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The earliest Eocene mammal fauna of the Erquelinnes Sand Member near the French-Belgian border.

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ABSTRACT: The earliest Eocene Erquelinnes site was discovered in 1880, but its mammal fauna has been frequently ignored. This paper provides the first detailed overview of the Erquelinnes mammals since 1929. The new faunal list doubles the known diversity at Erquelinnes to a total of 16 species, now also including amphilemurids, hyaenodontids, mesonychids, louisinids, equids and diacodexeids. The majority of the Erquelinnes species is also present in the earliest Eocene Dormaal MP7 reference fauna, with as most notable exceptions the presence of a potentially dwarfed specimen of *Dissacus,* and of two perissodactyl taxa at Erquelinnes. The ceratomorph perissodactyl *Cymbalophus cuniculus* is also known from the earliest Eocene of England, but a specimen identified as cf. *Sifrhippus sandrae* is closely similar to contemporaneous primitive North American equids. This specimen represents the oldest unambiguous European equid and highlights faunal similarities between Europe and North America during this time interval. Faunal differences between Erquelinnes and Dormaal seem mostly due to depositional differences, and the Erquelinnes fauna represents a typical earliest Eocene fauna, closely similar to other MP7 and PEI faunas in Europe.

KEYWORDS: MP7 reference level, "Late Landenian", Tienen Formation, Belgium, France

1. Introduction

In August 1880, a well preserved mammal dentary was found in a sand quarry at Erquelinnes. The specimen was donated to the Royal Belgian Institute of Natural Sciences (RBINS) and was referred to the Lower Eocene perissodactyl *Pachynolophus maldani* (Rutot, 1881). The specimen represented the first Lower Tertiary mammal from Belgium, and additional fieldwork in 1891, 1922, 1924 and 1958 increased the Erquelinnes mammal collection to 38 identifiable dental and postcranial specimens. Faunal lists for the Erquelinnes site were published by Dollo (1909), Dollo & Teilhard de Chardin (1924), Teilhard de Chardin (1921, 1927) and Simpson (1929). The monograph of Teilhard de Chardin (1927) was the only paper to provide illustrations and some details of the Erquelinnes mammal specimens. By then however, scientific attention had already shifted towards the contemporaneous Dormaal fauna about 90 km NE of Erquelinnes, which yielded thousands of specimens rather than only a few dozen (Teilhard de Chardin, 1927).

Quinet and Verlinden (1970) and Hooker (1984) discussed the taxonomic affinities of the perissodactyl jaw in more detail, and Hooker (1994) illustrated a plesiadapid incisor from Erquelinnes and included it into a new species, *Platychoerops georgei*. Mammal specimens from Erquelinnes were further mentioned in some taxonomic notes focusing on the Dormaal fauna (Smith et al., 1996; Smith, 1999; Smith & Smith 2001, 2010). In the past 75 years however, the Erquelinnes mammal fauna was never studied as a whole, and as a result its faunal composition has become unclear and in need of a modern revision.

Here we provide an updated faunal list for the Erquelinnes mammal site, giving a more precise identification for six of the eight taxa listed by Teilhard de Chardin (1927) and moreover doubling the taxonomic diversity to 16 taxa.

2. Materials and Methods

Due to the closing and filling of the historic Erquelinnes quarries, the Erquelinnes Sand Member is currently no longer exposed anywhere. Stratigraphic information presented here was mostly compiled from available literature. Some additional observations and analyses were however made on a core 10 cm in diameter and almost 2 m thick collected by Jean de Heinzelin and colleagues from a cleaned face on the last outcrop in November 1978 for biostratigraphic analysis (De Coninck et al, 1981).

Institutional abbreviations: BMNH-British Museum of Natural History, London, UK; IRSNB-Royal Belgian Institute of Natural Sciences, Brussels, Belgium; IM-Ipswich Museum, Suffolk, UK; MNHN-Musée National d'Histoire Naturelle, Paris, France; MPZ-Musea Paleantalogica, Universidad de Zaragoza, Zaragoza, Spain; UM-University of Michigan, Ann Arbor, USA.

Other abbreviations: **Fm-** Formation; **L**-Length; **Mb**-Member; **W**-Width.

3. Geographical and Geological setting

The Belgian village of Erquelinnes is located right on the French-Belgian border, about 20 km SE of Mons (Fig. 1). Although situated at the southern edge of the Mons Basin, strictly speaking it does not belong to the Mons Basin, but is separated from it by the Variscan Front and a Hercynian basement high. The Erquelinnes area is located south of this structural high and belongs to a N60°E sub-basin, aligned along the Sambre River and connected to the Avesnois Paleocene and Lower Eocene succession (Quesnel, 2006).

At the end of the 19th and the beginning of the 20th century, Upper Cretaceous and Lower Paleogene sediments were exposed at Erquelinnes in a series of sand quarries on both sides of the border. Lower Paleogene vertebrates including partial and complete skeletons have been found in several of these quarries (Dollo, 1884; Zangerl, 1971; Sigogneau-Russell & de Heinzelin, 1979; Delfino et al, 2005; Delfino & Smith, 2009).

The perissodactyl dentary discovered in 1880 was found in the '*Sablière n°1*' (Rutot, 1881). Historical records at the RBINS show that additional mammal specimens were collected in 1891, 1922, 1924 and 1954, but do not allow to establish with certainty the precise geographic origin for the other mammal specimens. However, most of the specimens were found during the 1922 fieldwork supervised by Dollo. For at least some of these specimens, Teilhard de Chardin (1927) mentions the French town Jeumont, rather than Erquelinnes, as the location and de Heinzelin identified three quarries in France where the Dollo specimens might have come from (Sigogneau-Russell & de Heinzelin, 1979).

In the Erquelinnes quarries, four stratigraphic units have been described below the Pleistocene loess (see Steurbaut, 1998). They are, in ascending order (Fig. 2): the marine Upper Cretaceous Saint-Vaast Chalk, the shallow marine Thanetian Grandglise

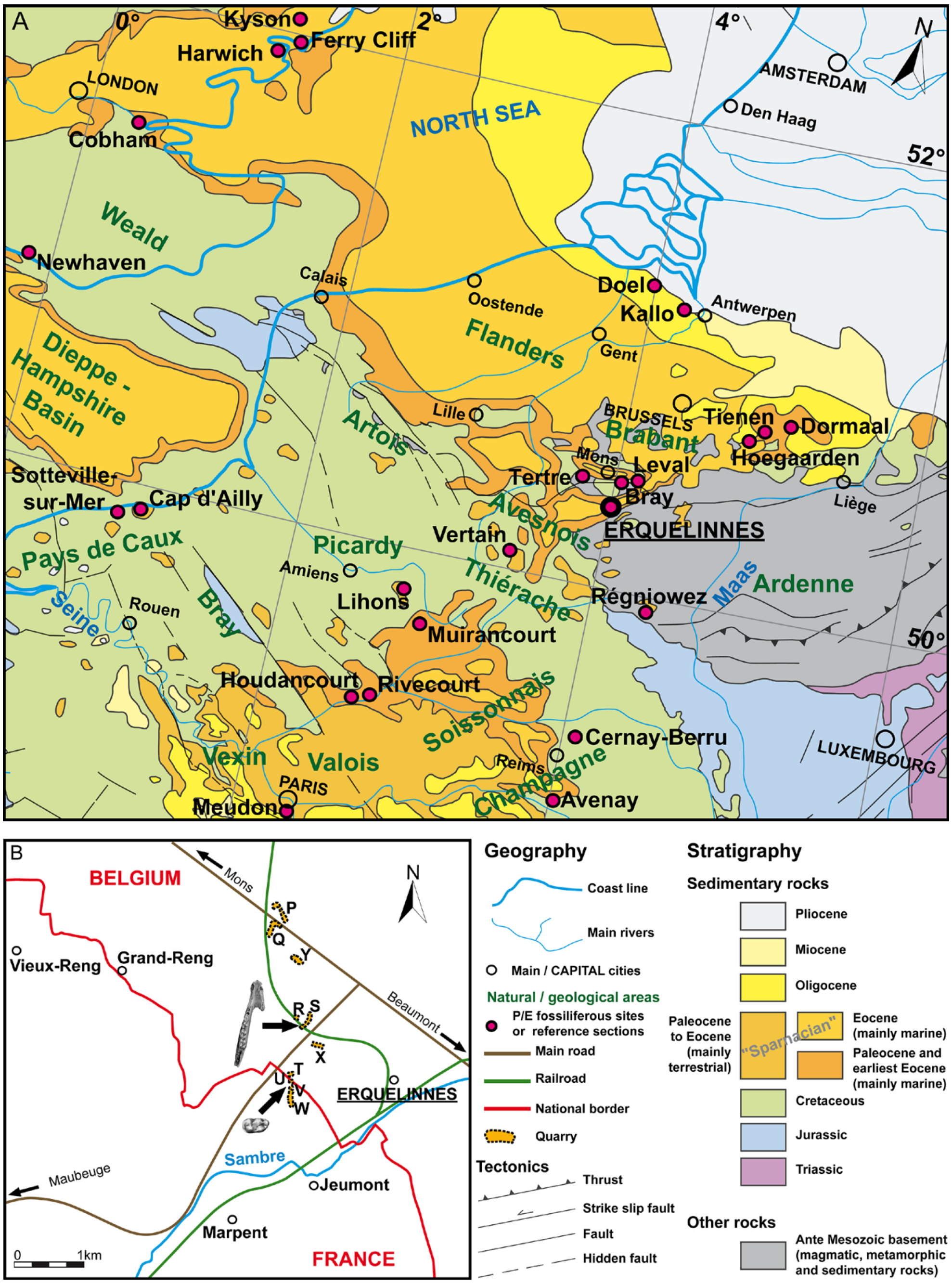

Figure 1. Geographical setting of the earliest Eocene Erquelinnes mammal fauna. A: Geological map of southern North Sea Basin and part of the Dieppe-Hampshire and Paris Basins (modified after IGME and Chantraine et al, 2003); B: Local geographical setting of the historic Erquelinnes sand quarries (modified after de Heinzelin, 1979 and Quesnel, 2006). Images of the *Cymbalophus* jaw and isolated cf. *Sifrhippus* molar respectively indicate the probable origin of the *Cymbalophus* specimen found by Gravis in 1880 and of the specimens collected by Dollo in 1922.

Sand Mb and Bois-Gilles Sand Mb (Hannut Fm), and the fluvial earliest Eocene Erquelinnes Sand Mb (Tienen Fm).

The very irregular scoured contact of the basal Erquelinnes Sand Mb incised up to 5 m into the shallow marine to littoral sands of the Bois-Gilles Sand Mb (Sigogneau-Russell & de Heinzelin, 1979; De Coninck et al, 1981). This very erosive surface is overlain by a basal gravel bed (flint dominant, quartz and local Devonian rocks of the Hercynian basement), characterized by a lenticular geometry and an irregular thickness (few cm up to one meter). The gravel bed contains lenses very rich in vertebrate fossils (Rutot, 1881, 1903; Stevens, 1919; Sigogneau-Russell & de Heinzelin, 1979), some reworked and rounded from the underlying Upper Thanetian marine sands (among which are numerous shark teeth) and other terrestrial autochthonous ones (mammals, crocodiles, turtles, *Lepisosteus* scales and other remains). The basal gravel bed is overlain by a sand set, 4 to 5 m thick, containing less vertebrate remains, occasional silicified wood debris, and characterized by trough cross bedding and planar cross bedding (Rutot, 1903; Sigogneau-Russell & de Heinzelin, 1979). Clay clasts are present at the bottom of the cross bedded sand set, as well as lignite lenses, 30 to 40 cm thick, and lignite laminae (Stevens, 1919; Sigogneau-Russell & de Heinzelin, 1979). Clay and marl lenses, 30 cm to 3 m thick, sometimes containing root or leaf casts, occur locally within the cross bedded sands, more in its upper half.

This fluvial succession constitutes the Erquelinnes Sand Mb (Fig. 2), that was formerly exposed in some of the historic Erquelinnes quarries. This fluvial unit has in the past been attributed to the “Late Landenian” and to the Upper Landen Fm (Vincent & Rutot, 1879; Moorkens, 1973) but was more recently stratigraphically ascribed to the Tienen Fm (Steurbaut, 1998). The gravel beds and cross bedded sands, with lignitic material in beds and lenses, may be interpreted as deposited rapidly in channels of braided rivers, while the marl and clay lenses and beds probably correspond to the lateral floodplain environment.

Similar fluvial gravels, sands, lignite, clay and occasional marl units as those of Erquelinnes sand Mb are widespread in the same lithostratigraphic position in northern France (Avesnois, Artois, Thiérache, Pays de Caux), southwestern Belgium (Tertre, Leval-Trahegnies, Bray) and eastern Belgium (Tienen, Dormaal, Hoegaarden). They belong to the so-called “Late Landenian”, and they fill fluvial channels incising marine Thanetian sediments or Upper Cretaceous chalk units, exhibit local cross-stratification, produce floral or vertebrate fossils (Vertain, Régniowez, Erquelinnes, Leval, Dormaal, Hoegaarden) or are

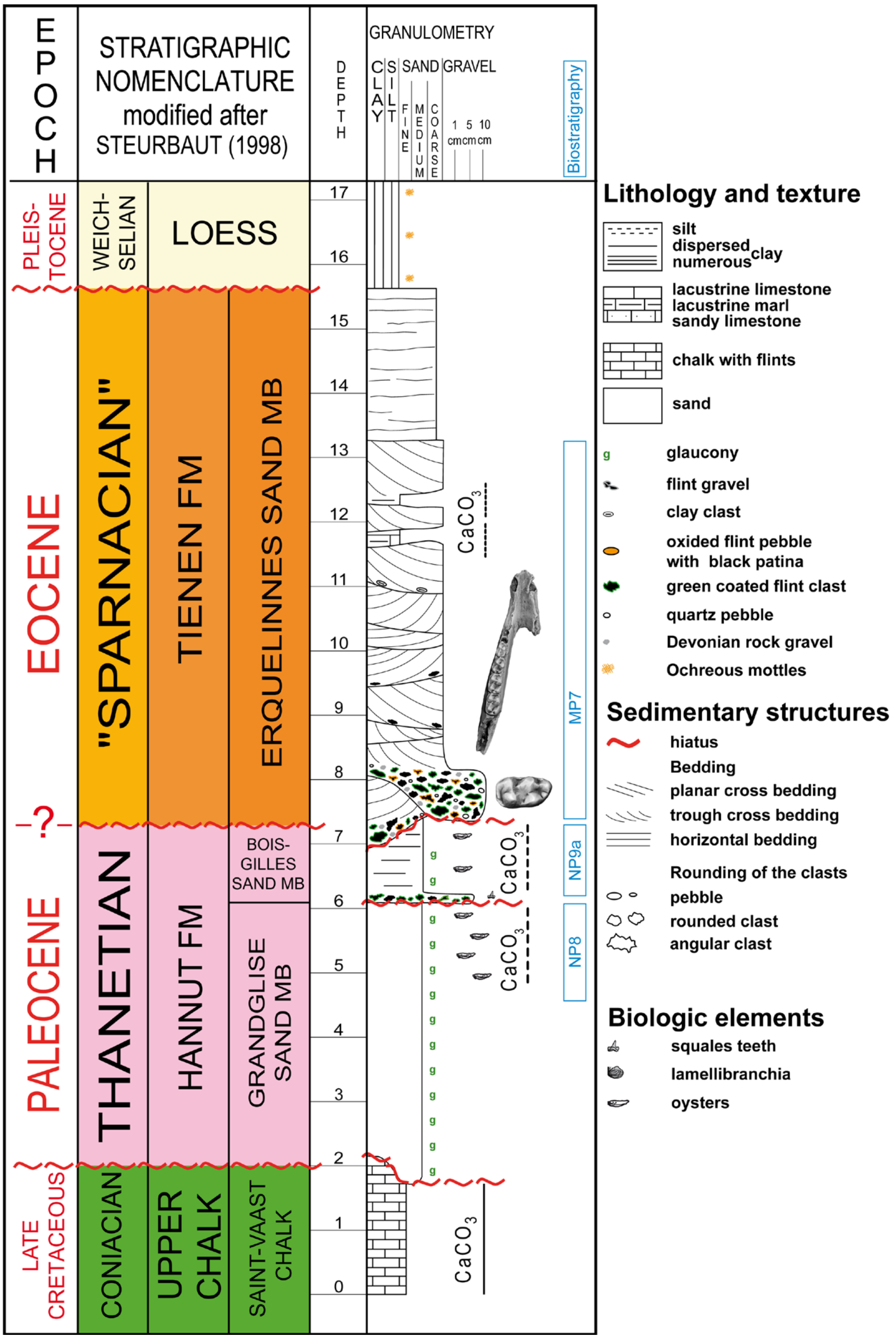

Figure 2. Geological setting of the earliest Eocene Erquelinnes mammal fauna. Log of the Erquelinnes sand quarry (modified after T point of Sigogneau-Russell & de Heinzelin, 1979). Images of the *Cymbalophus* jaw and isolated cf. *Sifrhippus* molar respectively indicate the probable origin of the *Cymbalophus* specimen found by Gravis in 1880 and of the specimens collected by Dollo in 1922.

intensively silicified (i.e. silcretes) with sometimes root or leaf casts (Quesnel, 2006). Such fluvial sediments and silcretes are also recognized in the first units of the Paris Basin "Sparnacian" Mortemer and Soissonnais Fms (Aubry et al, 2005) and of the London and Hampshire Basins Reading Beds Fm (Quesnel et al, 2009 and references therein).

The incision of these "Upper Landenian" fluvial channels may have been triggered by the latest Paleocene sea level fall (Hardenbol et al 1998), related to a significant uplift induced by the North Atlantic Igneous Province initiation (Knox, 1996). In terms of sequence stratigraphy, the "Upper Landenian" or "Sparnacian" fluvial sands filling those channels would correspond to the proximal part of the lowstand system tract. They record onland the beginning of the sea level rise and transgressive trend, further enhanced by the floodplain, swampy, lacustrine, then lagoonal facies evolution, until the open marine depositional environment setting at the beginning of the Ypresian *sensu stricto* (NP10).

Almost all mammal specimens from Erquelinnes were found in the lenticular deposits of the basal gravel bed of the Erquelinnes Sand Mb. Only the perissodactyl dentary was found in a different horizon, namely the overlying cross-bedded sands. Except for dental wear and dissociation into isolated teeth, the specimens are generally very well preserved, without clear signs of taphonomic abrasion or fracturing, and can therefore be interpreted as representing the original mammal fauna present at the time of deposition of the sediments.

4. Systematic Palaeontology

Class Mammalia Linnaeus, 1758
Cohort Placentalia Owen, 1837
Grandorder Glires Linnaeus, 1758
Order Rodentia Bowdich, 1821
Family Ischyromyidae Alston, 1876
Genus *Pseudoparamys* Michaux, 1964
Type species: *Pseudoparamys teilhardi* (Wood, 1962)

cf. *Pseudoparamys* sp.
Fig. 3 (A)

Referred specimens: IRSNB M 2119, right M^2 (L x W: 1.74 mm x 2.08 mm).

Discussion: A number of earliest Eocene Belgian rodent specimens from Dormaal and Erquelinnes were originally identified as '*Paramys lemoinei*', a species described from younger specimens from Epernay in France (Teilhard de Chardin, 1921, 1927). '*Paramys lemoinei*' as defined and used by Teilhard de Chardin has however been shown to be invalid and to contain specimens from multiple species, including most notably *Pseudoparamys teilhardi* (Wood, 1962; Michaux, 1964) Among the Erquelinnes rodent fossils, specimen IRSNB M 2119 features the distinctive near parallel and well developed protoloph and metaloph of *Pseudoparamys* (Michaux, 1964) as well as the strong mesostyle and metaconule typical of this genus (Escarguel, 1999) , but the heavy wear of the specimen precludes a more definitive identification.

Genus *Euromys* Escarguel, 1999
Type species: *Euromys thaleri* (Michaux, 1964)

***Euromys* sp.**
Fig. 3 (B-C)

Referred specimens: IRSNB M 2120, right M^1 (L x W: 2.04 mm x ca 2.41 mm); IRSNB M 2121, right M$_1$ (L x W: 2.21 mm x 1.99 mm).

Discussion: These two specimens were originally also identified as '*Paramys lemoinei*' but they display distinct cusps and weakly developed lophs. These features distinguish them from IRSNB M 2119 and other specimens of *Pseudoparamys*, but are also seen in the genus *Euromys*. IRSNB M 2120 resembles *Euromys* by the subequal paraconule and metaconule, the distinct hypocone, and the distinct lingual sinus. IRSNB M 2121 further resembles *Euromys* by the very large mesoconid and the lingually open talonid basin, by the isolation of the mesoconid and of the entoconid, and by the incipient doubling of the hypoconulid (Escarguel, 1999; Rana et al, 2008).

These Erquelinnes specimens resemble material from Dormaal identified as '*Paramys metacingularis'* and '*Paramys hemicingularis'* in their size, general shape and smooth enamel, by the development of the conules, hypocone and lingual sinus on the upper molars, and by the shape of the hypoconulid and the relative isolation of the mesoconid and entoconid on the lower molars (Quinet, 1964). These and possibly other species from Dormaal are however probably synonymous, representing a single species of *Euromys* (Escarguel, 1999). Awaiting further systematic revision of the Lower Eocene rodents from Dormaal and elsewhere, we therefore refrain from identifying the Erquelinnes specimens at the species level.

Grandorder Archonta Gregory, 1910
Order Plesiadapiformes Simons, 1972
Family Plesiadapidae Trouessart, 1897
Genus *Platychoerops* Charlesworth, 1855
Type species: *Platychoerops richardsoni* Charlesworth, 1855

***Platychoerops georgei* Hooker, 1994**
Fig. 3 (D-E)

Holotype: MNHN Try-15-L, left I^1.

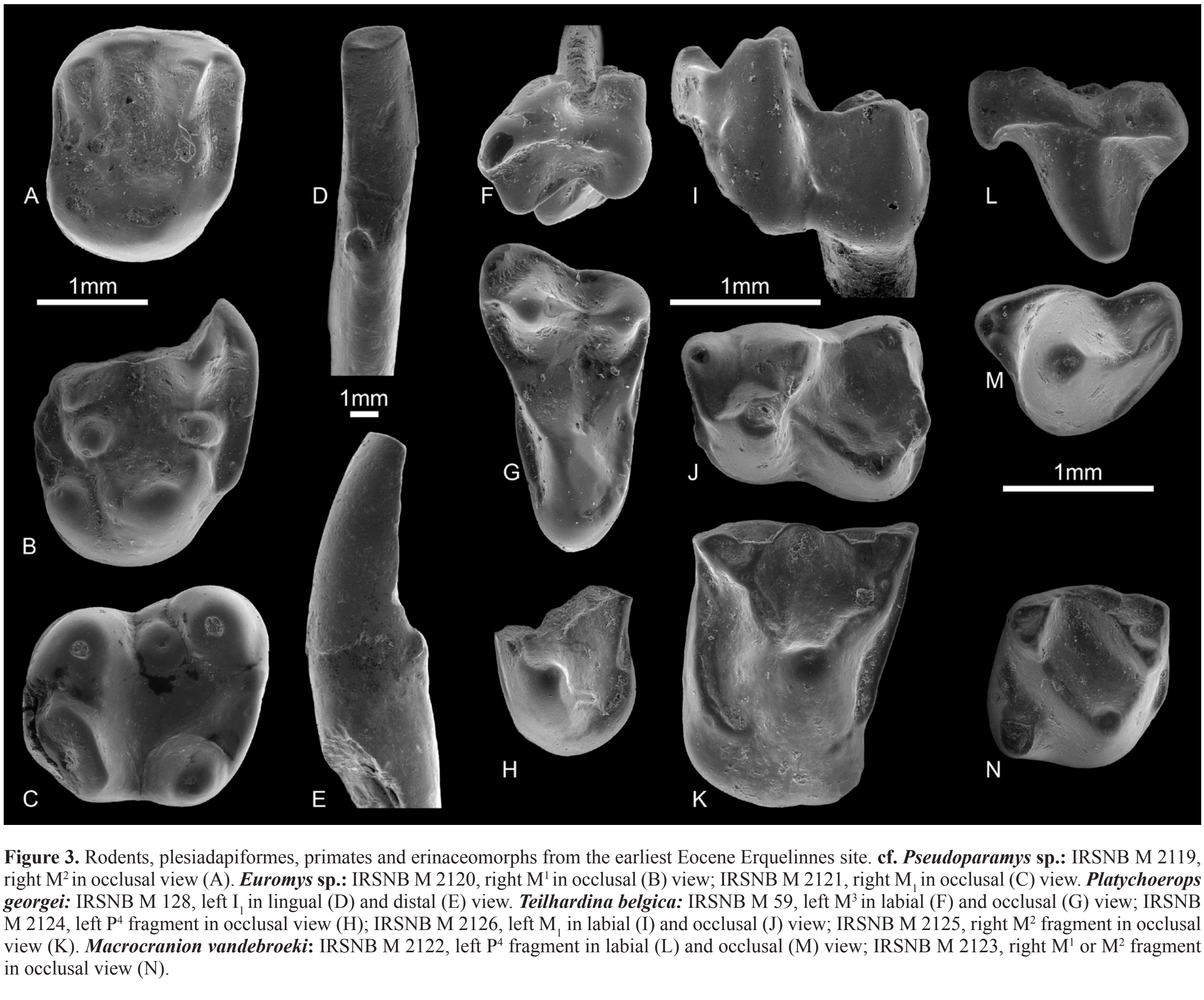

Figure 3. Rodents, plesiadapiformes, primates and erinaceomorphs from the earliest Eocene Erquelinnes site. **cf. *Pseudoparamys* sp.:** IRSNB M 2119, right M^2 in occlusal view (A). ***Euromys* sp.:** IRSNB M 2120, right M^1 in occlusal (B) view; IRSNB M 2121, right M$_1$ in occlusal (C) view. ***Platychoerops georgei:*** IRSNB M 128, left I$_1$ in lingual (D) and distal (E) view. ***Teilhardina belgica:*** IRSNB M 59, left M^3 in labial (F) and occlusal (G) view; IRSNB M 2124, left P^4 fragment in occlusal view (H); IRSNB M 2126, left M$_1$ in labial (I) and occlusal (J) view; IRSNB M 2125, right M^2 fragment in occlusal view (K). ***Macrocranion vandebroeki*:** IRSNB M 2122, left P^4 fragment in labial (L) and occlusal (M) view; IRSNB M 2123, right M^1 or M^2 fragment in occlusal view (N).

Type horizon and locality: earliest Eocene Marnes de Dormans, Try, France.

Referred specimen: IRSNB M 128, left I_1 (L: 2.79 mm, Depth: 4.56mm).

Discussion: This specimen was first identified and illustrated as *Plesiadapis* sp. (Teilhard de Chardin, 1927), but was later reassigned to *Platychoerops georgei*, together with other isolated earliest Eocene specimens found at Try, Sufffolk Pebble Beds and Dormaal (Hooker, 1994, 1996). In their description of a new Upper Paleocene species of *Platychoerops*, Boyer et al. (2012) suggested that *P. georgei* might represent a chimera of at least two different plesiadapid taxa. They notably questioned the affinities of the isolated upper first incisors identified as *P. georgei*, including also the name-bearing type specimen. The taxonomy of these plesiadapid specimens from the earliest Eocene of Europe is clearly in need of a detailed study. Such a task is however beyond the scope of this study of the Erquelinnes mammal fossils, and awaiting this we conservatively continue to identify this lower plesiadapid incisor from Erquelinnes as *Platychoerops georgei*.
A second specimen from Erquelinnes identified as '*Plesiadapis* or *Paramys*' (Teilhard de Chardin, 1927, p.27) seems to be missing from the collection, but given its very small size, it more likely belonged to a rodent than to a plesiadapid

Order Primates Linnaeus, 1758
Family Omomyidae (Trouessart, 1897)
Genus *Teilhardina* Simpson, 1940
Type species: *Teilhardina belgica* (Teilhard de Chardin, 1927)

***Teilhardina belgica* (Teilhard de Chardin, 1927)**
Fig. 3 (F-K)

Lectotype: IRSNB M 64, left dentary with P_3-M_3.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimens: IRSNB M 59, left M^3 (paralectotype, L x W: 1.14 mm x 2.05 mm); IRSNB M 2124, left P^4 fragment; IRSNB M 2125, right M^2 fragment; IRSNB M 2126, left M_1 (L x W: 1.65 mm x 1.24 mm).

Discussion: This small, primitive omomyid is a marker species for the earliest Eocene of Europe (Smith et al, 2006), and was first described from the Belgian Dormaal and Erquelinnes sites (Teilhard de Chardin, 1927). Teilhard de Chardin (1927) did not select a type specimen, making all his illustrated specimens the syntypes of the new taxon. He however failed to mention that the left upper last molar in his type series, IRSNB M 59, originated from Erquelinnes rather than from Dormaal like all other syntypes. It was only later, when Szalay (1976) selected IRSNB M 64 as his lectotype and IRSNB M 59 became a paralectotype that Dormaal truly became the unambiguous type locality of *T. belgica*. No significant morphological differences exist between the Erquelinnes specimens and the Dormaal ones. This is especially the case for the M_1 that is exactly at the same evolutive stage than that of the holotype of *Teilhardina belgica* (Smith et al, 2006).

Grandorder Lipotyphla Haeckel, 1866
Order Erinaceomorpha Gregory, 1910
Family Amphilemuridae Hill, 1953
Genus *Macrocranion* Weitzel, 1949
Type species: *Macrocranion tupaiodon* Weitzel, 1949

***Macrocranion vandebroeki* (Quinet, 1964)**
Fig. 3 (L-N)

Holotype: IRSNB M 66, left dentary with P_4 in place.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimens: IRSNB M 2122, left P^4 fragment (L: 1.41 mm); IRSNB M 2123, right M^1 or M^2 fragment.

Discussion: Both dental fragments were previously unlabelled, but they very closely match the morphology of the primitive erinaceomorph *Macrocranion* common in early Eocene mammal sites. In size these specimens only match *M. vandebroeki* from Dormaal and *M . junnei* from the Bighorn Basin in Wyoming (Smith & Smith, 1995; Smith et al, 2002). Morphologically, the P^4 from Erquelinnes differs from *M. junnei* and resembles *M. vandebroeki* by the more anteriorly projecting parastyle and the stronger metastylar lobe, so we identify both specimens as *M. vandebroeki*. IRSNB M 2122 is somewhat smaller than average for this taxon and IRSNB M 2123 has a rather rounded posterolingual border, but both specimens fall well within the normal size and morphological range of variation seen in *M. vandebroeki* from Dormaal.

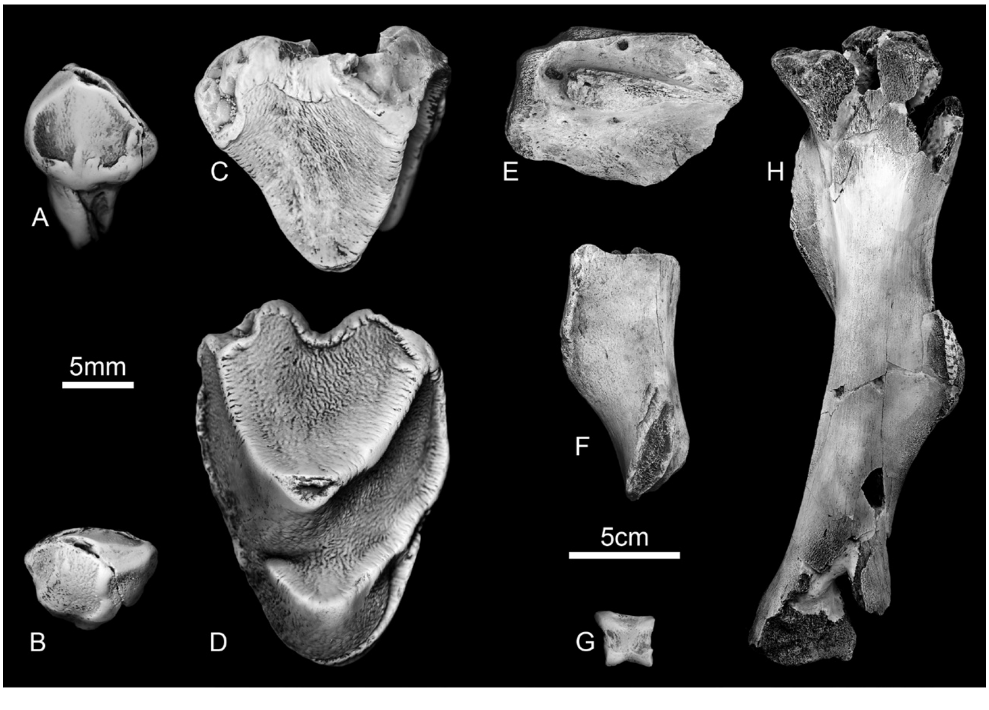

Figure 4. ***Coryphodon eocaenus*** from the earliest Eocene Erquelinnes site. IRSNB M 2127, left $I^{3?}$ in labial (A) and occlusal (B) view; IRSNB M 2128, left $P^{3?}$ in labial (C) and occlusal (D) view; IRSNB M 2130, left scapula fragment in dorsal view (E); IRSNB M 2131, left humerus fragment in anterior view (F); IRSNB M 2132, phalanx in dorsal view (G); IRSNB M 132: Juvenile left femur in anterior view (H).

Grandorder Ferae Linnaeus, 1758
Order Pantodonta Cope, 1873
Family Coryphodontidae Marsh, 1876
Genus *Coryphodon* Owen, 1845
Type species: *Coryphodon eocaenus* Owen, 1845

***Coryphodon eocaenus* Owen, 1845**
Fig. 4

Holotype: BMNH M27848, right dentary with damaged M_2 and M_3.

Type horizon and locality: Early Eocene Harwich Fm, dredged offshore between Harwich and St Osyth's, Essex, England.

Referred specimens: IRSNB M 132: Juvenile left femur (L x W: ca 29 cm x ca 10 cm); IRSNB M 2127, left $I^{3?}$ (L x W: 9.25 mm x 6.78 mm); IRSNB M 2128, left $P^{3?}$; IRSNB M 2129, left P_x fragment; IRSNB M 2130, left scapula fragment, glenoid portion; IRSNB M 2131, left humerus, distal fragment; IRSNB M 2132, phalanx (L x W: 25 mm x 28 mm).

Discussion: The presence of *Coryphodon* in the Erquelinnes fauna was first noted by Dollo (1909), and Teilhard de Chardin (1927) mentioned three specimens, illustrating only the juvenile *Coryphodon* femur IRSNB M 132. In total, six specimens in the Erquelinnes collection are assigned to *Coryphodon* mainly based on size, but only the juvenile femur and an isolated upper premolar can be more positively identified. The femur lacks all articular epiphyses, typical of a juvenile individual, but its general shape closely matches that of other femora assigned to *Coryphodon* (Cope, 1884). The general shape of IRSNB M 2128 is typical of a *Coryphodon* upper premolar, most probably a P^3 based on the development of the protocone and lingual cingula. It lacks the open stylar shelf of *C. oweni* and best matches the size of *C. eocaenus*, being larger than *C. oweni* and smaller than *C. anthracoideus*. Hooker (2010) synonymized *C. anthracoideus* with *C. eocaenus* finding no significant differences between both forms, but even regardless his results, we uphold Dollo's original identification of the Erquelinnes pantodont specimens as *C. eocaenus* (Dollo, 1909).

Order Hyaenodontida Leidy, 1869
Family Hyaenodontidae Van Valen, 1967
Genus *Arfia* Van Valen, 1965
Type species: *Arfia opistothoma* (Matthew, 1901)

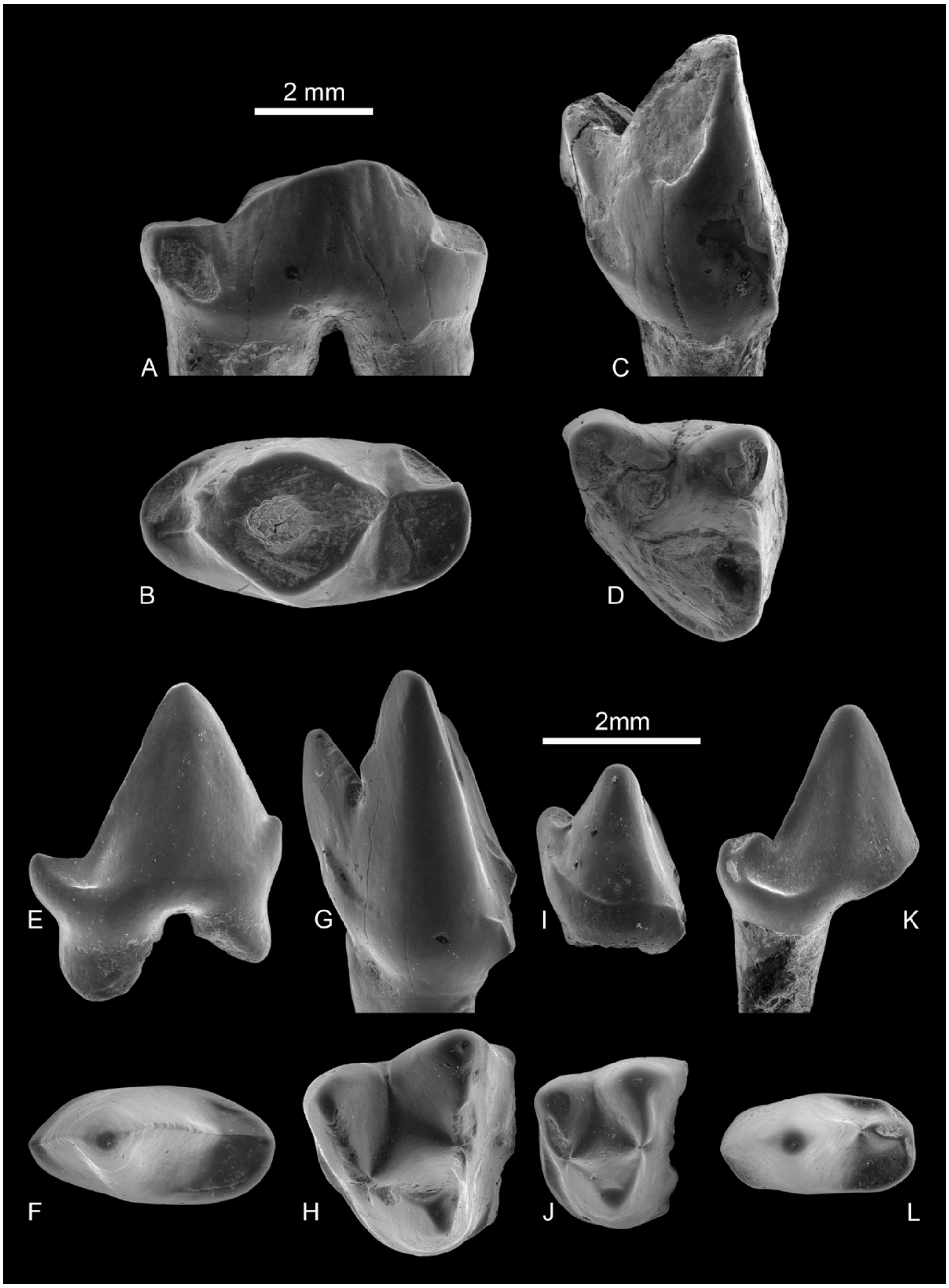

Figure 5. Hyaenodontidans and carnivoramorphans from the earliest Eocene Erquelinnes site. ***Arfia gingerichi:*** IRSNB M 2133, right P_4 in labial (A) and occlusal (B) view; IRSNB M 2134, left M_3 trigonid labial (C) and occlusal (D) view. ***Miacis latouri:*** IRSNB M 2135, right P_3 in labial (E) and occlusal (F) view; IRSNB M 2137, left M_1 trigonid in labial (G) and occlusal (H) view; IRSNB M 2138, left M_2 trigonid in labial (I) and occlusal (J) view. ***Gracilocyon solei:*** IRNSB M 1327, right P_4 in labial (K) and occlusal (L) view.

Arfia gingerichi **Smith and Smith, 2001**
Fig. 5 (A-D)

Holotype: IRSNB M 1275, right M_3.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimens: IRSNB M 2133, right P_4 (=Eq2 of Smith & Smith, 2001; L x W: 5.76 mm x 2.93 mm); IRSNB M 2134, left M_3 trigonid (=Eq1 of Smith & Smith, 2001; Trigonid L x W: 4.08 mm x 3.72 mm).

Discussion: In their description of *A. gingerichi* from Dormaal, Smith and Smith (2001) also referred a P_4 and an M_3 trigonid from Erquelinnes to their new species. Both specimens showing a crenulated enamel are worn and imperfectly preserved, and do not add to the knowledge of *A. gingerichi*, except showing its presence at Erquelinnes.

Order Carnivora Bowdich, 1821
Family 'Miacidae' Cope, 1880
Genus *Dormaalocyon* Solé et al, 2013
Type species: *Dormaalocyon latouri* (Quinet, 1966)

Dormaalocyon latouri **(Quinet, 1966)**
Fig. 5 (E-J)

Holotype: IRNSB M 1360, left M^1.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimens: IRSNB M 2135, right P_3 (L x W: 3.19 mm x 1.55 mm); IRSNB M 2136, left P_3 (L x W: 3.05 mm x 1.52 mm); IRSNB M 2137, left M_1 trigonid (Trigonid L x W: 2.55 mm x 2.70 mm); IRSNB M 2138, left M_2 trigonid (Trigonid L x W: 1.73 mm x 2.15 mm).

Discussion: '*Miacis' latouri*, one of the earliest miacids, was first described from Dormaal where it is abundantly present. The morphological and size variability of this taxon is now known in great detail allowing to refer it to the new genus *Dormaalocyon* (Solé et al, 2013). Four specimens from Erquelinnes can also unambiguously be assigned to this species, resembling the Dormaal specimens in size, in the small paraconid and simple talonid of P_3, in the development of the anterolabial cingulum of the lower molars, in the height of the M_1 trigonid cusps, and in the uncompressed M_2 trigonid with distinct cusps.

Genus *Gracilocyon* Smith and Smith, 2010
Type species: *Gracilocyon winkleri* (Gingerich, 1983)

Gracilocyon solei **Smith and Smith, 2010**
Fig. 5 (K-L)

Holotype: IRNSB M 1327, left M^1.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimen: IRSNB M 2139, right P_4 (=Eq18 of Smith & Smith, 2010; W:1.34 mm).

Discussion: IRSNB M 2139 is a very small, transversely P_4 with a high protoconid and remnants an accessory posterior cusp on the talonid, and by these characters it can be identified as belonging to *G. solei,* a diminutive species of miacid carnivorans described from Dormaal (Smith & Smith, 2010).

Grandorder 'Ungulata' Linnaeus, 1758
Order Procreodi Matthew, 1915
Family Arctocyonidae Giebel, 1855
Genus *Landenodon* Quinet, 1966
Type species: *Landenodon woutersi* Quinet, 1966

Landenodon woutersi **Quinet, 1966**
Fig. 6 (A-D)

Holotype: IRSNB M 1345, left dentary with P_4-M_3.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimens: IRSNB M 2140, left DP_4 talonid (Talonid L x W: 1.94 mm x 2.19 mm); IRSNB M 2141, left M_1 trigonid (Trigonid L x W: 2.51 mm x 2.64 mm).

Discussion: *Landenodon woutersi* is one of the most abundant relatively large taxa in the Dormaal fauna. Two partial teeth from Erquelinnes can also be attributed to *L. woutersi*, resembling the specimens reported by Quinet (1966) and Godinot (1980) in size, in the long and narrow, relatively high cusped talonid of the DP_4 specimen, and in the clear labial cingulum and the high, anterior paraconid separated from the metaconid by a distinct groove of the M1 specimen.

Order Acreodi Matthew, 1903
Family Mesonychidae Cope, 1875
Genus *Dissacus* Cope, 1881a
Type species: *Dissacus navajovius* Cope, 1881

Dissacus europaeus **Lemoine, 1891**
Fig. 6 (E-F)

Holotype: MNHN CRL982, right dentary, reconstructed as having P_4-M_3 in place.

Type horizon and locality: Late Paleocene, 'Conglomérat de Cernay', Cernay-lès-Reims, France.

Referred specimen: IRSNB M 2142, left $M_{1?}$ (L x W: 9.55 mm x 4.25 mm).

Discussion: This specimen from Erquelinnes was originally identified as '*Hyaeonodictis'* (Dollo, 1909) and later reidentified as '*Dissacus* sp.', but erroneously noted as found in Dormaal (Teilhard de Chardin, 1921). IRSNB M 2142 is smaller than *D. europaeus* specimens from the Late Paleocene of Cernay and Berru, but similar in size to *D.* cf. *europaeus* reported from the Early Eocene of Palette (Godinot et al., 1987). Overall though, the size range of these Upper Paleocene and Lower Eocene *Dissacus* specimens is not unacceptably large for their inclusion in a single species. A number of morphological differences was noted between *D. europaeus* and *D.* cf. *europaeus* (Godinot et al., 1987), but P_2 height and development of diastemata are difficult to reliably asses from the Palette specimen, while all other differences can be seen to be highly variable in the *D. europaeus* specimens from Cernay and Berru (see also Russell, 1964). In the absence of clear morphological distinctions, we consider all these specimens to represent a single species *D. europaeus*. We do however note that the two known Lower Eocene specimens are about 13% smaller than the Upper Paleocene specimens, a pattern reminiscent of the dwarfing of mammal species observed in North America during the PETM period (Gingerich, 2006).

Order 'Condylarthra' Cope, 1881
Family Louisinidae Sudre and Russell, 1982
Genus *Paschatherium* Russell, 1964
Type species: *Paschatherium dolloi* (Teilhard de Chardin, 1927)

Paschatherium **cf.** ***yvettae*** **Gheerbrant, Abrial and Cuenca, 1997**
Fig. 6 (I-T)

Referred specimens: IRSNB M 2144, right P^4 fragment (L: 1.70 mm); IRSNB M 2145, right M^1 (L x W: 1.67 mm x 2.11 mm); IRSNB M 2146, right P_4 (L x W: 1.76mm x 1.09 mm); IRSNB M 2147, right P_4 (L x W: 1.77 mm x ca 0.94 mm); IRSNB M 2148, right M_1 (L x W: 1.65 mm x 1.18 mm); IRSNB M 2149: worn and broken left M_2 (L x W: ca 1.78mm x 1.63mm).

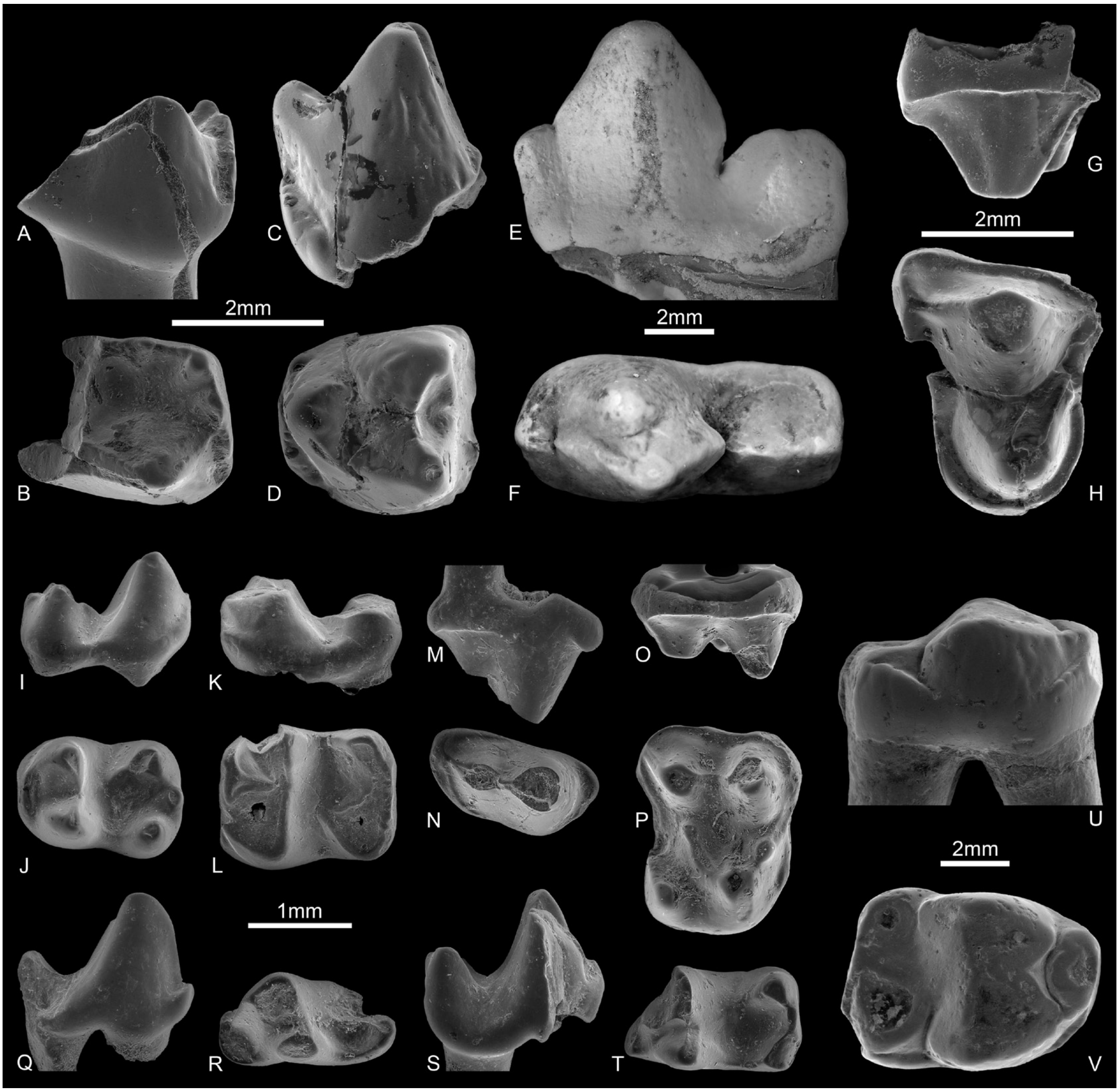

Figure 6. Primitive ungulates and artiodactyls from the earliest Eocene Erquelinnes site. ***Landenodon woutersi:*** IRSNB M 2140, left DP_4 talonid in labial (A) and occlusal (B) view; IRSNB M 2141, left M_1 trigonid in labial (C) and occlusal (D) view. ***Dissacus europaeus:*** IRSNB M 2142, left $M_{1?}$ in labial (E) and occlusal (F) view. ***Diacodexis gigasei:*** IRSNB M 2143, right P^4 in labial (G) and occlusal (H) view. ***Paschatherium* cf. *yvettae:*** IRSNB M 2148, right M_1 in labial (I) and occlusal (J) view; IRSNB M 2149, left M_2 in labial (K) and occlusal (L) view; IRSNB M 2144, right P^4 fragment in labial (M) and occlusal (N) view; IRSNB M 2145, right M^1 in labial (O) and occlusal (P) view; IRSNB M 2147, right P_4 in labial (Q) and occlusal (R) view; IRSNB M 2146, right P_4 in labial (S) and occlusal (T) view. ***Phenacodus teilhardi:*** IRSNB M 129, right P_4 in labial (U) and occlusal (V) view.

Discussion: *Paschatherium* is a very abundant taxon in European mammal sites around the Paleocene-Eocene Boundary, and it is also the most abundant small taxon in the collection from Erquelinnes. The *Paschatherium* specimens from Erquelinnes seem to be markedly smaller in size and less bunodont than most *P. dolloi* specimens from Dormaal, in both aspects closer to the much more rare *P. yvettae* specimens reported from Dormaal (Lopez-Martinez et al., 2006). The *P. dolloi* specimens from Dormaal, however, vary considerably in size and degree of bunodonty, making the distinction between both forms rather ambiguous. Lopez-Martinez et al. (2006) further characterised *P. yvettae* as having an M_2 that is markedly wider transversely than the M_1. The two *Paschatherium* lower molars from Erquelinnes reported here do display this difference in width, but the quantity and quality of our specimens would make any interpretation highly speculative. In the original description from the Cernaysian of Campo, *P. yvettae* was characterised as having a distinct premetacristid on the lower molars and an upper molar paracone that is markedly larger than the metacone (Gheerbrant et al., 1997). Of these traits, only the latter is to some degree present in the *Paschatherium* material from Erquelinnes. Although the specimens from Erquelinnes most closely resemble *P. yvettae* we here identify them as *P.* cf. *yvettae,* indicating the difficulty to unambiguously separate them from specimens of *P. dolloi* and the absence of at least one trait originally considered diagnostic of *P. yvettae*.

Family Phenacodontidae Cope, 1881
Genus *Phenacodus* Cope, 1873
Type species: *Phenacodus primaevus* Cope, 1873

Phenacodus teilhardi **Simpson, 1929**
Fig. 6 (U-V)

Lectotype: IRSNB M 88, right M_1 or M_2.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimen: IRSNB M 129, right P_4 (L x W: 7.98 mm x 5.62 mm).

Discussion: Originally identified as a lower molar of *Arctocyonides*? (Teilhard de Chardin, 1927), this specimen distinctly differs from arctocyonids by the transversely wider shape and submolariform trigonid. Instead, the limited bunodonty, the distinct anterolabial cingulum and paraconid and the wide talonid basin with a small entoconid is typical of the mostly North American condylarth genus *Phenacodus* (Thewissen, 1990). Among North American forms, IRSNB M 129 is similar in size to *P. vortmani* and *P. bisonensis*, but differs from these forms by the shorter, more rounded trigonid and the wider talonid with a distinct entoconid. Only three European phenacodontids are known, *P. teilhardi*, *P. lemoinei* and *P. condali*, of which *P. teilhardi* from Dormaal is the oldest and smallest (Thewissen, 1990). IRSNB M 129 from Erquelinnes compares favorably with *P. teilhardi* from Dormaal by its size and morphology, resembling the Dormaal specimens by the crenulated enamel, the anteroposteriorly short shape and the rounded anterior side of the trigonid. We therefore identify IRSNB M 129 as *P. teilhardi*, making it the first P_4 known for this species.

Order Artiodactyla Owen, 1848
Family Diacodexeidae Krishtalka and Stucky, 1985
Genus *Diacodexis* Cope, 1882
Type species: *Diacodexis secans* (Cope, 1881)

***Diacodexis gigasei* Smith, Smith and Sudre, 1996**
Fig. 6 (G-H)

Holotype: IRSNB M 1815: Right M_2.

Type horizon and locality: earliest Eocene Dormaal Mb of the Tienen Fm, Dormaal, Belgium.

Referred specimen: IRSNB M 2143, right P^4 (L x W: ca 2.91 mm x 3.59 mm).

Discussion: Although this specimen was originally labeled as '? *Plesiadapis'* by Teilhard de Chardin in the RBINS collection, the proportions and morphology of this specimen differ markedly from *Plesiadapis* specimens. Instead, the length-width ratio and the development of the cusps and a complete pericingulum very closely matches that of the primitive artiodactyl *Diacodexis*

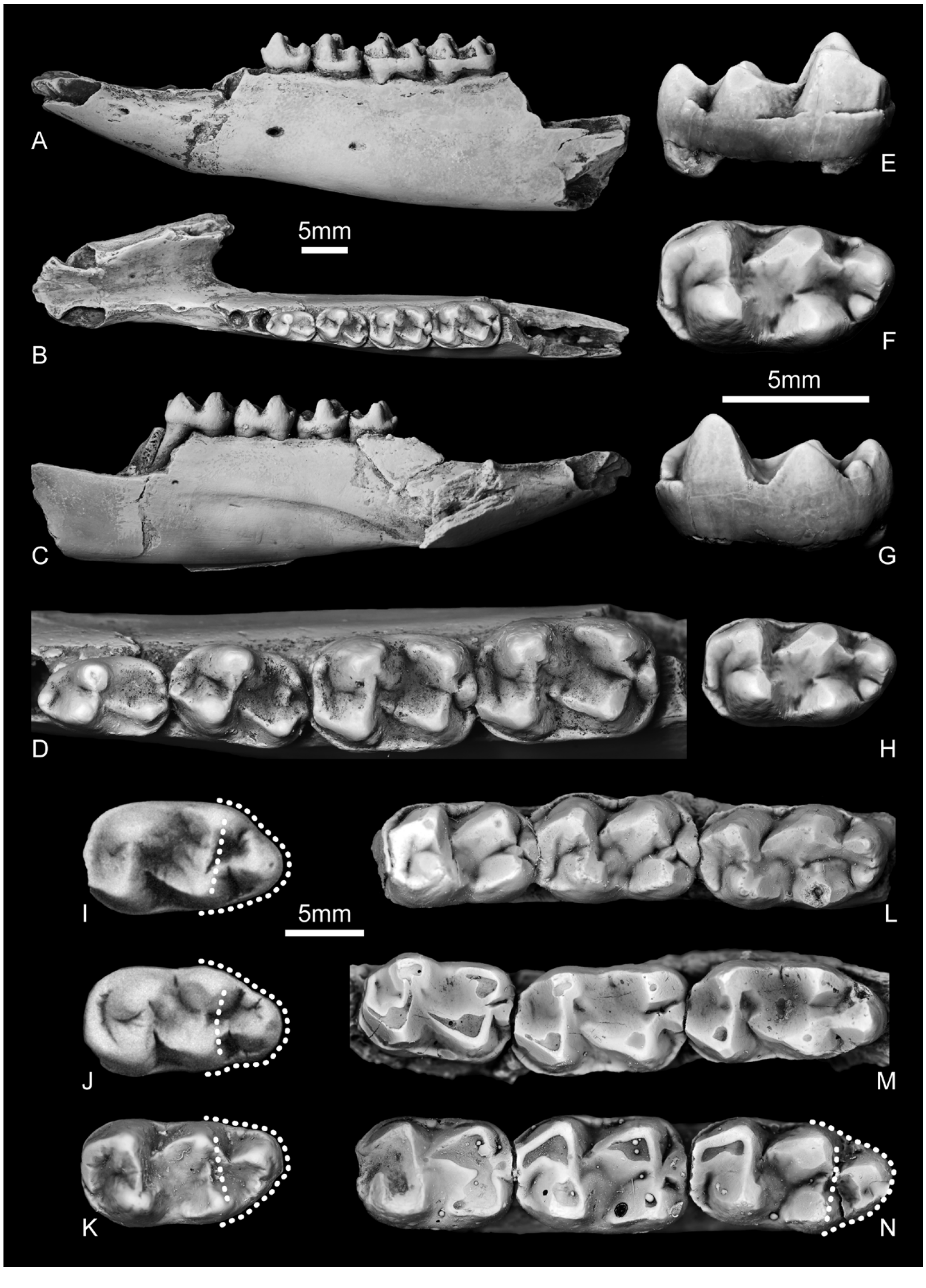

Figure 7. Perissodactyls from the earliest Eocene Erquelinnes site and comparative specimens. ***Cymbalophus cuniculus:*** IRSNB M 167, left dentary with P_3-M_2 in place in labial (A), occlusal (B, D) and lingual (C) view. **cf. *Sifrhippus sandrae:*** IRSNB M 130, right M_3 in labial (E), occlusal (F,H), lingual (G) view. ***Cymbalophus cuniculus:*** BMNH M14113, left M_3 (I); IM 1951.28.25, left M_3 (J); BMNH M29710, right M_3 (K). ***Sifrhippus sandrae:*** UM 83567 (holotype), right M_{1-3} (L); UM 83459, left M_{1-3} (M). ***Cymbalophus cuniculus:*** BMNH M36494, right M_{1-3} (N). I-N all in occlusal view, images I and J modified from Hooker (1984). Note the characteristic development of a hypolophid crest and M_3 hypoconulid lobe in *Cymbalophus*, which is absent or indistinct in *Sifrhippus*.

gigasei from Dormaal (Smith et al, 1996), to which we also assign this specimen.

Order Perissodactyla OWEN, 1848
Family Isectolophidae Peterson, 1919
Genus *Cymbalophus* Hooker, 1984
Type species: *Cymbalophus cuniculus* (Owen, 1842)

***Cymbalophus cuniculus* (Owen, 1842)**
Fig. 7 (A-D)

Lectotype: BMNH M36569, left M^3.

Type horizon and locality: Lower Eocene Suffolk Pebble Beds, Kyson, England.

Referred specimen: IRSNB M 167, left dentary with P_3-M_2 in place (L x W, P_3: 5.43 mm x 3.24 mm, P4: 5.95 mm x 4.08 mm, M1: 6.79 mm x 4.95 mm, M2: 7.53 mm x 5.21 mm).

Discussion: This is the original specimen reported in 1881 by Rutot, and represents one of the oldest, most complete and best preserved Lower Eocene perissodactyl specimens from Europe. In recent studies, it is conventionally referred to *Cymbalophus cuniculus* known from the Lower Eocene Suffolk Pebble Beds (e.g. Hooker, 1984; Froehlich, 2002) and our detailed comparison with *C. cuniculus* illustrations and casts [Fig. 7 (I-K,N] shows no morphological differences, so we support this identification. The Suffolk Pebble Beds are distinctly younger than the Erquelinnes Sand Mb, but the mammal specimens found in them were most probably reworked from basal Eocene deposits (Hester's Brown Sands) much closer in age to the Erquelinnes specimens (Hooker, 1996).

This specimen is the only known *Cymbalophus* specimen where the anterior portion of the jaw is preserved, and yielded the only unambiguously identified premolars (Hooker, 1984). The jaw of *C. cuniculus* is characterised by three small incisors and a distinct canine on both sides, by diastemata behind both the canine and the reduced first premolar, and by a relatively long, unconstricted symphysis. Based on its alveoli, the second premolar was not much smaller than P_3. The third premolar has a small paraconid and a well-developed protoconid and metaconid. The last premolar has a fully developed trigonid, and a talonid with a strong hypoconid, a conspicuous hypolophid and entoconid, and a small hypoconulid. Additionally, the unworn molars of this specimen present a clearly twinned metaconid and appear less lophodont than the more worn specimens known from the Suffolk Pebble Beds.

Nevertheless, this well-published specimen (Rutot, 1881; Teilhard de Chardin, 1921; Quinet & Verlinden, 1970; Hooker, 1984) has been underappreciated in recent phylogenetic studies (Froehlich, 2002; Danilo et al, 2013). Most notably perhaps, one analysis grouped *C. cuniculus* with the basal tapiromorph *Systemodon tapirinum*, noting that "*Cymbalophus* can be distinguished from *Systemodon* only on size and geography"(Froehlich, 2002: p.184). The *C. cuniculus* jaw from Erquelinnes however clearly differs from *Systemodon* by the shape of the mandibular symphysis, by the anterior diastemata, and by the molarisation of $P_{3\text{-}4}$. All of these features are readily observed on IRSNB M 167, and should be taken into account in future morphological or cladistic analyses of perissodactyl phylogeny.

Family Equidae
Genus *Sifrhippus* Froehlich, 2002
Type species: *Sifrhippus sandrae* (Gingerich, 1989)

cf. *Sifrhippus sandrae* (Gingerich, 1989)
Fig. 7 (E-H)

Referred specimen: IRSNB M 130, right M_3 (L x W: 8.06 mm x 4.53 mm).

Discussion: This isolated M_3 was referred to a primitive hyracotheriid (Teilhard de Chardin, 1927) and has often been implicitly assumed to belong to the same species as the lower jaw found at Erquelinnes (Simpson, 1929). However, originally this specimen had been attributed to the condylarth *Ectocion* (Teilhard de Chardin, 1925), and in his later study Teilhard de Chardin explicitly noted that it could be more primitive than even '*Hyracotherium' cuniculus*, based on the reduced paraconid, the paralophid running towards the metaconid, the twinned hypoconulid and the complete absence of a hypolophid (Teilhard de Chardin, 1927, p. 28). IRSNB M 130 further differs from the M_3 of *Cymbalophus* by a slightly smaller size and by a smaller, less posteriorly projecting hypoconulid lobe. All of these features, and especially the weak to absent hypolophid are however typical of the *Sifrhippus* (*Hyracotherium*) *sandrae*, a primitive hippomorph perissodactyl from the earliest Eocene of North America (Gingerich, 1989). *Sifrhippus sandrae* specimens occupy a distinct morphological range of variation [Fig. 7 (L-M)] from which we find IRSNB M 130 to be indistinguishable, but that is clearly distinct from that of *Cymbalophus* based on the development of the hypolophid and hypoconulid lobe. Nevertheless, taking into account the limitations involved in identifying a single isolated specimen, we conservatively identify IRSNB M 130 here as cf. *Sifrhippus sandrae*.

5. Discussion

The last comprehensive study of the Erquelinnes mammal fauna was published in 1927, and the last faunal list in 1929 (Teilhard de Chardin, 1927; Simpson, 1929). The present paper provides a detailed overview and illustration of all identifiable specimens from Erquelinnes, as well as an updated faunal list (Table 1). It identifies 16 fossil mammal species, doubling the published taxonomic diversity. Many of the published taxa are identified more precisely, and the Erquelinnes fossil fauna is shown to also include erinaceomorphs, hyaenodontids, mesonychids, louisinids, equids and diacodexeid artiodactyls.

The most interesting result of this paper is probably the identification of two distinct perissodactyl species at Erquelinnes. The alleged ceratomorph *Cymbalophus cuniculus* has long been known to be present at Erquelinnes represented by a beautifully preserved jaw (Hooker, 1984; Froehlich, 2002; Danilo et al., 2013). This study however shows that the isolated M_3 IRSNB M 130 represents a different, smaller and less lophodont taxon, closely similar to primitive equids from the earliest Eocene of North America. It is identified here as cf. *Sifrhippus sandrae* and currently represents the only hippomorph known from the earliest Eocene of Europe. Because this taxon is only known from a single specimen, we refrain from giving it a definitive, species-level identification, but regardless of that its affinities are clear. Phylogenetically, it represents the oldest hippomorph from Europe and might be close to the origin of European hippomorphs such as pachynolophs and palaeotheres (Froehlich, 1999; Danilo et al., 2013). Biogeographically, the specimen indicates faunal exchange between Europe and North America at the base of the Eocene, reinforcing a pattern of earliest Eocene mammal genera present on both continents to which perissodactyls seemed to form an exception (Smith & Smith, 1994, 2001, 2010; Smith et al., 1999, 2002, 2006)

It is also noteworthy that the *Cymbalophus* jaw from Erquelinnes is the only mammal specimen from the cross-bedded sands of the Erquelinnes Sand Mb (Rutot, 1881). This makes the *Cymbalophus* jaw ever so slightly younger than the cf. *Sifrhippus* molar from the basal gravel beds, which seems consistent with their difference in size and lophodonty. On the other hand, the age difference between both levels might be extremely short, making it irrelevant even during a period of rapid morphological and faunal evolution.

Next to the perissodactyl results on Erquelinnes, this work also shows the presence of a potentially dwarfed form of *Dissacus europaeus*, the first P_4 known for *Phenacodus teilhardi* and the surprising absence of *Paschatherium dolloi* and presence of *P.* cf. *yvettae* in the site. All of these results represent potentially meaningful data points for future systematic, biochronologic and biogeographic studies of European early Eocene mammals.

Of the 16 identified species, 12 taxa are also present in the nearby and much better sampled earliest Eocene Dormaal fauna, chosen as the international reference level for the earliest Eocene

- Grandorder Glires
  - Order Rodentia
    - Family Ischyromyidae
      - **cf. *Pseudoparamys* sp.**
      - ***Euromys* sp.**
- Grandorder Archonta
  - Order Plesiadapiformes
    - Family Plesiadapidae
      - ***Platychoerops georgei***
  - Order Primates
    - Family Omomyidae
      - ***Teilhardina belgica***
- Grandorder Lipotyphla
  - Order Erinaceomorpha
    - Family Amphilemuridae
      - ***Macrocranion vandebroeki***
- Grandorder Ferae
  - Order Pantodonta
    - Family Coryphodontidae
      - ***Coryphodon eocaenus***
  - Order Creodonta
    - Family Hyaenodontidae
      - ***Arfia gingerichi***
  - Order Carnivora
    - Family "Miacidae"
      - ***Dormaalocyon latouri***
      - ***Gracilocyon solei***
- Grandorder "Ungulata"
  - Order Procreodi
    - Family Arctocyonidae
      - ***Landenodon woutersi***
  - Order Acreodi
    - Family Mesonychidae
      - ***Dissacus europaeus***
  - Order "Condylarthra"
    - Family Louisinidae
      - ***Paschatherium* cf. *yvettae***
    - Family Phenacodontidae
      - ***Phenacodus teilhardi***
  - Order Artiodactyla
    - Family Diacodexeidae
      - ***Diacodexis gigasei***
  - Order Perissodactyla
    - Family "Isectolophidae"
      - ***Cymbalophus cuniculus***
    - Family Equidae
      - **cf. *Sifrippus sandrae***

Table 1. Overview table of the earliest Eocene Erquelinnes mammal fauna.

of Europe (MP7 in Schmidt-Kittler, 1987, Smith, 1999). The four remaining taxa are known from other early Eocene sites. *Dissacus europaeus*, *Cymbalophus cuniculus* and cf. *Sifrhippus sandrae* have been reported from Palette, Suffolk Pebble Beds and the Bighorn Basin respectively (Hooker, 1984; Godinot et al., 1987; Gingerich, 1989), whereas *Coryphodon eocaenus* was found in several sites in both Europe and North America (see Hooker, 2010). Consequently, the present study confirms the suggested earliest Eocene age of the Erquelinnes mammal fauna, and the distinctiveness of the earliest Eocene MP7 reference-level and PEI biozone (Schmidt-Kittler, 1987; Hooker, 1996; Smith, 1999). Faunal differences between Erquelinnes and Dormaal conspicuously involve the larger species present in Erquelinnes, whereas larger bodied forms are rare to absent in the Dormaal fauna. These differences clearly result from a strong bias towards small and medium sizes at Dormaal (Smith, 1999). This could be due to the different velocity of the rivers which deposited the fossiliferous channel lags at Dormaal and Erquelinnes, although depositional environments may have been rather similar (probably braided rivers). However, given that *Cymbalophus* and cf. *Sifrhippus* are comparable or slightly smaller in size than *Phenacodus teilhardi*, which is rare but present at Dormaal, different river velocities alone may not fully explain the faunal differences with Dormaal, and we cannot exclude the possibility of small differences in local topography or environment, causing minor ecological and faunal differences. In this view, the Dormaal and Erquelinnes collections might also be considered as complementary samples of the same earliest Eocene mammal fauna. Our study therefore indicates the importance and value of studying historical collections, even those considered well-known, and of also taking into account smaller, less diverse faunas.

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