

## New mammals from the marine Selandian of Maret, Belgium, and their implications for the age of the Paleocene continental deposits of Walbeck, Germany

Eric DE BAST, Etienne STEURBAUT & Thierry SMITH

*O.D. Earth and History of Life, Royal Belgian Institute for Natural Sciences, Rue Vautier 29, 1000 Brussels, Belgium*

**ABSTRACT.** The early to middle Selandian fossiliferous Orp Sand Member of the Heers Formation in Belgium has regularly been excavated at its type-locality Maret for its rich and diversified selachian fauna. Among the abundant vertebrate remains, extremely rare mammal specimens have been found. Three isolated teeth have been published previously, all with uncertain affinities. The purpose of this study is to present new specimens from the same deposits, including a small well-preserved dentary of an adapisoriculid attributable to “*Afrodon*” *germanicus*, a fragmentary upper molar, referred to *Berrulestes* sp., and a premolar of a large arctocyonid. Among the previous specimens we identified *Arctocyonides* cf. *weigelti*. The adapisoriculid dentary offers new clues that allow transferring “*Afrodon*” *germanicus* to the genus *Bustylus*. The five mammal taxa from Maret indicate an age intermediate between reference-levels MP1-5 of Hainin, Belgium and MP6 of Cernay, France and present the greatest correlation with the rich Walbeck fauna in Germany. The deposits from Walbeck were usually thought to be slightly older than the late Thanetian deposits of Cernay. We infer here that the age of Walbeck is likely to be Selandian. The strong differences observed between Hainin on the one hand, and Walbeck and Cernay on the other hand, document a dispersal event from North America to Europe around the Danian-Selandian boundary.

**KEYWORDS:** Orp Sand Member, Heers Formation, Biostratigraphy, Paleobiogeography, Adapisoriculidae

### 1. Introduction

Paleocene continental deposits of northwestern Europe are extremely discontinuous, both in space and time. This is essentially because a large part of Europe’s surface was flooded by shallow epicontinental seas and the remaining continental sedimentary archive was largely destroyed by the many subsequent vast marine transgressions (Vinken, 1988; Pomerol, 1989; Steurbaut, 1998). The stratigraphic position and age of these continental deposits are particularly difficult to establish, essentially because of the lack of suitable biostratigraphic markers. This prevents easy and accurate correlation between the terrestrial and marine records and with the Geological Time Scale. The often short time span covering many of the continental strata and the scarcity of well-studied localities are not helping either. Palynomorphs provide one of the rare keys for disentangling the continental-marine relationships (Steurbaut et al., 2003). Another key that helps in constraining the age estimates of continental faunas are remains of continental vertebrates found in marine deposits (Smith & Smith, 2003; Smith et al., 2004).

Among Paleocene MP levels (international mammal reference-levels for the European Paleogene, see Schmidt-Kittler, 1987 and BiochroM’97, 1997), only MP6, which corresponds to the upper Thanetian, has been definitely identified based on the mammal fauna from Cernay. The fauna of Hainin (Mons Basin, Belgium) is the only European fauna that is clearly older than the typical Cernaysian MP6 level. It is therefore the only representative for the interval MP1-5, which needs to be redefined and subdivided in the future when new intermediate mammal faunas are found. In his study on the Paleocene mammals of Europe, Russell (1964) noticed that many taxa of the continental fauna of Walbeck (Germany) showed slightly more primitive features than similar taxa from Cernay. Walbeck was later suggested to represent MP?5 (Schmidt-Kittler, 1987, BiochroM’97, 1997; Gheerbrant et al., 1999; Smith & Smith, 2003), but the aberrant mammal assemblage coupled with the lack of stratigraphic control prevented scientists from considering Walbeck as a reference-level (Schmidt-Kittler, 1987).

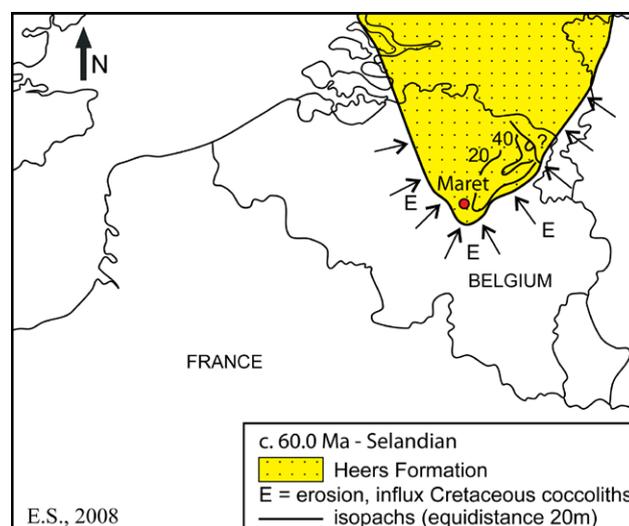
New fossil terrestrial mammal specimens have recently been collected from the Orp Sand Member at Maret, the type-locality of this stratigraphic unit (Steurbaut, 1998) (Fig. 1). At this particular site, these Mid-Paleocene sands are renowned for their rich marine selachian fauna, and they represent the locus typicus and stratum typicum of one genus and several species of sharks (Herman, 1973, 1977; Cappetta & Nolf, 2005). Extremely rare terrestrial vertebrate remains have been found in association with the marine vertebrates (Dollo, 1890; Herman, 1973), among which are a few mammal specimens (Quinet et al., 1971;

Herman & Sigé, 1975). Unfortunately, the specimens figured by Herman and Sigé (1975) were not deposited in a public institution or even numbered, and seem to be lost. However, casts of the specimens were recovered in the collection of the University of Montpellier; these casts are now deposited at the RBINS with type and figured specimen numbers. These previously mentioned specimens, together with the new Orp Sand records, including an adapisoriculid jaw, are discussed here and compared to other Paleocene mammal faunas of Europe.

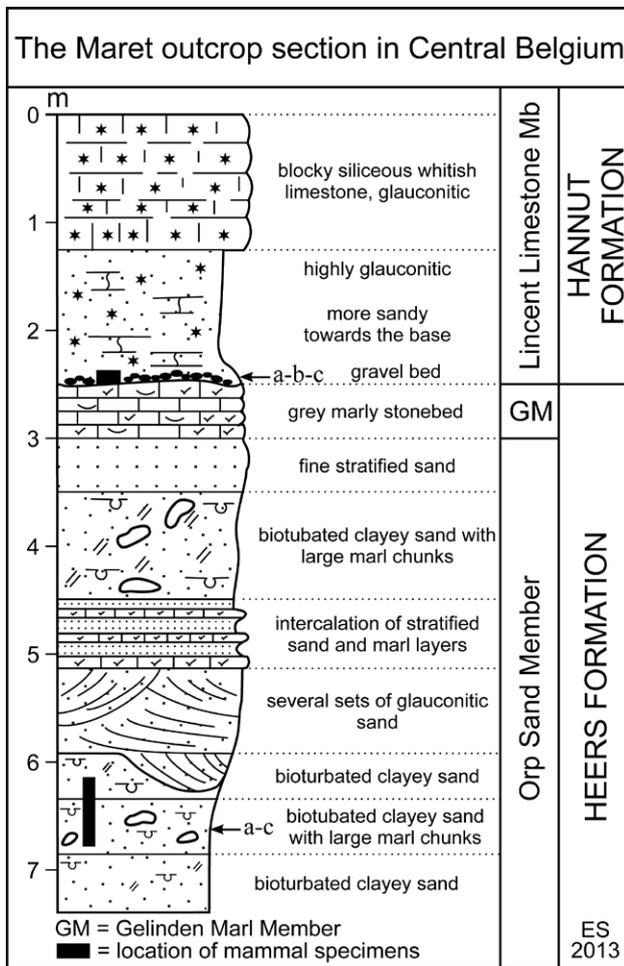
Institutional abbreviations—**IRSNB**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **MLU Wa**, Walbeck, Institut für Geologische Wissenschaften und Geiseltalmuseum, Martin-Luther-Universität Halle-Wittenberg, Germany.

### 2. The Maret site and its spatial and temporal setting

The fossiliferous outcrops of Maret, a hamlet of the village Orp-le-Grand, about halfway between the towns of Leuven and Liège, have been intermittently but intensively investigated since the end of the 19<sup>th</sup> century (see Herman & Sigé, 1975 for an overview). The mammal remains studied here have been collected on both sides of the Maret railway track, and at different spots in the over 100 m wide exposure zones (coordinates 50°42’40”N, 4°59’59”E). Herman & Sigé (1975) sampled on the North and



**Figure 1.** Current distribution of the Heers Formation in Belgium with thickness estimates and location of the fossiliferous site of Maret.



**Figure 2.** Lithology and lithostratigraphic interpretation of the Maret outcrop (logged on the southern side of the railtrack on June 16<sup>th</sup> 1992), with location of the mammal finds: a. Herman, 1973 and Herman & Sigé, 1974; b. Quinet et al., 1971; c. this paper.

South sides of the track, all others (Quinet et al., 1971; this paper) only on the South side (see Herman & Sigé, 1975 for a detailed map of the area). This southern site, last re-excavated in the early 1990s, was logged in 1992 (Fig. 2).

Of the six mammal specimens discussed here, three come from the Orp Sand Member, which at Maret, as nearly everywhere in its deposition area, is overlain by the Gelinden Marl Member. Both are subdivisions of the Heers Formation, the lithostratigraphic equivalent of the Heersian Stage, a regional chronostratigraphic unit, defined in Belgium (Dumont, 1851), which internationally is considered to be obsolete and replaced by its correlative, the Selandian (for discussion see De Geyter et al., 2006). The correlation between the Orp Sand Member and the lower part of the Selandian was based on lithological grounds and micropaleontological evidence. Both units, the Orp Sand Member and the Gelinden Marl Member, contain similar calcareous nannofossil associations, marked by high degrees of Cretaceous reworking and attributable to zonal interval NP4-NP5 (Thomsen & Heilmann-Clausen, 1985; Steurbaut, 1998; Hooyberghs et al., 2001; Clemmensen & Thomsen, 2005). Both units also contain similar dinoflagellate cyst associations (Schumacher-Lambry, 1978; Vlerick, 1988) characterized by the co-occurrence of *Palaeoperidinium pyrophorum* and *Glaphyrocysta pastielsi*, typical markers of North Sea dinoflagellate Zone 2 and Zone 3 of Heilmann-Clausen (1985). The absence in the Orp Sands of *Thalassiphora delicata* and *Alisocysta margarita* (Vlerick, 1988), and the presence of *Isabelidinium? viborgense* (E.S., personal observation: middle part of Orp Sand at 209 m depth in Eisden borehole), is more consistent with the middle part of Zone 2, corresponding to the upper part of the Kerteminde Marls in Denmark. The Orp Sands are therefore referred to the early to middle Selandian.

At Maret, the Orp Sands, of which only the upper 4 m are exposed, consist of a heterogeneous complex of essentially sandy sediments, with intermittent influxes of whitish marl material, sometimes forming thin beds, but mostly restricted to centimetric to decimetric large irregular marl lumps (Fig. 2). The high carbonate content of these marls is due to the presence of reworked Cretaceous coccoliths (Fig. 1). Sedimentation took place in a shallow marine context, with temporary estuarine influences, at the edge of the continent, with exposed chalk strata (cliffs? Bless & Fernández-Narvaiza, 1996, fig. 36; Dreesen et al., 1998). This is evidenced by the presence of bioturbated and horizontally stratified sands and thin marl beds, pointing to rather calm sedimentation conditions, and the reworked marl lumps, the concentrations of glauconite and the channeling, reflecting high-energy input.

The three other isolated mammal teeth from Maret were encountered in the basal gravel of the Lincent Limestone Member. This siliceous limestone to calcareous sandstone unit, overlying a thin basal gravel, represents the lower Member of the Hannut Formation. In agreement with its attribution to the lower part of nannofossil zone NP8, it belongs to the lower middle Thanetian. The basal gravel layer in Maret has yielded a rich selachian fauna.

In between the Orp Sand Member and the Lincent Member occurs a whitish crumbly marly chalk, the Gelinden Marl Member, the thickness of which is reduced to less than 1 m at Maret. The age estimate of the Gelinden Marl Member is mid to late Selandian on the basis of the calcareous nannofossil (upper NP4-NP5) and dinoflagellate associations (Zone 3 of Heilmann-Clausen (1985), recorded in the upper part of the Æbelø Formation and base of the Holmehus Formation in Denmark (Sheldon et al., 2012).

### 3. Systematic Palaeontology

Class Mammalia Linnaeus, 1758

Grandorder Euarchonta? Waddell, Okada, and Hasegawa, 1999

Family Adapisoriculidae Van Valen, 1967

Genus *Bustylus* Gheerbrant & Russell, 1991

Type species: *Bustylus cernaysi* Gheerbrant & Russell, 1991

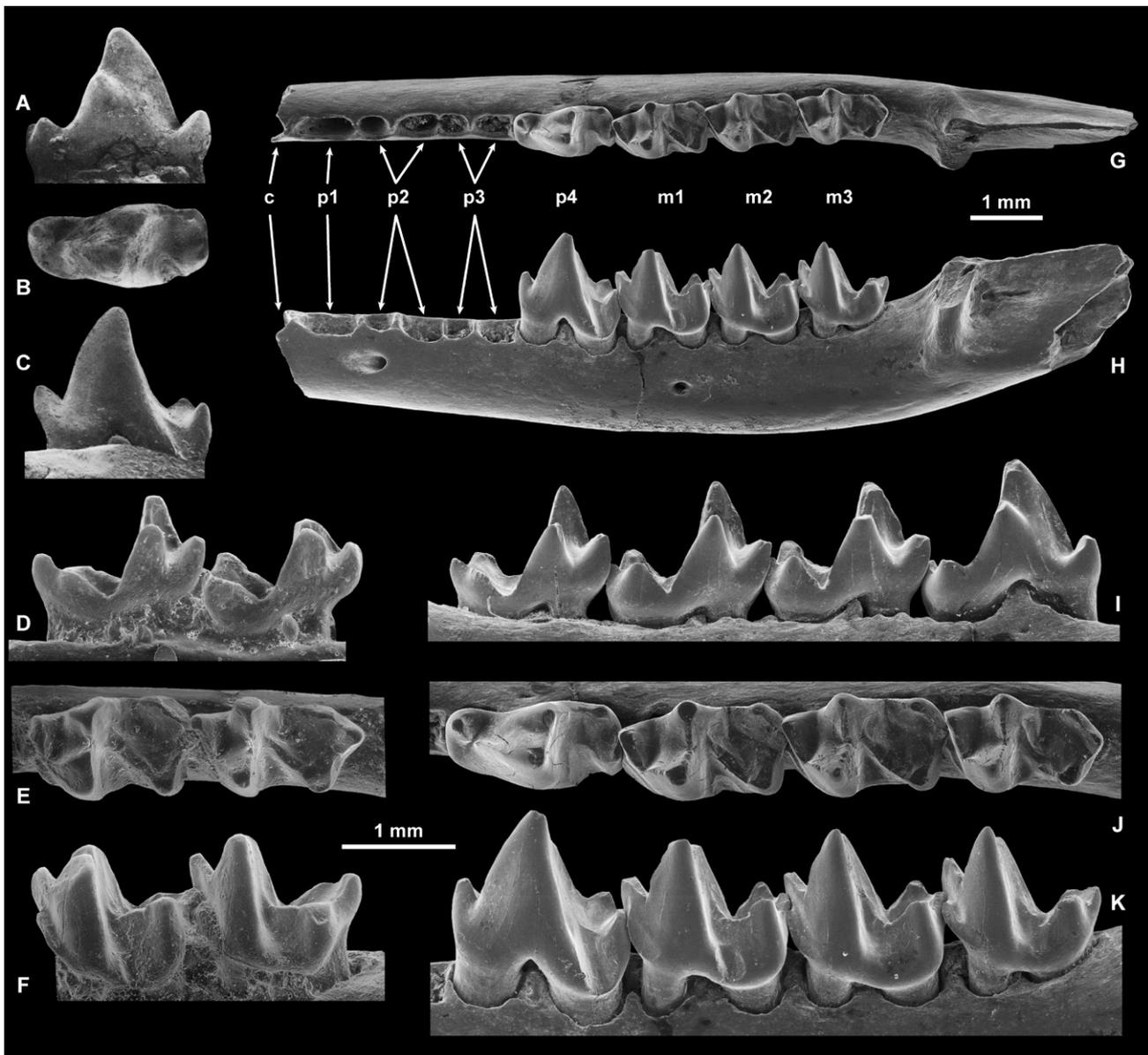
#### *Bustylus germanicus* (Russell, 1964) comb. nov.

(Fig. 3C)

Referred specimens: IRSNB M2017, left dentary with p3-m3 in place, from the Orp Sand Member of the Heers Formation at Maret.

Measurements: p4: L = 1,41 mm, l = 0,67 mm; m1: L = 1,35 mm, l = 0,74 mm; m2: L = 1,31 mm, l = 0,75 mm; m3: L = 1,27 mm, l = 0,70 mm.

Description and discussion: The best preserved mammal specimen from Maret is a nearly complete dentary bearing p4 and m1 to m3, and the alveoli of p1 to p3 (Fig. 3C). The size and morphology, including the sharp cusps with little height difference between the trigonid and talonid, and the large paraconid, indicate that the specimen belongs to the family Adapisoriculidae. The specimen from Maret is the most complete adapisoriculid specimen known to date as it displays 5 preserved alveoli in front of p4. The most anterior complete alveolus is interpreted here as that of p1; its shape and size indicates that the p1 was procumbent. We cannot exclude the possibility that this most anterior complete alveolus is that of the canine; however, this would imply that the p1 was lost, which would be unusual for a small Paleocene insectivorous mammal. Moreover, the species *Bustylus foliae* from Hainin displays small diastemata in front of and behind p2 (De Bast et al., 2012), which is somewhat inconsistent with the loss of p1, often coupled with a shortening of the tooth row. The hypothesis of the first full alveolus of the specimen from Maret being that of p1 is therefore retained here. Due to the shape and direction of the two alveoli posterior to the alveolus of p1, the p2 was certainly biradicate. The alveolus of the canine is not separated from that of p1 by a diastema, indicating that the canine was relatively small and low. This observation is confirmed by the shallowness and narrowness of the dentary under the canine region. The morphology of the lower molars corresponds well



**Figure 3.** Comparison of the lower dentitions of *Bustylus germanicus* from the Orp Sand Member (Selandian) in Maret, and from Walbeck (Germany). A-C. p4 (MLU Wa/383), from Walbeck. D-F. Associated m2-m3 (MLU Wa/358, holotype) from Walbeck. G-K. Dentary (IRSNB M2017) from Maret. Views are lingual (A, D and I), occlusal (B, E, G and J) and labial (C, F, H and K).

with the non-dilambdodont genera *Afrodon* and *Bustylus*. The slight approximation of the hypoconulid and entoconid, and the slightly larger size of the hypoconid compared to the entoconid are more consistent with the genus *Bustylus* than with *Afrodon*. However, it is the species "*Afrodon*" *germanicus* described from Walbeck that presents the most similar lower molars to those of the specimen from Maret (see Fig. 3A-B). Specimens referred to this species from Cernay by Gheerbrant & Russell (1989) are judged misidentified (see section 4.2). The differences are the 10% larger size of "*A.*" *germanicus* and the more protruding hypoconulid on m3. The intraspecific morphological variation within adapisoriculid species is not documented, but even a small amount of variation of the lower molars would be sufficient to erase the differences between species, and specific attribution within the family is thus uncertain based only on lower molars (see also Gheerbrant & Russell, 1989). The p4 seems to carry more useful information for classification. There is a relatively marked morphocline between the most primitive *Afrodon* and the most derived *Adapisoriculus* (Gheerbrant, 1995; De Bast et al., 2012). The p4 of *Afrodon chleuhi*, the type species of the genus, is premolariform with a very small metaconid and one talonid cuspid (shared with *A. gheerbranti* but not with "*A.*" *germanicus* and *A. tagourtensis*), the p4 of *Bustylus cernaysi*, the type species of the genus, is premolariform with a larger metaconid and two talonid cuspids (shared with all species of the genus), and the

p4 of *Adapisoriculus* is submolariform with a relatively large metaconid and a talonid with two large cuspids and a small basin. The relatively large paraconid, the small but well individualized metaconid and the two-cusped talonid on the p4 of the specimen from Maret are typical features of the genus *Bustylus*. However, the p4 resembles that of "*A.*" *germanicus* more closely than those of *B. cernaysi* from Cernay and of *B. marandati* and *B. foliae* from Hainin. The differences observed between the specimen from Maret and "*A.*" *germanicus* are extremely minor, with the slightly more posterior position of the hypoconulid and the slightly more mesially projecting paraconid. The specimen from Maret confirms the association of the p4 of "*A.*" *germanicus* with the molars; thanks to this confirmation and the recently described specimens from Hainin (De Bast et al., 2012), the importance of the morphology of the p4 in the systematics of adapisoriculids becomes more and more clear. Until recently, the systematics of adapisoriculids was mainly based on upper molars, and styler cuspids were considered taxonomically useful. However, as shown recently, because they have no particular role in the occlusion process, styler cuspids can display much intraspecific variability in marsupials (Ladevèze et al., 2012). Even though they are not phylogenetically related, upper molars of adapisoriculids are morphologically close to those of peradectid marsupials (see Crochet & Sigé, 1983; Gheerbrant, 1991). Given that adapisoriculid samples are too low to study variability, one

should consider the information about styler cusps with care. The morphology of p4 can therefore become an additional accurate and reliable character for generic attribution of adapisoriculids. The morphological comparisons thus indicate a close relationship with the species ‘*A. germanicus*’ from Walbeck that we here transfer to the genus *Bustylus* (see also section 4.2).

Order Lipotyphla Haeckel, 1866  
 Family Adapisoricidae Schlosser, 1887  
 Genus *Adapisorex* Lemoine, 1883  
 Type species: *Adapisorex gaudryi* Lemoine, 1883

***Adapisorex* sp.**

(Fig. 4.1)

Referred specimen: IRSNB M2018 (cast of the specimen), right DP4, from the Orp Sand Member of the Heers Formation at Maret.

Measurements: L = 2,12 mm, l = 1,86 mm.

Description and discussion: The DP4 figured by Herman & Sigé (1975) under the name *Adapisorex* sp. (Fig. 4.1) shares with the DP4 of *Adapisorex abundans* from Walbeck and *Adapisorex gaudryi* from Cernay-Berru the long protocone, small hypocone, lack of ectoflexus, relatively small protofossa, and presence of cingula at the anterior base of the protocone and distolingual base of the metacone. The specimen differs from the identified DP4 of *A. abundans* and *A. gaudryi* by the larger parastylar area, the larger paracone relative to metacone, the lower protocone, the less sharp cusps, and the more rounded outline. It further differs from *A. gaudryi* by the smaller protofossa and the smaller hypocone. The specimen from Maret shares with the fragmentary upper molar of *Berrulestes* sp. (see below) the particularly large paracone relative to the metacone, and is of similar size. However, it differs very strongly from the referred DP4 of *Berrulestes phelizoni* (Hooker & Russell, 2012, fig. 10D), notably by the much smaller protofossa, much smaller conules, much smaller hypocone, distolabial orientation of the postmetacrista, and much larger metastylar area. It also differs from the DP4 of *Walbeckodon krumbiegei* (Russell, 1964, Pl. III, fig. 4b), although in a lesser degree, by the absence of the ectoflexus, the wider metastylar region, the much smaller hypocone, the smaller conules, the smaller protocone, the distolabial orientation

of the postmetacrista, the smaller protofossa, and the shallower postflexus. These differences are stronger than between the tooth from Maret and *Adapisorex*, therefore suggesting that the two specimens from Maret belong to separate taxa. Taking into account the differences between the DP4 from Maret and those of *A. abundans* and *A. gaudryi*, we follow the decision of Herman & Sigé (1975) and do not refer the tooth to either of the two species.

Order “Condylarthra” Cope, 1881  
 Family Louisinidae Sudre & Russell, 1982  
 Genus *Berrulestes* Hooker & Russell, 2012  
 Type species: *Berrulestes phelizoni* Hooker & Russell, 2012

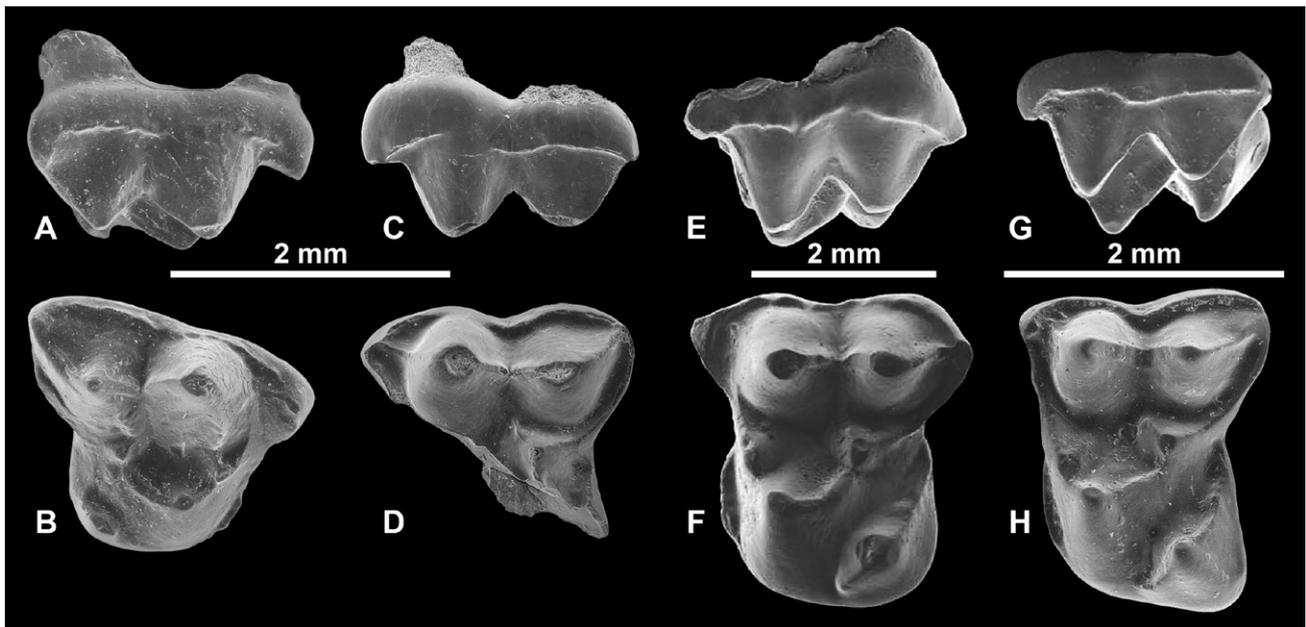
***Berrulestes* sp.**

(Fig. 4.2)

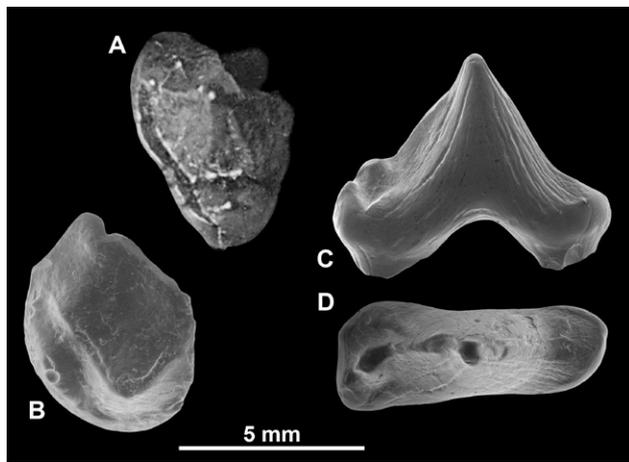
Referred specimens: IRSNB M2019, left upper molar fragment, from the Orp Sand Member of the Heers Formation at Maret.

Measurements: p4: L = 1,99 mm, width could not be measured.

Description and discussion: An upper molar fragment (Fig. 4.2) is referred to the recently described genus *Berrulestes* from Cernay-Berru, France (Hooker & Russell, 2012). The orientation of the preparacrista and the shape of the ectoflexus indicate an M1 rather than M2. The specimen from Maret shares with *Berrulestes* the diagnostic characters of the large and prominent, mesially pointed parastyle, and indistinct, mesiolabially oriented preparacrista. The rounded distolabial part of the tooth and the sharp triangular metaconule placed anteriorly to the metacone and close to its base offer the best comparison with *Berrulestes phelizoni* (Fig. 5.3). However, the distinctly smaller size, the higher and more labiolingually expanded paracone compared to the metacone and the mesiolabially oriented postmetacrista do not compare well with any described *Berrulestes* species, but better with *Walbeckodon krumbiegei* (Fig. 5.4) from Walbeck, Germany. The specimen from Maret differs from those from Walbeck by the even more labiolingually expanded paracone, the slightly stronger height difference between the paracone and metacone, and the interrupted cingulum at the labial base of the paracone. The two former characters are plesiomorphic in Louisinidae. Several species of the genus *Adapisorex* from Walbeck and Cernay also present a triangular metaconule in a similar position. They differ from the molar from Maret by



**Figure 4.** Small insectivorous mammals from Maret. A-B. DP4 (IRSNB M2018, cast) of *Adapisorex* sp. from the Orp Sand Member (Selandian). C-D. M1 (IRSNB M2019) of *Berrulestes* sp. from the Orp Sand Member in Maret (Selandian); E-F. M1 (MNHN.F.CR-937) of *Berrulestes phelizoni* from Cernay (reversed). G-H. M1 (MLU Wa/386) of *Walbeckodon krumbiegei* from Walbeck (cast). Views are labial (A, C, E, G) and occlusal (B, D, F, H). E, F and G from Hooker & Russell, 2012.



**Figure 5.** Arctocyonids from Maret. A-B. *Arctocyonides cf. weigelti* from the base of the Lincent Limestone Member (Thanetian). A. Upper P4 (not numbered). B. Fragmentary upper molar (IRSNB M2020, cast). C-D. *Arctocyonidae indet.* (IRSNB M2021) from the base of the Lincent Limestone Member (Thanetian). Views are occlusal (A, B, D) and labial (C). A from Quinet et al., 1971.

having a paracone not expanded labiolingually, a much more curved postmetacrista, and a rounder and smaller parastylar area. The fragmentary upper molar from Maret has therefore an intermediate morphology between *Berrulestes phelizoni*, from Cernay, and *Walbeckodon krumbiegeli*, from Walbeck. The diagnosis of *Berrulestes* includes characters that are visible on the specimen from Maret, which is the reason of the generic attribution proposed here. However, several characters indicate a very primitive morphology of the specimen from Maret, even compared to the most primitive lousinids *Walbeckodon*, suggesting that a revision of these two primitive lousinid genera may be needed in order to better discriminate them. Lousinid taxa have recently been attributed to *Macroscelidea* (Zack et al., 2005a, 2005b; Hooker & Russell, 2012), although direct evidence of a relationship between lousinids and *Macroscelidea* is still to be demonstrated. For that reason, the term ‘*Condylarthra*’ was used here, awaiting further analysis.

Order Procreodi Matthew, 1915

Family Arctocyonidae Giebel, 1855

Genus *Arctocyonides* Lemoine, 1891

Type species: *Arctocyonides trouessarti* Lemoine, 1891

*Arctocyonides cf. weigelti* Russell, 1964

(Fig. 5.1-2)

Referred specimens: Unnumbered right P4; IRSNB M2020 (cast of the specimen), right fragmentary upper molar, from the Lincent Limestone Member of the Hannut Formation at Maret.

Measurements: P4: L = ~6 mm, l = ~6 mm (from Quinet et al., 1971, original specimen could not be found); M1 dimension could not be measured.

Description and discussion: Of the three teeth previously reported from the locality of Maret, two come from the base gravel of the Lincent Member and feature a rather typical arctocyonid-like morphology. The upper P4 named “*Condylarthre* ?” (Fig. 5.1; Quinet et al., 1971) and the lingual fragment of an upper molar named “*Condylarthre arctocyonidé ? indet.*” (Fig. 5.2; Herman & Sigé, 1975) appear to be closely related to the species *Arctocyonides weigelti* from Walbeck. The P4 matches well the morphology of that of *A. weigelti*, both sharing the small protocone and absence of a labial cingulum; *A. weigelti* differs from the specimen from Maret by the slightly broader postcingulum, and slightly less individualized protocone. The P4 of *Arctocyonides arenae* from Cernay-Berru differs from that from Maret by the markedly larger protocone, the presence of a labial cingulum, and the straight postparacrista. The P4 of *Arctocyonides trouessarti* from

Cernay-Berru also differs from the specimen from Maret by the larger protocone, the broader postcingulum and the presence of a small precingulum. The fragmentary upper molar is compatible in size and morphology with *A. weigelti*. The hypocone is smaller than in many other European arctocyonids including *Arctocyonides arenae*, *Mentoclaenodon walbeckensis*, *Arctocyon* spp. Its position is slightly more labial than in *A. weigelti* but this is not incompatible with the relatively high degree of intraspecific variation observed in arctocyonids. The only other species of similar size and morphology is *Arctocyonides trouessarti* from Cernay, which differs from *A. weigelti* mainly by its slightly smaller size. Due to the rarity of the species from Cernay, and the higher resemblance of the P4 from Maret with the specimens of *A. weigelti* from Walbeck, we think it is more probable that both specimens from Maret belong to one same species, *A. cf. weigelti*.

*Arctocyonidae indet.*

(Fig. 5.3)

Referred specimens: IRSNB M2021, left dp3?, from the Lincent Limestone Member of the Hannut Formation at Maret.

Measurements: L = 7,63 mm, l = 3,12 mm.

Description and discussion: A lower premolar of large size is referred to the family Arctocyonidae because of its size, lateral compression, and crenulated enamel. The absence of a paraconid is incompatible with a p4. The hollow roots and narrowness of the tooth suggest that it is a deciduous premolar. The known dp4s of arctocyonids feature a three-cuspid talonid, very different from what is observed in the specimen from Maret. The morphology of a tooth interpreted as the dp3 of *A. primaevus* presents a series of features also recorded in the tooth from Maret, including a long and narrow outline, a talonid slightly wider than the trigonid, and the absence of a paraconid. The differences in the specimen from Maret essentially lie in the proportionally higher and narrower main cuspid of the trigonid. The high variability observed in anterior premolars of known species, suggesting a similar or even higher variability in the deciduous dentition, and the lack of specimens of anterior deciduous premolars, do not allow referring this tooth to a species or even genus. However, the large size, especially considering the anterior position of the tooth, is compatible only with *Arctocyon primaevus* or *Mentoclaenodon walbeckensis*.

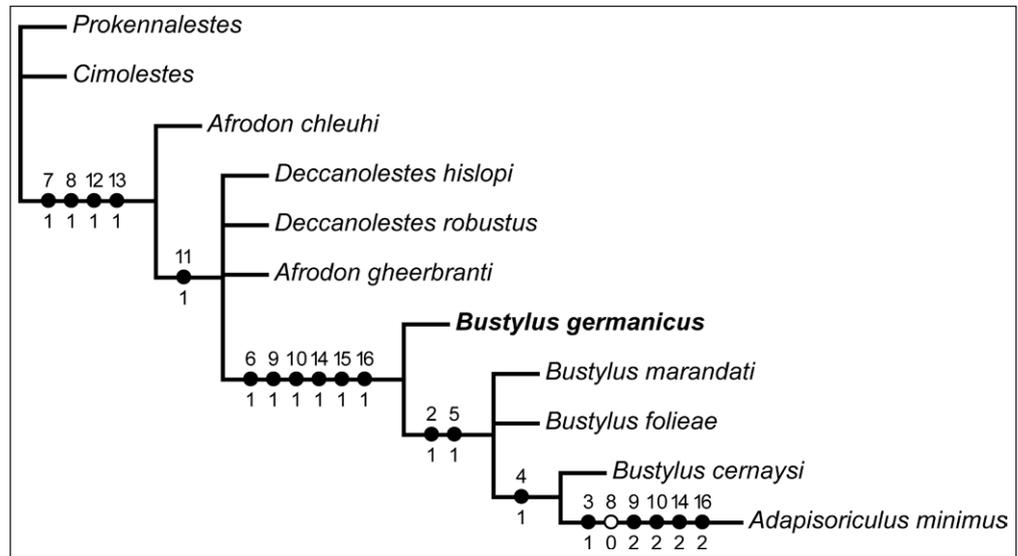
## 4. Discussion

### 4.1. Taphonomic and stratigraphic considerations on the Maret mammal fauna

The presence of terrestrial faunal elements in a marine context involves particular taphonomic processes. The record of isolated very rare and small mammal teeth in the Orp Sand Member can largely be explained by the marginal marine to estuarine character of this unit at Maret. The vicinity of a river mouth, through which mammal remains can be brought into the shallow marine depositional system, is a possible explanation for the occurrence of mammals at Maret. This is corroborated by the sedimentological data (substantial high-energy input as shown by the channeling) and by the associated remains of fluvial taxa, such as the choristoderan reptile *Champsosaurus* and the holostean fish *Amia* (Herman, 1973). The rarity of these non-marine finds, as well as their particular position (restricted to a few discrete levels) also seems to point to occasional river input and to exclude substantial reworking. This leads us to believe that the mammal teeth are contemporaneous with the Orp sands, indicating an early to middle Selandian age (~61 to 60 Ma based on Cohen et al., 2013).

The record of mid-size mammal teeth in the base of the Lincent Limestone Member probably results from reworking, as is the case of the abundant selachian remains with which they were found (Herman & Sigé, 1975). The relatively large size, robustness, and the patina of the mammal specimens are additional indicators of reworking. The isolated character of the finds suggests that they

**Figure 6.** Strict consensus of 6 most parsimonious cladograms obtained from the cladistic analysis of adapisoriculids. The analysis confirms that the species ‘*Afrodon*’ *germanicus* should be included in the genus *Bustylus*. For each node, the list of the synapomorphies is given, each synapomorphy being represented by a point (black for unambiguous synapomorphy and white for homoplasies) accompanied by the character number above and character state below.



do not originate from a subsequently eroded continental unit (cf. Dormaal, Steurbaut et al., 1999), but were accidentally introduced into a marine sedimentation system, subsequently removed at Maret. This reworking explains why their age cannot accurately be estimated. From the local stratigraphical context it is most probable that the teeth are younger than the lower part of the Gelinden Marl, which is still preserved at Maret, although it is not excluded that they are remnants of the erosion of the Orp sands, which occurred in the surroundings of Maret. The position at the base of the Lincient Member of these uppermost mammal remains from Maret also reveals that they are older than the Lincient Member. As a result, that their age ranges from middle Selandian (~60 Ma) to early Thanetian (~59 Ma). The similarity between the in situ recorded selachian fauna of the Orp Sand Member and the reworked selachian fauna in the base of the Lincient Limestone Member (Herman, 1977) is in favor of situating these vertebrate finds in the older part (middle Selandian) of this time range.

**4.2. Phylogenetic affinities of the adapisoriculid from Maret**

The adapisoriculid dentary from Maret constitutes the best preserved specimen of the family known to date. The morphology of the molars and especially the p4 allows its allocation to the genus *Bustylus*, known from Hainin, Walbeck and Cernay; the p4 is almost undistinguishable from that of ‘*Afrodon*’ *germanicus*. This species was described essentially on the basis of specimens from Walbeck, although some molars from Cernay were included. Close examination of the upper molars of ‘*A.*’ *germanicus* indicates some morphological differences between the specimens from Cernay and from Walbeck, such as the deeper postflexus and the lower paracone in the specimens from Walbeck. The only figured lower molar from Cernay also slightly differs from the specimens from Walbeck, mainly by its central hypoconulid. This suggests that there are probably two different species, as is the case in all other genera common to Walbeck and Cernay (Russell, 1964; Hooker & Russell, 2012), and that ‘*A.*’ *germanicus* is therefore only present at Walbeck. The specimens from Cernay attributed to ‘*A.*’ *germanicus* probably belong to a new species

of the genus *Afrodon* based on the shape of the ectoflexus, the size of the paracone, and the presence of strong internal crests of conules. The faunas of Walbeck and Cernay therefore seem to share no single species, only genera being shared.

In order to study the phylogenetic position of ‘*Afrodon*’ *germanicus*, a cladistic analysis was conducted based on the matrix from De Bast et al. (2012). The taxon sampling was simplified: only relatively well-known species were included, and *Remiculus* was removed because of possible convergences with *Adapisoriculus*. As a result of this simplification, three characters became uninformative and were removed from the analysis. Two additional characters were added (see Appendix 1). The resulting matrix (Appendix 2) includes 11 taxa and 16 characters. The cladistic analysis was performed using TNT 1.1 (Goloboff et al., 2003), with collapsing rule 3 (max branch length = 0) and all other parameters set to default; all characters were considered unordered. The analysis delivered six most parsimonious cladograms of 21 steps each. The strict consensus tree (Fig. 6) had a consistency index CI = 0.952 and a retention index RI = 0.972. As in the cladogram obtained by De Bast et al. (2012), *Deccanolestes* and *Afrodon* are mixed at the base of the tree. ‘*Afrodon*’ *germanicus* is sister group to the clade containing all *Bustylus* species and *Adapisoriculus minimus*. The clade formed by ‘*Afrodon*’ *germanicus*, *Bustylus* spp., and *Adapisoriculus minimus* is supported by 6 unambiguous true synapomorphies: M2 parastylar lobe less projecting labially than metastylar lobe (character 6); m1,2 hypoconid slightly larger than entoconid (character 9); hypoconulid slightly closer to the entoconid (character 10); p4 metaconid well differentiated but smaller than the protoconid (character 14); talonid of p4 with two cusps (character 15); and p4 paraconid small but forming a distinct cuspid (character 16). It seems therefore better to separate *Afrodon* and *Bustylus* at this node rather than at the next one. In conclusion, due to the relatively derived morphology of the p4 attributed to ‘*Afrodon*’ *germanicus* from Walbeck, to the confirmation of the association based on the new specimen from Maret, and to the results of the cladistic analysis, we transfer the species *germanicus* to the genus *Bustylus*.

**Table 1.** List of the taxa present in Maret, their stratigraphic position, and the most closely related species in Walbeck (MP25) and Cernay (MP6). Taxa in bold are those that are mentioned in this paper for the first time.

	Taxa from Maret	Most closely related species from	
		Walbeck	Cernay
Lincient Member	<i>Arctocyonides</i> cf. <i>weigelti</i> Arctocyonidae indet.	<i>Arctocyonides weigelti</i> <i>Mentoclaenodon walbeckensis</i>	<i>A. trouessarti</i> / <i>A. arenae</i> <i>Arctocyon primaevus</i>
Orp Sand Member	<b><i>Bustylus germanicus</i></b> <b><i>Berrulestes</i> sp.</b> <i>Adapisorex</i> sp.	<i>Bustylus germanicus</i> <i>Walbeckodon krumbiegeli</i> <i>Adapisorex abundans</i>	<i>Bustylus cernaysi</i> <i>Berrulestes phelizoni</i> <i>Adapisorex gaudryi</i>

### 4.3. Comparisons with the European Paleocene continental faunas

Comparison of the Maret mammal fauna with other European faunas reveals its close relationship with the Walbeck fauna. The upper molar of *Berrulestes* sp. from Maret is close to *Berrulestes phelizoni* from Cernay, but also shows similarities with *Walbeckodon krumbiegei* from Walbeck. The complete DP4 mentioned by Herman & Sigé (1975) under the name *Adapisorex* sp. compares better with the DP4 referred to *Adapisorex* than with that referred to *Walbeckodon*, and better with the species *A. abundans* from Walbeck than with *A. gaudryi* from Cernay. The adapisoriculid dentary is referred to *Bustylus germanicus*, a species that is only otherwise definitely known in Walbeck, following reidentification of the Cernay material as a species of *Afrodon* (see discussion in section 4.2). The upper P4 described by Quinet et al. (1971) seems very similar in size and morphology to that of *Arctocyonides weigelti* from Walbeck. The two other *Arctocyonides* species from Cernay both differ in their more derived morphology of the P4. The fragmentary upper molar figured by Herman & Sigé (1975) corresponds well in size and morphology to *A. weigelti*; however, there are too few diagnostic features to ascertain the attribution. The anterior lower premolar of the unidentified arctocyonid does not carry enough diagnostic characters to be useful in the comparison with other European faunas.

### 4.4. Implications for the age of Walbeck

Several of the specimens from Maret show a close resemblance to those of the Walbeck fauna, to the point that some seem almost identical (see Table 1). This is especially true for the taxa belonging to the genera *Bustylus* and *Arctocyonides*.

The Walbeck deposits consist of a karstic crack filled during the Oligocene with fossiliferous sands containing an assemblage of reworked marine fossils from the surrounding Triassic Muschelkalk, reworked terrestrial vertebrates from the Paleocene, and marine and terrestrial remains of Oligocene age (Weigelt, 1939; Russell, 1964). The Paleocene vertebrate fauna was therefore never accurately dated. Despite its complex taphonomy, the mammal fauna that it contains is clearly of Paleocene age, and can be considered as representative of a single chronological age (Russell, 1964). The slightly more primitive condition of the species compared to the Cernay specimens tends to indicate an older age for Walbeck, but accurate estimation of the age is difficult, notably due to the lack of comparable faunas in Europe. The Walbeck mammals have most often been assigned to the late Paleocene (Weigelt, 1960; Gheerbrant & Russell, 1989; Storch, 2008; De Bast et al., 2012), but also to the middle Paleocene (Russell, 1964; Quinet et al., 1975), the earliest Thanetian (Savage & Russell, 1983), or, more recently, the late Selandian (Smith & Smith, 2003; Hooker & Russell, 2012). The newly recovered Maret mammal specimens suggest that the Paleocene mammals from Walbeck are close in age with those from the Orp Sand Member of the Heers Formation, indicating a Selandian age for the mammals from Walbeck.

The presence in the Belgian Selandian of mammal taxa that are mostly very different from those of Hainin suggests that there is an important lapse of time between Cernay (MP6) and Hainin (MP1-5). Walbeck could represent an intermediate level, but was never chosen as reference-level due to the obvious biases in the composition of the fauna (Schmidt-Kittler, 1987). The difference in the mammal fauna between Hainin in Belgium and Walbeck in Germany could be interpreted as a result of geographic isolation rather than age difference, but the discovery of mammals in the Selandian of Maret, geographically close from Hainin, but morphologically close to those of Walbeck, suggests a substantial difference in age between Hainin and Walbeck, and also between Hainin and Maret. Moreover, the much stronger difference in the mammal assemblage observed between Hainin (earliest Selandian in Steurbaut, 1998; late Danian in Steurbaut & Sztrákos, 2008) and Walbeck (Selandian according to the correlation proposed here) than between Walbeck and Cernay (late Thanetian) evidences an undocumented dispersal event from North America towards Europe around the Danian-Selandian boundary. Indeed, several

taxa present in Walbeck and Cernay, such as *Arctocyon* and *Plesiadapis*, offer far closer relationships with North American faunas than with the preceding Hainin mammal fauna.

## 5. Conclusion

Several new mammal specimens were discovered in the marine Selandian of Maret, Belgium, including an adapisoriculid dentary referable to *Bustylus germanicus*, and a fragmentary upper molar of *Berrulestes* sp. Coupled with the previous described DP4 of *Adapisorex* sp. and two fragmentary teeth referable to *Arctocyonides* cf. *weigelti*, these mammals suggest that the best correlation for the poorly dated deposits of Walbeck is with the Orp Sand Member of the Heers Formation, dated early to middle Selandian. The presence in the Selandian of mammals that are very different than those found at Hainin moreover proves that Walbeck represents an intermediate MP level between Hainin and Cernay, and that a mammal turnover event existed between Hainin and Walbeck. A relatively large scale dispersal event probably occurred around the Danian-Selandian boundary, after the deposition of the Hainin fauna but before the development of the Walbeck fauna, as several taxa from Walbeck and Cernay seem closer to North American groups than to the Hainin fauna.

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**Appendix 1.** List of characters and character definitions used in the cladistic analysis of adapisoriculids.

1. mesostyle: absent (0), present (1)
2. postparaconule crest: marked (0); faint (1)
3. centrocrista: straight (0), dilambdodont (1)
4. stylar cusps: crestiform (0), cusped (1)
5. M2 ectoflexus: deep and asymmetrical (0), deep and symmetrical (1)
6. M2 size of parastylar lobe versus metastylar lobe: parastylar lobe more or equally projecting labially than metastylar lobe (0), parastylar lobe less projecting labially than metastylar lobe (1)
7. paracone size: markedly larger than metacone (0), slightly larger or similarly sized (1)
8. paracone and metacone shape: much higher than long (0), slightly higher than long (1)
9. m1,2 hypoconid size: similar to the entoconid (0), slightly larger than entoconid (1), much larger than entoconid (2)
10. hypoconulid place: median (0), slightly closer to the entoconid (1), very close to the entoconid (2)
11. talonid width: narrower than trigonid (0), equally wide (1)
12. trigonid length: compressed antero-posteriorly and much shorter than the talonid (0), trigonid about as long as the talonid (1)
13. trigonid height: more than twice the height of the talonid (0), trigonid less than twice the height of the talonid (1)
14. p4 metaconid: absent or present only as a slight bulge on the side of the protoconid (0), well differentiated but smaller than the protoconid (1), size similar to that of the protoconid (2)
15. talonid of p4: with one cuspid (0), two cuspids (1)
16. size of p4 paraconid: very small, barely present as individual cuspid (0), small but forming a distinct cuspid (1), almost as large as m1 paraconid (2)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Prokennalestes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cimolestes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>D. hislopi</i>	0	0	0	0	0	0	1	1	0	0	1	1	1	?	?	?
<i>D. robustus</i>	0	0	0	0	0	0	1	1	0	0	1	1	1	?	?	?
<i>A. chleuhi</i>	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0
<i>A. germanicus</i>	(01)	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
<i>B. gheerbranti</i>	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0
<i>B. cernaysi</i>	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>B. marandati</i>	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
<i>B. folieae</i>	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. minimus</i>	1	1	1	1	1	1	1	0	2	2	1	1	1	2	1	2