

Diversity of the adapisoriculid mammals from the early Palaeocene of Hainin, Belgium

ERIC DE BAST, BERNARD SIGÉ, and THIERRY SMITH



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Adapisoriculidae are an enigmatic group of small mammals known from the late Cretaceous of India, and from the early Palaeocene to early Eocene of Europe and Africa. Based on their primitive dental morphology, they have been classified as didelphids, nyctitheriids, leptictids, mixodectids, tupaiids, and palaeoryctids. While the latest hypothesis based on dental morphology suggests an affinity with Lipotyphla, postcranial remains indicate a close relationship with Euarchonta. Here, we present new adapisoriculid dental remains from the early Palaeocene locality of Hainin (Belgium). Adapisoriculidae are particularly abundant in Hainin, where they represent about one third of the mammalian fauna, offering new insights into both their specific and generic phylogenetic interrelationships. We describe three new species (*Afrodon gheerbranti* sp. nov., *Bustylus folieae* sp. nov. and *Proremiculus lagnauxi* gen. et sp. nov.) and document the previously unknown lower dentition of *Bustylus marandati*. The diversity of dental morphologies observed in the Hainin fauna suggests different interrelationships than previously suggested. In particular, the genus *Proremiculus* is considered morphologically intermediate between *Afrodon* and *Remiculus*, and the latter is no longer recognised as the sister group of *Adapisoriculus*. Although the highest diversity of adapisoriculids occurs in Europe, the oldest and most primitive members of the family were found in India and Africa, respectively. The geographic origin of the family could thus be located in any of these three continents, depending on the importance attributed to each of these factors. The coexistence of primitive and derived adapisoriculids at Hainin might indicate a very quick diversification in Europe, probably starting around the K-T boundary.

Key words: Mammalia, Adapisoriculidae, phylogeny, early Palaeocene, Hainin, Belgium.

Eric De Bast [eric.debast@naturalsciences.be] and Thierry Smith [thierry.smith@naturalsciences.be], Royal Belgian Institute of Natural Sciences, Department of Paleontology, Rue Vautier 29, B-1000 Brussels, Belgium; Bernard Sigé [bernard-sige@orange.fr], Laboratoire de Paléontologie, Institut des Sciences de l'Évolution, cc064, Université Montpellier II, place Eugène Bataillon, 34095 Montpellier cedex 05, France.

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Introduction

The Hainin vertebrate fauna was discovered in the early 1970s when several boreholes were drilled in order to reach the marine Danian (Lower Palaeocene) deposits of the Mons Basin in South West Belgium (Fig. 1) (Godfriaux and Robaszynski 1974). The continental vertebrate fauna occurred between Danian and Thanetian (Upper Palaeocene) deposits, both of which are marine, and a well was dug on the emplacement of the borehole which yielded the fossils in order to collect them (Godfriaux and Thaler 1972). The vertebrate species already described from the Hainin well include osteoglossid fish (Taverne et al. 2007), freshwater turtles (Groessens-Van Dijk 1984), scincoid lizards (Folie et al. 2005), different species of anurans and urodeles (Folie 2007) and several species of mammals. This fauna, although not exactly dated, was correlated with the earliest Selandian based on stratigraphic evidence (Sturbaut 1998), but could also be late Danian based on its mammalian contents (e.g., McKenna and Bell 1997). It therefore constitutes the oldest European Cenozoic continen-

tal vertebrate fauna, and was chosen as reference level MP1–5 on the mammalian biochronological scale of the European Palaeogene (Schmidt-Kittler 1987). Despite the fact that the entire mammalian fauna is not yet known, several taxa have been described, including multituberculates (Vianey-Liaud 1979), an arctocyonid and a louisinine condylarth (Sudre and Russell 1982), a plesiadapid (Sigé and Marandat 1997) and one adapisoriculid (Crochet and Sigé 1983).

Adapisoriculidae represent an enigmatic family of small mammals whose members have been placed in various systematic positions (Gheerbrant and Russell 1989). *Adapisorex minimus* from the late Palaeocene of Cernay, France was the first species to be described (Lemoine 1883). Later, Lemoine (1885) remarked on the originality of the species and placed it in the new genus *Adapisoriculus*. Teilhard de Chardin (1922) suggested a marsupial affinity for this species, which was followed by Simpson (1929), who suggested an affinity with Didelphidae. However, in his classification of mammals, he placed the taxon in both ?Didelphidae and ?Insectivora, while adding a note in the section on Nyctitheriidae regarding its

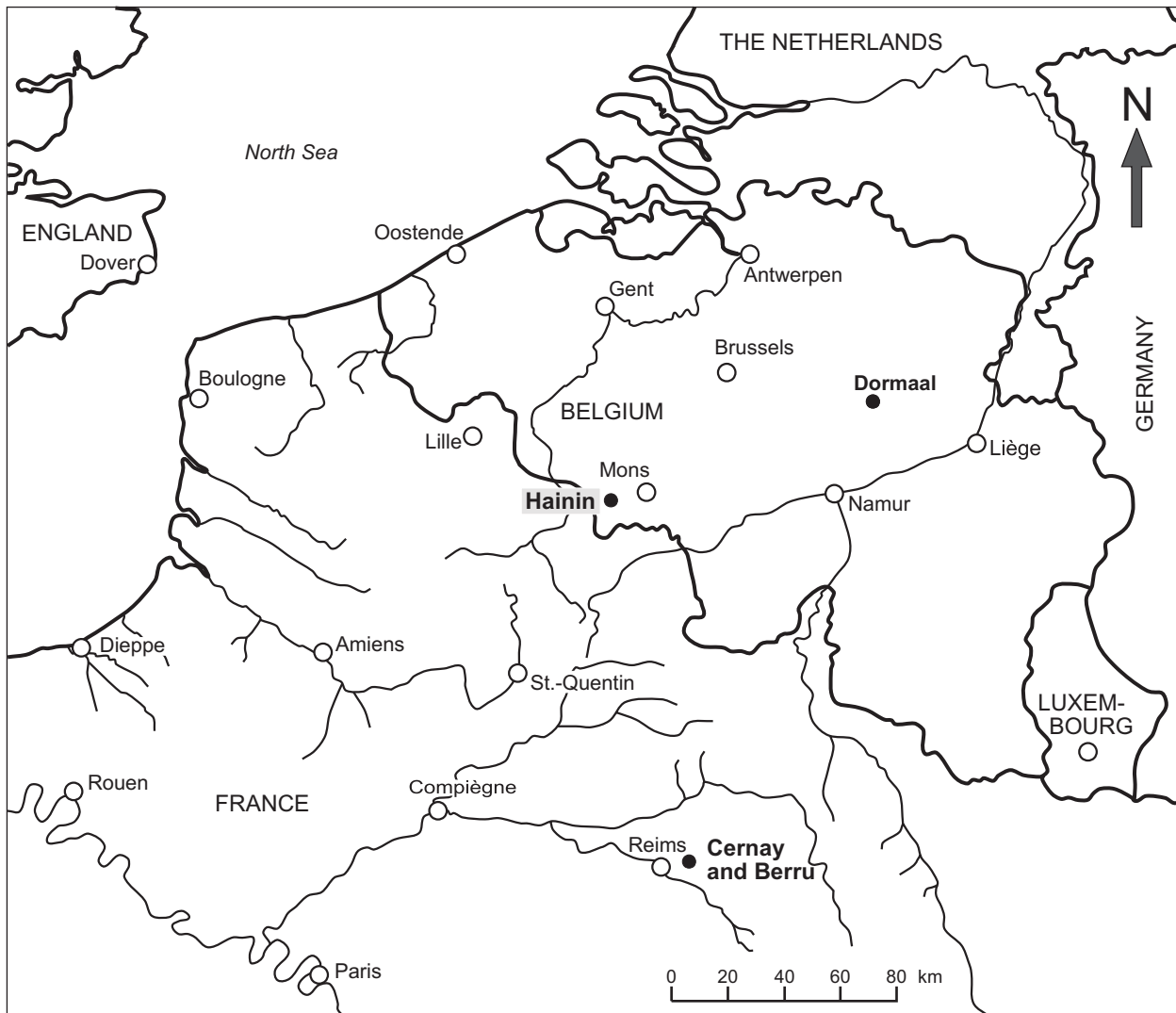


Fig. 1. Geographic map indicating the position of the Hainin Formation in the Mons Basin, South Western Belgium.

probable affinities with this group (Simpson 1945). Saban (1958) referred *Adapisoriculus* to Nyctitheriidae. In his monograph, Russell (1964) described two new species from the late Palaeocene of Walbeck, Germany: *Adapisoriculus? germanicus*, placed in the Leptictidae; and *Remiculus deutschi*, considered a member of the Mixodectidae, with both groups being classified as lipotyphlan insectivores. Van Valen (1967) created the subfamily Adapisoriculinae to contain *Adapisoriculus* (including *Adapisoriculus? germanicus*), and placed it in the family Tupaiidae (tree shrews). Butler (1972) suggested that *Adapisoriculus* may belong to the Mixodectidae, a family considered lipotyphlan at that time, but now classified as dermopterans by McKenna and Bell (1997). Crochet and Sigé (1983), based on upper molars from Hainin, described the new species *Peradectes marandati* (Marsupialia, Didelphidae). Crochet (1984) published *Garatherium mahboubii* from the early Eocene of El-Kohol, Algeria as a didelphid, while Gheerbrant (1988) described *Afrodon chleuhi* from the late Palaeocene of Adrar Mgorn 1, Morocco, and discussed the possible family-level affinities of this genus with *Adapisori-*

culus and *Remiculus*. During the same year, Prasad and Sahni (1988) described *Deccanolestes hislopi* from the Maastrichtian intertrappean beds of Naskal, India, and suggested a palaeoryctid affinity for this very primitive species. Gheerbrant and Russell (1989) placed the previously described *Adapisoriculus? germanicus* in the genus *Afrodon*, and referred this genus, together with *Adapisoriculus*, to the family Adapisoriculidae. They also suggested that *Remiculus* should be placed within Adapisoriculidae, which they considered to form part of ?Lipotyphla. Subsequently, Gheerbrant and Russell (1991) described two new adapisoriculids, *Bustylus cernaysi* from the late Palaeocene of Cernay, France, and *Bustylus cf. cernaysi* from the late Palaeocene of Walbeck, Germany. Gheerbrant (1991) also transferred *Peradectes marandati* to the new genus *Bustylus* and later described *Afrodon tagourtensis* from the early Eocene of N'Tagourt 2, Morocco, as well as *Afrodon cf. chleuhi* from the late Palaeocene of Adrar Mgorn 1bis, Morocco (Gheerbrant 1993). He also described another three taxa, including *Afrodon* sp. and ?*Adapisoriculus* sp. from the late Palaeocene of Ihadjamène, Mo-

rocco, and ?*Garatherium* sp. nov. from the late Palaeocene of Adrar Mgorn 1, and suggested that *Garatherium* should be referred to Adapisoriculidae (Gheerbrant 1995). In the meantime, Prasad et al. (1994) described *Deccanolestes robustus* and *Deccanolestes* cf. *hislopi* from the Maastrichtian of Naskal, India. In their classification of mammals, McKenna and Bell (1997) identified Adapisoriculidae as basal lipotyphlans, but with *Remiculus* set apart and considered a nyctitheriid. Simultaneously, Smith (1997) described the youngest European species of Adapisoriculidae known to date, *Remiculus delsei*, *Remiculus* cf. *deutschi*, and *Bustylus* sp., from the earliest Eocene of Dormaal, Belgium. One year later, Gheerbrant et al. (1998) described ?*Garatherium todrae* from the late Palaeocene of Ihdjamène, Morocco, while *Afrodon ivani* was described from the late Palaeocene of the Pyrenees, Spain, by Lopez-Martinez and Peláez-Campomanes (1999). Femora and humeri from Walbeck were described and attributed to Adapisoriculidae by Storch (2008). These bones resembled those of plesiadapiforms, and Storch (2008) suggested a close affinity between these two groups. In 2010, two research teams working independently showed that *Deccanolestes* belongs to the family Adapisoriculidae (Prasad et al. 2010; Smith et al. 2010). Furthermore, Prasad et al. (2010) also described a new species, *Deccanolestes narmadensis*, from the Maastrichtian of the Deccan intertrappean beds of India, and, based on teeth of *Deccanolestes* from India and *Afrodon* from France and Morocco, assigned the genus *Deccanolestes* to Adapisoriculidae. Based on tarsal bones of adapisoriculids from Belgium and their comparison with those of *Deccanolestes*, Smith et al. (2010) also included *Deccanolestes* in Adapisoriculidae, and reassigned the entire family to Euarchonta because of several derived characters they shared with Dermoptera. Finally, based on forelimb bones, Boyer et al. (2010) showed that *Deccanolestes* presents characters usually considered as synapomorphies of Euarchonta.

In total, six genera have thus been referred to Adapisoriculidae up to now: *Deccanolestes*, *Afrodon*, *Bustylus*, *Adapisoriculus*, *Garatherium*, and *Remiculus*. Among these genera, *Afrodon* and *Adapisoriculus* are present both in Africa and Europe, whereas *Deccanolestes* is endemic to India, *Garatherium* to Africa and *Bustylus* and *Remiculus* only occur in Europe. While *Deccanolestes* and *Adapisoriculus* are restricted to the Maastrichtian and the late Palaeocene, respectively, *Afrodon*, *Bustylus*, *Remiculus*, and *Garatherium* occur in both the Palaeocene and early Eocene. *Wyonycteris* was cited as either a possible adapisoriculid or nyctitheriid (Smith 1995), but is now generally considered an unusual nyctitheriid (e.g., Gingerich and Smith 2006).

The tooth morphology of the Adapisoriculidae is relatively plesiomorphic, especially in the primitive genus *Afrodon* (Gheerbrant and Russell 1989). The upper molars are transversely elongated, the parastyle and stylocone are always well marked and other stylar cusps are variably present, the wide stylar shelf features long prepara- and postmetacristae, and the paracone and metacone are well separated down to their bases with a rectilinear or dilambdodont

centrocrista. In the lower molars, there is little difference in height between the trigonid and talonid, the talonid is well developed, and the crista obliqua extends high on to the posterior wall of the trigonid (Gheerbrant 1995). Evolutionary tendencies within the family include a progressive development of dilambdodonty (V-shaped centrocrista) and a mesostyle, and a reduction of the transverse development of the upper molars. The lower molars in derived taxa tend to display a larger and more labially displaced hypoconid and, consequently, a wider talonid, a hypoconulid shifted towards the entoconid, and a crista obliqua extending higher on to the posterior wall of the trigonid. These characters are particularly visible in the dilambdodont genera *Adapisoriculus* and *Garatherium*. *Deccanolestes* and *Afrodon* are the most primitive genera, whereas *Bustylus* displays a morphology intermediate between *Afrodon* and *Adapisoriculus*. *Remiculus*, the only other dilambdodont genus, differs from the other genera in the rectangular aspect of its upper molars, which bear marked pre- and postcingula with a small crestiform hypocone, and the more massive aspect of its lower molars.

Institutional abbreviations.—IRSNB M, Royal Belgian Institute of Natural Sciences, mammal types and figured specimens.

Other abbreviations.—N1 to Z2, Hainin, general collections of the IRSNB. All specimens have a general collection number whose first part is composed of the level of the well which yielded the specimen (e.g., N1). Double-letter numbers indicate that the precise level which yielded the specimen could not be determined, and instead represent the depth range within which the latter was found.

Material and methods

The deposits from Hainin yielded 254 complete and fragmentary molars and posterior premolars, of which 54 are referred with certainty to the family Adapisoriculidae. At least 29 additional molar fragments can be related to several of the species described here. Adapisoriculidae thus represent about one third of the Hainin mammal fauna.

The sediments collected from the Hainin well went through a first step of screen washing. The remaining hard parts were treated with formic acid (5%) with tricalcic phosphate ($\text{Ca}_3(\text{PO}_4)_2$) used as a buffer. A second step of screen washing was then performed. Pictures of the dental specimens were taken using a FEI Qanta200 scanning electron microscope.

Systematic palaeontology

Class Mammalia Linnaeus, 1785

Order Euarchonta Waddell, Okada, and Hasegawa, 1999

Family Adapisoriculidae Van Valen, 1967

Genera included.—*Adapisoriculus* Lemoine, 1885 (type genus); *Remiculus* Russell, 1964; *Garatherium* Crochet, 1984; *Afrodon* Gheerbrant, 1988; *Deccanolestes* Prasad and Sahni, 1988; *Bustylus* Gheerbrant and Russell, 1991; *Proremiculus* gen. nov.

Stratigraphic and geographic range.—latest Cretaceous of India; Palaeocene and early Eocene of Western Europe and North Africa.

Genus *Afrodon* Gheerbrant, 1988

Type species: *Afrodon chleuhi* Gheerbrant, 1988; Thanetian (late Palaeocene), Adrar Mgorn 1 (Morocco).

Other species included.—*Afrodon germanicus* (Russell, 1964); *Afrodon tagourtensis* Gheerbrant, 1993; *Afrodon ivani* Peláez-Campomanes, 1999; *Afrodon gheerbranti* sp. nov.

Afrodon gheerbranti sp. nov.

Fig. 2; Table 1.

Etymology: In honour of Dr Emmanuel Gheerbrant who described the first species of the genus *Afrodon*, and his contribution to the knowledge of the family Adapisoriculidae.

Type material: Holotype: IRSNB M1982 (N2-17), right M2. Paratypes: IRSNB M1985 (Q2-28), right M1; IRSNB M1983 (N2-16), right M3; IRSNB M1986 (Q2-32), right p4; IRSNB M1987 (N2-13), right m1; IRSNB M1988 (Q1-06), right m2; and IRSNB M1989 (N2-06), left m3.

Type locality: Hainin, Hainaut province, Belgium.

Type horizon: Early Palaeocene, Hainin Formation, Mons Basin.

Referred material.—R1-13, right M1; Q2-35 right M2; R1-47, left M2; R1-82, right M2; R1-70, left M3; R1-71, left M3; N2-34, left p4; N2-12, left m1; N2-13, right m1; O1-03, left m1; Q2-31, left m2; Y1-6, right m2; N2-62, antero-labial part of right M1; N2-09, anterolabial part of right M2; R1-33, lingual part of left M1 or M2; Q2-08, trigonid of right m1; R1-22, trigonid of right m1; R1-42, talonid of left m3; P2-05, trigonid of left m2 or m3; Q2-17, trigonid of right m2 or m3; Y1-04, trigonid of left m2 or m3.

Diagnosis.—Differs from other species of the genus in its larger size and smaller degree of transverse development of the upper molars. Differs from *A. germanicus* in the presence of a less deep ectoflexus and an anteroposteriorly longer protocone of the upper molars. Lower molars differ from *A. chleuhi* in possessing a talonid as wide as the trigonid, and from *A. germanicus* and *A. ivani* in the presence of a medial hypoconulid and a less strongly developed hypoconid. p4 differs from that of *A. germanicus* and *A. tagourtensis* in the presence of a single talonid cusp and a smaller metaconid.

Measurements.—See Table 1.

Description.—The M1 (Fig. 2A) shows a moderate degree of transverse development. The wide styler shelf bears two well marked cusps, the parastyle and stylocone. The ectoflexus is moderately deep and asymmetrical. The parastylar lobe is long and directed anteriorly, whereas the metastylar lobe points posterolabially. The prepara- and postmetacristae are long, the latter being more oblique with regards to the labio-

Table 1. Measurements (in mm) of the cheek teeth of *Afrodon gheerbranti* sp. nov. cheek teeth from the early Palaeocene of Hainin. Hyphen designates dimensions that could not be measured.

Specimen number	IRSNB number	Position	Length	Width
Q2-28	M1985	M1	2.02	2.10
N2-17	M1982	M2	1.90	2.26
Q2-35		M2	1.80	2.26
R1-47		M2	1.80	2.34
N2-16	M1983	M3	1.46	2.30
R1-70		M3	1.38	–
R1-71		M3	1.46	2.38
Q2-32	M1986	p4	2.12	1.08
N2-34		p4	–	1.00
N2-12		m1	2.24	1.20
O1-03		m1	2.16	1.02
N2-13	M1987	m1	2.14	1.12
Q1-06	M1988	m2	1.90	1.14
Q2-31		m2	1.88	1.20
Y1-06		m2	1.98	1.12
N2-06	M1989	m3	2.16	1.04

lingual axis of the tooth. The preparacrista extends up to the stylocone. The paracone and metacone are well separated and linked by a rectilinear centrocrista. The paracone is taller and situated more labially than the metacone. The paracingulum is well marked; the metacingulum is very narrow, short and terminates at the posterolingual base of the metacone. The lingual part of the tooth is more developed transversely than its labial part. The protofossa is deep, wide and well delimited. The paraconule and metaconule are well developed and have long and sharp internal cristae. The postparaconule crista extends on to the lingual flank of the paracone, giving a triangular aspect to its base (along with the preparacrista and the centrocrista). The protocone is markedly procline, and is the smallest of the three main cusps.

The M2 (Fig. 2B) is similar to M1, with a larger styler shelf and a greater degree of transverse development. The tooth is slightly shorter anteroposteriorly, and the parastylar lobe points anterolabially. The preparacrista disappears halfway between the bases of the parastyle and stylocone, and the protofossa is narrower than on M1.

The M3 (Fig. 2C) is similar to M2 in size. The anteroposterior development of the tooth is less than that of M2, and the metacone is slightly reduced. The metastylar lobe is absent, while the parastylar lobe is well developed. The preparacrista is directed towards the parastyle and disappears just before reaching its base. One of the specimens identified as M3 has small pre- and postcingula.

The p4 (Fig. 2D) has a premolariform morphology. The trigonid is compressed labiolingually. The paraconid is very small and occupies an anterolingual position, and there is no precingulid. The metaconid occurs as a tiny cusp slightly pos-

terior to the protoconid, while the postmetacristid is well marked and sharp. The talonid is short, lacks a basin, and carries only one cusp occupying the position of the hypoconulid. No crista obliqua is visible, and the hypoflexid occurs along the entire width of the talonid.

The m1 (Fig. 2E) is robust and marked by an antero-posteriorly long trigonid resembling the talonid in both height and width. The trigonid cusps are sharp and strong at their bases. The precingulid is moderately developed. The paraconid, though large, is the smallest cusp of the trigonid. The metaconid is slightly protruding lingually and lower than the protoconid. The protoconid is located slightly anterior to the metaconid, resulting in the posterior wall of the trigonid being somewhat oblique with respect to the antero-posterior axis of the tooth. The postmetacristid is well developed, giving the trigonid a markedly procline aspect. The talonid cusps are equidistant and of similar size. The talonid basin is moderately deep. The crista obliqua reaches the posterior wall of the trigonid halfway between the protoconid and the metaconid and extends up towards the tip of the latter. The hypoflexid is wide and relatively shallow.

The m2 (Fig. 2F) is very similar to m1. The trigonid is slightly wider than the talonid and more compressed antero-posteriorly, making m2 shorter than m1. The protoconid and metaconid are more widely spaced than on m1.

The m3 (Fig. 2G) is similar to m2. The metaconid is situated more anteriorly than on m1 and m2, and the posterior wall of the trigonid is consequently less oblique. The talonid is narrower than the trigonid. The hypoconulid is more developed than the hypoconid and entoconid, and shifted posteriorly.

Discussion.—*A. gheerbranti* shares the following morphological features with Adapisoriculidae: transversely elongated upper molars; stylar cusps well marked (at least parastyle and stylocone); wide stylar shelf with long prepara- and postmetacristae; paracone and metacone well separated down to their bases, with a rectilinear or dilambdodont centrocrista. Lower molars show little height difference between trigonid and talonid; well-developed talonid; crista obliqua extends up the posterior wall of the trigonid (see Gheerbrant and Russell 1989). Upper molar characters shared with the genus *Afrodon* include: rectilinear centrocrista; wide stylar shelf; stylar cusps little marked; strongly asymmetrical ectoflexus; large transverse development of the tooth; sharp internal crests of the conules; absence of precingulum and postcingulum. Lower molars share with the genus: massive cusps; metaconid posterior to the protoconid; submedial hypoconulid (see Gheerbrant and Russell 1989).

The upper molars of *A. gheerbranti* are morphologically similar to those of *A. germanicus*, but are 35% larger in size and proportionally less developed transversely. The upper molars of *A. chleuhi* are even more transversely developed than those of *A. germanicus*, and have a wider stylar shelf than those of either of the other two species. The upper molars of *A. ivani* are also very wide transversely, but the stylar shelf is narrower than in other species of *Afrodon*. *A. tago-*

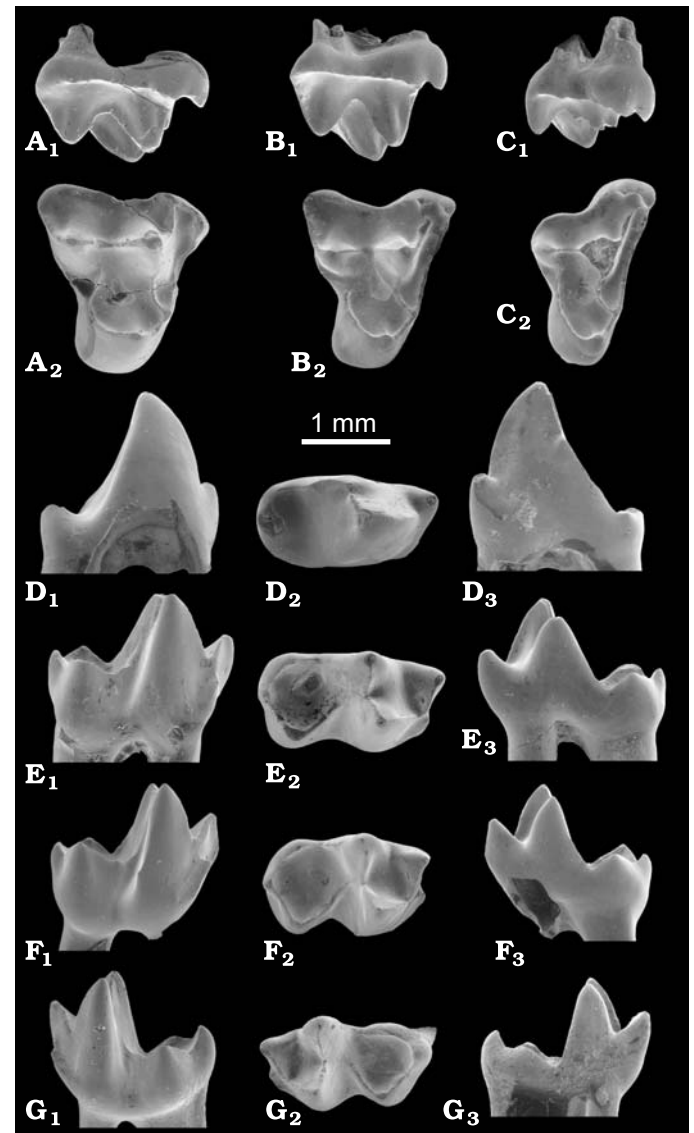


Fig. 2. SEM pictures of the adapisoriculid *Afrodon gheerbranti* sp. nov. from the early Palaeocene of Hainin (Belgium). **A.** Right M1, IRSNB M1985 (Q2-28), in labial (A₁) and occlusal (A₂) views. **B.** Holotype: right M2, IRSNB M1982 (N2-17), in labial (B₁) and occlusal (B₂) views. **C.** Right M3, IRSNB M1983 (N2-16), in labial (C₁) and occlusal (C₂) views. **D.** Right p4, IRSNB M1986 (Q2-32), in labial (D₁), occlusal (D₂), and lingual (D₃) views. **E.** Right m1, IRSNB M1987 (N2-13), in labial (E₁), occlusal (E₂), and lingual (E₃) views. **F.** Right m2, IRSNB M1988 (Q1-06), in labial (F₁), occlusal (F₂), and lingual (F₃) views. **G.** Left m3, IRSNB M1989 (N2-06), in labial (G₁), occlusal (G₂), and lingual (G₃) views.

urtensis is markedly smaller than *A. gheerbranti*, and characterised by an M1 with a more triangular aspect, a well developed paracingulum, and a less procline protocone. The M1 attributed here to *Afrodon gheerbranti* is rather large compared to M2, with a more anteroposteriorly developed protocone. This is unusual in adapisoriculids, but in line with the particularly long m1. The p4 with only one talonid cusp is closer to *A. chleuhi* and *A. ivani* than to *A. germanicus* or *A. tagourtensis*. Unlike *A. chleuhi*, the lower molars of *A. gheerbranti* have a talonid as wide as the trigonid.

A. gheerbranti resembles *A. ivani* and *A. germanicus* in having sharp lower molar cusps, whereas the African species *A. chleuhi* and *A. tagourtensis* are marked by more massive cusps. The talonid of *A. ivani* has a more square aspect, with a relatively strong hypoconid, a feature it shares only with *A. germanicus*. *A. gheerbranti* is morphologically intermediate between *A. germanicus* and *A. chleuhi*, with a smaller stylar shelf and a smaller degree of transverse development of the upper molars than observed in *A. chleuhi*.

Stratigraphic and geographic range.—Known only from the early Palaeocene of the Mons Basin, Belgium.

Genus *Bustylus* Gheerbrant and Russell, 1991

Type species: *Bustylus cernaysi* Gheerbrant and Russell, 1991; Thanetian (late Palaeocene), Cernay (France).

Other species included.—*Bustylus marandati* (Crochet and Sigé, 1983); *Bustylus folieae* sp. nov.

Bustylus marandati (Crochet and Sigé, 1983)

Figs. 3, 4; Table 2.

Type material: Holotype: IRSNB M1974 (N2-03), right M2. Paratypes: IRSNB M1990 (Q2-39), left P4; IRSNB M1975 (N2-02), left M1; IRSNB M1984 (R1-68), left M3; IRSNB M1991 (N2-22), left jaw fragment with p4, talonid of m1 and alveoli of p3; IRSNB M1992 (Q2-05), left m1; IRSNB M1993 (R1-27), left m2; IRSNB M1994 (Q2-42), left m3.

Type locality: Hainin, Hainaut province, Belgium.

Type horizon: Early Palaeocene, Hainin Formation, Mons Basin.

Referred material.—Right M2; Q2-06, right M3; Q2-29, right m1 or m2; R1-89, posterolabial part of M1 or M2; R1-88, lingual part of left M3; Q1-13, lingual part of right dp4 or m1; talonid of right m1; Q2-15, trigonid of right m2; Q2-18, talonid of left m2; Q1-14, trigonid of left m3; R1-19, trigonid of left m2 or m3; R1-29, trigonid of m2 or m3.

Emended diagnosis.—Differs from *B. cernaysi* and *B. folieae* in its smaller size (30% smaller than *B. cernaysi* and 15% smaller than *B. folieae*). Upper molars differ from those of *B. cernaysi* in their less developed stylar cusps and narrower lingual region, from *B. folieae* in a transversely less wide M1 and from both species in the presence of longer and more marked internal crests. Lower molars differ from those of *B. cernaysi* and *B. folieae* in the presence of a proportionally narrower m1 with a particularly long and narrow trigonid, and from *B. folieae* in the presence of a smaller precingulid and less compressed trigonid on m2. p4 differs from those of *B. cernaysi* and *B. folieae* in the presence of a slightly smaller paraconid and a less individualised metaconid.

Measurements.—See Table 2.

Description.—The P4 (Fig. 3D) is strongly developed transversely. The stylar shelf is reduced, only developed posteriorly, and bears one cusp in the position of the metastyle. The parastyle is broken at the base, but seems less developed. The postmetacrista is directed posterolabially and slightly curved. The paracone is high, while the metacone is reduced to a small bulge on the crest linking the paracone to the metastyle. There

Table 2. Measurements (in mm) of the cheek teeth of *Bustylus marandati* (Crochet and Sigé, 1983) cheek teeth from the early Palaeocene of Hainin. Hyphen designates dimensions that could not be measured.

Specimen number	IRSNB number	Position	Length	Width
Q2-39	M1990	P4	0.96	1.34
N2-02	M1975	M1	1.22	1.18
N2-03	M1974	M2	1.08	1.48
W2-01		M2	1.20	—
R1-68	M1984	M3	0.92	1.54
Q2-06		M3	0.88	1.56
N2-22	M1991	p4	1.18	0.56
Q2-05	M1992	m1	1.20	0.64
R1-27	M1993	m2	1.22	0.80
R1-34		m2	1.24	0.84
MZ1-01		m2	1.22	0.96
Q2-42	M1994	m3	1.24	0.68

is neither a paracingulum nor a metacingulum. The lingual region of the tooth is more developed than its labial part. The profossa is large and shallow. No metaconule is visible, and the paraconule is barely noticeable as a protuberance on the preprotocrista. The postparaconule crista is the only visible internal crest, and climbs up on to the paracone. The protocone is small and shifted anteriorly.

The M1 (Fig. 3A) is relatively long and narrow compared to M2 and shows a moderate degree of transverse development. The stylar shelf is wide and shows three cusps: the parastyle, stylocone and mesostyle. The ectoflexus is relatively deep and rather symmetrical. The parastylar lobe points labially, whereas the metastylar lobe is directed posterolabially. The preparacrista and postmetacrista are relatively long and oblique to the anteroposterior axis of the tooth. The paracone and metacone are well separated and linked by a rectilinear centrocrista. The paracingulum is relatively wide, whereas the metacingulum is very narrow, short and terminates at the posterolingual base of the metacone. The lingual part of the tooth is more developed transversely than its labial part. The profossa is deep, relatively small and well delimited. The metaconule, and even more so the paraconule, are well developed and carry sharp internal cristae. The protocone is slightly procline and smaller than the paracone and metacone.

The M2 (Fig. 3B) is relatively similar to M1, but much more developed transversely. The prepara- and postmetacristae are more parallel to the transverse axis of the tooth and the stylar shelf is wider.

The M3 (Fig. 3C) is similar in size to M2. The parastylar lobe is even more developed than on M2, whereas the metastylar lobe is almost absent. The metacone is moderately reduced. The profossa is slightly smaller than on M2.

Specimen IRSNB M1991 (Fig. 3H) is a dentary preserving p4 in situ, as well as the alveoli for p3. The p3 appears slightly shorter than p4; both p3 and p4 are biradicate. Relatively short diastemata are present in front of and behind p3.

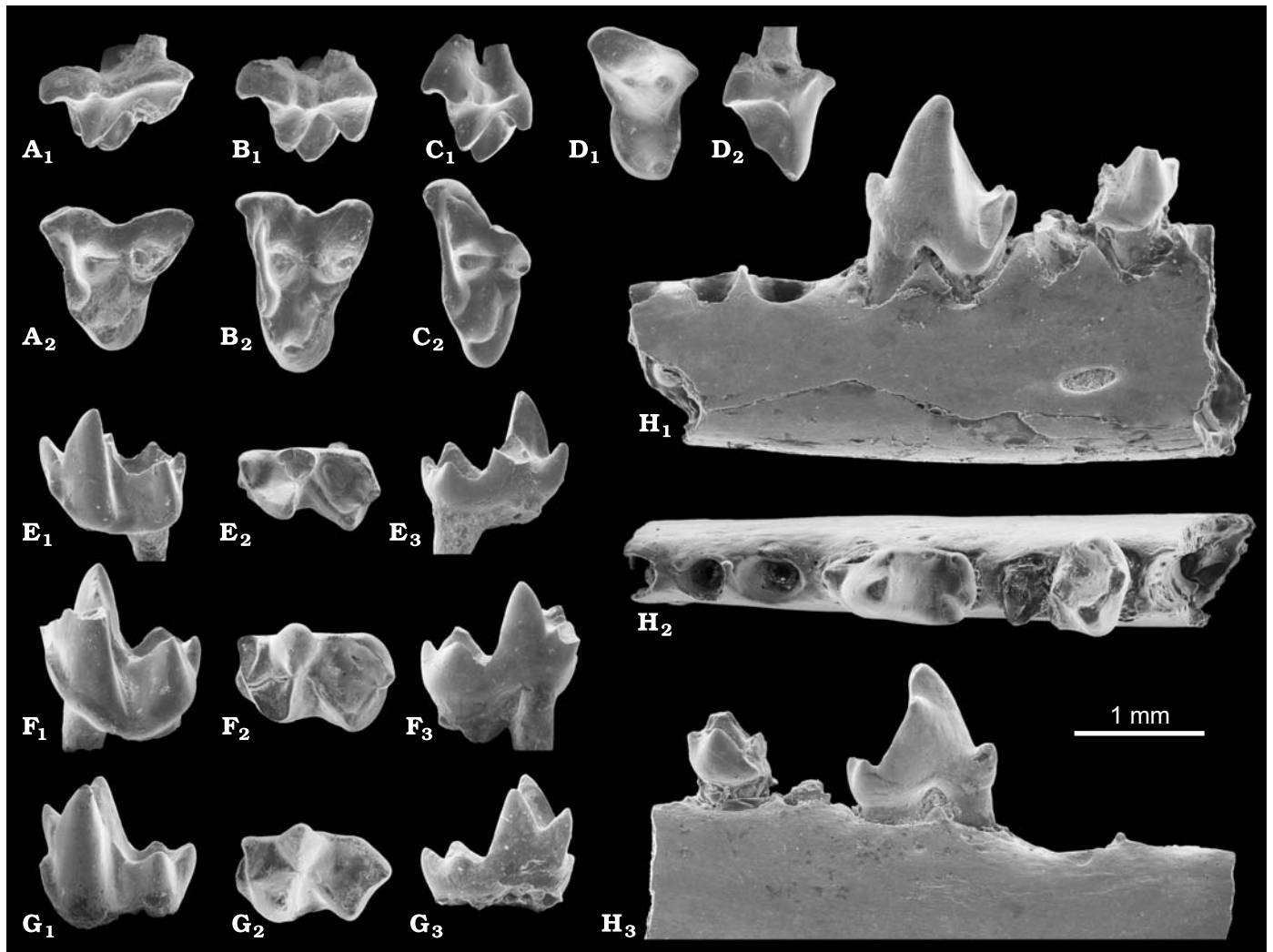


Fig. 3. SEM pictures of the adapisoriculid *Bustylus marandati* (Crochet and Sigé, 1983) from the early Palaeocene of Hainin (Belgium). **A.** Left M1, IRSNB M1975 (N2-02), in labial (A₁) and occlusal (A₂) views. **B.** Holotype: left M2, IRSNB M1974 (N2-03), in labial (B₁) and occlusal (B₂) views. **C.** Left M3, IRSNB M1984 (R1-68), in labial (C₁) and occlusal (C₂) views. **D.** Right P4, IRSNB M1990 (Q2-39), in labial (D₁) and occlusal (D₂) views. **E.** Left m1, IRSNB M1992 (Q2-05), in labial (E₁), occlusal (E₂), and lingual (E₃) views. **F.** Left m2, IRSNB M1993 (R1-27), in labial (F₁), occlusal (F₂), and lingual (F₃) views. **G.** Left m3, IRSNB M1994 (Q2-42), in labial (G₁), occlusal (G₂), and lingual (G₃) views. **H.** Left jaw fragment with p4, talonid of m1 and alveoli of p3, IRSNB M1991 (N2-22), in labial (H₁), occlusal (H₂), and lingual (H₃) views.

The dentary is moderately high (slightly higher than the crown of p4) and has a dental foramen under the anterior root of m1.

The p4 (Fig. 3H) is premolariform. The trigonid is much longer than the talonid, but of similar width. The paraconid is small and situated at the anterolingual base of the protoconid. There is no precingulid, and the protoconid is the highest cusp. The reduced metaconid is partially fused to the protoconid and located slightly posterior to it. The postmetacristid is well developed. The talonid has two cusps, corresponding to the entoconid and hypoconid, respectively. A poorly developed crista obliqua is visible, but delimits no basin.

The m1 (Fig. 3E) is narrow, with little height difference between the trigonid and talonid. The trigonid is narrower than the talonid and rather long. The trigonid cusps are sharp, but have a robust base. The precingulid is moderately developed. The paraconid, the smallest cusp of the trigonid, is re-

duced, points lingually and anteriorly, and is aligned with the metaconid along the anteroposterior axis of the tooth. The slightly lingually protruding metaconid is lower than the protoconid. The latter is located anterior to the metaconid, resulting in an oblique and almost vertical posterior wall of the trigonid. The postmetacristid is relatively well marked. The hypoconid is the most voluminous cusp of the talonid and is shifted labially. The three talonid cusps are equidistant, and the talonid basin is deep. The crista obliqua reaches the trigonid lingual to the protocristid notch and extends up towards the tip of the metaconid. The hypoflexid is narrow and deep, and the tooth is slightly narrower (labiolingually) in this area.

The m2 (Fig. 3F) is morphologically similar to m1, but more robust, distinctly wider, and slightly longer. The trigonid is markedly compressed anteroposteriorly. The hypoconulid is slightly closer to the entoconid than to the hypoconid.

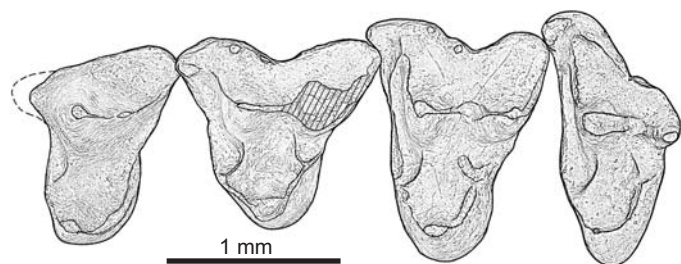


Fig. 4. Occlusal sketch of the reconstructed upper tooth row, from P4 to M3, of *Bustylus marandati* (Crochet and Sigé, 1983), the best known species from Hainin as regards the upper dentition.

The m3 (Fig. 3G) is very similar to m2. The talonid is slightly narrower than the trigonid, while the hypoconulid is bigger than on m1 and m2, and shifted posteriorly.

Discussion.—The lower teeth referred here to *Bustylus marandati* conform in their size, morphology and occlusal pattern to those of Adapisoriculidae. Their affinity with the family Adapisoriculidae was discussed by Gheerbrant (1991). The upper molars share with other species of *Bustylus* the presence of a mesostyle and a rectilinear centrocrista, a rather short protocone, and internal crests of the conules less marked than in *Afrodon*.

The upper molars of *Bustylus marandati* differ from those of *Bustylus cernaysi* in their smaller size (70%), more crestiform stylar cusps, a shorter lingual region, less transverse development and more marked internal crests. The M1 (IRSNB M1273) of *Bustylus* sp. from Dormaal, Belgium (Smith 1997) is very similar to that of *B. marandati*, but differs from *B. marandati* in its slightly smaller size (90%), a lesser degree of transverse development, more individualised stylar cusps, a shallower and less asymmetrical ectoflexus, and a shorter postmetacrasta. *B. marandati* is the best known species as regards the upper molars, and a tentative reconstruction of the jugal teeth is proposed in Fig. 4. Among the specimens initially attributed to *B. marandati* by Crochet and Sigé (1983), the M3 IRSNB M1976 is here transferred to *Bustylus folieae* sp. nov. (see discussion of that species). The p4 is morphologically very similar to that of *B. cernaysi*, but is slightly less molariform, with a smaller paraconid and a less individualised metaconid. The lower molars are very similar to those of other species of Adapisoriculidae. The talonid is much deeper than in *Afrodon*, but similar to other species of *Bustylus*. The hypoconid is larger and located more labially than in all species of *Afrodon*. The m1 (IRSNB M1274) of *Bustylus* sp. (Smith 1997) is remarkably similar in size and morphology to that of *B. marandati*. The trigonid of the figured m1 is unusually narrow and somewhat resembles the shape of a dp4, except for the relatively steep paraconid. The m1 talonid preserved in the jaw fragment (IRSNB M1991) is slightly wider, and the possibility of the isolated m1 being a dp4 can not be excluded. However, the narrowness of m1 seems compatible with the relatively small degree of transverse development of M1, and we therefore here regard the isolated tooth as an m1.

Stratigraphic and geographic range.—Known only from the early Palaeocene of the Mons Basin, Belgium.

Bustylus folieae sp. nov.

Fig. 5, Table 3.

Etymology: In honour of Dr. Annelise Folie, for her contribution to the knowledge of the herpetofauna of Hainin.

Type material: Holotype: IRSNB M1996 (Y1-01), left M1. Paratypes: IRSNB M1997 (R1-40), left M2; IRSNB M1976 (N2-04), left M3; IRSNB M1998 (N2-06b), left mandible fragment with p3–m2 and alveoli of p2; IRSNB M1999 (P2-14), left p3; IRSNB M2000 (R1-31), left p4; IRSNB M2001 (N2-08), right dp4; IRSNB M2002 (P2-04), left m1; IRSNB M2003 (N1-01), left m2; IRSNB M2004 (R1-10), right m3.

Type locality: Hainin, Hainaut province, Belgium.

Type horizon: Early Palaeocene, Hainin Formation, Mons Basin.

Referred material.—IRSNB M1995 (Z2-01), left dp4, Q2-38, left M3; O1-08, right p4; N2-07, right m1; O2-01, right m1; Q2-09, left m3; R1-34, left m3; Q1-18, left m3; P1-09, lingual part of right M1; R1-77, lingual part of right M2; P2-08, labial part of right p4; R1-91, trigonid of left dp4; Q2-22, trigonid of right m1; R1-20, talonid of left m1; N1-10, trigonid of left m3.

Diagnosis.—Size intermediate between *B. marandati* and *B. cernaysi* (20% smaller than *B. cernaysi* and 15% larger than *B. marandati*). Upper molars differ from those of *B. cernaysi* in their less developed stylar cusps and a narrower lingual region, and from *B. marandati* and *B. cernaysi* in the presence of a transversely wider M1. Lower molars differ from those of *B. marandati* and *B. cernaysi* in the presence of a much larger precingulid and a deeper and wider hypoflexid. p4 morphology similar to that of *B. cernaysi*, and differs from that of *B. marandati* in the presence of a larger paraconid and a lower and more individualised metaconid.

Measurements.—See Table 3.

Description.—The dp4 (Fig. 5G) is morphologically similar to M1, but is slightly longer anteroposteriorly and much less developed transversely, especially in the stylar shelf region. The paracone and metacone are less sharp than on M1. The parastylar lobe points more anteriorly, and the metastylar lobe is directed more labially. The ectoflexus is somewhat deeper, and the stylar cusps are almost invisible. Some of these differences may be explained by the high level of wear that the tooth exhibits.

The M1 (Fig. 5H) shows a moderate degree of transverse development. The stylar shelf is wide and exhibits four marked cusps: the parastyle, stylocone, mesostyle and D cusp. The metastyle is a very faint bulge at the labial end of the postmetacrasta. The ectoflexus seems relatively shallow owing to wear on the labial edges of the parastylar and metastylar lobes, but was probably relatively deep. It forms two relatively symmetrical lobes. The metastylar lobe is slightly smaller than the parastylar lobe and points more posteriorly. The preparacrasta and postmetacrasta are long, the latter being more oblique to the labiolingual axis of the tooth. The paracone and metacone are well separated down to their bases, linked by a rectilinear centrocrista, similar in size and aligned anteroposteriorly. The paracingulum is relatively

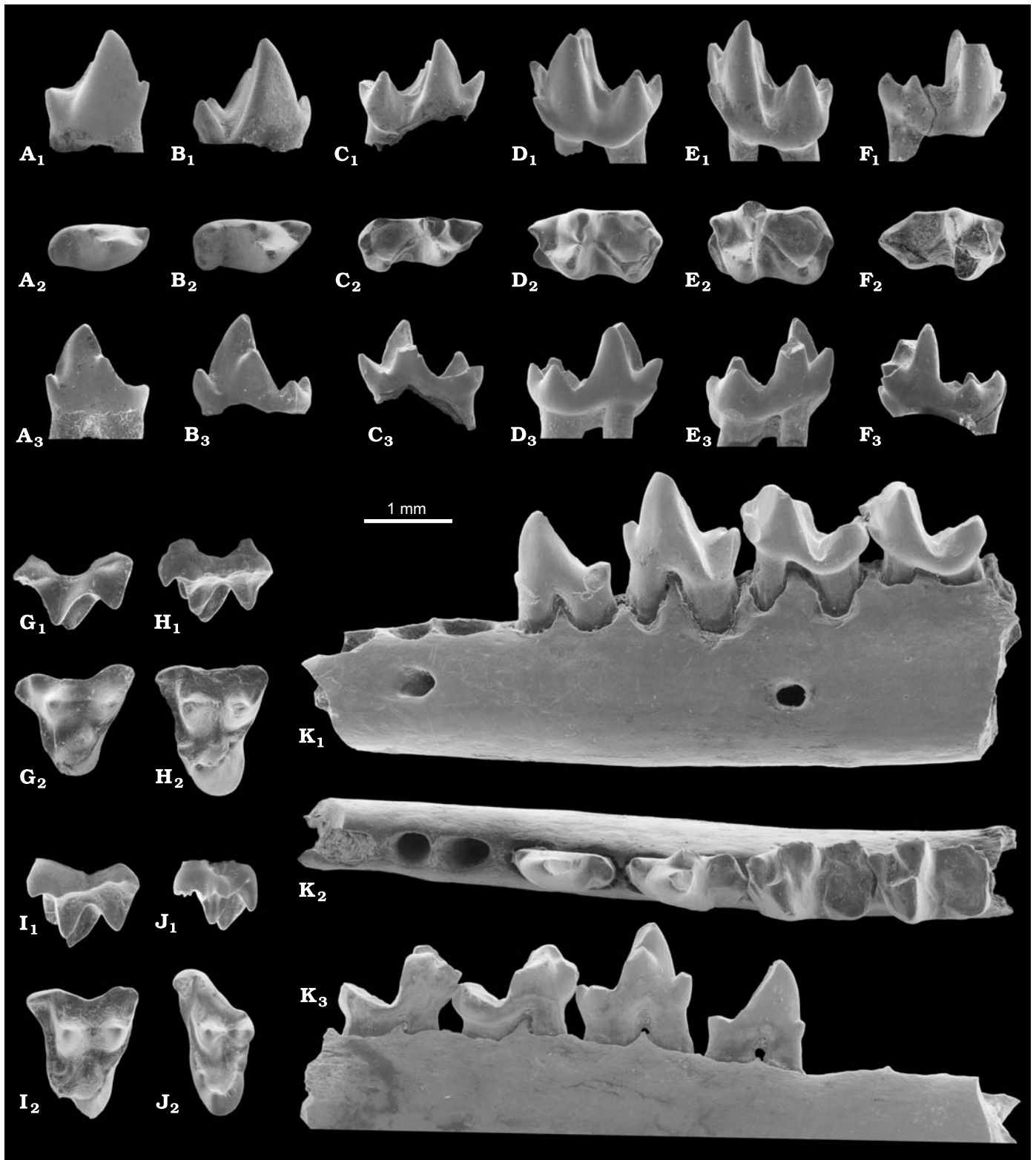


Fig. 5. SEM pictures of the adapisoriculid *Bustylus folieae* sp. nov. from the early Palaeocene of Hainin (Belgium). **A.** Left p3, IRSNB M1999 (P2-14), in labial (A₁), occlusal (A₂), and lingual (A₃) views. **B.** Left p4, IRSNB M2000(R1-31), in labial (B₁), occlusal (B₂), and lingual (B₃) views. **C.** Right dp4, IRSNB M2001 (N2-08), in labial (C₁), occlusal (C₂), and lingual (C₃) views. **D.** Left m1, IRSNB M2002 (P2-04), in labial (D₁), occlusal (D₂), and lingual (D₃) views. **E.** Left m2, IRSNB M2003 (N1-01), in labial (E₁), occlusal (E₂), and lingual (E₃) views. **F.** Right m3, IRSNB M2004 (R1-10), in labial (F₁), occlusal (F₂), and lingual (F₃) views. **G.** Left dp4, IRSNB M1995 (Z2-01), in labial (G₁) and occlusal (G₂) views. **H.** Holotype: left M1, IRSNB M1996 (Y1-01), in labial (H₁) and occlusal (H₂) views. **I.** Left M2, IRSNB M1997 (R1-40), in labial (I₁) and occlusal (I₂) views. **J.** Left M3, IRSNB M1976 (N2-04), in labial (J₁) and occlusal (J₂) views. **K.** Left jaw fragment with p3-m2 and alveoli of p1-p2, IRSNB M1998 (N2-06b), in labial (K₁), occlusal (K₂), and lingual (K₃) views.

Table 3. Measurements (in mm) of the cheek teeth of *Bustylus folieae* sp. nov. cheek teeth from the early Palaeocene of Hainin. Hyphen designates dimensions that could not be measured.

Specimen number	IRSNB number	Position	Length	Width
Z2-01	M1995	dP4	1.42	1.34
Y1-01	M1996	M1	1.32	1.52
R1-40	M1997	M2	1.28	–
N2-04	M1976	M3	0.98	1.68
Q2-38		M3	1.06	1.70
N2-06b	M1998	p3	1.18	0.44
P2-14	M1999	p3	1.20	0.52
N2-06b	M1998	p4	1.34	0.62
R1-31	M2000	p4	1.26	0.60
O1-08		p4	1.26	0.64
N2-08	M2001	dp4	1.44	0.66
N2-06b	M1998	m1	1.48	0.90
P2-04	M2002	m1	1.50	0.86
N2-07		m1	1.50	0.90
O2-01		m1	1.44	0.80
N2-06b	M1998	m2	1.38	0.94
N1-01	M2003	m2	1.44	0.94
R1-10	M2004	m3	1.48	0.80
Q2-42		m3	1.24	0.68
Q2-09		m3	1.36	0.78

wide, whereas the metacingulum is very narrow, short and terminates at the posterolingual base of the metacone. The lingual part of the tooth displays a greater degree of transverse development than the labial part, and is slightly shifted anteriorly. The protofossa is deep and well delimited. The paraconule and metaconule are well developed, whereas the internal crests are not well marked, and rather short. The protocone is slightly procline and similar in height to both the paracone and metacone.

The M2 (Fig. 5I) is similar to M1, but is characterised by a slightly greater degree of transverse development and a wider protofossa. The styler cusps are less visible than on M1 and the metacingulum extends more labially.

The M3 (Fig. 5J) presents a well-developed parastylar lobe, whereas its metastylar lobe is reduced. The metacone is relatively small, and the protofossa is shorter anteroposteriorly than on M1 and M2. The conules are well developed and present no internal crests.

Specimen IRSNB M1998 (Fig. 5K) is a fragmentary left dentary bearing the posterior part of the alveolus for p1, the alveoli for p2, and p3 to m2. The alveoli for p2–p4 are biradicate, with those for p2 and p3 being similar in length and somewhat shorter than p4. A short diastema is present in front of p3. The dentary is relatively high (1.5 times the height of the crown of p4) and carries two dental foramina below the anterior roots of p2 and m1.

The p3 (Fig. 5A) resembles p4, but is shorter and lower and displays a somewhat simpler morphology. The trigonid

is narrower, the paraconid smaller, and the metaconid much more reduced and posterior in position. The talonid is smaller and exhibits a single cusp in the position of the hypoconid.

The p4 (Fig. 5B) is pre- to semi-molariform. The trigonid is much longer and higher than the talonid, but has the same width. The paraconid is of moderate size and situated at the anterolingual base of the protocone. There is no precingulid. The protoconid is the biggest cusp of the trigonid, while the slightly reduced metaconid protrudes lingually and is posteriorly shifted compared to the protoconid. The postmetacristid is well developed. The talonid has two cusps corresponding to the entoconid and hypoconid, respectively. There is no trace of a crista obliqua.

The dp4 (Fig. 5C) is much narrower than m1, but has about the same length. The paraconid is large and located anteriorly, while the talonid is wider than the trigonid and separated from the latter by a lateral constriction.

The m1 (Fig. 5D) is relatively robust, with little height and width difference between the trigonid and talonid, although the trigonid is slightly narrower than the talonid and relatively long. The trigonid cusps have very sharp apices, but also strong bases. The precingulid is well developed. The paraconid, the smallest cusp of the trigonid, is projecting anterolingually, and is shifted labially compared to the metaconid. The metaconid, slightly protruding lingually, has about the same height as the protoconid. The latter is located slightly anterior to the metaconid, making the posterior wall of the trigonid, which itself is almost vertical, slightly oblique to the anteroposterior axis of the tooth. The postmetacristid is relatively well developed. The hypoconid is the largest cusp of the talonid, and the three talonid cusps are equidistant. The talonid basin is deep. The crista obliqua reaches the posterior wall of the trigonid lingual to the protocristid notch, and extends high on the trigonid wall towards the tip of the metaconid. The hypoflexid is narrow and deep.

The m2 (Fig. 5E) is morphologically very similar to m1, although the trigonid is markedly shorter and wider, the paraconid is located in a more lingual position, and the metaconid is protruding more lingually.

The m3 (Fig. 5F) is similar to m2, with the talonid being longer and narrower, and the hypoconid being larger and shifted anteriorly.

Discussion.—*Bustylus folieae* is placed in the family Adapisoriculidae and the genus *Bustylus* for the same reasons as *B. marandati*.

The dp4 (IRSNB 1995) was interpreted as an M1 of *B. marandati* by Crochet and Sigé (1983). However, its relatively larger size, as well as other features, such as the small size of the styler shelf and the anterior development of the parastylar lobe, do not correspond to the morphology of other M1s assigned to this species. Based on this relatively different morphology (as compared to other M1s), the high level of wear, the relatively thin enamel, and the absence of root insertions, we prefer to interpret this tooth as a dp4, rather than a worn M1, with its size matching *B. folieae* better than *B. marandati*. The upper molars are similar to those of

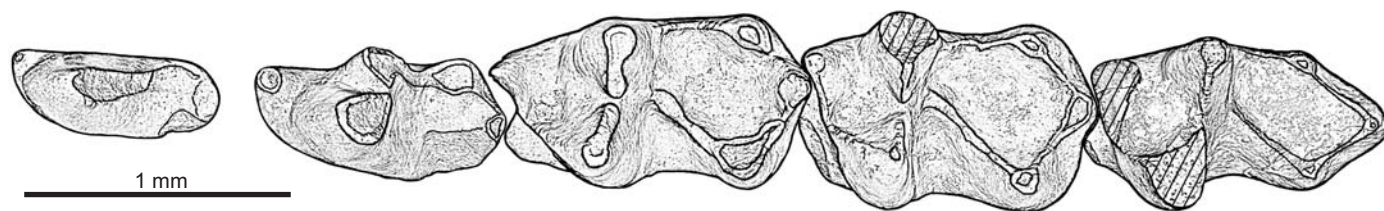


Fig. 6. Occlusal sketch of the reconstructed lower tooth row, from p3 to m3, of *Bustylus folieae* sp. nov., the best known species from Hainin as regards the lower dentition.

B. marandati, but slightly bigger, with M1 being wider transversely, and the styler cusps being slightly more individualised and the internal crests less developed, or even absent, on M3. By contrast, *B. cernaysi* has much better developed styler cusps and is also larger. The M1 (IRSNB M1273) referred to *Bustylus* sp. (Smith 1997) differs from *B. folieae* in showing a smaller degree of transverse development and in the presence of more individualised styler cusps. The p4 differs from that of *B. marandati* in the presence of a slightly larger hypoconid, a longer talonid, a less marked postmetacristid and a larger and more individualised metaconid. The morphology of this tooth seems to be close to that of *B. cernaysi*, but the only p4 reported for the latter is partially broken. The lower molars are similar to those of *B. marandati*, but slightly larger, with a much larger precingulid and a deeper and wider hypoflexid. The width of m1 much more resembles that of m2 than is the case in *B. marandati*, and the talonid of m3 is relatively longer. *B. cernaysi* has a more labially protruding hypoconid and sharper cusps. The m1 (IRSNB M1274) of *Bustylus* sp. from Dormaal (Smith 1997) is very similar, but has a smaller precingulid and is slightly smaller overall. *B. folieae* is the best known species as regards the lower molars, and a tentative of reconstruction of the jugal teeth is proposed in Fig. 6.

Stratigraphic and geographic range.—Known only from the early Palaeocene of the Mons Basin, Belgium.

Genus *Proremiculus* nov.

Etymology: Refers to the primitive molar morphology of this *Remiculus*-like adapisoriculid genus.

Type species: *Proremiculus lagnauxi* sp. nov., see below; by monotypy.

Diagnosis.—As for the type species.

Proremiculus lagnauxi sp. nov.

Fig. 7; Table 4.

Etymology: In honour of Hector Lagnaux, for his efforts in manually sinking the Hainin well reaching a depth of 27 metres, with a diameter of one metre.

Type material: Holotype: IRSNB M2006 (R1-46): left M2. Paratypes: IRSNB M2005 (Q2-44), left M1; IRSNB M2007 (R1-38), right m1; IRSNB M2008 (R1-74), left m1 or m2.

Type locality: Hainin, Hainaut province, Belgium.

Type horizon: Early Palaeocene, Hainin Formation, Mons Basin.

Referred material.—N2-43, talonid of left m1 or m2.

Diagnosis.—General morphology of upper molars similar to

that of *Afrodon*, with only two styler cusps (parastyle and stylocone), marked internal crests of the conules, and a typically “predilambdodont” morphology with a rectilinear centrocrista. Differs from all species of *Afrodon* in the presence of a lower paracone and metacone, the presence of pre- and postcingula, and a less asymmetrical hypoflexus on the upper molars, as well as more massive cusps and a wider talonid on the lower molars. Differs from all species of *Remiculus* in the presence of a rectilinear centrocrista, the absence of a mesostyle, and a less developed lingual cingulum on the upper molars, as well as a slightly less strongly developed hypoconid and a medial hypoconulid on the lower molars.

Measurements.—See Table 4.

Table 4. Measurements (in mm) of the cheek teeth of *Proremiculus lagnauxi* sp. nov. cheek teeth from the early Palaeocene of Hainin. Hyphen designates dimensions that could not be measured.

Specimen number	IRSNB number	Position	Length	Width
Q2-44	M2005	M1	–	2.20
R1-46	M2006	M2	2.02	2.64
R1-38	M2007	m1	2.18	1.20
R1-74	M2008	m1, m2	2.04	1.30

Description.—The M1 (Fig. 7A) described here is incomplete, lacking the metacone, the metastylar lobe and part of the postcingulum. The styler shelf is relatively short and bears two well-defined cusps (parastyle and stylocone). The preparacrista is short and almost parallel to the labiolingual axis of the tooth. The paracone and metacone are well individualised and the postparacrista is oriented anteroposteriorly, indicating that the entire centrocrista was rectilinear. The paracingulum is very narrow. The lingual part of the tooth is more developed than the labial part. The paraconule is well defined, while the postparaconule crista is marked but not very visible owing to poor preservation of the tooth. The precingulum and the partially broken postcingulum are long and almost join on the lingual side of the protocone.

The M2 (Fig. 7B) is the only complete upper tooth. The relatively short styler shelf bears two marked cusps (parastyle and stylocone). The preparacrista and postmetacrista are long, the latter being more oblique with respect to the labiolingual axis of the tooth. The ectoflexus is moderately deep and slightly asymmetrical. The parastylar lobe has about the same

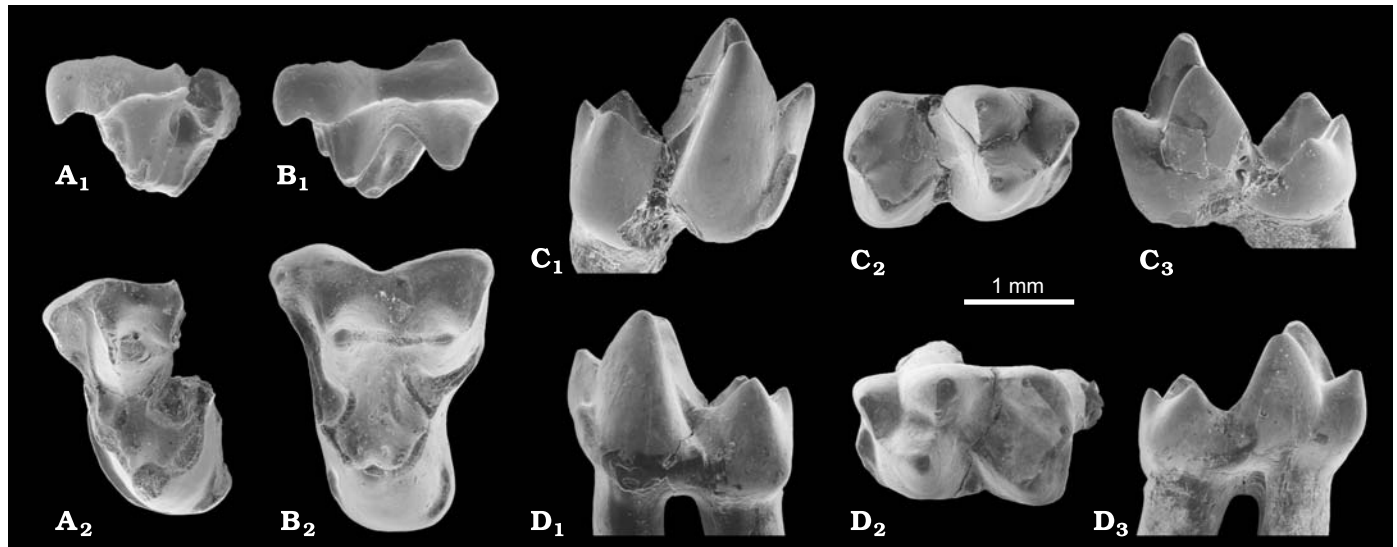


Fig. 7. SEM pictures of the adapisoriculid mammal *Proremiculus lagnaui* sp. nov. from the early Palaeocene of Hainin (Belgium). **A.** Left M1, IRSNB M2005 (Q2-44), in labial (A₁) and occlusal (A₂) views. **B.** Holotype: left M2, IRSNB M2006 (R1-46), in labial (B₁) and occlusal (B₂) views. **C.** Right m1, IRSNB M2007 (R1-38), in labial (C₁), occlusal (C₂), and lingual (C₃) views. **D.** Left m1,2, IRSNB M2008 (R1-74), in labial (D₁), occlusal (D₂), and lingual (D₃) views.

size as the metastylar lobe, but is oriented more labially. The paracone and metacone are well separated down to their bases and linked by a rectilinear centrocrista. The paracone is higher and situated slightly more labially than the metacone. The lingual part of the tooth is much more transversely developed than the labial part. The protofossa is moderately developed, and the paraconule is better individualised than the metaconule. The internal crests are well marked, with the post-paraconule crista extending on to the lingual face of the paracone. The protocone is the largest cusp of the tooth and has a massive and slightly procline aspect. The presence of a very small precingulum and large postcingulum enlarges the base of the protocone anteroposteriorly. There is no hypocone on the postcingulum.

The m1 (Fig. 7C) is massive, with strong and low cusps. There is little difference in height between the trigonid and the talonid, with the latter being slightly wider than the former. The precingulid is moderately developed. The paraconid, though relatively large, is the smallest trigonid cusp, points anteriorly, and is located slightly labial to the metaconid. The metaconid has the same height as the protoconid and is situated more posteriorly than the latter, resulting in the posterior wall of the trigonid being oblique to the anteroposterior axis of the tooth. The posterior wall of the trigonid is not very steep anteroposteriorly. The three talonid cusps are equidistant, with the hypoconid being slightly larger than the two other cusps, and projecting labially. The talonid basin is relatively deep. The crista obliqua reaches the posterior wall of the trigonid halfway between the protoconid and metaconid, and extends up towards the metaconid. The hypoflexid is wide and shallow.

Specimen IRSNB M2008 (Fig. 7D) represents either m1 or m2, and is the only other known lower tooth. It is very similar to m1 in its size and morphology, with a slightly smaller

and more posteriorly situated paraconid. However, the somewhat shorter trigonid could be a reason to consider this tooth an m2, rather than m1.

Discussion.—The morphology of *Proremiculus lagnaui* resembles that of *Afrodon*, showing marked internal crests, a rectilinear centrocrista, only two stylar cusps on the upper molars, and a small hypoconid on the lower molars. However, its lower paracone and metacone, anteroposteriorly longer protocone, small precingulum and postcingulum, relatively square upper molars and relatively shallow talonid basin, as well as the bulbous cusps of its lower molars resemble the genus *Remiculus*, although these derived features are not as well developed as in *R. deutschii* or *R. delseitei*. The presence of such derived characters excludes this species from the genus *Afrodon*. At the same time, the absence of other derived characters such as a mesostyle, D cusp, and dilambdodont centrocrista excludes it from the genus *Remiculus*, thus justifying its inclusion in the new genus *Proremiculus*.

Stratigraphic and geographic range.—Known only from the early Palaeocene of the Mons Basin, Belgium.

Genus *Adapisoriculus* Lemoine 1885

Type species: Adapisoriculus minimus (Lemoine, 1883), Cernay-lès-Reims, late Palaeocene; by monotypy.

?*Adapisoriculus* sp.

Fig. 8.

Material.—IRSNB M2009 (W2-02), right M3, early Palaeocene of Hainin, Hainaut province, Belgium..

Measurements.—M3: L = 1.30 mm; W = 1.97 mm.

Description.—The M3 is the only known complete molar of this taxon. The tooth is strongly dilambdodont and the wide stylar shelf has three cusps (parastyle, stylocone and meso-

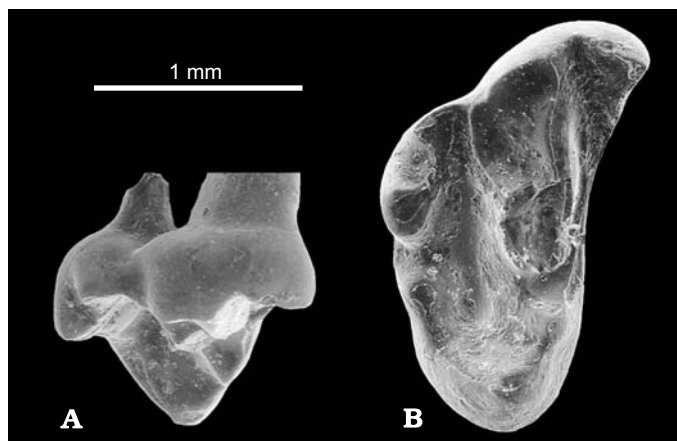


Fig. 8. SEM pictures of the adapisoriculid ?*Adapisoriculus* sp. from the early Palaeocene of Hainin (Belgium). Right M3, IRSNB M2009 (W2-02), in labial (A) and occlusal (B) views.

style). The metastylar lobe is absent, whereas the parastylar lobe accounts for more than one third of the occlusal surface. The preparacrista is long and runs parallel to the labiolingual axis of the tooth, isolating a portion of the parastylar lobe lower than the stylar shelf. There is no postmetacrista. The paracone and metacone are well separated down to their bases, and linked by a strongly dilambdodont centrocrista. The metacone is greatly reduced and points posteriorly, with the paracone occupying a more lingual position than the latter. The paracingulum is very narrow and there is no metacingulum. The protofossa is wide and deep, and delimited by poorly marked crests. The paraconule and metaconule are clearly visible, but the internal crests are indistinct.

Discussion.—The M3 attributed to ?*Adapisoriculus* sp. shares with *A. minimus* a high degree of dilambdodonty, a wide protofossa with no clearly marked internal crests, and a rounded lingual region of the protocone. The comparison with *A. minimus* is difficult, both because no M3 has been described for that species and because the tooth described here is damaged, making it difficult to observe the exact topology of the cusps and crests. However, the stylar cusps seem less developed than in *A. minimus*, possibly indicating the presence of another species. The metacone of M3 is markedly more reduced than in *Afrodon* and *Bustylus*, which is probably a derived character.

Discussion

Diversity of adapisoriculids.—In the Hainin mammal collection, Adapisoriculidae is the most abundant group, accounting for more than 30% of the known fauna. The diversity of Adapisoriculidae in Hainin seems higher than in other European or African Palaeocene deposits, with five species (including one unidentified taxon), present in a fauna represented by less than 400 mammalian teeth. In comparison, six species (*Afrodon germanicus*, *Bustylus cernaysi*, *Adapisoriculus minimus*, *Remiculus deutschii*, and two unidentified species)

are known from Cernay-Berru and Walbeck together, with both localities being represented by more than 10,000 dental remains each (Russell 1964).

The family Adapisoriculidae now includes 16 defined species grouped into 7 genera: *Deccanolestes hislopi* Prasad and Sahni, 1988; *Deccanolestes robustus* Prasad, Jaeger, Sahni, Gheerbrant, and Khajuria, 1994; *Deccanolestes narmadensis* Prasad, Verma, Gheerbrant, Goswami, Khosla, Parmar, and Sahni, 2010; *Afrodon chleuhi* Gheerbrant, 1988; *Afrodon germanicus* (Russell, 1964); *Afrodon tagourtensis* Gheerbrant, 1993; *Afrodon ivani* Peláez-Campomanes, 1999; *Afrodon gheerbranti* sp. nov.; *Bustylus marandati* (Crochet and Sigé, 1983); *Bustylus cernaysi* Gheerbrant and Russell, 1991; *Bustylus foliae* sp. nov.; *Adapisoriculus minimus* (Lemoine, 1883); *Garatherium mahboubii* Crochet, 1984; *Proremiculus lagnaui* gen. et sp. nov.; *Remiculus deutschii* Russell, 1964; and *Remiculus delstatei* Smith, 1997.

Additional taxa in open nomenclature include *Deccanolestes* cf. *hislopi* (Prasad et al. 1994); *Afrodon* cf. *chleuhi* (Gheerbrant 1993); *Afrodon* sp. (Gheerbrant 1995); *Bustylus* cf. *cernaysi* (Gheerbrant and Russell 1991); *Bustylus* sp. (Smith 1997); ?*Adapisoriculus* sp. (Gheerbrant 1995); ?*Adapisoriculus* sp. (this work); *Remiculus* cf. *deutschii* (Smith 1997); *Remiculus* (?) nov. sp. (Russell et al. 1966); ?*Garatherium* sp. nov. (Gheerbrant 1995); and ?*Garatherium todrae* (Gheerbrant et al. 1998).

One additional species and genus from the Cretaceous of India, designated as *Sahnitherium rangapurensis*, has been reported as closely related to *Deccanolestes* (Rana and Wilson 2003). The only species of the genus is represented by a single upper tooth resembling *Deccanolestes*, and could thus represent another adapisoriculid.

Phylogeny.—*Afrodon germanicus* seems somewhat more derived than *A. chleuhi*, *A. ivani*, and *A. gheerbranti* with regard to several characters. The more developed hypoconid and the slight but constant lingual displacement of the hypoconulid, combined with a p4 bearing a stronger metaconid and a two-cusp talonid are all characters indicating a more advanced evolutionary stage, close to what can be observed in the genus *Bustylus*. However, the lack of a mesostyle, the marked internal crests, and a more asymmetrical hypoflexus than present in *Bustylus* justify its placement in the genus *Afrodon*. *Afrodon gheerbranti* seems to occupy a phylogenetic position intermediate between *A. chleuhi* and *A. germanicus*: while the upper molars of *A. gheerbranti* resemble those of *A. germanicus* in their reduced stylar shelf and a comparatively less asymmetrical ectoflexus, the species still retains a smaller hypoconid and a hypoconulid located in a medial position on its lower molars, as well as a p4 characterised by a single-cusp talonid. By contrast, *Afrodon ivani* seems somewhat derived with respect to *A. chleuhi* in a different way from *A. germanicus* and *A. gheerbranti*, possessing a reduced stylar shelf and a larger protofossa.

Bustylus cernaysi is clearly more derived than *B. foliae* and *B. marandati* in bearing much more marked stylar cusps.

The evolutionary position of *Bustylus folieae* seems intermediate between *B. marandati* and *B. cernaysi*, based on the intermediate development of the styler cusps and internal crests of the upper molars, as well as the better developed metaconid of p4 and the more oblique crista obliqua in *B. cernaysi* and *B. folieae* as compared to *B. marandati*.

The new genus *Proremiculus* might represent an intermediate stage between *Afrodon* and *Remiculus*. Likewise, *Bustylus* is morphologically intermediate between *Afrodon* and *Adapisoriculus*, and might thus be considered as a transitional form. As dilambdodonty is generally regarded as a strong synapomorphy at low taxonomic levels, *Remiculus* and *Adapisoriculus* might be closely related, with *Bustylus* forming the sister group of a clade including the former two genera. On the other hand, the morphology of *Proremiculus* might suggest a different phylogenetic scenario, with *Afrodon* giving rise to two different lineages, one leading to *Remiculus*, with *Proremiculus* representing an intermediate stage, and the other leading to *Adapisoriculus*, with *Bustylus* as a transitional form. According to this hypothesis, dilambdodonty would have appeared twice. However, given that many other orders seem to have developed this feature independently (Butler 1996), there may be reason to think that the dilambdodonty observed in *Remiculus* and *Adapisoriculus* actually represents a case of evolutionary convergence.

The adapisoriculids from Hainin mainly consist of primitive genera such as *Afrodon* and *Bustylus*, and only a single upper tooth of a derived form was identified here. The same relative abundances can be observed in the Palaeocene of North Africa, where only *Afrodon* is present with certainty during the Palaeocene, with a few isolated teeth having been uncertainly referred to *Adapisoriculus* or *Garatherium* (Gheerbrant 1995). In Cernay and Walbeck, *A. germanicus* seems to be the most derived member of the genus *Afrodon*, while *B. cernaysi* appears more derived than the two species of *Bustylus* from Hainin. The more derived character of the faunas from Cernay and Walbeck, as inferred from both the species of *Afrodon* and *Bustylus* they contain and the presence of other much more derived genera of the family in these two localities, supports an early Palaeocene age for Hainin.

Cladistic analysis.—In order to test the new hypothesis of two distinct lineages, one represented by *Bustylus* and *Adapisoriculus* and the other by *Proremiculus* and *Remiculus*, a cladistic analysis of the family Adapisoriculidae was performed using PAUP 4.0b10 (Swofford 2003). A set of 17 characters was chosen in order to resolve the 6 different genera of the family. All defined adapisoriculid species were included in the analysis, except for *Garatherium mahboubii*, which is known only from a single upper tooth. Two outgroups were chosen from among primitive Cretaceous eutherians: *Prokennalestes trofimovi* Kielan-Jaworowska and Dashzeveg, 1989 and *Cimolestes incisus* Marsh, 1889. All characters were considered unordered, except for characters 9, 10, 16, and 17. For

these characters, a gradual morphocline and an intermediate state can be observed, implying that their evolution is better considered ordered. Multistate characters were treated as polymorphism. Morphology was assessed through a review of the literature (Marsh 1889; Russell 1964; Clemens 1973; Gheerbrant 1988, 1995; Gheerbrant and Russell 1989, 1991; Kielan-Jaworowska and Dashzeveg 1989; Prasad et al. 1994, 2010), as well as through direct observation of fossils and casts. The analysis yielded 416 equally parsimonious cladograms of 34 steps each, with a consistency index of 0.735 and a retention index of 0.836. The strict consensus tree (Fig. 9) had a consistency index of 0.694 and a retention index of 0.800, and confirmed our hypothesis of an early separation between the lineages leading to *Remiculus* and *Adapisoriculus*, respectively.

The clade comprising *Bustylus* and *Adapisoriculus* was supported by 4 unambiguous synapomorphies: presence of a mesostyle (character 1); postparaconule crest faint (character 2); M2 ectoflexus deep and symmetrical (character 6); and hypoconulid slightly displaced towards the entoconid (character 11). The clade formed by *Proremiculus* and *Remiculus* was also supported by 4 unambiguous synapomorphies: pre- and post-cingulum present (character 4); styler shelf accounting for less than one third of the transverse development of the tooth (character 7); paracone and metacone longer than high (character 9); and relatively low crown and rounded cusps (character 12).

In this analysis, *Afrodon chleuhi* was found to be the most primitive member of the family based on the talonid being less wide than the trigonid (character 13). Other species of *Afrodon* and *Deccanolestes* were mixed at the level of two subsequent polytomies, thus implying these two taxa to be polyphyletic. However, the very low level of specialisation of the different members of these two genera is an obstacle to an accurate description of their phylogenetic relationships. More material, such as anterior teeth, skull and tarsal bones, would help to resolve the polytomies observed here and determine whether it is necessary to revise the genera *Afrodon* and *Deccanolestes*. *B. cernaysi* was found to be the sister group of *Adapisoriculus*, rendering the genus *Bustylus* paraphyletic. The clade formed by *B. cernaysi* and *A. minimus* was supported by only one synapomorphy: well individualised styler cusps (character 5). Once again, more fossil material is needed to confirm the paraphyly of this genus. Gheerbrant (1995) already suggested that *Afrodon* and *Bustylus* might be paraphyletic, but refrained from drawing any firm conclusions owing to a lack of material.

Palaeobiogeography.—From a biogeographical point of view, Hainin is interesting in understanding the migrations that likely occurred during early Palaeocene. The presence of *Afrodon* in Hainin, the oldest record of the genus, suggests an early (i.e., prior to the formation of the Hainin deposits) migration out of India, where *Deccanolestes* was already present during the Cretaceous (Smith et al. 2010). The presence of a dilambdodont tooth seems to indicate that the migration

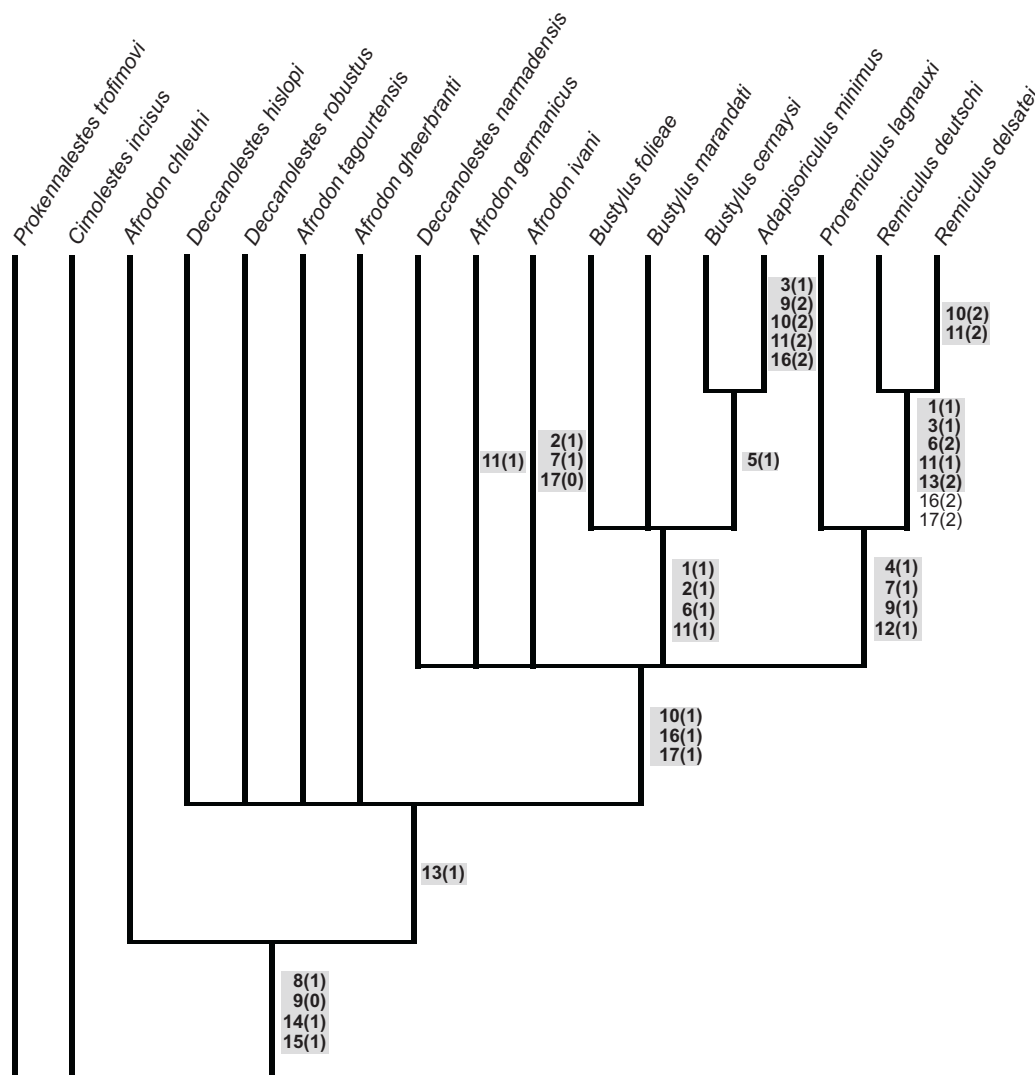


Fig. 9. Strict consensus of the 416 most parsimonious trees constructed from the data matrix in Appendix 2. The tree shows the separation of Adapisoriculidae into two main lineages, one leading to *Bustylus* and *Adapisoriculus*, and the other leading to *Proremiculus* and *Remiculus*. Unambiguous apomorphies are displayed in grey boxes and bold characters.

events actually occurred long before, probably around the Cretaceous–Palaeogene boundary, with diversification occurring rapidly in Western Europe. Alternatively, the high European diversity of adapisoriculids at the beginning of the Palaeocene, combined with the relatively poor knowledge of the continental late Cretaceous of Western Europe might indicate a European origin of this group, with subsequent dispersal of a *Deccanolestes*-like species to India during the Cretaceous, and of *Afrodon*-like and *Adapisoriculus*-like species to Africa during the Palaeocene. Finally, the presence of *Afrodon chleuhi*, the most archaic member of the family, in the late Palaeocene of Africa might imply a late Cretaceous African origin, although there is currently no fossil evidence to support this scenario. In summary, while the highest diversity of adapisoriculids is found in Europe, the oldest record of the family is known from India, and the most primitive member occurs in Africa. The geographical origin of the family could thus be located in any of these three conti-

nents, depending on the importance attributed to each of these factors.

The genus *Garatherium* and the other dilambdodont taxa reported as Adapisoriculidae by Gheerbrant (1995) seem closer to *Adapisoriculus* than to *Remiculus*, and probably represent a second dispersal event between Europe and Africa during the late Palaeocene. *Garatherium* and *Adapisoriculus* are indeed very similar in their morphology, with sharp molars, strong dilambdodonty and large, well differentiated stylar cusps. They mainly differ in the length of the lingual region of the upper molars, which is much shorter in *Garatherium*.

Afrodon and *Deccanolestes* display very similar morphologies which probably resemble the ancestral morphotype. A *Deccanolestes*-like ancestor diversified in Europe into two main lineages and several genera, *Bustylus* and *Adapisoriculus* representing one lineage, and *Proremiculus* and *Remiculus* the second one.

Conclusions

Three new species, including one belonging to a new genus (*Afrodon gheerbranti* sp. nov., *Bustylus folieae* sp. nov., and *Proremiculus lagnauxi* gen. et sp. nov.), as well as the lower teeth of *Bustylus marandati* (Crochet and Sigé, 1983), and one taxon in open nomenclature were identified in Hainin. The family Adapisoriculidae thus now includes 16 species and at least 11 additional taxa in open nomenclature, placed within seven genera. The high diversity of adapisoriculids in Hainin confirms the identity of the different genera, but also raises new questions about their evolutionary relationships. Dilambdodonty seems to have appeared twice in the family, in a lineage leading from *Afrodon* to *Bustylus* to *Adapisoriculus* to *Garatherium*, and in another lineage leading from *Afrodon* to *Proremiculus* to *Remiculus*. The family proved to be an excellent disperser as it underwent at least one long-distance dispersal event, either from Europe or Africa to India, or from India to Europe and Africa, most likely around the Maastrichtian (see Smith et al. 2010; Prasad et al. 2010).

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Appendix 1

List of characters and character definitions used in our cladistic analysis of adapisoriculids.

1. Mesostyle absent (0), present (1)
2. Postparaconule crest marked (0), faint (1)
3. Straight centrocrista (0), dilambdodont (1)
4. Precingulum and postcingulum absent (0), present (1)
5. Styler cusps crestiform (0), well individualised (1)
6. M2 ectoflexus deep and asymmetrical (0), deep and symmetrical (1), shallow (2)
7. Styler shelf larger than 1/3 of total transverse development of the tooth (0), smaller than 1/3 (1)
8. Paracone markedly larger than metacone (0), slightly larger or similarly sized (1)
9. Paracone and metacone as high as long (0), longer than high (1), higher than long (2)
10. m1, 2 hypoconid size similar to the entoconid (0), slightly larger than the entoconid (1), much larger than the entoconid (2)
11. Hypoconulid medial (0), slightly closer to the entoconid (1), very close to the entoconid (2)
12. Lower molars with high crowns and pointed cusps (0), relatively low crowns and rounded cusps (1)
13. Talonid narrower than trigonid (0), equally wide (1), significantly wider (2)
14. Trigonid compressed anteroposteriorly and much shorter than the talonid (0), trigonid about as long as the talonid (1)
15. Trigonid more than twice the height of the talonid (0), trigonid less than twice the height of the talonid (1)
16. p4 metaconid absent or almost absent (0), well differentiated but smaller than the protoconid (1), size similar to that of the protoconid (2)
17. Talonid of p4 with one cusp (0), two cusps (1), three cusps (2)

Appendix 2

Character matrix used to assess genus-level phylogenetic relations within Adapisoriculidae. Missing or unknown characters are marked “?”.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Prokennalestes</i>	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Cimolestes</i>	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Deccanolestes hislopi</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	?	?
<i>Deccanolestes robustus</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	?	?
<i>Deccanolestes narmadensis</i>	?	?	?	?	?	?	?	?	?	1	0	0	1	1	1	?	?
<i>Afrodon chleuhi</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
<i>Afrodon germanicus</i>	0,1	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	1
<i>Afrodon ivani</i>	0	1	0	0	0	0	1	1	0	1	0	0	1	1	1	1	0
<i>Afrodon tagourtensis</i>	0	0	0	0	0	?	0	1	0	0	0	0	1	1	1	?	?
<i>Afrodon gheerbranti</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0
<i>Bustylus cernaysi</i>	1	1	0	0	1	1	0	1	0	1	1	0	1	1	1	1	1
<i>Bustylus marandati</i>	1	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1
<i>Bustylus folieae</i>	1	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1
<i>Adapisoriculus minimus</i>	1	1	1	0	1	1	0	1	2	2	2	0	1	1	1	2	1
<i>Proremiculus lagnaui</i>	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	?	?
<i>Remiculus deutschii</i>	1	0	1	1	0	2	1	1	1	1	1	1	2	1	1	2	2
<i>Remiculus delsatei</i>	1	0	1	1	0	2	1	1	1	2	2	1	2	1	1	?	?