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A land micro-mammal fauna from the Early Eocene marine Egem deposits (NP12, Belgium) and the first occurrence of the peradectid marsupial *Armintodelphys* outside North America

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ABSTRACT. Dental remains of land mammals are sometimes discovered in shallow marine Paleogene deposits of the North Sea Basin. Such is the case for eleven specimens we describe here from the Early Eocene Egemkapel Clay Member in the middle part of the Tielt Formation, found in Ampe quarry at Egem in Northwestern Belgium. The small fauna consists of 6 taxa, including the neoplagiaulacid multituberculate *Ectypodus*, the erinaceomorph insectivore *Macrocranion*, the nyctitheriid *Leptacodon*, an eochiropteran bat possibly belonging to a palaeochiropterygid, an unidentified perissodactyl possibly belonging to an equoid, and a new species of the peradectid marsupial *Armintodelphys*. The latter represents the first European occurrence of the genus, which was previously only known from the North American late Early and early Middle Eocene of the Wind River and Green River basins in Wyoming and the Uinta Basin in Utah. Biogeographic and biostratigraphic analyses of peradectid marsupials suggest that *Armintodelphys* dispersed between North America and Europe around the time of the Early Eocene Climatic Optimum. The Egemkapel Clay Member has been dated as middle NP12, early late Ypresian, whereas the Egem mammal fauna can be correlated to the fauna of Avenay from the Paris Basin, which is the international reference-level MP8+9 of the mammalian biochronological scale for the European Paleogene.

KEYWORDS: MP8+9 reference level, Tielt Formation, Ypresian, North Sea Basin

1. Introduction

While some continental areas contain hundreds of Paleocene and Early Eocene mammal localities such as the Clark's Fork Basin in Northwestern Wyoming (Gingerich & Klitz, 1985), early Paleogene mammal deposits of Northwestern Europe are much rarer. Moreover, they are often deposited on unconformities and/or intercalated between marine deposits making mammal evolution more difficult to understand and document than in the more continuously fossiliferous subsiding basins of North America. However, some shallow marine deposits, especially along the North Sea Basin, also yield mammal remains, which allows for more accurate age estimates of mammal-bearing horizons by comparison with the international stratigraphic scale based on biostratigraphic indicators occurring in marine layers (e.g. Hooker, 1996; Hooker & Millbank, 2001; Smith & Smith, 2003; Smith et al., 2004).

This is particularly true for the Early Eocene Egem section, the stratigraphy of which has been intensively studied (see Steurbaut 1988, 1998, 2006). Excavations in the Ampe quarry at Egem (51°00'45" N, 003°13'56" E, see Vanhove at al., 2012), situated 40 km west of Gent in West Flanders, Northwestern Belgium (Fig. 1), have been carried out for decades because of the presence there of well-preserved elasmobranch teeth. Thousands of shark and ray teeth have been collected from tons of extracted fossiliferous sediments by different collectors at different levels in the section. Included in these collections are

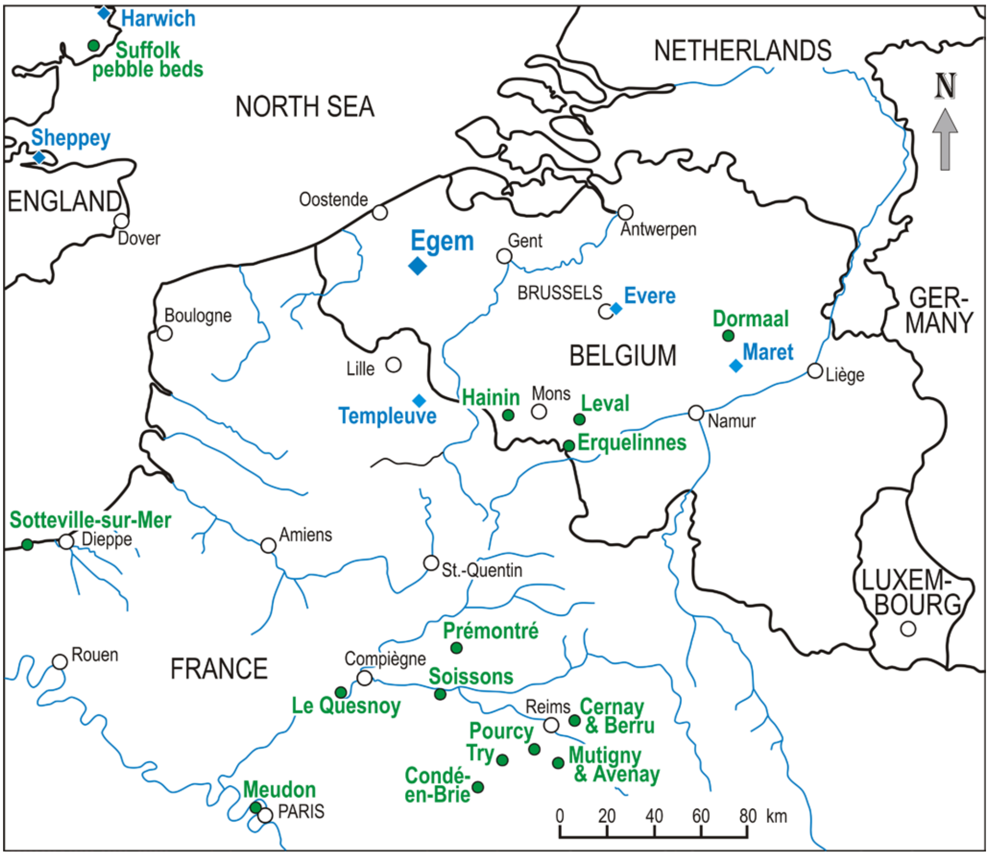

Figure 1. Geographic map around the North Sea Basin indicating Paleocene and Early Eocene localities that have yielded land mammals including the Early Eocene locality of Egem in Northwestern Belgium. Continental deposits are in green and marine deposits in blue.

Figure 2. A. Bottom of the Ampe quarry in Egem at the level of the Egemkapel Clay Member during excavations by P. De Schutter in 2005. B. Section in 2002 crossing lenticular fine sands from the base of the Egemkapel Clay Member (Layer IV *sensu* Steurbaut 1998, 2006) from which the mammal specimens have been collected. C. Close-up on the lens showing bivalve ghosts indicated by an arrow.

some small land mammal remains (Smith & Smith, 2003). These mammal discoveries seem to always originate from the same basal bed in the middle part of the Tielt Formation that represents a shallow marine deposit. They can be accurately dated as NP12 calcareous nannoplankton zone corresponding to the middle part of the Ypresian (Steurbaut, 2006).

Here we describe new dental mammal remains from the Ampe quarry of Egem that have all been found by screenwashing of lenticular fine glauconitic sands at the base of a silty clay named the Egemkapel Clay Member (Layer IV *sensu* Steurbaut 1998, 2006). The base of this member exhibits channel structures and is rich in elasmobranch teeth, phosphatic remains, and worm-tubes of the serpulid polychaete *Ditrupa* (Fig. 2).

Institutional abbreviations — **AL**, Argiles et Lignites du Soissonnais; **AMNH**, American Museum of Natural History, New York; **CB**, Condé-en-Brie; **CLO**, Le Clot; **CM**, Carnegie Museum of Natural History, Pittsburgh; **CR**, Cernay-lès-Reims; **FSL**, Faculté des Sciences, Lyon; **HLMD (Me)**, Hessisches Landesmuseum, Darmstadt (Messel); **IRSNB**, Institut royal des Sciences naturelles de Belgique, Brussels; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **Mu**, Mutigny; **RI**, Rians; **Sn Bn**, Soissons Collection Braillon; **UM**, Université de Montpellier II, Montpellier; **UMMP**, University of Michigan, Museum of Paleontology, Ann Arbor.

2. Systematic Paleontology

Class Mammalia Linnaeus, 1758
Infraclass Allotheria Marsh, 1880
Order Multituberculata Cope, 1884
Family Neoplagiaulacidae Ameghino, 1890
Genus *Ectypodus* Matthew & Granger, 1921
Type-species: *Ectypodus musculus* Matthew & Granger, 1921

***Ectypodus* sp.**
(Fig. 3)

Referred specimens: IRSNB M2150, right M^1 (L x W: 3.03 mm x 1.29 mm); IRSNB M2151, fragment of right P^4 (W: 0.73 mm)

Discussion: A complete M^1 with a cusp formula from labial to lingual rows of 9:12:6 and an anterior half P^4 bearing two cusps on the labial row belong to a small neoplagiaulacid multituberculate (Weil & Kraus, 2008). By size and general morphology they perfectly fit together and probably belong to the same species.

Among the nine neoplagiaulacid genera generally accepted (Weil & Kraus, 2008) only two genera are recognized in Europe, *Neoplagiaulax* that has mostly been described from the Late Paleocene (Vianey-Liaud, 1986, Jehle et al., 2012) and *Ectypodus* that is only known from the Early Eocene (Hooker, 2010; Marandat et al., 2012). The two genera are not easy to discriminate morphologically. However, *Neoplagiaulax* includes the largest species of Neoplagiaulacidae (Weil & Kraus, 2008) with the exception of *Neoplagiaulax sylvani* and some very small specimens referred to *N. annae* from Cernay (Vianey-Liaud, 1986) that are similar in size to *Ectypodus* species.

The M^1 from Egem is complete but unfortunately this dental position is generally considered as not very diagnostic in neoplagiaulacids (see Weil & Kraus, 2008). It resembles MNHN Mu1135 of *Neoplagiaulax* aff. *sylvani* from Mutigny (MP8+9, Paris Basin) except that the latter possesses 13 cusps on the middle row instead of 12. It resembles also the fragmentary M^1 UM CLO43 of ?*Ectypodus riansensis* from Le Clot (MP7, Corbières, Southern France) by the size and lingual row cusp formula that are similar. Teeth referred to *Ectypodus* or *Paraectypodus* from the Institut Saint-Pol of Soissons (MP8+9, Paris Basin) figured by Louis (1996) include an M^1. The M^1 MNHN Sn58Bn from Saint-Pol differs by the cusp formula but also by the lingual row that is much longer than on the M^1 from Egem. The fragment of P^4 from Egem, previously referred to *Neoplagiaulax* aff. *sylvani* (Smith & Smith, 2003), resembles the P^4's MNHN CR4473 of *Neoplagiaulax annae* from Cernay (MP6, Paris Basin, Northeast France), MNHN RI414 of ?*Ectypodus riansensis* from Rians (MP7, Provence, South France), and MNHN Mu1124 of *Neoplagiaulax* aff. *sylvani* from Mutigny (MP8+9, Paris Basin), by its small size and by the presence of only two cusps on the labial row. However, it differs from P^4 MNHN Sn57Bn of *Ectypodus* or *Paraectypodus* from Saint Pol of Soissons (Louis, 1996) by having only two cusps on the labial row instead of three and by the slope of the lingual row that is much less strong.

One of the main characters differentiating *Neoplagiaulax* from *Ectypodus* is the posterior part of the crown of P^4 where the highest cusp of the lingual row is the ultimate cusp of the tooth. It is however the penultimate or antepenultimate cusp that is the highest on the crown of P^4 in *Neoplagiaulax* and *Paraectypodus* (Weil & Krause, 2008 modified from Sloan, 1981). Unfortunately, as the posterior part of P^4 is missing in IRSNB M2151 we cannot identify the genus with certainty. However, the anterior slope that

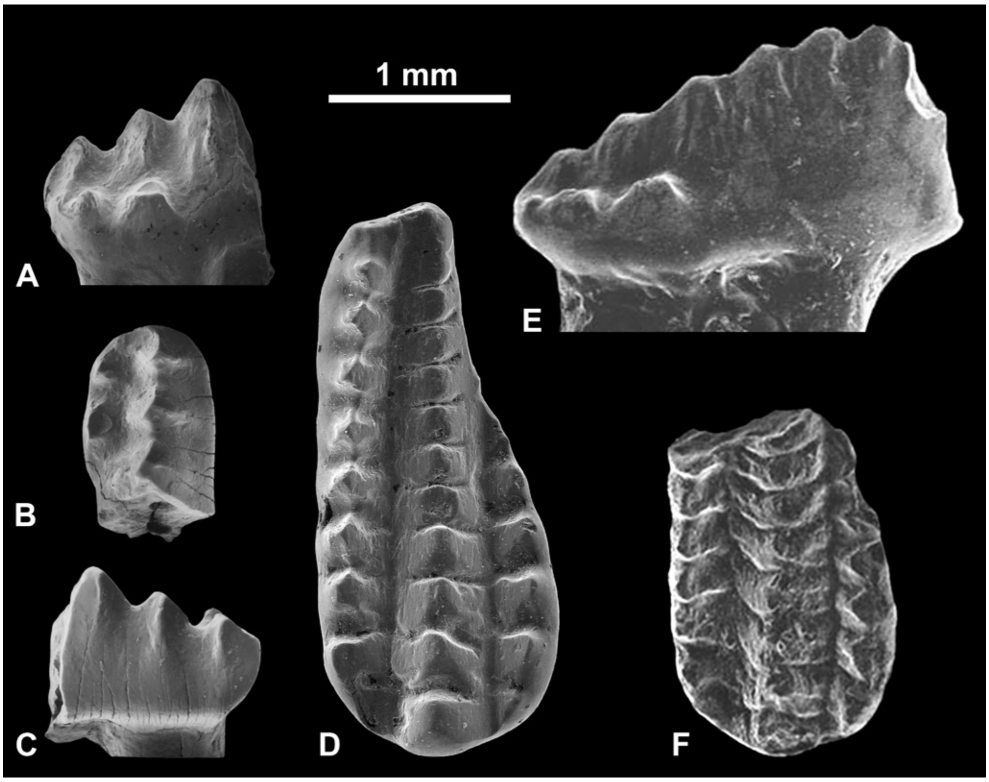

Figure 3. ***Ectypodus*** **sp.** IRSNB M2151, fragment of right P^4 in labial (A), occlusal (B), and lingual (C) views; IRSNB M2150, right M^1 in occlusal view (D). ***?Ectypodus riansensis*** from Southern France, MP7, MNHN RI414, left P^4 (reversed) in labial view (E); UM CLO43, fragment of left M^1 (reversed) in occlusal view (F); images modified from Marandat et al. (2012).

is straight in profile preserved on this specimen is in favor of an attribution to *Ectypodus*. Moreover, the presence of ridges that have wrinkled enamel from the top of the base of each main cusp of the tooth of ?*Ectypodus riansensis* (Marandat et al., 2012) is a common character with the Egem species. These characters combined with the small size of the Egem taxon and the fact that *Ectypodus* and *Paraectypodus* are the only genera that cross the P/E boundary in North America (Weil & Kraus, 2008) allow us to provisionally refer this taxon to *Ectypodus* sp. Finally, the teeth from Egem fit perfectly in size and relatively well in morphology with ?*Ectypodus riansensis*.

Infraclass Holotheria Wible et al., 1995
Supercohort Theria Parker & Haswell, 1897
Cohort Metatheria Huxley, 1880 (=Marsupialia Illiger, 1811)
Order Didelphimorphia Gill, 1872
Family Peradectidae Crochet, 1979
Genus *Armintodelphys* Krishtalka & Stucky, 1983
Type species: *A. blacki* Krishtalka & Stucky, 1983

Armintodelphys dufraingi **sp. nov.**
(Fig. 4)

Holotype: IRSNB M2152, fragment of right dentary with M_{2-4} (L x W, M_2: 1.42 mm x 0.75 mm, M_3: 1.43 mm x 0.76 mm, M_4: 1.44 mm x 0.71 mm)

Paratype: IRSNB M2153, right M_3 (L x W: 1.48 mm x 0.78 mm)

Diagnosis: Small species of *Armintodelphys* differing from *A. blacki* and *A. dawsoni* by having high ratio length/width on lower molars, narrower talonids, smaller hypoconulids, and posterior wall of the trigonids more oblique.

Etymology: after Léo Dufraing (Beerse) who discovered the holotype specimen.

Type locality and horizon: Clay-sand pit Ampe, Egem, West Flanders, Belgium. Egemkapel Clay Member, Tielt Formation, middle NP12, Ieper Group (*sensu* Steurbaut 1998).

Description: The best preserved specimen is a fragment of a right dentary with M_{2-4}, and the alveoli of M_1 and the posterior alveolus of P_3. A small mental foramen is present below the posterior root of M_1. The three molars have the same length, and M_1 was probably about the same size based on its alveoli dimensions that are similar to those of M_{2-4}. The trigonids are low, relatively open lingually, and the posterior wall is strongly oblique. The metaconid is thus distinctly posterior to the protoconid. The oblique crest is slightly ascending. The shallow talonids are somewhat shorter and narrower than the trigonids on M_{2-3} and very narrow on M_4. The hypoconulid is progressively farther from the entoconid from M_2 to M_4 respectively, displacing the hypoconulid more to the median axes of the teeth. The hypoconulid and entoconid are connected by a crest. The entoconids are the lowest cusps of the talonids. The labial and posterior cingula are very weak to nearly absent.

A second specimen is represented by an isolated lower molar. Based on the width of the trigonid it corresponds to an M_3 which is the widest tooth. This identification is confirmed by the crest between the entoconid and hypoconulid that is longer than in M_2 and shorter than in M_4.

Discussion: These very small mammal dental specimens show a general morphology that resembles that of a nyctitheriid-type insectivore (Smith & Smith, 2003). However, they can be attributed to a marsupial by the well-developed trigonid with a strong paraconid that is anteriorly oriented on all the molars, the hypoconulid that is situated near the entoconid, and the posterior mental foramen that is situated below the posterior root of M_1. Moreover, the presence of a crest between the entoconid and hypoconulid is indicative of the family Peradectidae (instead of a notch that is characteristic of contemporaneous herpetotheriid marsupials, Ladevèze et al., 2012). Early Eocene peradectid marsupials are relatively rare in Europe and mainly known from the eastern Paris Basin (Crochet, 1980). A few isolated specimens have also been reported from Rians in Provence (Godinot, 1981), Fordones in Corbières (MP7, Southern France, Marandat, 1991), Abbey Wood in the London Basin (MP8+9, Hooker, 2010), and Sotteville-sur-Mer in Upper Normandie (MP7?, Smith et al., 2011). Moreover, they all belong to *Peradectes*, a genus that differs from the Egem taxon by higher trigonids and talonids, especially the entoconid and hypoconulid, and much wider teeth. Only a few lower teeth from Avenay and Condé-en-Brie (MP8+9, Paris Basin) referred to undetermined *Peradectes* species (MNHN CB226; Crochet, 1980: p. 49-51) share with the Egem marsupial a

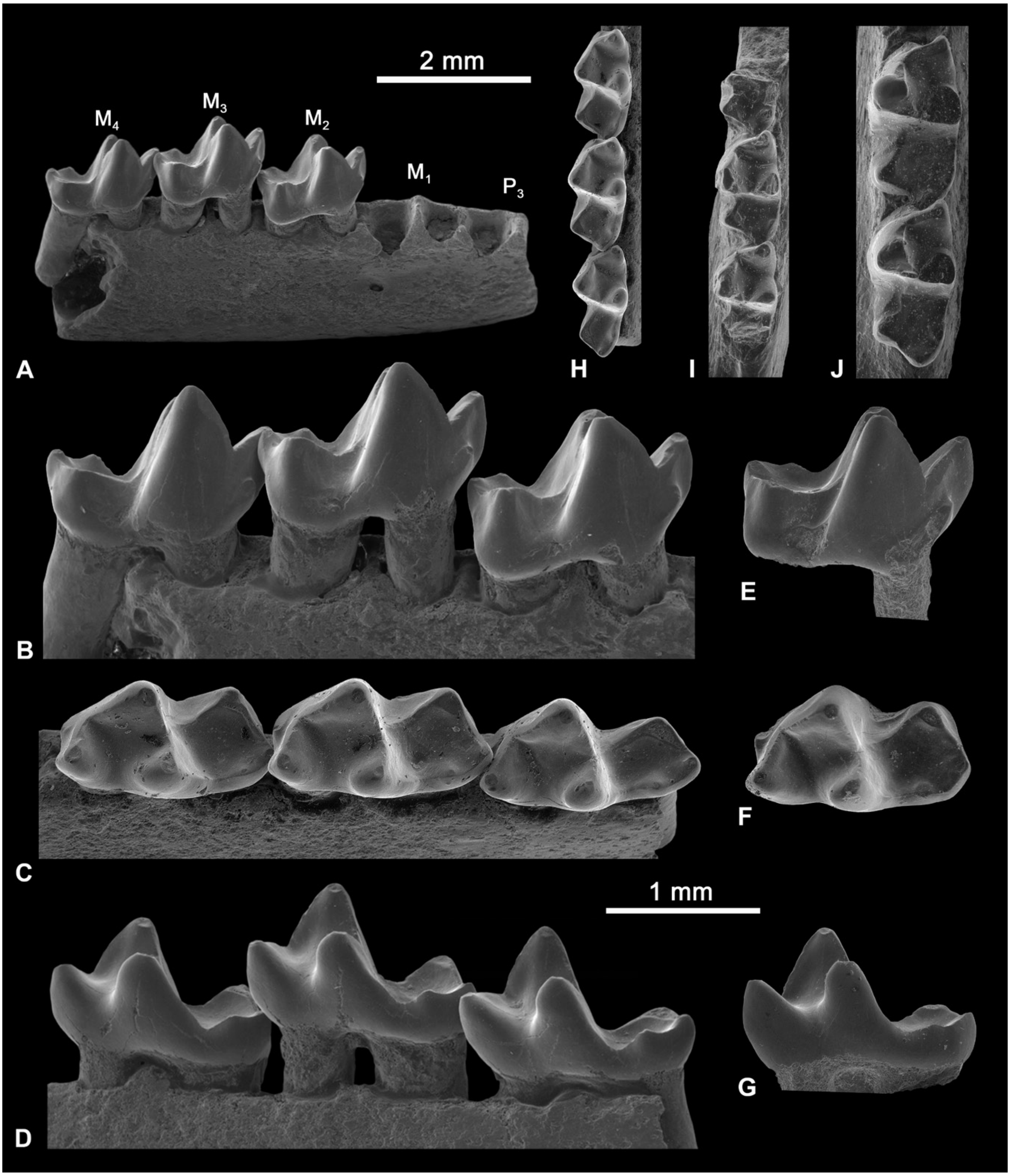

Figure 4. ***Armintodelphys dufraingi*** **sp. nov.** from Egem, IRSNB M2152, fragment of right dentary with $M_{2\text{-}4}$ in labial view with tooth positions (A); close up on $M_{2\text{-}4}$ in labial (B), occlusal (C), and lingual (D) views.; IRSNB M2153, right M_3 in labial (E), occlusal (F), and lingual (G) views. Comparison of molar dentition in occlusal view between ***A. dufraingi*** IRSNB M2152 from Egem (H), ***A. dawsoni*** CM 55569 (I) and ***A. blacki*** CM 41159 (J) from the late Early Eocene Wind River Basin, Wyoming.

very small size, a longer talonid, and a less posterior hypoconulid on M_4. However, the rest of the morphology is different with a rectilinear lingual edge, a hypoconulid that is more lingual and an entoconid more developed and crestiform.

The marsupial from Egem can be assigned to the genus *Armintodelphys* based on the presence of long and narrow molars, low trigonids and talonids, and reduced talonid cusps, especially the entoconid. This genus is only known from the late Early and early Middle Eocene of North America by two species: *Armintodelphys blacki* described from the late Wasatchian North American Land Mammal Age (NALMA) to earliest Bridgerian NALMA of the Wind River Formation (Wind River Basin), Wyoming, and *A. dawsoni* described from the early Bridgerian of the Wind River Formation, Wyoming (Krishtalka & Stucky, 1983). *A. dawsoni* also occurs in the early Bridgerian Powder Wash locality of the Green River Formation in the Uinta Basin, Utah (Krishtalka & Stucky, 1984). Two specimens referred under the name cf. *Armintodelphys* sp. have also been reported from the early Bridgerian of the Southern Green River Basin in Wyoming (Gunnell, 1998). Like the species from Egem, the two American species present a curved talonid lingual edge whereas this edge is rectilinear in *Peradectes*.

The *Armintodelphys* species from Egem is much smaller than the type-species *A. blacki* and similar in size to *A. dawsoni*. It

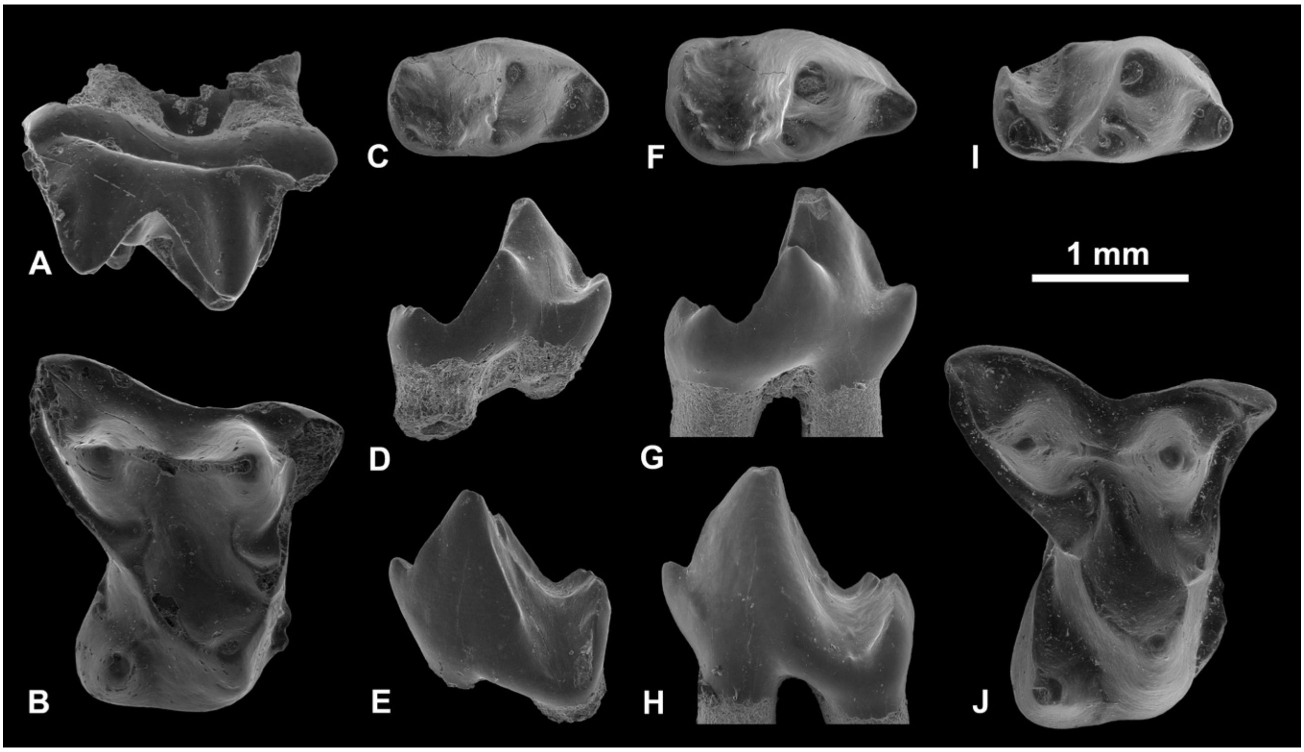

Figure 5. ***Macrocranion* cf. *nitens*** from Egem, IRSNB M2154, right M^1 in labial (A), and occlusal (B) views; IRSNB M2155, left P_4 in occlusal (C), lingual (D), and labial (E) views; IRSNB M2156, left P_4 in occlusal (F), lingual (G), and labial (H) views. ***Macrocranion* cf. *nitens*** from Mutigny, Paris Basin, MP8+9, MNHN Mu457, left P_4 in occlusal view (I); MNHN Mu5985, right M^1 (reversed) in labial view (J).

differs from both species by the talonid structure that is narrower especially the talonid of M_4. The hypoconulid is also narrower and more reduced, and the posterior wall of the trigonid is more oblique than in the two American species. These characters allow attribution of the Belgian taxon to a new species for which we propose the name *Armintodelphys dufraingi* sp. nov.

Supercohort Eutheria Huxley, 1880
Cohort Placentalia Owen, 1837
Grandorder Lipotyphla Haeckel, 1866
Order Erinaceomorpha Gregory, 1910
Family Amphilemuridae Hill, 1953
Genus *Macrocranion* Weitzel, 1949
Type species: *Macrocranion tupaiodon* Weitzel, 1949

Macrocranion* cf. *nitens
(Fig. 5)

Referred specimens: IRSNB M2154, right M^1 (L x W: 2.02 mm x 2.30 mm); IRSNB M2155, left P_4 (L x W: 1.33 mm x 0.74 mm); IRSNB M2156, left P_4 (L x W: 1.58 mm x 0.83 mm)

Discussion: The presence of the hedgehog-like insectivore *Macrocranion* at Egem is attested by three typical teeth. An upper molar about as long as wide with a short labial shelf, a shallow ectoflexus, a parastyle anteriorly oriented, two strong conules, and a strong hypocone is indeed characteristic of an M^1. Two similar exodaenodont lower premolars with a crestiform paraconid, a reduced metaconid, a short and wide labially open talonid clearly indicate P_4 of *Macrocranion*. The P_4 IRSNB M2156 is a little larger than IRSNB M2155. However, the two teeth are morphologically identical differing only by the metaconid slightly more developed and the paraconid a little more cuspidate on IRSNB M2156. These differences correspond to intraspecific variation such as is observed in the case of *Macrocranion vandebroeki* from Dormaal (MP7, Belgium, Smith & Smith, 1995).

The respective sizes of the M^1 and the two P_4's compared to the same dental positions of different species of *Macrocranion* such as *M. vandebroeki* from Dormaal (MP7, Belgium, Smith & Smith, 1995), *M.* cf. *nitens* from Mutigny and Avenay (MP8+9, Paris Basin, France, Russell et al., 1975), *M. junnei* from the Bighorn Basin (Wa-0, Wyoming, Smith et al., 2002), and *M. tenerum* from Messel (MP11, Germany, Tobien, 1962) strongly suggest that the three teeth belong to the same species.

Morphological comparisons indicate that M^1 from Egem differs from those of *M. vandebroeki* from Dormaal by the shorter labial shelf and more massive paracone and metacone. These characters are however similarly developed in some teeth of *M.* cf. *nitens* from Mutigny and Avenay described by Russell et al. (1975). The two P_4's from Egem differ from those of *M. vandebroeki* in being much narrower like in the case of *M.* cf. *nitens* from Mutigny and Avenay. For these reasons we attributed the *Macrocranion* species from Egem to *M.* cf. *nitens*. Nevertheless, the teeth from Egem are closer in size to the teeth from Avenay than to those of Mutigny. The important variation in *M.* cf. *nitens* and the larger size of the population of Mutigny has been already underlined by Russell et al. (1975).

M. cf. *nitens*, known from hundreds isolated teeth from Mutigny and Avenay, has always stayed in open nomenclature because of its strong resemblance to *M. nitens* from the Early Eocene of North America. The American species has been recognized in numerous localities from different areas and different ages but showing substantial variation. Therefore, it probably represents different species. A detailed restudy of the American holotype specimen and a comparison with referred specimens discriminated by stratigraphic levels and geographic origins would be useful for a better comparison with the European taxa.

Order uncertain
Family Nyctitheriidae Simpson, 1928
Genus *Leptacodon* Matthew & Granger, 1921

***Leptacodon* sp.**
(Fig. 6)

Referred specimen: IRSNB M2157, left M^1 (L x W: 1.32 mm x 1.67 mm)

Discussion: The nyctitheriid genus *Leptacodon* is recognised by a small and gracile upper molar, wider than longer, with relatively deep ectoflexus, a straight centrocrista, an anteriorly oriented parastyle, a labially oriented metastyle, two conules, a developed postcingulum bearing a small but distinct hypocone, and a distinct

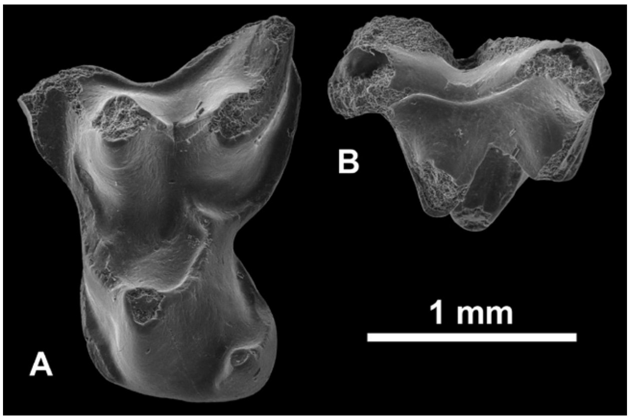

Figure 6. ***Leptacodon*** **sp.** from Egem IRSNB M2157, left M^1 in occlusal (A), and labial (B) views.

precingulum. These characters are typical of an M^1.

Leptacodon is present in different Early Eocene localities of Europe but has only been formally described from Dormaal (MP7, Belgium) with the species *L. dormaalensis* (Smith, 1996) and from Silveirinha (MP7, Portugal) with the species *L. nascimentoi* (Estravis, 1996). The species from Egem differs from *L. dormaalensis* by the greater extension of the metastyle in labial direction and by the absence of a postparaconule crista. However, this latter character is shared with *L. nascimentoi*. A few teeth referred to *Leptacodon* sp. or *Saturninia* sp. have been reported from Fordones (MP7, Corbières, Southern France) by Marandat (1991) but they preserve the postparaconule crista like *L. dormaalensis*. Numerous dental specimens of *Leptacodon* are also present in higher stratigraphic levels such as Avenay and Mutigny (MP8+9, personal observations) and their description would be particularly useful for a detailed comparison of the different European species of this genus including the specimen from Egem.

Order Chiroptera Blumenbach, 1779
Suborder "Eochiroptera" Van Valen, 1973
Family Palaeochiropterygidae? Revilliod, 1917

Gen. et sp. indet.
(Fig. 7)

Referred specimen: IRSNB M2158, left M^2 (W: 1.72 mm); IRSNB M2159, trigonid of right M$_2$ or M$_3$ (W: 0.79 mm)

Discussion: Although the metastyle area is broken in IRSNB M2158, several important characters are visible on this very small upper molar. Among them are the protocone that is antero-posteriorly narrow with a small postero-lingual postcingulum, the metaconule is absent, the ectoflexus is very deep, narrow, and anterior, and the centrocrista is long and joins the labial border. This typical chiropteran morphology indicates an M^1 or M^2. The labially oriented parastyle suggests more an M^2 than an M^1. IRSNB M2159 is represented by a trigonid somewhat antero-posteriorly compressed showing a strong paraconid antero-lingually oriented, protoconid and metaconid relatively distant, and a well developed antero-labial cingulid suggest a chiropteran M$_2$ or M$_3$. The size of this lower molar fits perfectly with that of the upper molar.

Among the different early bat families that are recognized (Smith et al., 2012) several can be excluded. The Egem taxon differs from onychonycterids that have relatively square shaped upper molars, which are nearly as long as wide with the centrocrista that does not reach the labial border and the ectoflexus that is very shallow to nearly non-existent. The Egem bat is morphologically closer to icaronycterids and archaeonycterids by the deep ectoflexus but it is very anteriorly situated in the Belgian taxon while it is symmetric and well open in icaronycterids and archaeonycterids. Moreover, icaronycterids preserve two conules and archaeonycterids have a more massive protocone and the centrocrista, relatively short, does not join the labial border. A small unidentified "Eochiroptera" from the early Eocene of El Kohol in Algeria (Ravel et al., 2011) fits well in size with the Egem bat but as in *Icaronycteris* the African bat is more plesiomorphic by the retention of two conules and a short centrocrista that does not join the labial border. The mixopterygids and emballonurids can also be excluded by the development of a large postcingulum (Maitre et al., 2008) that is not present in the Egem bat. The latter also differs from philisids (Sigé, 1985, 1991; Gunnell et al., 2008; Ravel et al., 2012) that have lost the conules and that have a large protocone. It resembles more the hassianycterids and palaeochiropterygids by the anteriorly situated ectoflexus. However, hassianycterids are of relatively large size except "*Hassianycteris*" *joeli* described by Smith and Russell (1992) from the Early Eocene of Evere (Brussels, Belgium). However, this species has recently been removed from the genus *Hassianycteris* and tentatively allied with the onychonycterid *Honrovits* (Smith et al., 2012).

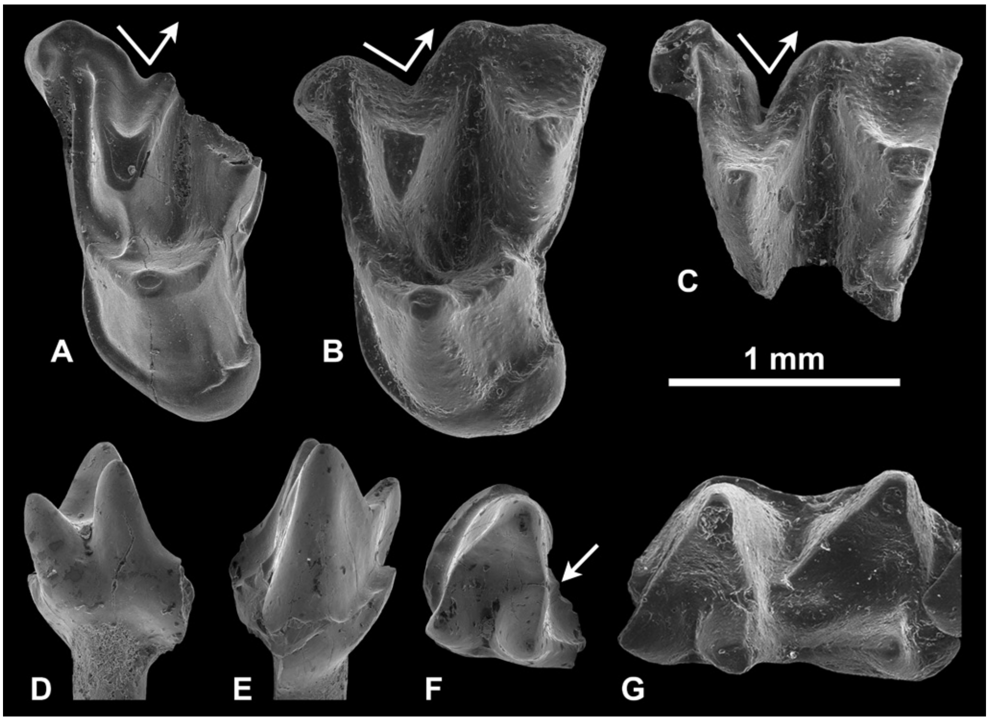

Figure 7. Palaeochiropterygidae? gen. et sp. indet. from Egem, IRSNB M2158, left M^2 in occlusal view (A); IRSNB M2159, trigonid of a right M$_2$ or M$_3$ in lingual (D), labial (E), and occlusal (F) views. ***Palaeochiropteryx tupaiodon*** from the Middle Eocene of Messel, Germany, MP11, HLMD 4271 (Me26), left M^1 (B); HLMD 517 (Me43), left partial M^2 (C) and left M$_2$ (reversed) (G) in occlusal views. The folded arrows in A, B, and C indicate the anteriorly situated narrow ectoflexus typical of Palaeochiropterygidae. The arrow in F indicates the very lingual position of the crista obliqua characteristic of Palaeochiropterygidae.

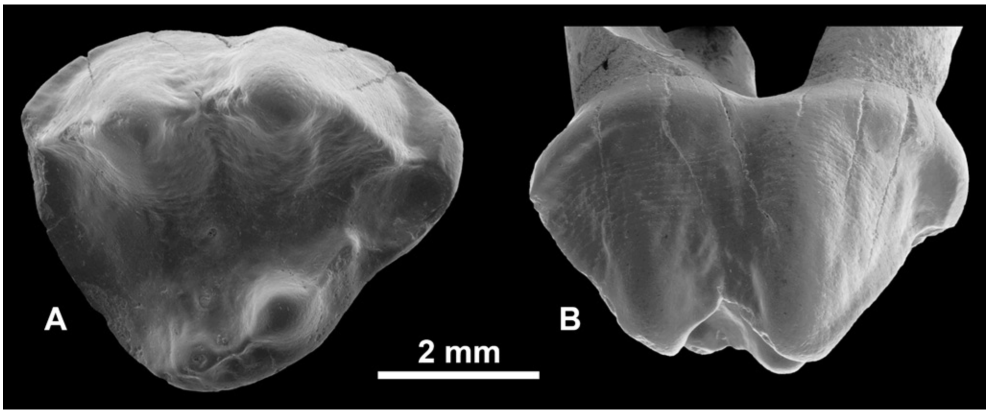

Figure 8. Equoidea? gen. et sp. indet. from Egem. IRSNB M2160, cast of right P^2 in occlusal (A) and labial (B) views.

The upper molar from Egem shares several important diagnostic characters with the palaeochiropterygids such as the anteriorly situated narrow ectoflexus, the short protocone, and the very long centrocrista that joins the labial border. Finally, palaeochiropterygids are among the smallest early bats and the very small upper molar from Egem fits in size and general morphology with an M^2 of *Palaeochiropteryx tupaiodon* from the Middle Eocene of Messel (MP11, Germany). The base of the posterior wall of the trigonid of IRSNB M2159 preserves the beginning of the crista obliqua. This one is in a very lingual position such as in *P. tupaiodon*.

However, the two teeth from Egem are a little smaller, and the M^2 is more gracile with a less massive protocone, and preserves a postparaconule crista. These characters probably indicate another species.

If the palaeochiropterygid affinities of these teeth could be confirmed this would represent the oldest occurrence of the family in Europe.

Order Perissodactyla OWEN, 1848
Suborder Hippomorpha WOOD, 1937
Superfamily Equoidea? GRAY, 1821

Gen. et sp. indet.
(Fig. 8)

Referred specimen: IRSNB M2160, cast of right P^2 (L x W: 5.70 mm x 4.71 mm)

Discussion: Despite its small size, this specimen is the largest mammal tooth found at Egem. By its very simple rounded outline with bunodont paracone and metacone, absence of conules, wide and rounded parastyle, and a reduced lingual part it can be attributed to a P^2 of a perissodactyl. However, very few P^2 of Early Eocene perissodactyls have been described. Only general comparisons can thus be done.

The Egem tooth seems to be distinguished from Ancylopoda. Indeed, it differs from the lophiodontid *Lophiaspis maurettei* from the Early Eocene of Palette in Southern France (MP7) known based on FSL2084, a right P^2-M^3. The P^2 from Egem is much smaller with less massive cusps especially the protocone, and the parastyle is more anteriorly developed than in *Lophiaspis* (Hooker & Dashzeveg, 2004). It differs also from the isectolophid *Cardiolophus radinskyi*, known from UMMP 68548, a skull from the Early Eocene Willwood Formation, Clarks Fork Basin, Wyoming (Gingerich, 1991; Hooker & Dashzeveg, 2004). The lingual part of the Egem tooth is more developed and the metacone is nearly the same size as the paracone whereas the metacone is absent in the P^2 of *Cardiolophus*.

The P^2 from Egem does not show a typical morphology for a Tapiroidea. Indeed, it differs from the helaletid *Helaletes mongoliensis* (specimen AMNH 19161) from the Middle Eocene of Mongolia (Radinsky, 1965) by the paracone and metacone well distinct from each other and the lingual part of the P^2 that is much less developed.

The well distinct paracone and metacone and the lingual part with a small protocone of the Egem upper premolar is reminiscent of the morphology of basal Hippomorpha such as *Propachynolophus*, *Pliolophus*, and *Hyracotherium*. The P^2 MNHN AL5196 referred to *Propachynolophus maldani* from the Sables à Unios et Térédines in the vicinity of Epernay also presents a rudimentary protocone (Russell et al., 1965) but is a little smaller and less antero-posteriorly elongated than the P^2 from Egem. The size of IRSNB M2160 seems to fit with the size of the equoid species *Propachynolophus levei*, *Pliolophus vulpiceps*, and *Hyracotherium leporinum*. It is difficult to go further in the identification because all these species are close to each other in size, and are of a similar age that is situated around the middle part of the Early Eocene like the Egem specimen.

3. Discussion

The small land mammal fauna from Egem in Northwestern Belgium consists of 6 taxa, including the multituberculate *Ectypodus*, a new species of the peradectid marsupial *Armintodelphys*, the erinaceomorph insectivore *Macrocranion*, the nyctitheriid *Leptacodon*, an eochiropteran bat possibly belonging to a palaeochiropterygid, and a perissodactyl possibly belonging to a primitive equoid.

Biochronological analysis indicates that the genera *Macrocranion* and *Leptacodon* are present in Europe already from the earliest Eocene of Dormaal. However, peradectid marsupials, multituberculates, bats, and perissodactyls are absent in Dormaal. Some of these groups are nevertheless present in other MP7 localities and all the groups are present together later in the MP8+9 reference level. The multituberculate *Ectypodus* has been recently identified in the localities of Rians and Le Clot (MP7 of Southern France). Moreover, the peradectid *Armintodelphys* represents the first European occurrence of the genus, which was previously only known from a short time span extended from the late Wasatchian to early Bridgerian (late Early to early Middle Eocene) in North America. *Macrocranion* cf. *nitens* characterised by a narrower P_4 than *M. vandebroeki* from Dormaal also suggests a relationship with middle to late Wasatchian (middle to late Early Eocene) of North America. Bats are however not present in North America before the late Wasatchian and are restricted to the families Icaronycteridae and Onychonycteridae (Smith et al., 2012) whereas their presence in Europe is confirmed from the early Early Eocene of Silveirinha (Portugal), Meudon (Paris Basin), and Rians, Palette, Fordones and Fournes (South France), and they are well diversified at the MP8+9. The bat from Egem possibly belongs to the family Paleochiropterygidae that is very abundant in the Middle Eocene of Messel (MP11, Germany). Russell et al. (1973) mentioned that a palaeochiropterygid could already be present in the late Early Eocene of Grauves (MP10, Paris Basin). Nonetheless, a tiny paleochiropterygid, *Microchiropteryx foliae*, is present in the middle Early Eocene of Vastan in India (Smith et al., 2007). Taking into account that more than 50 % of the mammal taxa from Vastan fauna are closely related to European faunas the presence of a paleochiropterygid since the Early Eocene of Europe would not be surprising. Primitive equoids are typical in the Early Eocene of both Europe and North America.

The Egem mammal fauna thus best correlates with the international reference-level MP8+9 of the mammalian biochronological scale for the European Paleogene for which the mammal fauna of Avenay from the Paris Basin is the reference fauna. However, more specimens and taxa need to be found to confirm the correlation. Moreover, the reference-level MP8+9 needs to be better defined as the time span between MP7 and MP10 seems very important. The mammals originated from the base of the Egemkapel Clay Member in the middle part of the Tielt Formation that has been dated as middle NP12 (VI) subzone, indicating the early late Ypresian about 51-52 Ma (*sensu* Steurbaut, 2006; Vanhove et al., 2011).

Biogeographical analysis based on the seeming absence of *Armintodelphys* before the late Wasatchian in North America and its presence for the first time in early late Ypresian deposits of Europe suggests that this peradectid marsupial belongs to a different migration wave than the main migration that took place around the Paleocene Eocene Thermal Maximum (Smith et al., 2006). The first occurrence of Cenozoic marsupials in Europe starts at the earliest Eocene, about 56 Ma with the herpetotheriid *Peratherium constans* at Dormaal (Teilhard de Chardin 1927; Ladevèze et al., 2012). Rapid intercontinental mammal dispersals have been suggested around the PETM. Similar paleoclimatic conditions seem to prevail around the Early Eocene Climatic Optimum (EECO) and this event could thus be favourable for another migration wave between Europe and North America. This would explain the presence of several late Wasatchian and early Bridgerian genera in the late Ypresian of Europe (upper "Sparnacian" and "Cuisian"). The diacodexeid artiodactyls *Bunophorus* and/or *Simpsonodus* have been identified in localities of Mutigny and Avenay (MP8+9) and Pourcy (MP7?) in the Paris Basin (Sudre et al., 1983; Stucky and Krishtalka 1990). The genus *Pontifactor*, known from the early Bridgerian (West, 1974) in North America, is present in the MP10 locality of Prémontré (Degrémont et al., 1985). A study on larger mammal associations than the one from Egem would be interesting to test this hypothesis of dispersals between Europe and North America around the EECO.

Taphonomic hypotheses have been proposed to explain the presence of land micro-mammals in marine layers either through the action of predatory sea birds or through fluvial transport (Smith & Smith, 2003). The large quantity of shark and ray teeth discovered together with the micro-mammal teeth indicates an additional concentration effect of the material in the marine deposit. All the mammal specimens discovered at Egem are of small to very small size. They all belong to small sized mammals except the perissodactyl tooth. Nevertheless, this tooth presents the same preservation aspect as the other mammal specimens suggesting that all these teeth do not result from the action of predatory sea birds. The perissodactyl tooth, a P^2, is among the smallest dental position of the tooth row suggesting that all the mammal teeth collected at Egem are the result of a granulometric sorting. The very good preservation of the specimens suggests that they have not been reworked but that they have been transported over a short distance toward the marine deposit.

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