plesiadapids, thus allowing gene flow between the continents within the family; or (2) plesiadapids dispersed once, likely from North America towards Europe (see De Bast and Smith, 2017), and underwent separate parallel evolution driven by similar adaptations to an environment changing similarly on both continents. Arguments for (1) include the similar development of seemingly independent dental characters in species from both continents. Arguments against (1) would be the difficulty of explaining the reason why plesiadapids were able to disperse whereas other similarly successful families of ‘plesiadapiforms’ and other groups occupying similar niches were not. Argument for (2) is that Europe and North America did suffer similar climatic changes during the second part of the Paleocene (e.g., Zachos et al., 2001) and it is not unlikely that the response of the vegetation was globally similar on both continents at large scale, hence driving parallel mammal evolution. Argument against (2) is that completely independent evolution is rarely parallel, similar vegetation does not imply similar adaptations of plant-eating mammals, and Europe was apparently more forested than North America (e.g., Hooker and Collinson, 2012), so that the conditions were not that similar on the two continents. In conclusion,

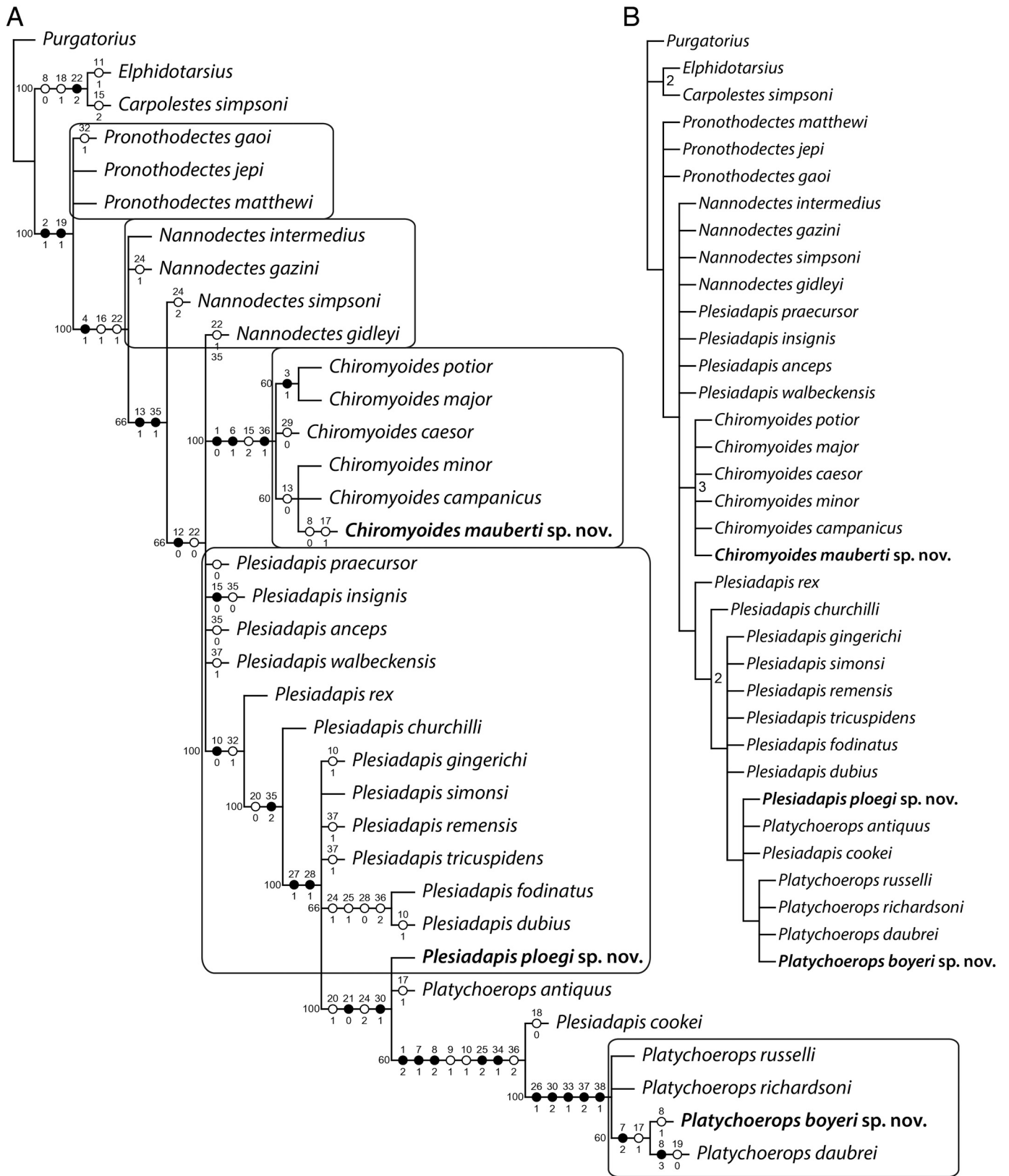


FIGURE 12. Consensus of the cladistic analysis of Plesiadapidae, based on the matrix of Boyer et al. (2012a, 2012b). **A**, majority-rule consensus of 1800 trees. The percentage of support is given to the left of the nodes; **B**, strict consensus of 1800 trees. Bremer support above 1 is given to the right of the corresponding nodes.

it seems more likely that plesiadapids dispersed at least twice between Europe and North America during the late Paleocene (hypothesis 1). The first dispersal was likely from North America towards Europe and concerned *Plesiadapis*, whereas the second involved *Chiromyoides*. This genus is present on both continents, from Ti3 in North America and after Paleocene, locality of Walbeck (likely Selandian, see De Bast et al., 2013; equivalent to Ti2 or Ti3) in Europe, so that the direction of this dispersal is harder to determine.

### Cladistic Analysis of Plesiadapidae

In order to study the phylogenetic position of the new plesiadapids from Petit-Pâtis, to confirm their generic attribution, and to test our hypothesis concerning the geographic origin of *Platychoerops*, a cladistic analysis was conducted. For this analysis, the three new species were added to the matrix of Boyer et al. (2012a, 2012b). The matrix was further modified, first by removing cranial characters that are known only for very few taxa, thus suffering from a bad distribution of the characters; when run with these cranial and postcranial characters (not coded for the new taxa), the resulting strict consensus was identical, whereas the majority-rule consensus was slightly more resolved without the cranial and postcranial characters. Several additional dental characters were also included (see Appendix 1 for the list of characters and character states). The matrix (Appendix 2) was analyzed with TNT 1.1 (Goloboff et al., 2008). All characters were considered unordered, except for characters 7, 8, 16, 25, 26, 31, 36, and 38, for which a gradual morphocline and an intermediate state can be observed, implying that their evolution is better considered ordered. Multistate characters were treated as polymorphisms. The whole matrix was checked and a few miscodings were corrected (mainly concerning the inclusion of polymorphisms for *Ples. tricuspidens*), and the morphology of the additional characters was assessed based on casts and illustrations (see Appendix S1). Traditional search was preferred because the number of taxa is reasonable and was driven with 100 random seeds and a maximum of 10,000 trees saved for each replication. The analysis delivered more than 600,000 equally parsimonious cladograms of 85 steps each, with a consistency index (CI) = 0.576 and a retention index (RI) = 0.836. The strict consensus (Fig. 12B) has a CI = 0.426 and a RI = 0.700. Because this strict consensus displayed several large polytomies, a majority-rule consensus was also constructed (Fig. 12A), with 50% support cutoff, with a CI = 0.538 and a RI = 0.809. Running the analysis with all characters unordered did not change the resulting consensus except for a slightly better resolution in the large polytomy including derived species of *Plesiadapis*.

The consensus trees found only *Chiromyoides* to be monophyletic, *Pronothodectes* to be paraphyletic, and *Nannodectes*, *Plesiadapis*, and *Platychoerops* to be polyphyletic. The relationships between the species of *Plesiadapis* are mostly unresolved; the species cluster in two large polytomies. At the transition between *Plesiadapis* and *Platychoerops*, both genera are intermixed, even in the majority-rule consensus, with *Plesiadapis cookei* basal to the derived species of *Platychoerops*, and *Plat. antiquus* and *Plesiadapis ploegi* in a trichotomy with the clade grouping *Ples. cookei* and the derived species of *Platychoerops*. Of the eight apomorphies of the clade containing *Ples. cookei* and *Platychoerops* spp., only the size of m3 is coded for *Plat. antiquus*. The lack of data for key tooth positions of *Plat. antiquus* is conspicuous; in particular, the absence of an upper incisor is unfortunate. Indeed, the morphology of this locus is very important: four of the eight previously mentioned apomorphies concern the upper incisor. Because this tooth is here used to classify *Ples. ploegi* in the genus *Plesiadapis*, it would thus be very useful for further detailed analysis of the relationships of *Plat. antiquus*, *Ples. ploegi*, *Ples. cookei*, and the clade of derived species of *Platychoerops*. If this tooth only has a vestigial laterocone as all other species of *Platychoerops*, it would mean that it is a ‘true’

*Platychoerops*, whereas the presence of a large laterocone would question the generic attribution and require a revision of the evolution of the genus *Platychoerops* and its relationships with *Plesiadapis*. Considering the morphology of the p4, very much like that of the derived species of *Platychoerops*, we expect a derived I1 without laterocone. Nevertheless, the high number of specimens of plesiadapids from Berru, coupled with the particular morphology of a derived upper incisor lacking a laterocone, would make it surprising that none was ever identified, but only two specimens of *Plat. antiquus* were ever identified; in contrast, incisors morphologically similar to that of *Ples. tricuspidens* are more likely to escape notice.

The results of the strict consensus highlight the complexity of the evolution of Plesiadapidae during the late Paleocene. Indeed, apart from *Chiromyoides*, all currently recognized genera are either paraphyletic or polyphyletic. This underlines the fact that plesiadapid evolution was quick, likely driven towards similar adaptations in separate lineages (parallel evolution), and the study of their relationships is further complicated by the high intraspecific variability observed in populations from single fossil localities.

Besides, the results of our analysis imply that either the metaconid on p4 was acquired twice independently or that *Ples. cookei* lost the metaconid on p4, thus reverting to the primitive state, which is contradictory to the specialization towards folivory by molarization of the p4 that is observed in Plesiadapidae at the end of the Paleocene. This highlights the likelihood of convergent evolution in plesiadapids of Europe and North America close to the PEB. Convergent evolution very likely occurred within Europe alone: the oldest *Platychoerops* from Berru is older than *Ples. ploegi* from Petit-Pâtis. Once again, the only alternative explanation to parallel evolution, at least for the molarization of the p4 and simplification of I1 in both lineages (the lineage from *Plesiadapis* to *Platychoerops* and that from *Ples. tricuspidens* to *Ples. ploegi*), would be that *Ples. ploegi* surprisingly reverted to a less derived p4 and likely to a less derived I1 from *Plat. antiquus*.

### CONCLUSIONS

The description of three new species of European Plesiadapidae from the latest Paleocene of Petit-Pâtis enriches the knowledge of the family, especially that of the relatively poorly known European Paleocene. More importantly, the concomitant presence of the very diagnostic central upper incisor in the three European genera in Petit-Pâtis demonstrates the coexistence in space and time of *Plesiadapis*, *Platychoerops*, and *Chiromyoides*. The adaptations of dental morphology that reflect a tendency to folivory and that characterize Plesiadapidae just before the PEB are here corroborated by the description of *Plesiadapis ploegi*, morphologically intermediate between *Plesiadapis tricuspidens* and the primitive species of *Platychoerops*, featuring a primitive I1 with a large laterocone but cheek teeth more derived towards folivory: semimolariform p4 with developed metaconid; small accessory crest on the oblique cristid of lower molars; shallow gash at the anterior base of the mesostyle; and marked dilambdodonty of the upper molars.

Plesiadapids likely dispersed several times between Europe and North America during the Paleocene, as evidenced by the parallel evolution in the genus *Plesiadapis* on both continents and the appearance of *Chiromyoides*. The tendency to folivory, illustrated by the development of crests on cheek teeth and the molarization of p4, is observed both in *Ples. cookei* and in *Ples. ploegi* (although more markedly in *Ples. ploegi*), so that either some dispersal occurred during the North American Clarkforkian, or its direction remains unclear, or *Ples. cookei* is representative of a lineage having developed adaptations to folivory convergently with the European *Platychoerops*.


Cladistic analysis fails to separate the historic genera as monophyletic groups, which is unsurprising given the variability observed in plesiadapids and the seniority of the most problematic genus *Plesiadapis*. The analysis also questions the generic position of *Ples. cookei*, which shares several characters with the

*Platychoerops* clade, and suggests either parallel evolution in North America and Europe when approaching the PEB or several reversals with intercontinental dispersal. Additional specimens of key taxa such as the oldest species of *Platychoerops*, *Plat. antiquus*, would be crucial for elucidating the phylogenetic relationships of *Ples. cookei* and *Platychoerops*.

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#### LITERATURE CITED

- Bloch, J. I., S. G. B. Chester, and M. T. Silcox. 2016. Cranial anatomy of Paleogene Micromomyidae and implications for early primate evolution. *Journal of Human Evolution* 96:58–81.
- Bloch, J. I., D. M. Boyer, P. D. Gingerich, and G. F. Gunnell. 2002. New primitive paromyid from the Clarkforkian of Wyoming and dental eruption in Plesiadapiformes. *Journal of Vertebrate Paleontology* 22:366–379.
- Bloch, J. I., D. C. Fischer, K. D. Rose, and P. D. Gingerich. 2001. Stratocladistic analysis of Paleocene Carpolestidae (Mammalia, Plesiadapiformes) with description of a new late Tiffanian genus. *Journal of Vertebrate Paleontology* 21:119–131.
- Bloch, J. I., M. T. Silcox, D. M. Boyer, and E. J. Sargis. 2007. New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. *Proceedings of the National Academy of Sciences of the United States of America* 104:1159–1164.
- Boyer, D. M., L. Costeur, and Y. Lipman. 2012a. Earliest record of *Platychoerops* (Primates, Plesiadapidae), a new species from Mouras Quarry, Mont de Berru, France. *American Journal of Physical Anthropology* 149:329–346.
- Boyer, D. M., A. R. Evans, and J. Jernvall. 2010. Evidence of dietary differentiation among late Paleocene–early Eocene plesiadapids (Mammalia, Primates). *American Journal of Physical Anthropology* 142:194–210.
- Boyer, D. M., C. S. Scott, and R. C. Fox. 2012b. New craniodental material of *Pronothodectes gaoi* Fox (Mammalia, “Plesiadapiformes”) and relationships among members of Plesiadapidae. *American Journal of Physical Anthropology* 147:511–550.
- Burger, B. J., and J. G. Honey. 2009. Plesiadapidae (Mammalia, Primates) from the late Paleocene Fort Union Formation of the Piceance Creek Basin, Colorado. *Journal of Vertebrate Paleontology* 28:816–825.
- Charlesworth, E. 1855. On several new vertebrate fossils. Report of the 24th Meeting of the British Association for the Advancement of Science. Liverpool 24(Miscellaneous Communications):80.
- Chester, S. G. B., J. I. Bloch, D. M. Boyer, and W. A. Clemens. 2015. Oldest known euarchontan postcrania and affinities of Paleocene *Purgatorius* to Primates. *Proceedings of the National Academy of Sciences of the United States of America* 112:1487–1492.
- Chester, S. G. B., T. E. Williamson, J. I. Bloch, M. T. Silcox, and E. J. Sargis. 2017. Oldest skeleton of a plesiadapiform provides additional evidence for an exclusively arboreal radiation of stem primates in the Palaeocene. *Royal Society Open Science* 4:170329. doi: 10.1098/rsos.170329.
- De Bast, E., and T. Smith. 2017. The oldest Cenozoic mammal fauna of Europe: implication of the Hainin reference fauna for mammalian evolution and dispersals during the Paleocene. *Journal of Systematic Palaeontology* 15:741–785.
- De Bast, E., E. Steurbaut, and T. Smith. 2013. New mammals from the marine Selandian of Maret, Belgium, and their implications for the age of the Paleocene continental deposits of Walbeck, Germany. *Geologica Belgica* 16:236–244.
- Fleagle, J. G. 1998. *Primate Adaptation and Evolution*, second edition. Elsevier Academic Press, London.
- Gagnaison, C., J. Prieur, and G. de Plöeg. 2009. Le gisement de vertébrés thanétiens (Paléocène supérieur, MP6) du Petit Pâtis près de Creil (Oise France). *Bulletin d'Information des Géologues du Bassin de Paris* 46(2):3–11.
- Gervais, P. 1877. Enumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine. *Journal de Zoologie (Paris)* 6:74–79.
- Gidley, J. W. 1923. Paleocene primates of the Fort Union, with discussion of relationships of Eocene primates. *Proceedings of the United States National Museum* 63:1–38.
- Gingerich, P. D. 1973. First record of the Paleocene primate *Chiromyoides* from North America. *Nature* 244:517–518.
- Gingerich, P. D. 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *Journal of Paleontology* 48:895–903.
- Gingerich, P. D. 1975. New North American Plesiadapidae (Mammalia, Primates) and a biostratigraphic zonation of the Middle and Upper Paleocene. *Contributions from the Museum of Paleontology, University of Michigan* 24:135–148.
- Gingerich, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *University of Michigan Papers on Paleontology* 15:1–140.
- Gingerich, P. D. 2012. Primates in the Eocene. *Palaeobiodiversity and Palaeoenvironments* 92:649–663.
- Gingerich, P. D., and J. A. Dorr Jr. 1979. Mandible of *Chiromyoides minor* (Mammalia, Primates) from the Upper Paleocene Chappo Member of the Wasatch Formation, Wyoming. *Journal of Paleontology* 53:550–552.
- Gingerich, P. D., and M. J. Schoeninger. 1979. Patterns of tooth size variability in the dentition of Primates. *American Journal of Physical Anthropology* 51:457–466.
- Godinot, M., D. Dutheil, A. Galoyer, E. Gheerbrant, A. Nel, G. de Plöeg, and D. E. Russell. 1998. The Plesiadapidae across the Paleocene-Eocene boundary in the Paris Basin. *Strata, série 1* 9:53–54.
- Goloboff, P., J. Farris, and K. Nixon. 2008. T.N.T.: a free program for phylogenetic analysis. *Cladistics* 24:1–13.
- Hooker, J. J. 1994. A new species of *Platychoerops* (Plesiadapiformes, Mammalia) from the latest Palaeocene of the Paris, London and Belgian basins. *Geobios* 27:343–352.
- Hooker, J. J. 2010. The Mammal Fauna of the Early Eocene Blackheath Formation of Abbey Wood, London. *Palaeontographical Society Monographs*, 165:634:162 pp.
- Hooker, J. J. 2015. A two-phase mammalian dispersal event across the Paleocene-Eocene transition. *Newsletters on Stratigraphy* 48:201–220.
- Hooker, J. J., and M. E. Collinson. 2012. Mammalian faunal turnover across the Paleocene-Eocene boundary in NW Europe: the roles of displacement, community evolution and environment. *Austrian Journal of Earth Sciences* 105:17–28.
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society, London* 43:649–662.



- Jepsen, G. L. 1930. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. *Proceedings of the American Philosophical Society* 69:463–582.
- Lemoine, V. 1880. Communication sur les ossements des terrains tertiaires inférieurs des environs de Reims. *Association Française pour l'Avancement des Sciences. Actes du Congrès* 8:585–594.
- Lemoine, V. 1887. Sur le genre *Plesiadapis*, mammifère fossile de l'éocène inférieur des environs de Reims. *Comptes Rendus de l'Académie des Sciences* année 1887:190–193.
- Louis, P. 1996. Recherches de mammifères paléogènes dans les départements de l'Aisne et de la Marne pendant la deuxième moitié du vingtième siècle; pp. 83–113 in M. Godinot and P. D. Gingerich (eds.), *Paléobiologie et évolution des mammifères paléogènes, Volume jubilaire en l'honneur de Donald E. Russell, Palaeovertebrata* 25, Fasc. 2–4.
- Louis, P., M. Laurain, C. Bolin, and L. Barta. 1983. Nouveau gisement de vertébrés dans le Cuisien supérieur de Saint-Agnan (Aisne) ses relations stratigraphiques avec les autres gisements yprésiens du Bassin parisien. *Bulletin d'Information des Géologues du Bassin de Paris* 20(4):3–20.
- Maas, M. C., D. W. Krause, and S. G. Strait. 1988. The decline and extinction of Plesiadapiformes (Mammalia: ?Primates) in North America: displacement or replacement? *Paleobiology* 14:410–431.
- Matthew, W. D. 1915. A revision of the Lower Eocene Wasatch and Wind River faunas, Part IV: Entelonychia, Primates, Insectivora (part). *Bulletin of the American Museum of Natural History* 34:429–484.
- Matthews, S. C. 1973. Notes on open nomenclature and synonymy lists. *Palaentology* 16:713–719.
- Missiaen, P., F. Quesnel, C. Dupuis, J.-Y. Storme, and T. Smith. 2013. The earliest Eocene mammal fauna of the Erquelinnes Sand Member near the French-Belgian border. *Geologica belgica* 16:262–273.
- Ni, X., D. Y. Hu, Y. Wang, and C. Li. 2005. A clue to the Asian origin of euprimates. *Anthropological Science* 113:3–9.
- Ni, X., Q. Li, L. Li, and K. C. Beard. 2016. Oligocene primates from China reveal divergence between African and Asian primate evolution. *Science* 352:673–677.
- Ni, X., D. Gebo, M. Dagosto, J. Meng, P. Tafforeau, J. J. Flynn, and K. C. Beard. 2013. The oldest known primate skeleton and early haplorhine evolution. *Nature* 498:60–64.
- Piton, L.-E. 1940. Paléontologie du gisement éocène de Menat (Puy-de-Dôme). *Vallier, Clermont-Ferrand, France*, 303 pp.
- Rose, K. D. 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. *University of Michigan Papers on Paleontology* 26:1–197.
- Rose, K. D. 2006. *The Beginning of the Age of Mammals*. The Johns Hopkins University Press, Baltimore, Maryland, 428 pp.
- Rose, K. D., and T. M. Bown. 1982. New plesiadapiform primates from the Eocene of Wyoming and Montana. *Journal of Vertebrate Paleontology* 2:63–69.
- Russell, D. E. 1964. *Les mammifères paléocènes d'Europe*. Éditions du Muséum, Université de Paris, Paris, 324 pp.
- Schlosser, M. 1921. Beiträge zur Kenntnis der Säugetierreste aus dem untersten Eocaen von Reims. *Palaeontographica* 63:97–144.
- Secord, R. 2008. The Tiffanian land-mammal age (middle and late Paleocene) in the northern Bighorn Basin, Wyoming. *Papers on Paleontology* 35:1–192.
- Silcox, M.T. 2001. A phylogenetic analysis of Plesiadapiformes and their relationship to euprimates and other archontans. Ph.D. dissertation, Baltimore, MD: The Johns Hopkins University.
- Silcox, M. T., and S. López-Torres. 2017. Major questions in the study of primate origins. *Annual Review of Earth and Planetary Sciences* 45:113–137.
- Silcox, M. T., and G. F. Gunnell. 2008. Plesiadapiformes; pp. 207–238 in C. M. Janis, G. F. Gunnell, and M. D. Uhen (eds.), *Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans and Marine Mammals*. Cambridge University Press, New York.
- Silcox, M. T., J. I. Bloch, D. M. Boyer, and P. Houde. 2010. Cranial anatomy of Paleocene and Eocene *Labidolemur kayi* (Mammalia: Apatotheria) and the relationships of the Apatemyidae to other mammals. *Zoological Journal of the Linnean Society* 160:773–825.
- Silcox, M. T., J. I. Bloch, E. J. Sargis, and D. M. Boyer. 2005. Euarchonta (Dermoptera, Scandentia, Primates); pp. 127–144 in K. D. Rose and J. D. Archibald (eds.), *The Rise of Placental Mammals*. Johns Hopkins University Press, Baltimore, Maryland.
- Silcox, M. T., E. J. Sargis, J. I. Bloch, and D. M. Boyer. 2008. Primate origins and supraordinal relationships: morphological evidence; pp. 831–859 in W. Henke and I. Tattersall (eds.), *Handbook of Paleoanthropology*. Springer, New York.
- Silcox, M. T., J. I. Bloch, D. M. Boyer, S. G. B. Chester, and S. López-Torres. 2017. The evolutionary radiation of plesiadapiforms. *Evolutionary Anthropology* 26:74–94.
- Simons, E. L. 1972. *Primate Evolution: An Introduction to Man's Place in Nature*. MacMillan Series in Physical Anthropology, Macmillan, New York, 322 pp.
- Simpson, G. G. 1935. The Tiffany fauna, Upper Paleocene. II. Structure and relationships of *Plesiadapis*. *American Museum Novitates* 816:1–30.
- Simpson, G. G. 1936. A new fauna from the Fort Union of Montana. *American Museum Novitates* 873:1–27.
- Simpson, G. G. 1955. The Phenacolemuridae, new family of early primates. *Bulletin of the American Museum of Natural History* 105:415–441.
- Smith, T., F. Quesnel, G. de Ploëg, D. De Franceschi, G. Métais, E. De Bast, F. Solé, A. Folie, A. Boura, J. Claude, C. Dupuis, C. Gagnaison, A. Iakovleva, J. Martin, F. Maubert, J. Prieur, E. Roche, J.-Y. Storme, R. Thomas, H. Tong, J. Yans, and E. Buffetaut. 2014. First Clarkforkian equivalent land mammal age in the latest Paleocene basal Sparnacian facies of Europe: fauna, flora, paleoenvironment and (bio)stratigraphy. *PLoS ONE* 9:e86229. doi: 10.1371/journal.pone.0086229.
- Soligo, C., and J. B. Smaers. 2016. Contextualising primate origins—an ecomorphological framework. *Journal of Anatomy* 228:608–629.
- Stehlin, H. G. 1916. *Die Säugetiere des schweizerischen Eocaens. Abhandlungen der schweizerischen paläontologischen Gesellschaft* 41:1299–1552.
- Szalay, F. S. 1972. Paleobiology of the earliest primates; pp. 3–35 in R. Tuttle (ed.), *The Functional and Evolutionary Biology of Primates*. Aldine-Atherton, Chicago, Illinois.
- Szalay, F. S., and E. Delson. 1979. *Evolutionary History of the Primates*. Academic Press, New York, 580 pp.
- Teilhard de Chardin, P. 1922. *Les mammifères de l'Éocène inférieur français et leurs gisements*. Masson, Paris, 132 pp.
- Trouessart, E.-L. 1897. *Catalogus mammalium tam viventium quam fossilium, Volume 1*. Friedländer und Sohn, Berlin, 664 pp.
- Wible, J. R., G. W. Rougier, and M. J. Novacek. 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature* 447:1003–1006.
- Winterfeld, G. F. 1982. Mammalian paleontology of the Fort Union Formation (Paleocene), eastern Rock Springs Uplift, Sweetwater County, Wyoming. *Contributions to Geology, University of Wyoming* 21:73–111.
- Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–693.

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#### APPENDIX 1. List of characters and characters states used in the phylogenetic analysis.

- (1) Incisor proportions: occlusal height short compared with area in occlusal plane (0); occlusal height intermediate (1); occlusal height high (2). (character 1 of Boyer et al., 2012b)
- (2) Basal cusp on lingual cingulum of i1: absent (0); present (1). (character 4 of Bloch et al., 2001)
- (3) i1 with squared tip: absent (0); present (1). (character 3 of Boyer et al., 2012b)
- (4) i2: present (0); absent (1). (character 4 of Boyer et al., 2012b)
- (5) i3: present (0); absent (1). (character 6 of Bloch et al., 2001)
- (6) Incisor size relative to molars: slightly larger (0); greatly enlarged (m1 area/i1 area <0.85) (1). (character 31 of Boyer et al., 2012b)
- (7) I1 laterocone: present and similarly sized as the anterocone (0); reduced, less than half the size of the anterocone (1); absent (2). Ordered. (character 6 of Boyer et al., 2012b, modified)
- (8) I1 posterocone: twinned (0); present (1); reduced (2); absent (3). Ordered. (character 7 of Boyer et al., 2012b)

- (9) I1 mediocone: present (0); reduced or absent (1). (character 8 of Boyer et al., 2012b)
- (10) I1 centroconule: present (0); reduced or absent (1). (character 9 of Boyer et al., 2012b)
- (11) I1 anterocone length: short, the length between the tip of the anterocone and the insertion point of the laterocone is significantly shorter than that between the insertion points of the laterocone and the posterocone (0); long, insertion point of the laterocone halfway between the base of the posterocone and the tip of the anterocone (1).
- (12) C1: present (0); absent (1). (character 10 of Boyer et al., 2012b)
- (13) c1: present (0); absent (1). (character 11 of Boyer et al., 2012b)
- (14) Diastemata between premolars and more anterior teeth: absent (0); present (1). (character 12 of Boyer et al., 2012b)
- (15) P1 or p1: present (0); absent (1). (character 13 of Boyer et al., 2012b)
- (16) p2: large (0); small (1); absent (2). Ordered. (character 14 of Boyer et al., 2012b)
- (17) Form of p2: premolariform with talonid heel (0); button-shaped (1). (character 15 of Boyer et al., 2012b)
- (18) Metaconid on p3: absent (0); present (1). (character 68 of Boyer et al., 2012a)
- (19) Metaconid on p4: absent (0); present (1). (character 16 of Boyer et al., 2012b; modified from character 14 of Bloch et al., 2001)
- (20) Paraconid on p4: present (0); absent (1). (d25 of Silcox, 2001)
- (21) Entoconid on p4: present (0); absent (1). (character 18 of Boyer et al., 2012b)
- (22) Trigonid of p4: present (0); absent (1). (character 19 of Boyer et al., 2012b)
- (23) Proportions of p4: buccolingually broad relative to mesio-distal length (0); narrow (1); extremely narrow, relatively large and with multiple in-line apical cusps (2). (character 20 of Boyer et al., 2012b)
- (24) P2: present (0); absent (1). (character 21 of Boyer et al., 2012b)
- (25) P3 paraconule: present (0); reduced (1); absent (2). Ordered. (character 22 of Boyer et al., 2012b)
- (26) P4 paraconule: present (0); reduced (1); absent (2). Ordered. (character 23 of Boyer et al., 2012b)
- (27) P4 molar-type paraconule: present (0); absent (1). (character 24 of Boyer et al., 2012b)
- (28) Entoconid of m1–m2: squared and lacking crest (0); curved with crest (1). (character 25 of Boyer et al., 2012b)
- (29) Length of m1: species sample mean less than 3.5 mm (0); greater than or equal to 3.5 mm (1). (character 26 of Boyer et al., 2012b)
- (30) Postvallid of m1: flush (0); stepped (1). (d80 of Silcox, 2001)
- (31) Accessory crest on the crista obliqua: absent (0); short or small tubercle (1); long (2). Ordered.
- (32) Size of m3 hypoconulid: small relative to talonid (0); large (1). (modified from d75 of Silcox, 2001)
- (33) Shape of m3 hypoconulid: rounded and unfissured (0); squared and fissured (1). (character 29 of Boyer et al., 2012b)
- (34) Posterior cingulid on m3: absent (0); present (1). (character 67 of Boyer et al., 2012a)
- (35) Size of m3 relative to that of *P. cookei*: smaller, i.e., less than 8.5 mm long on average (0); as long or longer (1). (character 69 of Boyer et al., 2012a)
- (36) M1–M2 mesostyles: absent (0); weakly present (1); strong (2). Ordered. (character 30 of Boyer et al., 2012b)
- (37) Premolar and/or molar form: cuspidate (0); blunt (1); creniform (2). Unordered. (character 32 of Boyer et al., 2012b)
- (38) Gash at the mesial base of the mesostyle: absent (0); shallow (1); deep, across the whole depth of the enamel to the roots (2). Ordered.

APPENDIX 2. Taxon-character matrix used for the phylogenetic analysis. **A**, 0, 1; **B**, 1, 2.

	10	20
<i>Purgatorius</i> sp.	1000000101	??00010000
<i>Elphidotarsius</i> sp.	10001000A1	0100011010
<i>Carpolestes simpsoni</i>	1000100011	000012?010
<i>Pronothodectes matthewi</i>	1100100101	0000110001
<i>Pronothodectes jepi</i>	1100100101	000011?001
<i>Pronothodectes gaoi</i>	1100100101	0000110001
<i>Plesiadapis praecursor</i>	1101100101	00A111?001
<i>Plesiadapis insignis</i>	1101100101	001110?0?1
<i>Plesiadapis anceps</i>	1101100101	00A111?001
<i>Plesiadapis walbeckensis</i>	1101100101	00111B?001
<i>Plesiadapis rex</i>	1101100100	001111?001
<i>Nannodectes intermedius</i>	1101100101	0000111001
<i>Nannodectes gazini</i>	1101100101	000011?001
<i>Nannodectes simpsoni</i>	110110?0???	000111?001
<i>Nannodectes gidleyi</i>	11011001?1	0011111001
<i>Chiromyoides minor</i>	0101110101	0?10?2????
<i>Chiromyoides campanicus</i>	0101110101	0?1012?001
<i>Chiromyoides caesor</i>	0?????10101	0?????????
<i>Chiromyoides potior</i>	0111110101	0?11?2????
<i>Chiromyoides major</i>	0111110101	0?11?2????
<i>Chiromyoides mauberti</i>	010??10001	0?1012?101
<i>Plesiadapis churchilli</i>	1101100100	00111B?001
<i>Plesiadapis gingerichi</i>	1?????0101	0?1112?001
<i>Plesiadapis simonsi</i>	???????????	???????????
<i>Plesiadapis remensis</i>	1101100100	0?1112?001
<i>Plesiadapis tricuspidens</i>	1A01100100	011112?001
<i>Plesiadapis fodinatus</i>	1101100100	001112?00A
<i>Plesiadapis dubius</i>	1101100101	001112?0?A
<i>Plesiadapis cookei</i>	2001101211	011112?00A
<i>Plesiadapis ploegi</i>	1A0??00100	0?1112?01A
<i>Platychoerops russelli</i>	2??1101211	111?12?0??
<i>Platychoerops antiquus</i>	???????????	?????????111
<i>Platychoerops daubrei</i>	2001102311	111112?110
<i>Platychoerops richardsoni</i>	?????0????	?1111?????
<i>Platychoerops boyeri</i>	2?0????2111	1?????1111
	30	38
<i>Purgatorius</i> sp.	0100110000	00000000
<i>Elphidotarsius</i> sp.	1120000001	01000000
<i>Carpolestes simpsoni</i>	1120000001	01000000
<i>Pronothodectes matthewi</i>	1100000001	01000000
<i>Pronothodectes jepi</i>	1100000001	01000000
<i>Pronothodectes gaoi</i>	1100000001	01100000
<i>Plesiadapis praecursor</i>	1100000001	01000000
<i>Plesiadapis insignis</i>	1100??0001	01000000
<i>Plesiadapis anceps</i>	1100000001	01000000
<i>Plesiadapis walbeckensis</i>	1100000001	01000101
<i>Plesiadapis rex</i>	1100000001	01100100
<i>Nannodectes intermedius</i>	1110000001	01000000
<i>Nannodectes gazini</i>	1101100001	01000000
<i>Nannodectes simpsoni</i>	1110200001	01000100
<i>Nannodectes gidleyi</i>	1110000001	01000100
<i>Chiromyoides minor</i>	?????????0?	??????1?
<i>Chiromyoides campanicus</i>	1100?00001	01000110
<i>Chiromyoides caesor</i>	110?????000	010??110
<i>Chiromyoides potior</i>	?????0000?	??????1?
<i>Chiromyoides major</i>	???????????	??????1?
<i>Chiromyoides mauberti</i>	110?????001	01000110
<i>Plesiadapis churchilli</i>	0100000001	0110020?
<i>Plesiadapis gingerichi</i>	010????0111	01100200
<i>Plesiadapis simonsi</i>	?????0111	011?020?
<i>Plesiadapis remensis</i>	0100000111	01100201
<i>Plesiadapis tricuspidens</i>	0100000111	A11A0201
<i>Plesiadapis fodinatus</i>	0100110101	0110022A
<i>Plesiadapis dubius</i>	0100110101	A1100220
<i>Plesiadapis cookei</i>	1001220111	11101220
<i>Plesiadapis ploegi</i>	1A0?210111	111A020A
<i>Platychoerops russelli</i>	????221?1?	21111222
<i>Platychoerops antiquus</i>	100????2111	11100????
<i>Platychoerops daubrei</i>	100?221111	21110222
<i>Platychoerops richardsoni</i>	????122111	21111222
<i>Platychoerops boyeri</i>	?00?????111	2????1222