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A new late Thanetian mammal fauna from Therdonne (Oise, France): new evidence for a Clarkforkian-equivalent biozone in Western Europe

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A new late Thanetian mammal fauna from Therdonne (Oise, France): new evidence for a Clarkforkian-equivalent biozone in Western Europe

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ABSTRACT
The Paleocene-Eocene transition is marked by dramatic global climatic change correlated with pronounced mammalian faunal change. A new late Paleocene mammal fauna from the Butte de Therdonne in the Paris Basin is described and compared with fossil assemblages of similar age elsewhere in Europe and North America. The Therdonne fauna is currently documented by *c.* 45 identifiable fossil specimens representing nine mammalian species. The stratigraphic position of this fossil assemblage in the early Paleogene Therdonne sequence indicates a late Thanetian age, and the taxonomic assemblage is consistent with the MP6b reference biochronological level defined on the basis of a mammalian fauna found in the Rivecourt sand Member in the Oise Valley, about 40 km east of Therdonne. The relative diversity of rodents and condylarthrans including the North American apheliscid *Aletodon* Gingerich, 1977, are the most striking characteristics of this fauna. Several lines of evidence, including biostratigraphy, sequence stratigraphic interpretation of the Therdonne section, and correlations with boreholes of the Paris Basin lead us to correlate the Therdonne and Rivecourt faunas. Therdonne therefore pertains to the MP6b biozone which corresponds roughly to the 1 Ma interval preceding the onset of the carbon isotope excursion (CIE) that marks the Paleocene-Eocene boundary.

KEY WORDS
Paleocene-Eocene transition,
Paris Basin,
fossil mammals,
PETM.

RÉSUMÉ
Une nouvelle faune de mammifères du Thanétien supérieur de Therdonne (Oise, France) : nouvelle preuve d'un équivalent du Clarkforkien en Europe occidentale.
La transition entre le Paléocène et l'Éocène est marquée par un spectaculaire changement climatique mondial, coïncident avec un renouvellement majeur des faunes de mammifères. Une nouvelle faune de mammifères du Paléocène supérieur provenant de la Butte de Therdonne, dans le bassin parisien, est décrite et comparée à des assemblages fossiles d'âge similaire provenant d'autres régions d'Europe et d'Amérique du Nord. La faune de Therdonne est actuellement documentée par environ 45 spécimens fossiles identifiables représentant dix espèces de mammifères. La position stratigraphique de cet assemblage fossile dans la séquence paléogène de Therdonne indique un âge thanétien supérieur et l'assemblage taxonomique est cohérent avec le niveau biochronologique de référence MP6b défini sur la base d'une faune mammifère trouvée dans le membre sableux de Rivecourt dans la vallée de l'Oise, à environ 40 km à l'est de Therdonne. La diversité relative des rongeurs, la présence de condylarthes, notamment de l'apheliscidé nord-américain *Aletodon* Gingerich, 1977 sont les caractéristiques les plus frappantes de cette faune. Plusieurs éléments, notamment la biostratigraphie, l'interprétation stratigraphique de la séquence de Therdonne et les corrélations avec les forages du bassin parisien, nous ont amenés à proposer un calibrage géochronologique pour les faunes de Therdonne et de Rivecourt, et donc pour la biozone MP6b qui correspond approximativement au million d'années précédant le début de l'excursion isotopique du ^{13}C (CIE) qui marque la limite Paléocène-Eocène.

MOTS CLÉS
Transition Paléocène-Eocène, Bassin de Paris, mammifères fossiles, PETM.

INTRODUCTION

In the past decades, the Paleocene-Eocene transition has been intensively studied because it is associated with a dramatic episode of greenhouse gas-induced global warming associated with changes in geochemical cycles and biotic interactions (e.g., Kennett & Stott 1991; Gingerich 2006; Röhl *et al.* 2007). Global temperature underwent a rapid rise of 5-9°C about 56 Ma ago and this event, known as the PETM (Paleocene-Eocene Thermal Maximum), induced worldwide environmental disruption for both marine and terrestrial ecosystems. There are still debated issues about the source of the massive injection of light ^{13}C depleted carbon in the atmosphere (e.g. Kender *et al.* 2021), and whether it was released as a single injection or in several pulses (e.g. Bowen *et al.* 2015). The PETM is marked geochemically by a short and abrupt negative carbon isotope excursion (CIE) registered in marine and terrestrial sediments (Zachos *et al.* 2008) followed by a body, and then recovery to pre-PETM $\delta^{13}C$ values, the duration of which does not exceed 200 ka (Harding *et al.* 2011). Coincident with this warming was a series of major biotic processes including inter-continental dispersals of terrestrial vertebrates, significant northward range extensions of continental floras in the northern hemisphere, and extinction of 35-50% of deep-sea benthic foraminifera species (McInerney & Wing 2011). It is now well documented that early representatives of several modern orders of mammals dispersed intercontinentally at this time, particularly across high latitude land bridges that then connected Asia with North America and North America with Europe (Beard & Dawson 1999; Bowen *et al.* 2002; Smith *et al.* 2006; Tong & Wang 2006; Beard 2008; Beard *et al.* 2010).

Terrestrial records of the PETM and associated abiotic and biotic patterns are best documented in Western North America. This transition has been most thoroughly studied in foreland basins of the North American Rockies, especially the Bighorn Basin of northern Wyoming, where long stratigraphic successions of fossiliferous localities provide the best record on Earth of biotic and environmental changes across the Paleocene-Eocene boundary (Rose 1981; Gingerich 1989, 2001; Gingerich & Smith 2006). The Bighorn Basin is where the Clarkforkian North American Land Mammal Age (NALMA) was originally defined (Rose 1981), where the onset of the CIE is registered in the uppermost part of the Clarkforkian NALMA in the Polecat Bench section (Bowen *et al.* 2015: fig. 1), which is the most complete continental section registering the Paleocene-Eocene transition. The first appearances of "modern" taxa (in this case rodents) in North America diagnose the Clarkforkian from the Tiffanian (Rose 1981). The Clarkforkian is currently recognized as the interval between the first appearance of Rodentia and the first appearance of Artiodactyla (Lofgren *et al.* 2004). The first artiodactyls appear early in the body of the CIE, along with perissodactyls and primates, not far above the P-E boundary, and mark the beginning (Wa-0 biozone) of the Wasatchian land-mammal age (Gingerich & Clyde 2001; Magioncalda *et al.* 2004). Yans *et al.* (2006) subsequently added precision in the faunal transition from Paleocene Clarkforkian to Eocene Wasatchian mammals in the southern Bighorn Basin by recognizing the Wa-M interval prior to Wa-0 based on the first and co-occurrence of *Meniscotherium* Cope, 1874 and a *Heptodon* Cope, 1882-like perissodactyl (Gingerich & Smith 2006).

Biozonation for most of the late Paleocene in North America was traditionally based on anagenetic evolutionary lineages of *Plesiadapis* Gervais, 1877 (e.g. Gingerich 1975, 2001), and associations of phenacodontids (Rose 1981), two taxa that are common in many Tiffanian and Clarkforkian fossil localities. The caveat of such an approach is the need for large fossil samples to identify species with confidence, and thus the placement of biozone boundaries. For these reasons Secord *et al.* (2006) have chosen to define new interval biozones based on the first occurrences of taxa that are not closely related to those that define the preceding or succeeding zones, and they have subdivided the Clarkforkian LMA into three interval zones (Cf-1, Cf-2, Cf-3) calibrated to the geomagnetic polarity time scale (GPTS) in the Bighorn Basin (Secord *et al.* 2006). Alternatively, the study of two Clarkforkian fossil assemblages from the Great Divide Basin and the nearby Washakie Basin of southwestern Wyoming led Anemone *et al.* (2024) to propose a bipartite subdivision of the Clarkforkian (Cf-1 and Cf-2) based exclusively on invasive taxa (immigrants from Asia) rather than endemic North American plesiadapids and phenacodontids which are claimed to be more prone to asynchronous range shifts in response to changes in regional climate or local environments. These dispersals and first appearances of invasive taxa seem to occur in two distinct phases, i.e., the appearance of rodents (*Acritoparamys* Korth, 1984 and *Paramys* Leidy, 1871) and the tillodont *Azygonyx* Gingerich, 1989 mark the base of the Clarkforkian (Cf-1), and the appearance of "miacid" carnivoraforms (*Uintacyon* Leidy, 1872) and the pantodont *Coryphodon* mark the "late" Clarkforkian (Cf-2). All these exogenous taxa are highly diagnostic when they appear (supposedly synchronously at the scale of the continent) in the fossil record of North America, and are thus well positioned for intercontinental correlations (at least with Asia). In this work, we will follow the biozonation proposed by Anemone *et al.* (2024: fig. 21) who recognize the Cf-1 – Cf-2 boundary by the first occurrence of *Coryphodon* in the Bighorn Basin, dated to *c.* 56.8 Ma (Secord *et al.* 2006). The biozonation of Anemone *et al.* (2024) merges the upper part of the Cf-2 biozone (index taxon *Plesiadapis cookei* Jepsen, 1930) and Cf-3 (index taxon *Copecion* Gingerich, 1989) of Secord *et al.* (2006) into a unique biozone characterized by the association of the Coryphodontidae and Miacidae. The top of the late Clarkforkian interval zone (Cf-2) of Anemone *et al.* (2024) is defined by the first appearance of Perissodactyla (i.e., Wa-0 biozone) while Gingerich & Smith (2006) defined the top of the Clarkforkian (their biozone Cf-3) in the Bighorn Basin as the lowest occurrence of *Meniscotherium priscum* Granger, 1915, which marks the base of Wa-M biozone, a short time interval preceding the Wa-0 biozone, and characterized by the association of the North American condylarths *Meniscotherium priscum* and *Haplomylus zalmouti* Gingerich & Smith, 2006. The Clarkforkian is a relatively brief interval of roughly 1.5 Ma (Anemone *et al.* 2024), forming a transitional period between typical Paleocene archaic Paleocene faunas and Eocene "modern" faunas.

In Europe, the sedimentary and fossil record is generally patchier than in North America, and two main areas have yielded fossil faunas subcontemporaneous to the PETM, i.e., the French-Anglo-Belgian Basin, and the Pyreneo-Provencal domain of southern France and northern Spain. In the Paris Basin, geologists of the 19th century detected a major change in mammalian faunas between that of the Conglomérat de Cernay (Thanetian) and that of the Conglomérat de Meudon (Sparnacian). While the Cernay mammalian fauna documented an extinct fauna inherited from the core fauna that diversified in Europe after the K-Pg boundary, the Meudon fauna marked the first appearance in the European fossil record of Rodentia, Primates, Artiodactyla and Perissodactyla, mammalian orders that are important elements of virtually all later continental faunas up to the present day. In North America, rodents make a similarly abrupt appearance in the Clarkforkian, whereas the first appearance of Primates, Artiodactyla and Perissodactyla (APP) occurred at the base of the Wasatchian (Gingerich 2001; Rose *et al.* 2012). In the Paris Basin, the Paleocene-Eocene boundary is bracketed by the biochronologic horizons MP6b, which is considered to be a Clarkforkian equivalent (Smith *et al.* 2014), and MP7 which is the oldest fauna in Europe that yielded APP (Steurbaut *et al.* 1999). It is worth noting that the MP7 biohorizon is supposed to correlate with the CIE of the PETM but none of the localities yielding a MP7 fauna known in Europe has actually registered the isotopic excursion *in situ*.

Paleocene continental deposits of northwestern Europe are extremely discontinuous, both in space and time. The Paris Basin, which then formed the southern margin of the North Sea, included paralic and coastal plain environments that were regularly flooded by shallow epicontinental seas. The few remaining continental sedimentary archives deposited during regressive intervals were largely destroyed by the many subsequent vast marine transgressions (Pomerol 1989; Steurbaut 1998; Vandenberghe *et al.* 1999). Here we report a new vertebrate assemblage collected from one of these Thanetian coastal-continental intervals that preceded the PETM. The Mont de Bourguillemont is located near the village of Therdonne (Oise), in the north-central part of the Paris Basin (Fig. 1). The stratigraphic position of the Therdonne local fauna (LF) is detailed in relation to the evolution of the sedimentary environments and their stacking pattern, and the paleontological content of the assemblage is integrated into the European mammalian biochronology and compared with the NALMA chronology.

GEOLOGICAL CONTEXT

The Mont de Bourguillemont is a residual hill that preserves early Paleogene strata resting unconformably on the Campanian chalk (Blondeau*et al.* 1970). At Therdonne, the contact between the chalk and the Thanetian Bracheux Formation is not visible, and the base of the Mont de Bourguillemont is thus comprised of the marine glauconitic sandstones of the Bracheux Formation, which is estimated to be 20-25 m thick based on borehole data (Blondeau*et al.* 1970). Accessible outcrops are

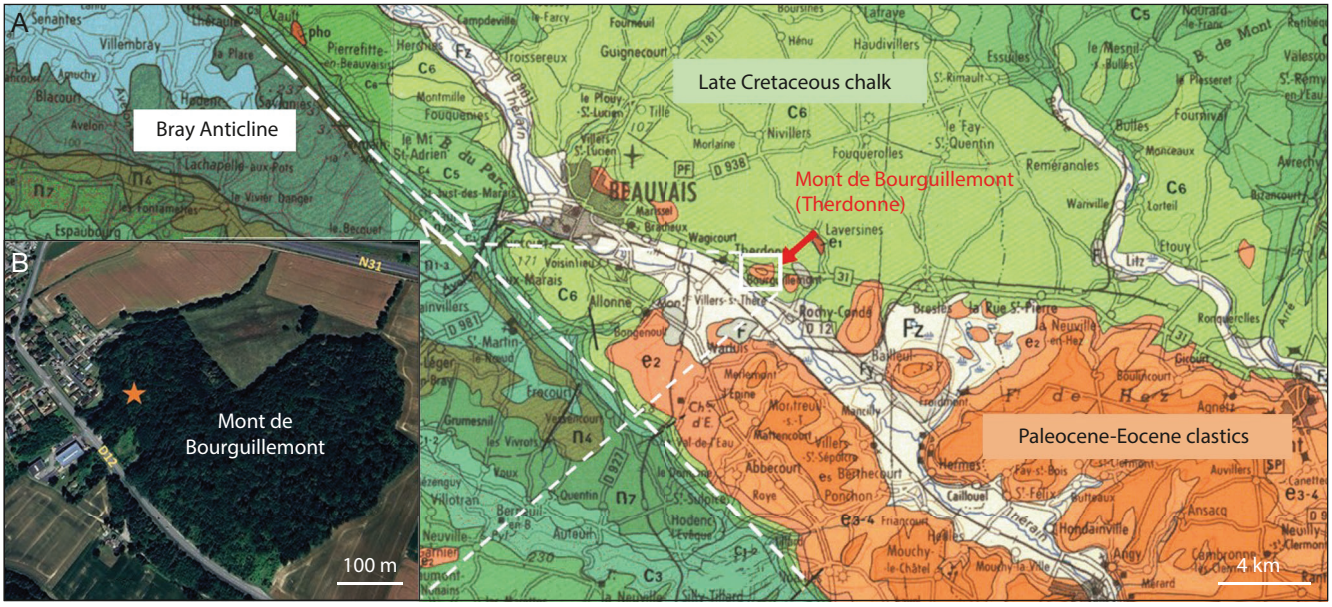


FIG. 1. — Locator map of the fossil locality (**orange star**) on the Mont de Bourguillemont near Therdonne Village: **A**, the geological map is from InfoTerre (BRGM) and Blondeau *et al.* (1970); **B**, the aerial photo is from https://geoportail.gouv.fr/.

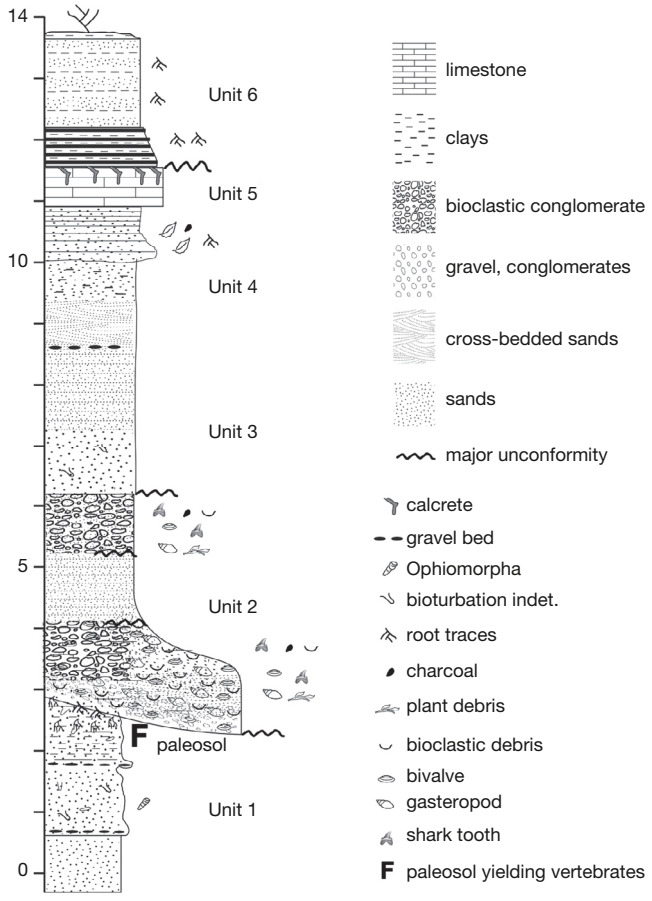


FIG. 2. — Measured stratigraphic section of the Therdonne fossil locality. Note that the fossil-bearing level is at the top of the Bracheux sands, and is capped by bioclastic conglomerate and sand bodies that constitute the base of the sables de Bouguillemont Formation.

often covered by vegetation and scree, and observations are often hampered. Describing the sequence overlying the mammal yielding horizon has required observation made along a transect of about 30 m from the fossil locality to an ancient quarry situated toward the South of the Mont de Bourguillemont. Also, the thickness of the different lithological units described below may vary or be truncated laterally, and the section presented here is a composite section (Fig. 2). The fossiliferous horizon yielding the fossil mammals reported here is an immature paleosol that lies on an erosional surface at the top of the glauconitic Bracheux sands (Unit 1, Fig. 3A, B). It consists of brownish well sorted sands with rounded quartz grains ("sables chocolat"), some burrows indicating a buried soil, and rare traces of roots have been observed. The thickness of this brownish to yellow-greyish paleosol varies laterally but never exceeds 50 cm at the sampled locality which is on the northwestern flank of the Mont de Bourguillemont (Fig. 1). Feugueur (1951) interpreted this lithological unit as the base (his unit B) of an estuarine transitional unit between the Thanetian marine sands and the overlying "Sparnacian" sands and marls (his unit D, E, F) on the basis of a section in an abandoned and backfilled quarry on the Southeast flank of the Mont de Bourguillemont. The paleosol yielding fossil mammals is incised (erosional contact) by 70 cm to 2 meters thick (this bed varies a lot laterally) coarse-grained greyish sands and greenish and flint pebbles with accumulations of both fragments of shells and complete mollusks (gastropods and bivalves with two valves in connection), shark teeth, charcoal and pieces of wood (Unit 2, Fig. 3A-C). There are different bodies of accumulation of shelly, bioclastic conglomerates separated by brownish well-sorted clayey sands forming flaser bedding in some places. This tidal system rests unconformably on the eroded paleosol yielding mammals through a sharp

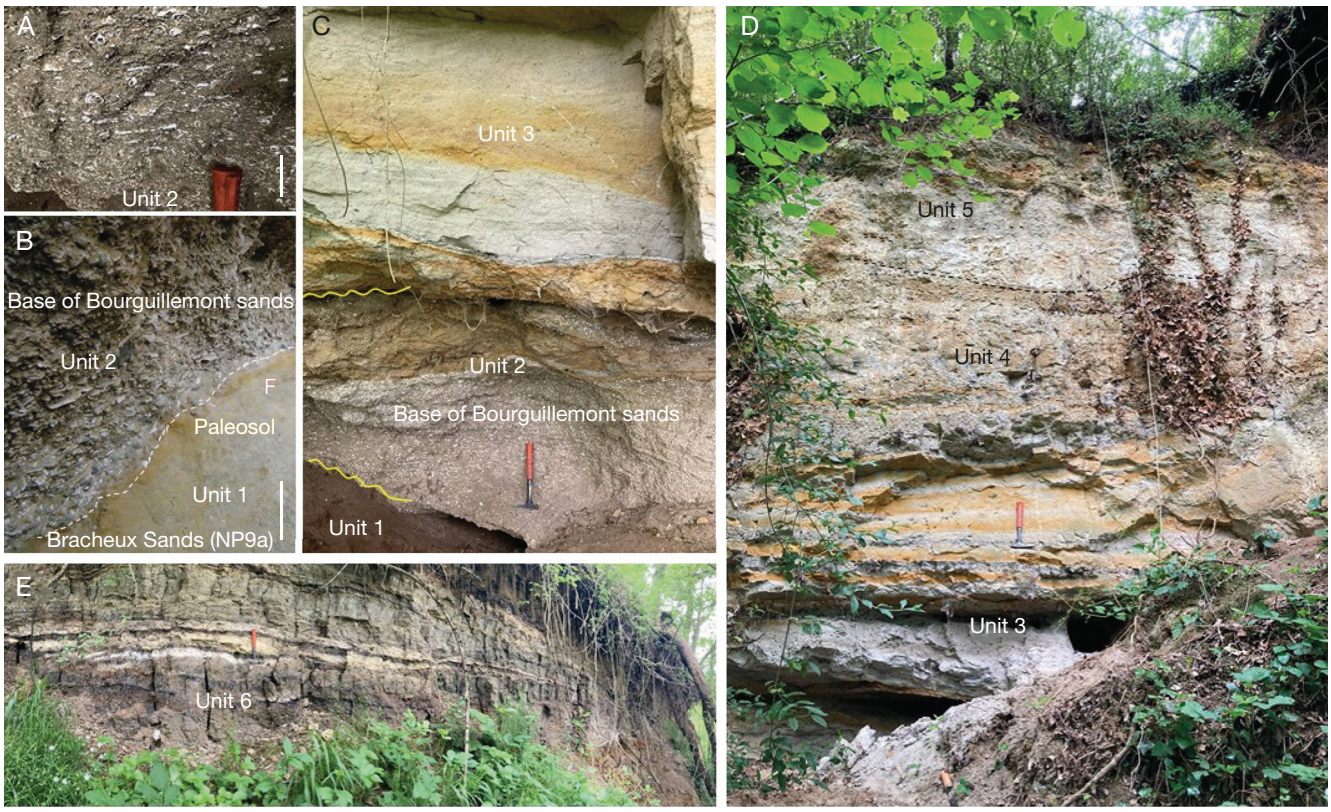


Fig. 3. — Paleogene sequence showing different identified lithological units exposed on the Mont de Bourguillemont in April 2026: **A**, detailed view of the bioclastic conglomerate forming the base of the Bourguillemont Sands; **B**, close-up showing the fossiliferous horizon where mammalian fossils were found near the top of the unit 1; **C**, view of the base of the section with the three lowermost units separated by erosional unconformities; **D**, the middle part of the section with the unit 3 to 5; **E**, the clayey unit 6 showing alternation of lignites, clays, and silts. The length of the rock hammer is about 30 cm. Scale bars: A, 5 cm; B, 10 cm. Credits: Grégoire Métais.

contact (Fig. 3A, B), and it corresponds to a littoral depositional environment, sometimes interpreted as storm-deposited beds (Dutheil *et al.* 2002). These tidal deposits are equivalent to the unit C of Feugueur (1951) and form the base of the Sables de Bourguillemont of Dutheil *et al.* (2002). As mentioned above, this basal lithological unit of the Bourguillemont sands has yielded a rich marine coastal fauna including mollusks, wood, shark teeth, osteichthyan, crocodiles and chelonian remains (Dutheil *et al.* 2002; Lapparent de Broin *et al.* 2025). The fossil assemblage from the Bourguillemont sands undoubtedly indicates a Thanetian age, notably the bivalves *Cucullaea crassatina* Lamarck, 1801, *Crassatella landinensis* Nyst, 1845, and *Glycymeris terebratularis* (Lamarck, 1805), all restricted to the Thanetian (Dutheil *et al.* 2002; Leroy *et al.* 2014; Lapparent de Broin *et al.* 2025). Likewise, the elasmobranch fauna from the base of the Bourguillemont sands shows no trace of reworking and includes ten taxa that are restricted to the Thanetian (Dutheil *et al.* 2002). The contact between the units 2 and 3 is erosional and the unit 3 consists of about 3 m of sandstone (the thickness varies laterally) with plant debris near the base of this unit and large-scale oblique bedding planes, which pass upward into whitish sands containing rare and poorly preserved brownish bioturbation (Fig. 3D). According to Dutheil *et al.* (2002), this tidal to infra-tidal unit would represent the maximum flooding surface of the sequence. The contact between the units 3 and 4 is erosional and the unit 4 consists of about 2 meters of well sorted and channelized sands with plant debris alternating with laminated beds of yellow-brownish-violet sandy clays and silts evoking an alluvial plain with channels and sand bars (unit 4, Fig. 3D). This fluvial sequence is capped by about 1 meter of highly altered lacustrine limestone, with calcretes near the top (unit 5, Fig. 3D). Dutheil *et al.* (2002) reported a paleokarst on the top of this limestone (not observed in our section) which is overlain (in some place) by about 2.5m beds of alternating brown-dark and whitish clays, and lignite (Fig. 3E) capping the hill in that area of the Butte. The calcretes and paleokarst (reported in Dutheil *et al.* 2002) indicate a continentalization of the area, marking a major unconformity in our section.

The Bourguillemont sands unit has long been considered as late Thanetian (Pomerol *et al.* 1977; Mégnien 1980; Dutheil *et al.* 2002) because it is stratigraphically bracketed by the Bracheux sands below and the "Sparnacian" lignitic clays lying above. Likewise, the marine fossil assemblage of the Bourguillemont sands clearly indicates a Thanetian age (Dutheil *et al.* 2002). The Bracheux sands Formation can be assigned to calcareous nannoplankton zone NP9a (Aubry *et al.* 2005). Based on the chart of third and fourth order stratigraphic cycles, Briais *et al.* (2016) identified a sharp transition (unconformity) between the wave-dominated

shore deposits of the Bracheux sands Formation and the fluvio-estuarine (tidal dominated) Bourguillemont sands Formation. Following a conjecture assumed by many workers (Pomerol *et al.* 1977; Laurain & Meyer 1986), Briais *et al.* (2016) consider this unconformity as time equivalent to the Cernay conglomerate Formation. This is probably erroneous and we will further discuss this assertion in this work, but the sequence stratigraphic interpretation of Briais *et al.* (2016: fig. 2) undoubtedly indicates a late Thanetian age for the Bourguillemont sands.

MATERIAL AND METHODS

Data acquisition

Two of us (JFL, DR) sampled and screen-washed (mesh 5, 2, 0.5 mm) a large volume (*c.* 1500 kg) of the brownish sands yielding fossils. Considerable time was dedicated to sorting vertebrates under a binocular microscope. Only the mammal remains are reported here, the rest of the fauna is still under study and a list of elasmobranchs and bony fishes from the bioclastic conglomerate are provided in Dutheil *et al.* (2002). Forty-seven teeth and fragments documenting nine species of mammals have been recognized in the assemblage so far. With few exceptions, there is no trace of mechanical erosion or traction by lateral transport (roundness, size sorting) suggesting relatively quiet hydrodynamic conditions, nor is there evidence of abrasive chemicals that would suggest digestive processes before burial. The absence of mechanical erosion suggests that fossil vertebrates from this bed have not been reworked.

Terminology

Dental terminology of the molar dental cusps and crests follows Van Valen (1967), and Escarguel (1999) for rodents. The method for measurements follows Gingerich (1983). In this paper, the upper premolars and molars are indicated by P or M, respectively, lower molars by m, and deciduous teeth are preceded by d. The measurements of a tooth are indicated in the referred specimen section under the form Length (L) and Width (W), and the values are in millimeters. The fossil material described in this paper is deposited in the collections of the Muséum national d'Histoire naturelle, Paris.

Notes on systematics

The Therdonne mammal fauna consists of isolated teeth, but most of the taxa they represent are well-known from more complete dentitions collected from upper Paleocene and/or lower Eocene strata of Europe or North America. Hence, we are reasonably confident in most identifications, and those for which questions remain are indicated appropriately and may be regarded as hypotheses subject to further testing and interpretation.

Abbreviations

Cf	Clarkforkian;
NALMA	North American Land Mammal Age;
Ther	Therdonne, Oise.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family Paramyidae Miller & Gidley, 1918
Subfamily Ailuravinae Michaux, 1968
[This subfamily is treated here as a clade within the paraphyletic 'Paramyidae']
Genus *Ailuravus* Rütimeyer, 1891

Ailuravus sp.
(Fig. 4A-E, H-J)

Type species. — *Ailuravus picteti* Rütimeyer, 1891.

Localities. — Various early to middle Eocene localities from Europe (see Vianey-Liaud & Marivaux 2021).

Referred specimens. — Ther-19, left M2 (L: 2.1-W: 2.51); Ther-20, left M2 (L: 1.96-W: 2.43); Ther-23, fragment of incisor (L: 2.77-W: 0.44); Ther-24, left m2 (L: 1.89-W: 1.75); Ther-25, right p4 (L: 1.92-W: 1.66); Ther-26, left dp4 (L: 1.73-W: 1.41).

Description

Of the two M2s, Ther-19 (Fig. 4H) is almost unworn, although its polished aspect suggests that the specimen has been transported. The outline is roughly trapezoidal and there is a prominent anteroloph extending lingually nearly two thirds of the width of the tooth and terminating buccally in a parastyle. The main cusps are relatively low and bulbous, the buccal cusps being the tallest. There is a hypocone separated from the larger protocone by a deep groove (sinus) that extends toward the disto-lingual base of the metacone, and a small hypostyle situated slightly more buccally along the posteroloph. Paracone and metacone have a lingual extension towards the paraconule and metaconule respectively. The conules are rounded, bulbous, and almost conical; the metaconule is slightly larger and somewhat more lingually placed. Pre- and postprotocrista are poorly expressed and join the base of the paraconule and metaconule respectively. The metacone has a faint crest extending buccally forming the distal wall of a sinus incising the ectoloph. The mesostyle is close to the paracone to which it is linked by a faint disto-buccal crest. The distal flank of the mesostyle forms the mesial wall of the sinus incising the ectoloph. There is no ectocingulum as in *A. cardosoi* Estravis, 2000 (Estravis 2000: plates 4-7a). The other M2, Ther-20 (Fig. 4I), is heavily worn, but shape and cusp pattern are similar to Ther-19. The metacone is more abraded than the paracone, and the small hypostyle situated slightly more buccally along the posteroloph is completely abraded, forming a marked wear facet.

Ther-24 (Fig. 4A-C) is a lower molar that we consider as a m2 because of its occlusal outline and its prominent hypoconid. However, the molar is a bit small for a m2, and we cannot exclude that this might be an m1. The cuspids are very bulbous, and crests and lophs are poorly expressed or absent. The talonid basin shows very faint irregularities on its surface, which may be interpreted as wrinkling. The metaconid is the tallest and the most voluminous cusp, followed by the protoconid and hypoconid which are about the same size (protoconid being taller), whilst the entoconid is smaller and

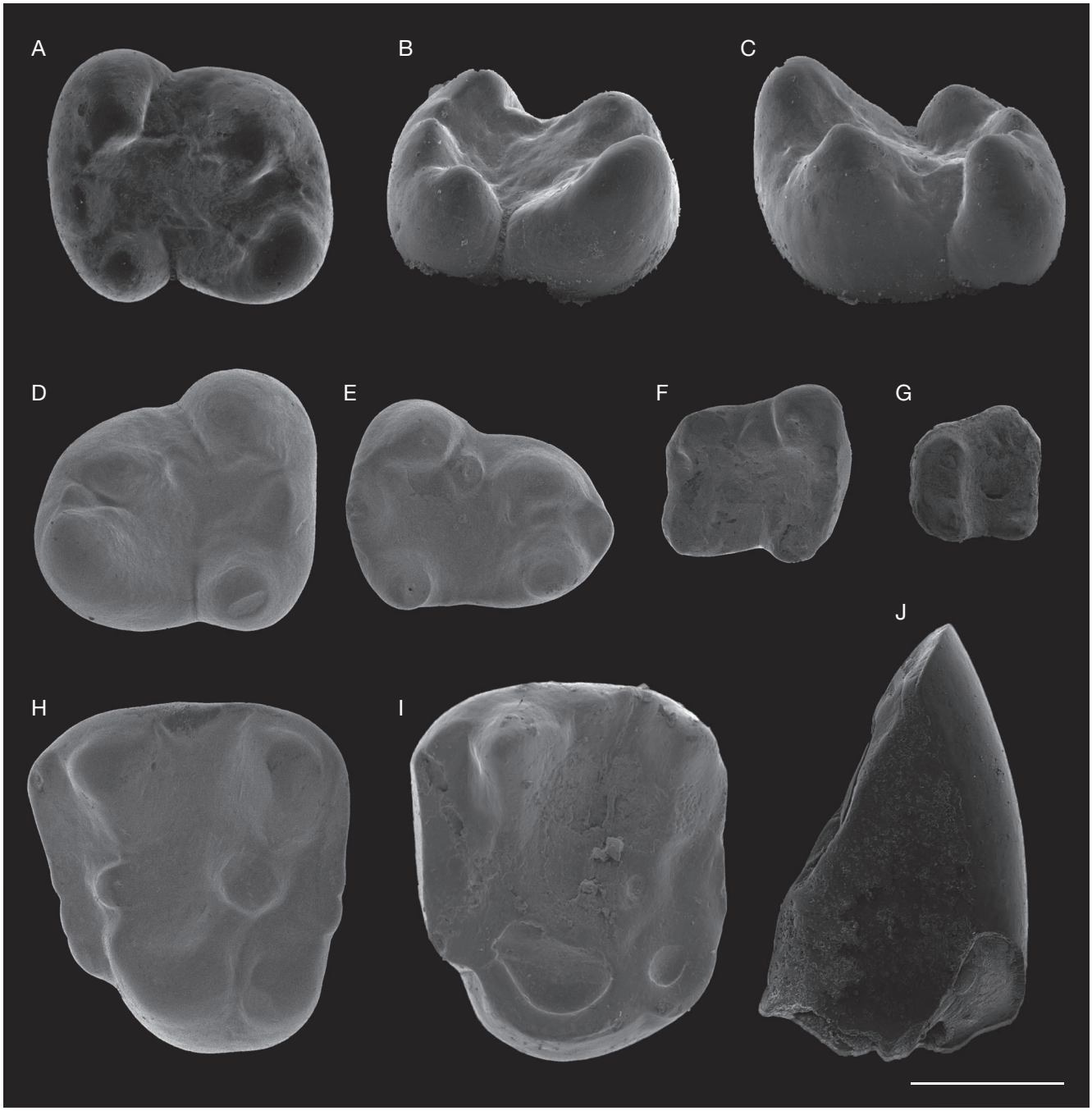


FIG. 4. — Rodents from Therdonne: **A**-**E**, **H**-**J**, *Ailuravus* sp. Ther-24, left m2 in occlusal (**A**), lingual (**B**), and buccal (**C**) views; Ther-25, right p4 in occlusal view (**D**); Ther-26, left dp4 in occlusal view (**E**); Ther-19, left M2 in occlusal view (**H**); Ther-20, left M2 in occlusal view (**I**); Ther-23, incisor in distal view (**J**); **F**, *Sparnacomys* sp. Ther-21, right m1-2 in occlusal view; **G**, Microparamyinae? indet. Ther-22, right m1? in occlusal view. Scale bar: 1 mm. Credits: Philippe Loubry.

lower. The protoconid has a transverse posterior arm directed-connected to the lingual metalophulid, disposition defined as a metalophulid II by Vianey-Liaud & Marivaux (2021). A tiny but distinct cuspid emerges from the lingual extension of the hypoconid; it is separated from the hypoconulid by a deep groove (sinusid). The entoconid is slightly more mesial in position than the hypoconid, and the metaconid is distinctly more mesial than the protoconid. There is no real transverse lophid across the trigonid, but a narrow lingual rib on the metaconid which may be interpreted as a faint and short metalophulid I. Likewise, these is a buccal rib on the protoconid that may be interpreted as a faint metalophulid II. The anterolophid is poorly marked and low. The sinusid is relatively shallow, as deep as in *Meldimys* Michaux, 1968, but less deep than in other *Ailuravus* species. The ectolophid is weak, and the mesoconid is barely visible, a condition that is unlike that seen in lower molars of *Euromys* Escarguel, 1999, where it is well-developed (Escarguel 1999; Estravis 2000).

The p4 (Fig. 4D) is relatively unworn, crests are overall poorly expressed, cuspids are bulbous, only the entoconid has substantial dietary wear. The metaconid is the most voluminous and tallest cuspid, the protoconid is the smallest. There is a distinct single hypoconulid, slightly mesio-distally compressed, and separated from the hypoconid by a groove. Another shallower groove separates the hypoconulid from the conical entoconid. The mesoconid is small and, closely appressed to the protoconid, and it is separated from the hypoconid by a deep sinusid. The talonid is much wider than the trigonid, and it is also reduced mesio-distally compared to that of m2. The close proximity of the protoconid and metaconid is more like the condition in *Euromys* and to a lesser extent *Meldimys* and *Ailuravus*, where these cusps are better separated. The protoconid is more distally placed with respect to the metaconid, and there is a small anteroconid between the two main cuspids of the trigonid.

The dp4 (Fig. 4E) shows moderate dietary wear. The talonid is much wider than the trigonid and the hypoconid is the tallest and most voluminous cuspid. The hypoconulid is large and transversely elongate, linked to the two main cuspids of the talonid by a crest becoming lower towards the base of the entoconid and hypoconid. The trigonid has three distinct cuspids, of which the protoconid and the metaconid are the largest and tallest; in this respect, it differs from the dp4 of *Sparnacomys* Hartenberger, 1971 and *Pantrogna* Hartenberger, 1971 in which the trigonid is nearly unicuspid. The buccal side of the metaconid is ribbed, and this may be interpreted as an incipient metalophulid I. Likewise, there is a faint crest extending postero-lingually from the protoconid. The anterolophid is lower and bears a cuspid medially. The ectolophid is weak, the mesoconid is moderately developed, and the sinusid relatively deep.

Comparisons and remarks

Morphology and size of the dental material best compares with ailuravine rodents, because of the overall bunodonty and bulbous aspect of cusps and cuspids, the absence or poor development of lophs and lophids, and the open trigonid on lower molars. The lower molar has a transverse posterior arm of the protoconid, directed--connected to the lingual metalophulid, disposition defined as a metalophulid II: there is no buccal transverse metalophulid from the apex of the protoconid (metalophulid I). A strong and oblique postprotocristid found in *Euromys* and other theridomorphs is absent here.

The upper and lower molars resemble the teeth identified as *Euromys* from Dormaal (Escarguel 1999), and from Erquelinnes (Missiaen *et al.* 2013). Further, our material is most similar to the smallest and most primitive species *cardoisi* from Silveirhinia (MP7), which has been successively referred to the genus *Meldimys* (Estravis 1992), *Euromys* (Escarguel 1999, Estravis 2000), and now to *Ailuravus* (Vianey-Liaud & Marivaux 2021). *Ailuravus cardosoi* from Portugal displays many common features with our material, including the trigon shape, the large, bulbous and subequal paraconule and metaconule, the large anteroloph and parastyle, the mesostyle on M2, and the poor development of transverse lophids, the isolation of the entoconid, and the absence of connection between hypoconid and hypoconulid on lower molars. However, the lower molar from Therdonne differs in having a reduced mesoconid. The unique upper molar (M1-2) from Rians referred to ?Ailuravinae, sp. indet. by Godinot (1981: plate 2, fig. 25) shows a different morphology with a more square occlusal outline, and a stronger parastyle. In terms of grade of evolution, the teeth from Therdonne closely correspond to *A. cardoisi* and the teeth referred to *Euromys* sp. from Dormaal. Awaiting more complete material, we prefer to leave the ailuravine from Therdonne as *Ailuravus* sp.

Infra-order THERIDOMORPHA Lavocat, 1955
Genus *Sparnacomys* (Hartenberger, 1971)

Sparnacomys sp.
(Fig. 4F)

Type species. — *Sparnacomys chandoni* Hartenberger, 1971.

Localities. — Various early Eocene (MP7-10) localities from France and Portugal.

Referred specimens. — Ther-21, right m1-2 (L: 1.1-W: 1.14).

Description

The unique lower molar is a fairly worn specimen, approximately equal in length and width; the four main cusps are peripheral in position, there is a well-developed talonid basin, and the trigonid is mesio-distally compressed; the prominent metaconid is situated at the anterolingual margin and connects directly to the anterior cingulid which is well developed, and separated buccally from the protoconid by a groove; the metaconid is elongate mesio-buccally to postero-lingually; the anterolophid seems to be confluent with the protoconid, unlike *Pantrogna russelli* (Michaux, 1964), where there is an intervening notch. The metalophulid is heavily worn but reaches the base of the metaconid. There is a rounded and well-developed mesoconid set in from the buccal side; the sinusid between the mesoconid and hypoconid is well-marked but not very deep; the hypoconid is strongly concave mesially; the rounded entoconid is separated by a groove from the lingual end of the posterolophid. The posterior cingulid connects to the entoconid. The short hypolophid crosses less than half the talonid basin, paralleling the posterior cingulum. The hypoconid curves into the posterior cingulid, on which there is a swollen and twinned hypoconulid.

Microparamyinae? indet.
(Fig. 4G)

Referred specimens. — Ther-22, right m1? (L: 0.87-W: 0.76).

Description

This is a fairly worn and partly damaged (badly corroded) lower molar (possibly a m1, the trigonid is not reduced enough transversely to identify it as a p4), that is significantly smaller

than the lower molar (Ther-21) identified as *Sparnacomys* sp. The occlusal outline is roughly square shaped and the trigonid is mesio-distally compressed with a small trigonid basin. Lingual cuspids are much higher than the labial ones, and there is a well-developed mesial cingulid which extends all along the buccal border of the tooth. The anterolophid is confluent with protoconid, and the metalophid is strong and high. The rounded mesoconid is present but heavily worn, and there is a complete and strong ectolophid. Because of the advanced wear stage, it is difficult to distinguish either a mesial cingulid or the hypoconulid on the relatively high posterolophid.

Comparisons and remarks

Ther-21 actually closely resembles in morphology and size the specimen AV5529 from Avenay (MP9) figured in Michaux (1968: plate 8) and then attributed to *Microparamys nanus* Teilhard de Chardin, 1927, but which is now considered as *Sparnacomys chandoni* Hartenberger, 1971 (Escarguel 1999; Vianey-Liaud & Marivaux 2021). Attribution of Ther-21 to the basal Theridomorpha is based on the presence of mesial, distal, and buccal cingulids, a trigonid that is anteroposteriorly compressed with a small trigonid basin; tendency toward strong transverse component in lophids of lower molars, with metalophid and hypolophid from short to complete; mesoconid in internal position; entoconid separated by barely visible groove from posterolophid, and a short ectolophid (Vianey-Liaud & Marivaux 2021). Ther-21 differs from lower m1-2 of *Pantrogna* Hartenberger, 1971 and *Hartenbergeromys* Escarguel, 1999 in its smaller size, its more concave cup-shaped talonid basin, short and incomplete entolophid, and its relatively high metaconid. However, the advanced wear of Ther-21 precludes the identification of all the dental features characterizing the only *Sparnacomys* species *S. chandoni*, and awaiting more complete material, we prefer to leave Ther-21 from Therdonne as *Sparnacomys* sp. Ther-22 is also heavily worn, hampering any firm taxonomic identification at this stage. However, Ther-22 closely resembles but is slightly smaller than the right m1 (M66051) attributed to Microparamyinae? undet. from the MP7 locality of Croydon (Hooker 2020: fig. 4). The microparamyine rodents are hypothesized to have originated in midlatitude North America and subsequently dispersed across a North Atlantic corridor to colonize western Europe (Dawson 2001). However, the presence of microparamyines in the early Eocene of Europe remains contentious. *Microparamys nanus* was identified at Dormaal (Belgium) by Teilhard de Chardin (1927), and additional fossil material of this taxon was reported by T. Smith (1999, unpublished PhD). Escarguel (1999) suggested that some specimens referred to *Microparamys nanus* at Dormaal may actually be teeth of *Sparnacomys* and *Pantrogna*. These two genera known from MP 8-9 and MP 8-10 localities respectively, were considered as most similar to North American Microparamyini by Escarguel (1999), whereas Vianey-Liaud & Marivaux (2021) consider *Sparnacomys* and *Pantrogna* as basal Theridomorpha, a clade exclusively known in Western Europe. *Sparnacomys* is restricted to the early Eocene of Western Europe (Vianey-Liaud & Marivaux 2021); it is known from Mutigny, Avenay (Escarguel 1999) and Abbey Wood (Hooker 2010). If our identification is correct, the currently limited fossil material from Therdonne would record the earliest known occurrence of the genus. The identification of Ther-22 as a possible Microparamyinae is tentative and raises the issue of their effective presence in Europe during the late Paleocene. In North America, Microparamyinae range from the latest Paleocene through the end of the Eocene, with their earliest occurrence in the Clarkforkian Cf-2 (in the sense of Secord *et al.* 2006) of the Bighorn Basin (Ivy 1990). *Microparamys cheradius* Ivy, 1990 occurs in the *Plesiadapis cookei* Jepsen, 1930 and *Phenacodus-Ectocion* biozone of the Clarkforkian in the Bighorn Basin (Ivy 1990; Secord *et al.* 2006). Microparamyinae are usually considered as close to paramyine rodents (*sensu* Wood 1962) which also show a Holarctic distribution. The oldest paramyines are *Paramys atavus* (Jepsen, 1937) and *P. adamus* Dawson & Beard, 1996 from the North American late Paleocene (early Clarkforkian, Cf-1, Dawson & Beard 1996) and diversified there during the middle Eocene, but paramyines are a minor element in the European Eocene faunas, which are dominated by various clades of Ischyromyoidea and Theridomorpha (Escarguel 1999; Vianey-Liaud & Marivaux 2021).

Clade CARNIVORAMORPHA Wyss & Flynn, 1993
Clade CARNIVORAFORMES Flynn,
Finarelli & Spaulding, 2010
Family 'Miacidae' Cope, 1880
Genus *Dormaalocyon* Solé, Smith, Coillot,
De Bast & Smith, 2013

Dormaalocyon sp.
(Fig. 5)

Type species. — *Dormaalocyon latouri* (Quinet, 1966).

Localities. — Belgium, Dormaal (Flemish Brabant); earliest Eocene, MP7.

Referred specimens. — Ther-1, left m3 (L: 2.1-W: 1.66); Ther-4, right trigonid of a dp4 (L: 2.31-W: 1.5); Ther-8, right P4 (L: 4.23-W: 4.26); Ther-5, trigonid of a left m1? (?-W: 2.94).

Description

The P4 (Ther-8; Fig. 5A, B) is an upper carnassial. The postmetacrista is much elongated but poorly developed distally. The paracone is prominent and only slightly mesially located. The parastyle is poorly developed. The paracone is linked to the parastylar area and metastyle and a continuous buccal cingulum is present. The lingual part of the crown is missing, but the breakage shows that there was a third, lingual root (Fig. 5B).

A mesiodistally compressed trigonid of a lower molar (Ther-5; Fig. 5E) bears a metaconid that is higher and larger than the paraconid. The metaconid is robust and elongated mesiodistally, aligned mesiodistally with the protoconid, and its apex is slightly tilted lingually. The protoconid is sharp, but it is not much higher than the paraconid and metaconid.

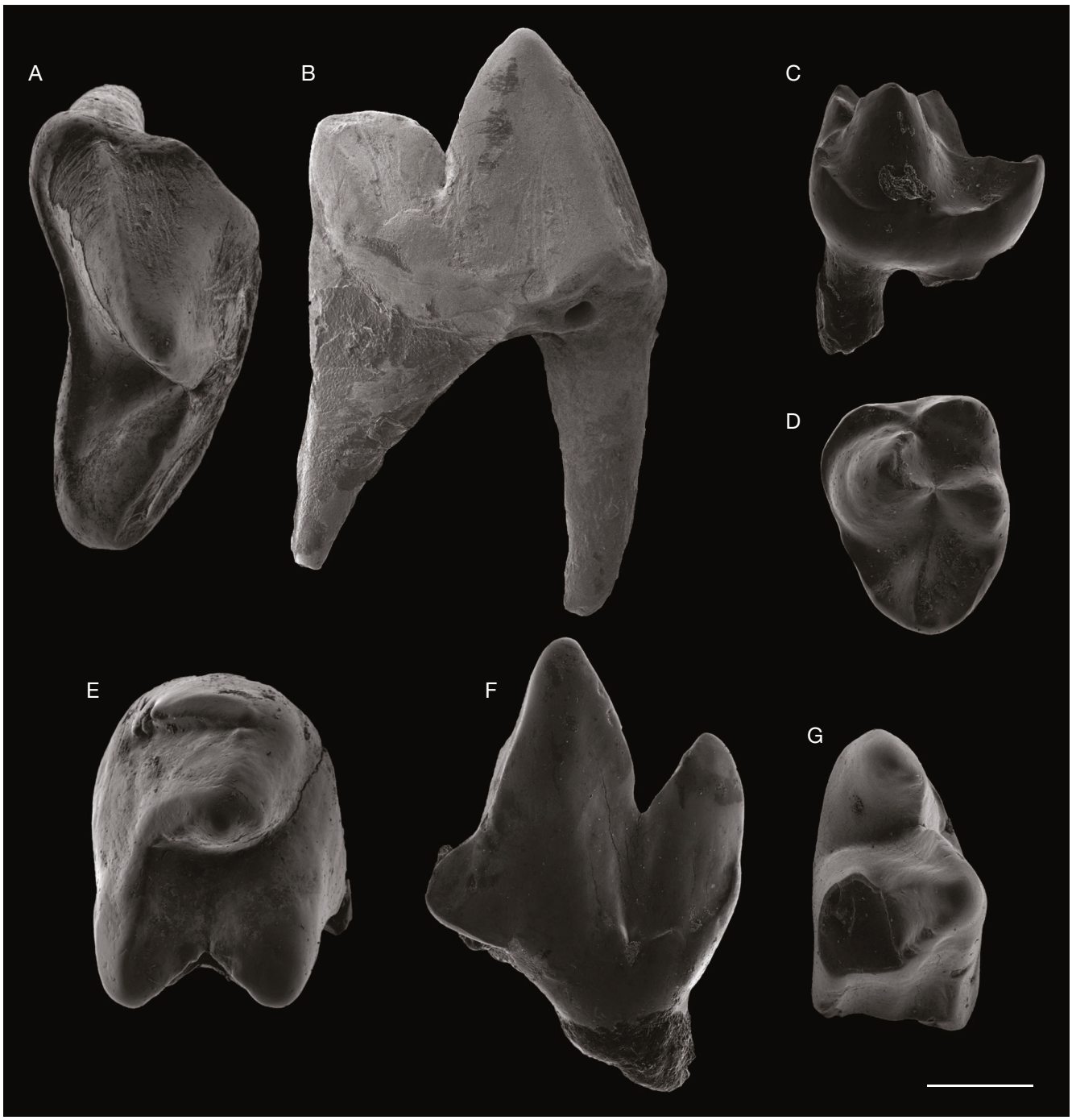


FIG. 5. — The miacid carnivoraform *Dormaalocyon* sp. from Therdonne: **A**, **B**, Ther-8, right P4 in occlusal (**A**) and lingual (**B**) views; **C**, **D**, Ther-1, left m3 in buccal (**C**) and occlusal (**D**) views; **E**, Ther-5, trigonid of a left m1? in occlusal view; **F**, **G**, Ther-4, trigonid of right dp4 in buccal (**F**) and occlusal (**G**) views. Scale bar: 1 mm. Credits: Philippe Loubry.

The m3 (Ther-1; Fig. 5C, D) is two-rooted and has a high trigonid and a transversely narrow talonid that is elongated mesiodistally. The paracristid is transversal. The paraconid and metaconid have almost the same height; the protoconid is slightly higher. The metaconid is aligned mesiodistally with the protoconid. As on m1, the paraconid projects only slightly mesially. The talonid is shorter than the trigonid and the hypoconid is the highest cusp; the entocristid becomes lower toward the lingual part. The entoconid and hypoconulid are not individualized. The buccal cingulid (pre-, ectocingulid) is continuous. The cristid obliqua is more oblique (distally shifted buccally) than in more anterior molars. The precingulid is well developed mesially.

The trigonid of dp4 (Ther-4; Fig. 5G) is mesiodistally elongated; the protoconid is the largest and most acute cusp, and the protoconid and metaconid are aligned transversely; the paraconid is low and shifted mesially; the apex of the metaconid

is broken, but it seems to have been as high as the protoconid. The trigonid is open lingually, forming a wide angle, unlike what is observed on the trigonid of the permanent molar. The broken part of the crown distal to the trigonid suggests a much lower talonid. This specimen resembles a specimen from Dormaal illustrated in Quinet (1966: plate IV, fig. 9-11), and erroneously referred to Arctocyonidae indet.

Comparisons and remarks

As much as we can judge from this limited sample, these dental elements display characters of "miacid" carnivoraforms, a paraphyletic assemblage of basal carnivoramorphs (Solé *et al.* 2016). The reduced parastyle and elongated postmetacrista on P4, and the morphology of m3 are reminiscent of *Dormaalocyon latouri* (Quinet, 1966) (Quinet, 1966), although the latter is noticeably smaller than the material from Therdonne. *D. latouri* is exclusively known from Dormaal, and it is also documented by tarsal bones (calcaneum and astragalus) which indicate arboreal capabilities for this species (Solé *et al.* 2014). The first appearance of carnivoraforms has long been considered as a marker of the Eocene in Europe until the report of *Vassacyon prieuri* Solé, Smith, De Bast, Codrea & Gheerbrant, 2016 from the late Paleocene of the Paris Basin (Solé *et al.* 2016). According to Solé *et al.* (2014) *Dormaalocyon* Solé, Smith, Coillot, De Bast & Smith, 2014 is one of the most primitive carnivoraforms and is closely related to *Vulpavus* Marsh, 1871 and *Miacis* Cope, 1872 known from the earliest Eocene (Wasatchian) of North American. The primitiveness of *Dormaalocyon* and its late Paleocene occurrence in Europe suggest a dispersal of carnivoraforms from Europe to North America during the Paleocene-Eocene transition.

"CONDYLARTHRA" Cope, 1881
Louisinidae Sudre & Russell, 1982

Genus *Paschatherium* Russell, 1964

Type species. — *Paschatherium dolloi* (Teilhard de Chardin, 1927).

Localities. — Late Thanetian, Cernay; Belgium, Erquelinnes, Dormaal, Zone PEI, Neustrian; United Kingdom, Ferry Cliff.

Paschatherium sp.
(Fig. 6)

Referred specimens. — Ther-29, right M1 (L: 1.24-W: 1.87); Ther-30, right M2 (L: 1.39-W: 1.88); Ther-31, left M3 (L: 1.25-W: 1.78); Ther-32, left m2 (L: 1.67-W: 1.18); Ther-33, left m2 (L: 1.55-W: 1.15); Ther-34, right m1-2 (L: 1.77-W: 1.27); Ther-28, lingual part of a left upper molar (L: 1.23-?).

Description

The M1 (Fig. 6A) has a distally expended metacone, straight centrocrista, paracone and metacone of equal size and height, a distinct precingulum, a confluent postcingulum-metacingulum and a weak postmetaconule crista that does not join the postcingulum-metacingulum. Ther-30 (Fig. 6G) is interpreted as a M2 which is larger than M1 in *Paschatherium* (Hooker & Russell 2012). The M2 has sharp pre- and postprotocristae; the paraconule is more lingually placed than the metaconule, and there is no post-metaconule crista. On lower molars (Fig. 6B, C, H, I) the paraconid is crestiform, the premetacristid is mesiobuccally curved, and the precingulid (although partly broken) is strong, extensive, and shelf-like. The cristid obliqua ascends the back of the trigonid a short distance; the hypoconulid is small and medially placed. The size of these molars makes it one of the smallest known *Paschatherium*. On the lower molar Ther-32 (Fig. 6H, I), the precingulid forms a large shelf bearing the crestiform paraconid, the hypoconulid is larger, more bulbous, and less integrated into the postcristid than in *Pa. yvettae* Gheerbrant et al., 1997. Although these specimens display characters of *Pa. dolloi* (Teilhard de Chardin, 1927), their size lies outside the range known for this species (López-Martínez *et al.* 2006).

Comparisons and remarks

Our sample consists of isolated teeth that are very difficult to allocate to a species with a reasonable degree of certainty. Representing over 60% of the specimens recovered at Dormaal, *Paschatherium* is a very common mammal across the Paleocene-Eocene transition in Europe, and this pattern of abundance for this taxon has been named the *Paschatherium* acme (López-Martínez *et al.* 2006). Five species of *Paschatherium* have been formally defined but they show important variation in both size and morphology, including along the molar row (López-Martínez *et al.* 2006). Given the small size and fragmentary nature (isolated teeth) of our sample from Therdonne, and pending additional fossil data regarding this taxon, these specimens are identified as *Paschatherium* sp.

Arctocyonidae Giebel, 1855

Genus *Landenodon* Quinet, 1966

Type species. — *Landenodon woutersi* Quinet, 1966.

Localities. — Various late Paleocene (MP6) to early Eocene (MP7-8) localities from Western Europe.

Referred specimens. — Ther-27, left m2; Ther-11, left m2 (L: 4.62-W: 3.02); Ther-13, right m2 (L: 4.17-W: 2.91); Ther-14, left m1 (L: 4.77-W: 3.4); Ther-6, trigonid of a left m1? (?-W: 2.3); Ther-15, talonid of a left m1? (?-W: 3.45); Ther-9, left upper molar trigon (?-W: 3.3); Ther-17, left M1 (L: 3.84-W: 4.83); Ther-18, right M1? (L: 4.0-W:3.91); Ther-10, left M3 (L: 2.12-W: 2.96); Ther-7, right P4 (L: 4.58-W: 4.37); Ther-16, left P4 (L: 3.87-W: 2.05).

Landenodon sp.
(Fig. 7)

Description

Upper and lower molars of a small arctocyonid are attributed to the genus *Landenodon* based on their overall dental morphology. Ther-18 is an upper molar (Fig. 7A), lacking a hypocone, and bearing crested paracone and metacone, both of which

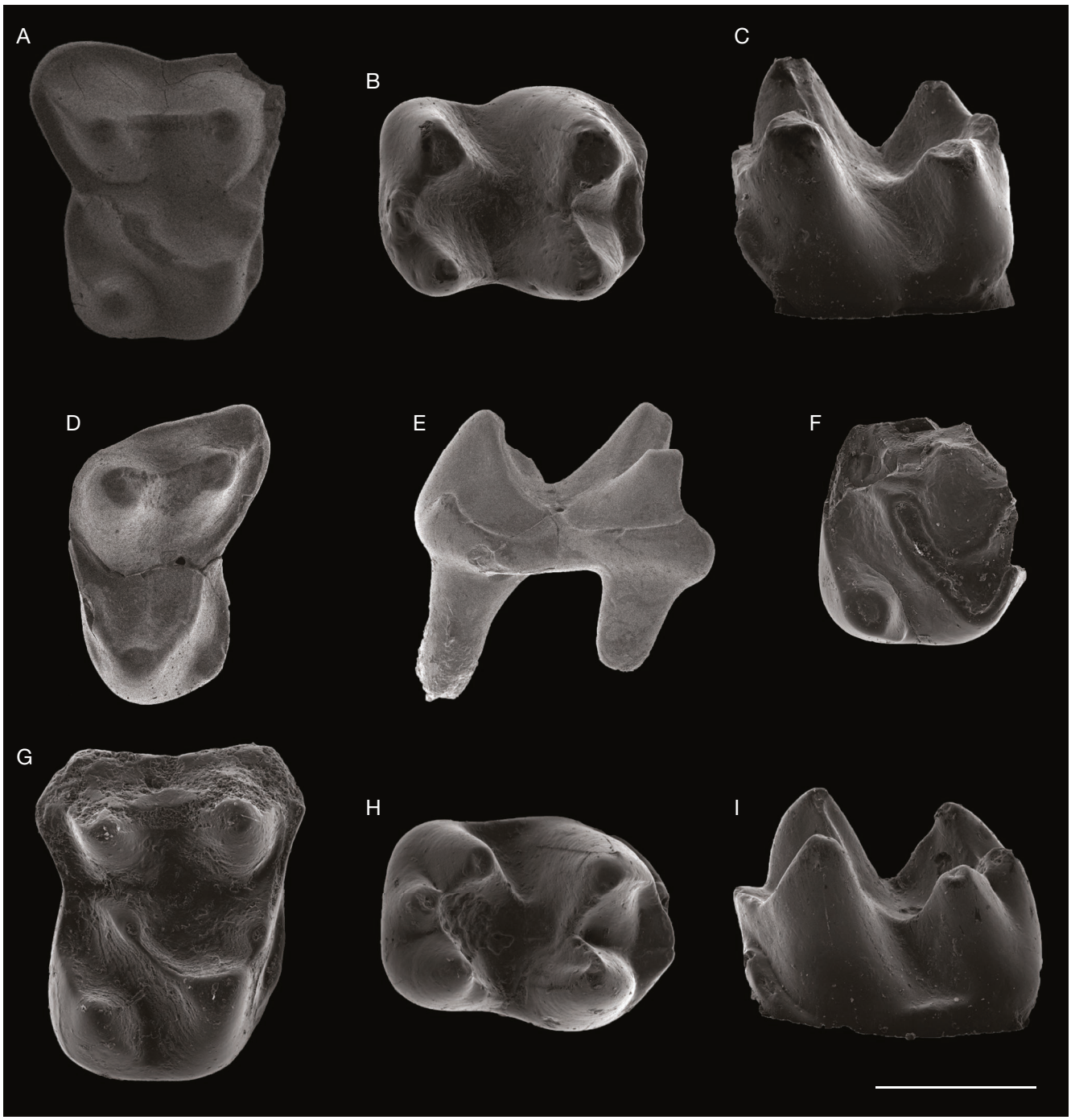


Fig. 6. — Louisinid *Paschatherium* sp. from Therdonne: **A**, Ther-29, right M1 in occlusal view; **B**, **C**, Ther-33, left m2 in occlusal (**B**) and buccal (**C**) views; **D**, **E**, Ther-31, left M3 in occlusal (**D**), and distal (**E**) views; **F**, Ther-28, lingual part of a right upper molar in occlusal view; **G**, Ther-30, right M2 in occlusal view; **H**, **I**, Ther-32, left m2 in occlusal (**H**), and buccal (**I**) views. Scale bar: 1 mm. Credits: Philippe Loubry.

display lingual crests linked to the paraconule and metaconule, respectively. Ther-17 bears a strong cingulum surrounding the entire crown while the lingual cingulum is interrupted below the protocone on Ther-18. In *Landenodon*, the M2 is wider transversely than M1, and parastyle and metastyle are absent. The M3 is much smaller than other molars, and it is on this basis that the small, asymmetrical M3 (Ther-10, Fig. 7E, F) is tentatively referred to this taxon here. This molar displays a thick mesial and buccal cingulum; paracone and metacone are about equal in size, but the paracone is more buccally placed, giving the molar an asymmetrical outline in occlusal view. It is probably too small to be a M3 of *Landenodon* cf. *woutersi*, and to match with the rest of the dental remains, but awaiting further data, this M3 is provisionally considered as *Landenodon* sp. The two P4s (Fig. 7C, D) each have a prominent and acute paracone, a rounded parastyle,

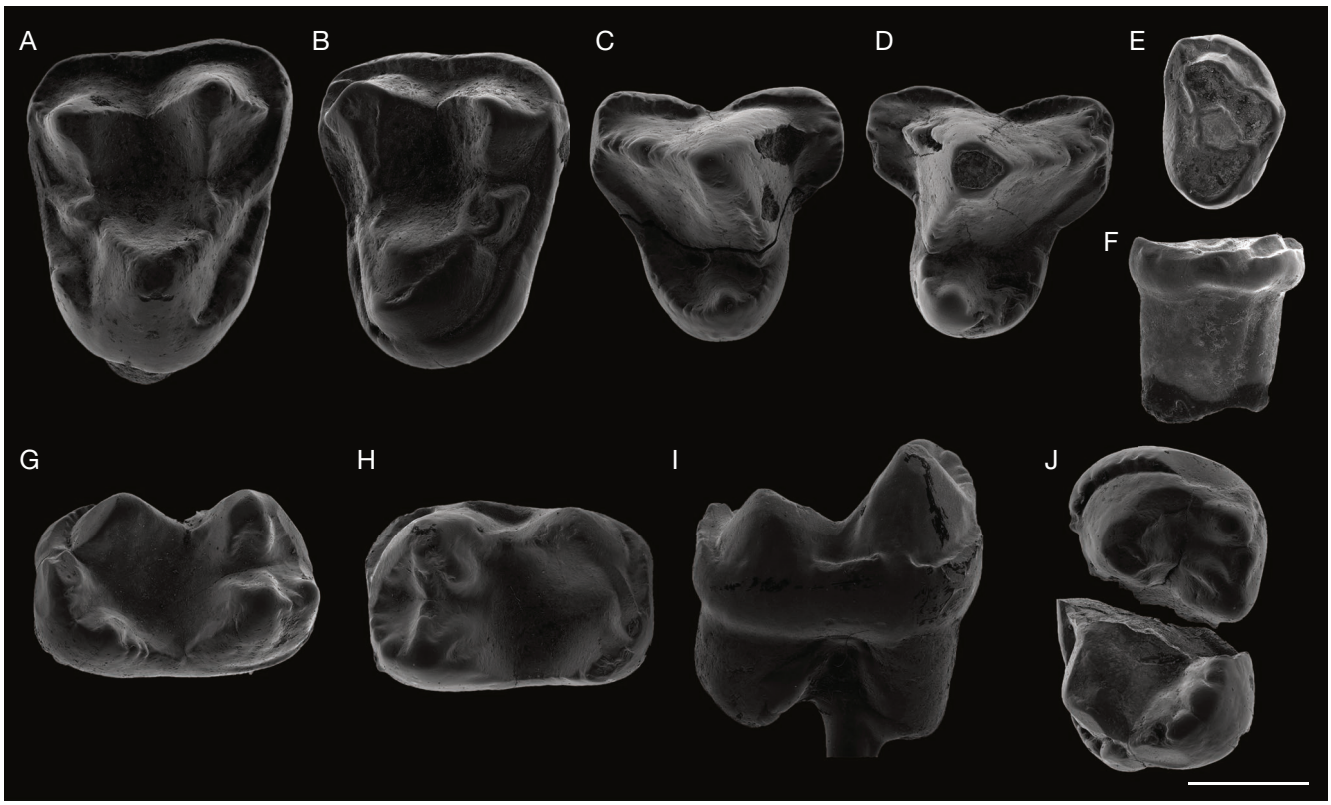


Fig. 7. — Arctocyonid *Landenodon* from Therdonne. *Landenodon* sp.: **A**, Ther-18, right M1? in occlusal view; **B**, Ther-17, left M1 in occlusal view; **C**, Ther-7, right P4 in occlusal view; **D**, Ther-16, left P4 in occlusal view; **E**, **F**, Ther-10, left M3 in occlusal (**E**), and proximal (**F**) views; **G**, Ther-14, left m1 in occlusal view; **H**, **I**, Ther-13, right m2 in occlusal (**H**), and buccal (**I**) views; **J**, Ther-6, trigonid, and Ther-15, talonid of a left m1 in occlusal view. Scale bar: 2 mm. Credits: Philippe Loubry.

and a postparacrista showing denticles. The protocone is acute and a thick cingulum which extends along the distal border, and buccally until half of the premolar mesio-distal length.

The size and position of the paraconid on lower molars of *L. woutersi* is very variable (Russell 1980). Some molars have a mesio-distally short trigonid with reduced paraconid, conjointly with a wide and elongated talonid (Fig. 7H-J) which matches the morphology of *Landenodon woutersi*. Another lower molar pattern (Fig. 7G) displays a mesiodistally extended trigonid with paraconid and metacoid about equal in size, a shorter, but narrower talonid with a very low entoconid that tends to fuse with the lingual border of the talonid. This second lower molar pattern rather resembles that of *L. lavocati* Russell, 1980 from Cernay (Russell 1980).

Comparisons and remarks

The dental material displays the diagnostic features of *Landenodon*: narrow and elongated lower molars, the anterior position of the voluminous paraconid on m1, the frequent absence of the paraconid on m2, the hypoconulid close to the small but distinct entoconid, the elevated hypoconid and the strong and continuous buccal cingulid. Beyond *L. woutersi*, two additional species are reported from the late Paleocene of Cernay-Berru (MP6), *L. lavocati* which is smaller and dentally more primitive, and *L. phelizoni* Russell, 1980 from Berru, a species only known by a lower jaw that is about the same size as *L. woutersi* (Russell 1980).

In *L. woutersi*, the talonid is never wider than the trigonid, and very often it is narrower. On m1-2 of *L. phelizoni* from Berru, the hypoconid is lower than in *L. woutersi*, but the entoconid is better marked than in the latter species. *L. phelizoni* mostly differs from *L. woutersi* by its wider talonid and lower hypoconid. On the m1 of *L. lavocati*, the paraconid is closer to the metaconid, and paraconid and entoconid are higher than in *L. woutersi*. Moreover, *L. lavocati* is slightly smaller than the two other species of *Landenodon*. The teeth included in our sample are smaller than the mean size of the same dental elements of *Landenodon woutersi* from Dormaal (Godinot 1980). *Landenodon* is abundant during the late Paleocene and earliest Eocene in Europe. *Landenodon woutersi* is one of the most abundant relatively large taxa in the Dormaal fauna (MP7), and this species is also present at Rivecourt (MP6b; Smith *et al.* 2014). Our sample is too limited to draw definitive conclusions, but there may be two species documented in Therdonne, *L. woutersi* and the more primitive *L. lavocati*.

Apheliscidae Matthew, 1918

Genus *Aletodon* Gingerich, 1977

Type species. — *Aletodon gunnelli* Gingerich, 1977.

Localities. — North America, Tiffanian and Clarkforkian localities of the Rocky Mountain Interior.

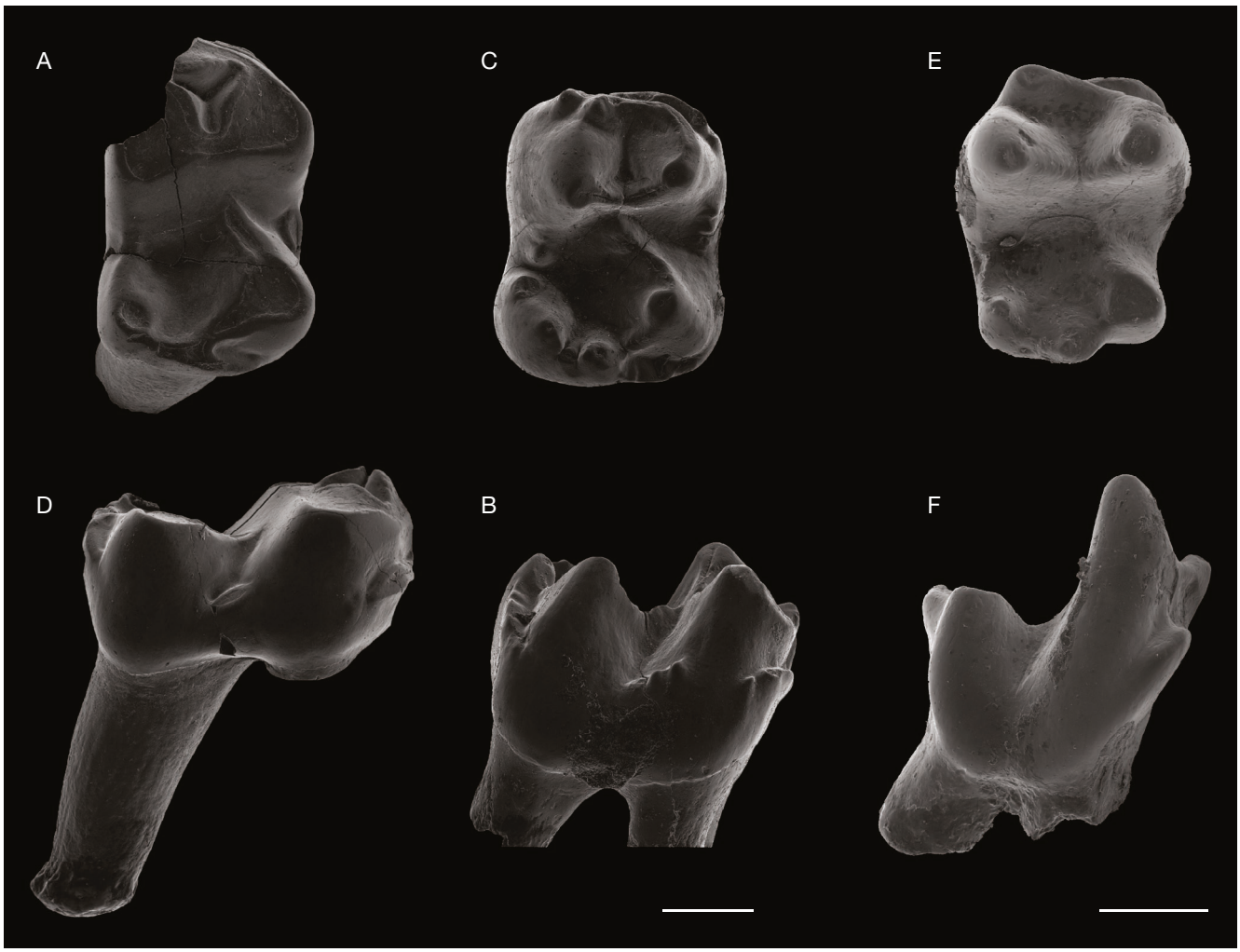


Fig. 8. — Condylarthra Apheliscidae gen. and sp. indet.: **A**, **B**, Ther-2, right m1-2 in occlusal (**A**), and buccal (**B**) views; **C**, **D**, Condylarthra Apheliscidae, *Aletodon* sp. Ther-3, m1-2 in occlusal (**C**), and buccal (**D**) views; **E**, **F**, Leptictida Pseudorhyncocyonidae, *Phakodon* sp.: Ther-46, right m1-2 in occlusal (**E**), and buccal (**F**) views. Scale bar: 1 mm. Credits: Philippe Loubry.

Aletodon sp.
(Fig. 8B, C)

Referred specimens. — Ther-3, m1-2 (L: 3.15-W: 2.32).

Description

Ther-3 is a transversely wide lower molar with bulbous cuspids. Trigonid and talonid are about equal in mesio-distal length, the former being slightly higher than the latter. The main cuspids are bulbous, inflated, the bent paracristid is well-marked, terminating in a small paraconid that stands at the mesial base of the voluminous metaconid. Below and slightly lingual to the paraconid, there is an accessory cuspid independent from the cuspidate precingulid which extends buccally up to the buccal base of the protoconid. The hypoconid is the largest and only crested cuspid of the talonid. The cristid obliqua is high and connects the postvallid centrally near the base of the V shaped metacristid. The entoconid is bulbous and bears an accessory cuspid on its mesial flank, and there is a metastylid at the distal base of the metaconid. The hypoconulid is strong, conical, centrally placed, and it is connected to the post-hypocristid, and separated from the entoconid by a groove. There is a postcingulid but only on the buccal half of the talonid. This cingulid extends buccally and joins the mesial cingulid. Buccally, the ectocingulid forms a crest with three accessory cusps.

Comparisons and remarks

Ther-3 shows the greatest similarities with certain members of the Hyopsodontidae *sensu lato*, especially Apheliscidae, and to a lesser degree with *Lessnessina* Hooker, 1979, an enigmatic genus known from the earliest Eocene of Mongolia and Western Europe (Hooker & Dashzeveg 2003). By its fairly massive, inflated cuspids, Ther-3 also resembles louisiniids such as *Berrulestes* Hooker & Russell, 2012, *Gigarton* Hooker & Russell, 2012, *Thryptodon* Hooker & Russell, 2012 or *Microhyus* from the Thanetian localities of Cernay-Berru (Hooker & Russell 2012). This resemblance between Ther-3 and these louisinids is mostly based on the bulbous cuspids of lower molars and the somewhat similar relative size of

the trigonid/talonid, but none of these louisinids show the combination of crest pattern, the development of cingulids, and the accessory cusps seen in Ther-3. The lower molar of the enigmatic *Lessnessina khushuensis* Hooker & Dashzeveg, 2003 from the Bumban Member, Tsagan Khushu, Mongolia, shares with Ther-3 the paraconid separated from (not fused to) the metaconid, relatively short talonid, the distinct hypoconulid with a robust entocristid that bears a small cuspid in front of the entoconid, and the development of cingulids. However, the lower molars of the three species of *Lessnessina* are about half the size of Ther-3, and all are overall more bunodont, and display a peculiar morphology that set them apart from the form from Therdonne.

Outside Europe, Ther-3 shares greatest dental features with the North American hyopsodontids *Haplomylus* Matthew, 1915 and *Aletodon* Gingerich, 1977 (Apheliscidae for Zack *et al.* 2005). These two genera display fairly bunodont lower molars with paraconids low and well separated from metaconids, hypoconulid not basally fused to entoconid, and not connected to entoconid by a crest. All these characters are present in Ther-3, which also bears many autapomorphic features. The lower molars of the Clarkforkian *Haplomylus simpsoni* Rose, 1981 share similar relative size of the trigonid/talonid, crest development of hypoconid, similar orientation of the paracristid, and development of cingulids, but differs in the reduced hypoconulid almost included in the postcristid, the lack of accessory cuspids, especially on the entocristid which is crestiform in *H. simpsoni* (Gingerich 1994; Gingerich & Smith 2006). *Aletodon* is known by three species restricted to the Tiffanian and the Clarkforkian (Gingerich 1977; Winterfeld 1982). Gingerich (1977: fig. 1) displays the penultimate lower molar (m2) of *Aletodon gunnelli* as lacking the paraconid (it is present in Ther-3), with the talonid about the same width as the trigonid, and the trajectory of the paracristid distinctly different from what is seen in Ther-3. Moreover, the lower molars of *A. gunnelli* displays a sharp and crested entocristid, and Ther-3 is about 30% smaller than the m1-2 of *A. gunnelli*. Finally, Ther-3 shows the greatest morphological affinities with and is close in size to *A. conardae* Winterfeld, 1982, known from the late Tiffanian of Wyoming, United States (Winterfeld 1982), although the latter lacks the accessory cuspids, and development of cingulids. Awaiting additional material for this taxon (notably the upper dentition), we prefer to leave Ther-3 as *Aletodon* sp. This is the first occurrence of the genus *Aletodon* in Europe, a genus so far restricted to the late Paleocene of North America.

Apheliscidae gen. and sp. indet.
(Fig. 8A, B)

Referred specimen. — Ther-2, right m1-2 (L: 3.83-W: 2.23).

Description

Ther-2 is a worn lower molar which has suffered breakage of its mesiolingual corner so that the paraconid and part of the metaconid are missing on the trigonid. Ther-2 is much larger than any known species of *Paschatherium* Russell, 1964, and the specimen differs from molars of *Landenodon* in lacking the thick buccal cingulid, and a mesially oriented cristid obliqua. Instead, and despite the wear, this lower molar (probably an m1) shows a long and thin mesial cingulid; the buccal cingulid is absent. The trigonid is higher and mesiodistally shorter than the talonid, the small hypoconulid is central in position although slightly closer to the entoconid than the hypoconid, and the cristid obliqua joins the base of the protoconid. The apparent connection of the entoconid to the posterior cingulid is due to wear. Because of the mesial breakage, it is impossible to state whether the paraconid and metaconid are coalescent. There is a small ectostylid, and the mesial cingulid extends slightly onto the buccal flank of the protoconid.

Comparisons and remarks

The lower molar Ther-2 shows some resemblance with the basal artiodactyl *Diacodexis* Cope, 1882, but the hypoconulid does not appear cuspidate in Ther-2, and the wear does not allow to distinguish a groove separating the hypoconulid and the hypoconid (Boivin *et al.* 2018), nor a continuous structure uniting the hypoconulid and the hypoconid resulting from heavy wear such as reported by Smith *et al.* (1996). Ther-2 closely resembles the lower m1 of Paleocene "hyopsodontids" (*sensu lato*) from North America, although it differs from them by its crown proportion (mesiodistal elongation and reduced width), less inflated cuspids, less-developed cingulids, and lack of cuspidate hypoconulid. The trigonid is not mesio-distally compressed in Ther-2 like in *Hyopsodus* Leidy, 1870, and the breakage hampers observation of the paraconid and paracristid that are important features to distinguish taxa within hyopsodontids (Zack *et al.* 2005). Among genera of Apheliscidae from North America, Ther-2 shares the highest resemblance in its overall structure with the lower molar m1-2 of *Litomylus* Simpson, 1935 which is a common genus known by six species from the Puercan to the Tiffanian of North America (Lofgren *et al.* 2004). However, the molar from Therdonne differs by its crown proportion (even when compared with a m1 of the type species *Litomylus dissentaneus* Simpson, 1935), its crescentic hypoconulid linked to the entoconid by crest, the trigonid and talonid cusps are not as swollen, and the lack of buccal cingulid. Further material of this taxon is needed to ensure its identification, but it is not referable to anything known in the Paleocene or early Eocene of Western Europe.

LEPTICTIDA McKenna, 1975
Pseudorhyncocyonidae Sigé, 1974

Genus *Phakodon* Hooker, 2013

Type species. — *Phakodon levei* (Russell, Louis& Poirier, 1966).

Localities. — France, Berru (MP6, late Paleocene).

Phakodon sp.
(Fig. 8E, F)

Referred specimen. — Ther-46, right m1-2 (L: 2.8-W: 1.9).

Description
The crown of m1 is subrectangular in occlusal outline, with the trigonid elevated above and narrower than the shallow talonid. The crests are overall poorly expressed. The strong, shelf-like precingulid is developed below the paraconid and paracristid. The apex of the paraconid is slightly lingual to the longitudinal axis of the crown, and this cuspid, which is about half the height of the metaconid, is more mesiodistally compressed than the other trigonid cusps. If the protoconid and metaconid are subconical and sub-equal in size; the metaconid is slightly higher than the protoconid. The paracristid extends mesiolingually from the base of the protoconid to the paraconid, which has no crest on its lingual side. The talonid is transversely narrower than the trigonid, and mesiodistally short. The hypoconid is the most voluminous and highest cuspid of the talonid; entoconid and hypoconulid are subequal in height. The hypoconulid is centrally placed, mesiodistally compressed, and positioned slightly posterior to the other talonid cusps. The cristid obliqua is faint and meets the postvallid surface slightly buccal to the protocristid notch, while the faint and straight pre-entocristid extends mesially from the apex of the entoconid but terminates just before reaching the postvallid surface.

Comparisons and remarks
This molar is identified as a m2 because of its short trigonid, and it is very similar in cusp and crest pattern to the pseudorhyncocyonid *Phakodon levei*, from the MP6 biochron of Cernay-Berru (Hooker 2013). The main differences are that Ther-46 displays a narrower and shorter talonid, smaller paraconid, less splayed protoconid and metaconid in occlusal view, relatively bunodont, weak entoconid and poor development of the pre-entocristid. Because of these morphological differences, and given the paucity of our fossil material, we leave Ther-46 as *Phakodon* sp. This genus was so far only recorded from the Berru locality (MP6), this occurrence in Therdonne extends its range to MP6b. It is worth noting that a possible pseudorhyncocyonid has also been reported from the latest Paleocene of Albas (Tabuce *et al.* 2025), but it is only documented by an upper molar, thus limiting comparison. Pseudorhyncocyonids are rare elements known from few Paleocene and Eocene localities of Europe (Hooker 2013).

DISCUSSION

Late Paleocene mammals of the Paris Basin are represented by the MP6 reference fauna of Cernay and Berru near Reims (Russell 1964), and by the slightly younger MP6b fauna from Rivecourt (Smith *et al.* 2014). Another mammal locality in the Thanetian Marne de Montchenot is also allocated to MP6 (Jehle *et al.* 2012). While the MP6 fauna is dominated by endemic European lineages, the MP7 fauna is characterized by the input of exogenous "modern" taxa, suggesting one or more episodes of dispersals from North America, and probably also from Asia. The southern and eastern parts of the Paris Basin were emerged in the Late Paleocene, and river systems together with estuaries or deltas developed on land and on the coasts. In the area of Therdonne, the environment is generally estimated as more marine, but the lithological succession, sedimentary structures, and (ichno)fossils clearly indicate continentalization of the area during the latest Thanetian.

Sequence stratigraphy
In Western Europe the Thanetian is marked by four transgressive-regressive third order-cycles that can be recognized in England (Powell *et al.* 1996), Belgium (Steurbaut 1998), and France (Briais *et al.* 2016). Depending on the location in the Paris Basin and the importance of hiatuses in the borehole, these four cycles are potentially identifiable because the tectonic overprint is very weak during the late Thanetian, which is a period of relative quiescence (Ruban *et al.* 2010). Correlation of the different orders of cycles can be proposed from well to well, but the observation of sequences directly on outcrop is generally more difficult because of limited rock exposures, scree, and relatively dense vegetation in non-cultivated areas. The third-order eustatic cycles of Haq *et al.* (1987) have been used to correlate sequences regionally and at larger scale for sequence stratigraphic correlation (e.g. Xu *et al.* 2023).

There are three different bounding surfaces that can be used in sequence stratigraphy (Catuneanu 2002). The maximum flooding surfaces (MFS) are important surfaces which generally contain biostratigraphic markers (foraminifera and calcareous nannofossils) allowing correlation because these onlapping surfaces are considered as essentially synchronous horizons in the Paris Basin (e.g. Guillocheau *et al.* 2000). We acknowledge that the proximity of the Bray Fault may bias a sequence stratigraphic approach for dating sedimentary sequences, but the activity and influence of the Bray Fault on the sedimentary-lithology pattern in the Therdonne area is not clearly demonstrated during the late Thanetian. Maximum regressive surfaces (MRS) and unconformities (UN) can also be used for correlation at the scale of a sedimentary basin (Catuneanu 2002; Catuneanu *et al.* 2011). An integrated biostratigraphic and sequence stratigraphic approach provides a useful mechanism for correlation of the sequence exposed at Therdonne with the boreholes known in the northern part of the Paris Basin. Because of paleogeography and local environmental conditions at any given time in the study area, local stratigraphic sections may reflect changes in eustasy, subsidence, and variation of sedimentary flux in the late Thanetian time interval.

Dutheil *et al.* (2002) interpreted the sequence exposed at the Mont de Bourguillemont as a transgressive-regressive sequence although the maximum flooding surface is poorly expressed and was not clearly identified. There is clearly a regressive trend from the shallow marine Bracheux Formation to the lacustrine limestone with calcretes, and this sequence is bounded by two major erosional surfaces which correspond

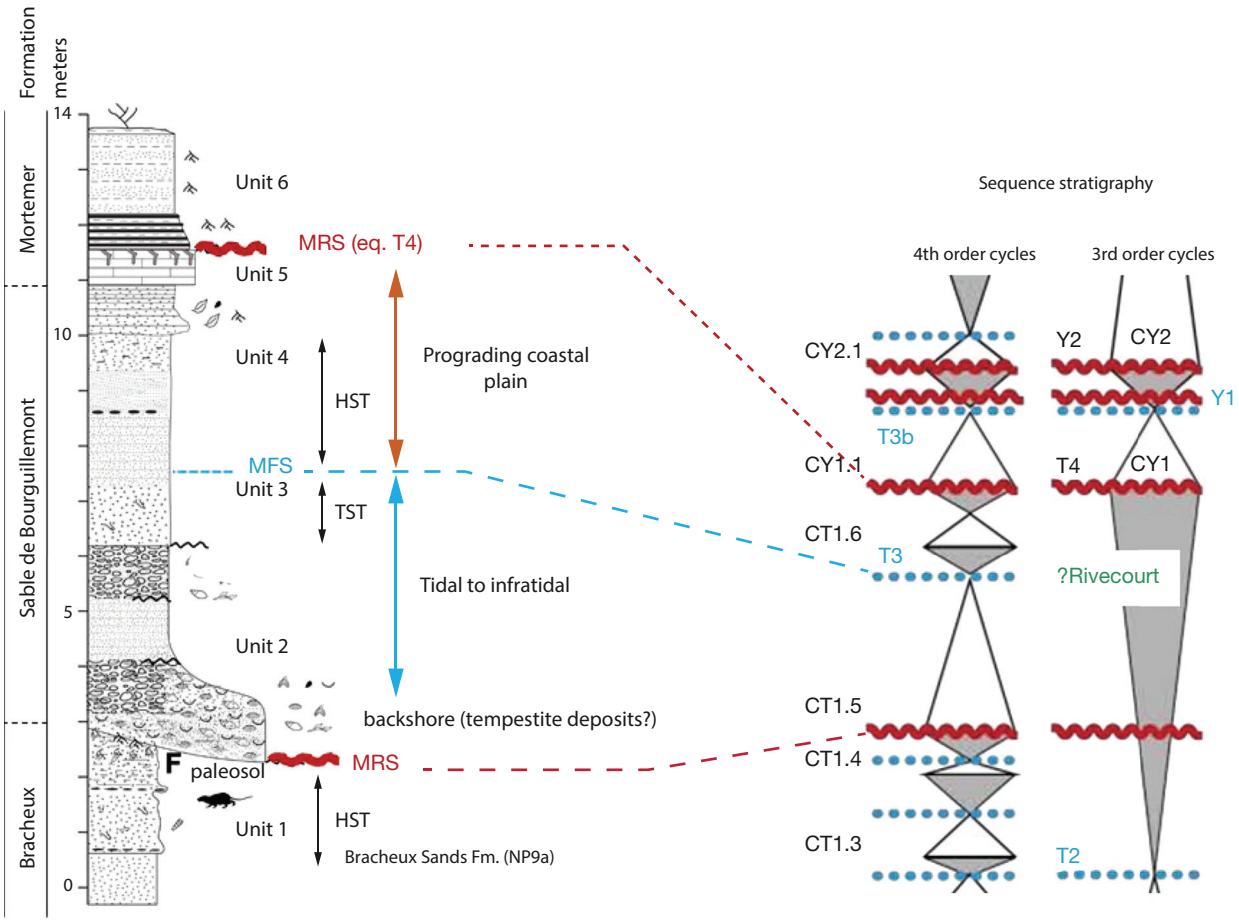


FIG. 9. — Sequence stratigraphic interpretation of the Therdonne section, and tentative correlation with the stratigraphic cycles of the Paleocene-Eocene sediments of the Paris Basin (adapted from Briais *et al.* 2016). The tentative position of Rivecourt in this sequence stratigraphic framework is discussed in the text. The interpretation of depositional environments and system tracts are adapted from Dutheil *et al.* (2002). CT and CY designate Thanetian and Ypresian transgressive-regressive stratigraphic cycles, respectively. Abbreviations: **HST**, highstand system tract; **MFS**, maximum flooding surface; **MRS**, maximum regressive surface; **TST**, transgressive system tract (Catuneanu *et al.* 2009, 2011).

to the paleosol incised by the Bourguillemont sands at the base, and the calcrete and paleokarst that developed on top of the lacustrine limestone at the top (Fig. 9). These two major erosional surfaces may equate to maximum regressive surfaces (MRS) corresponding to the shallowest or the most proximal surface along a depositional profile (Catuneanu *et al.* 2009). Dutheil *et al.* (2002) identified a massive sandstone with some bioturbations in their section (which is about 200 m SE of our fossil locality and section) as a transgressive system tract capped by a poorly expressed maximum flooding surface. We did not clearly identify this unit, but the vegetation and scree up section generally hamper precise observation, and we have missed this shallow marine unit. The thick sequence of fluvial sands and clays overlying the transgressive infra-tidal deposits certainly corresponds to a prograding alluvial plain passing upward to lacustrine deposits.

Briais *et al.* (2016) identified several sequence bounding surfaces defining fourth-order transgressive-regressive stratigraphic cycles in the late Thanetian on the Sailly-1 well situated 60 km to the east of Therdonne, and well-log correlations with the Cuise-la-Motte borehole situated 2 km away are also provided. The paleosol on top of the Bracheux sands corresponds to an erosional surface in a continental environment and is equivalent to an unconformity (UN) in the sense of Embry (2009) and thus corresponds to a MRS. This unconformity is recognized in the Sailly-1 and Cuise-la-Motte boreholes and corresponds to a sharp transition between the Bracheux Sands Formation (interpreted as Highstand System Tract, HST) and the fluvio-estuarine Bourguillemont Sands Formation (Briais *et al.* 2016: fig. 2). It is worth noting that this erosional surface is also present in the upper part of the Upnor Formation in the London Basin (Powell *et al.* 1996: fig. 10). The Upnor Formation contains calcareous nannoplankton indicative of the lower part of zone NP9, thus equivalent in age to the Bracheux Sands Formation. Therefore, this unconformity may be a regional erosional surface that occurs throughout northwest Europe and is most likely related to tectonic upheaval in the North Atlantic (Powell *et al.* 1996). Following the interpretation of earlier authors, Briais *et al.* (2016) suggest that this unconformity is the time equivalent of the Cernay conglomerate Formation which is exclusively in the Reims area, 150 km to the east. The relationship between the Thanetian marine formations exposed in the north of the Paris Basin and the

Thanetian lacustrine deposits in the eastern part of the Paris Basin remains to be established (Aubry *et al.* 2005). The mammal yielding Cernay conglomerate Formation lies just above the Sables de Rilly which may be decalcified facies of the Sables de Châlons-sur-Vesles (Aubry *et al.* 2005). However, the Berru lens which has also yielded mammals (Russell *et al.* 1966) is within the upper part of Sables de Rilly, and must be slightly older. The marine Châlons-sur-Vesles Formation is exposed in the eastern part of the Paris Basin, where it has yielded calcareous nannoplankton indicative of the lower part of zone NP8 (Aubry *et al.* 2005). This is consistent with the MP6 mammal assemblage of Cernay and Berru, which yielded "archaic" endemic European taxa without any modern taxa such as rodents or carnivoraforms that are present at the MP6b locality of Rivecourt in the Oise Valley. The European MP6 biohorizon has been correlated with the early Clarkforkian NALMA (Hooker & Millbank 2001) or with late Tiffanian NALMA (Beard & Dawson 1999; Smith *et al.* 2014; Jehle *et al.* 2019; Beard *et al.* 2020). The absence of rodents and tillodonts in the well-sampled Cernay fauna argues against a correlation with the Clarkforkian, and magnetostratigraphic study of the Mont de Berru Paleocene sequence would help further constraining the age of that fauna with respect to the C25r magnetochron.

The MRS indicated by the calcretes on top of the lacustrine limestone in Therdonne may be regarded as equivalent to the MRS T4 identified in the Sailly-1 and Cuise-la-Motte boreholes (Briais *et al.* 2016: fig. 2). It corresponds in the Paris Basin to the emersion attested by the sedimentary facies of the top of the Bracheux sands Formation (Pomerol *et al.* 1977). This erosional unconformity (T4, Fig. 9) is a major type 1 sequence boundary that has been recognized worldwide because it corresponds to a major drop of sea level that precedes the marine transgression, which starts just before the onset of the CIE, and continues during the PETM, thus marking the first Eocene transgressive pulse (Powell *et al.* 1996). This maximum regression occurs before the onset of the CIE and may correspond to the cooler event near the end of the Thanetian at 56.4 Ma (Briais *et al.* 2016). This MRS T4 is correlative with the upper boundary of the Tht-4 sequence of the London Basin (Powell *et al.* 1996). This major type 1 sequence boundary has also been recognized in the Gulf Coastal Plain, Mississippi, United States (Mancini & Tew 1995; Beard & Dawson 2009). In Europe, the Dormaal sand member of the Tienen Formation which yielded the reference MP7 fauna of Dormaal represents incised valley deposits (lowstand system tract), interpreted as an initial transgressive tract (TE 1.1 sequence of Steurbaut 1998: fig. 12). These incised valley-fill deposits rest unconformably upon shallow marine Grandglise sands of the Hannut Formation. In the Paris Basin, this MRS is within the Mont Bernon Group and may correspond to the Mortemer Formation which registered the CIE (Aubry *et al.* 2005; Quesnel *et al.* 2011).

Between the unconformity (MRS) incising the Bracheux sands and the T4 MRS that is situated near the base of the Mortemer Formation exists the fourth order maximum flooding surface (MFS) T3 which is a major MFS within this regressive trend and could define a cycle of intermediate order within this dominant trend (Briais *et al.* 2016). MFSs are important surfaces in sequence stratigraphy because they are time-lines allowing precise correlation within a basin (Baum & Vail 1988). This is applicable here because the late Thanetian is a period of relative quiescence in terms of local tectonics in the Paris Basin, which reduces the risk of truncated surfaces and thus diachronic correlations. According to Briais *et al.* (2016), T3 would correspond to the Marqueglise Marls Formation or its lateral equivalent the Bourguillemont Sands Formation which is generally regarded as localized protected marine deposits. This marine domain passed laterally to an area of nondeposition (hiatus), probably with fluvial bypassing. It is worth noting that Aubry *et al.* (2005) correlated the Marquéglise Marls with the NP9 at the Rollot Quarry (*c.* 40 km northeast of Therdonne) where the Mortemer Formation overlies the Marquéglise Marls Formation. In the London Basin, the MFS of the Tht-4 sequence is not well expressed at outcrop and lies at the base of a unit with *Ophiomorpha* burrows in the Upnor Formation, which is the same age as the Bracheux sands Formation (Powell *et al.* 1996). The MFS T3 is dated biostratigraphically and correlates with the W1 (*Wezellielacea*) zone and dinocysts D4c zone (Chateauneuf & Gruas Cavagnetto 1978, updated) suggesting an age interval of 56.9-55.8 Ma. Briais *et al.* (2016) combined chemostratigraphic (Cramer *et al.* 2011) and cyclostratigraphic (Laskar *et al.* 2011) data to propose an age of 56.9 Ma for T3. Therefore, the age of T3 provides a minimum age for the mammalian fauna reported here, since the paleosol is about 5 meters below the purported T3 identified by Dutheil *et al.* (2002). The age of the Therdonne mammal fauna is thus bounded by the age of the base of the nannoplankton zone NP9a (i.e., 57.2 Ma, Speijer *et al.* 2020) and the age of T3 which is estimated at 56.9 Ma (Briais *et al.* 2016).

The MP6b in the Paris Basin

The biohorizon MP6b was introduced on the basis of an atypical pre-PETM mammalian fauna from the Tremp Formation exposed in the Spanish central Pyrenees (López-Martínez & Peláez-Campomanes 1999). This MP6b reference fauna dated to the lower part of NP9 includes both Cernaysian and Neustrian taxa (Smith *et al.* 2014) and correlated with the lower Clarkforkian 1-2 (following the biozonation proposed by Secord *et al.* 2006), because of the low species richness and low diversity index (70% *Paschatherium*), and comparing with typical MP6 and MP7 assemblages (López-Martínez & Peláez-Campomanes 1999). Subsequently, the discovery in the Petit Pâtis Quarry in the Oise Valley of the Rivecourt biota, which is characterized by the first appearances of rodents and "miacid" carnivoraforms (both missing in the type MP6b localities of the Spanish Pyrenees) led Smith *et al.* (2014) to lump the localities of Tremp (Spain), Jibou (Romania) and Rivecourt (France) in a tentative new European Land Mammal Age, intermediate between Cernaysian (MP6) and Neustrian (MP7) faunas. This MP6b biozone does not correspond strictly to the PEI biozone defined by Hooker (1996), which includes pri-

mates and *Coryphodon* that are missing in Rivecourt (Smith *et al.* 2014). Considering that the MP6b correlates with the Clarkforkian-2 (Cf-2) (following the definition given by Anemone *et al.* 2024) as assumed in this work, there is still a hiatus in the Anglo-Belgian-Paris Basin between the Cernay and the Rivecourt-Therdonne faunas, which would roughly correspond to the Clarkforkian-1 (Cf-1) since it is generally admitted that the Cernaysian correlates with the late Tiffanian faunas (Beard & Dawson 1999) although the later correlation still needs to be confirmed with additional data. According to the calibration of the North American Tiffanian and Clarkforkian NALMA proposed by Anemone *et al.* (2024), the biozone Ti-6 straddles the magnetochron C25n and C25r while the biozone Ti-5 is in the C25r. A magnetostratigraphic study of the Paleogene sequence exposed on the Mont de Berru would certainly allow further testing of the age of the Cernay-Berru faunas, and therefore the importance of the hiatus between MP6 and MP6b faunas.

The Rivecourt fauna has been found in a sedimentary unit that plugs part of the hiatus in the Paris Basin between the Berru Sandstones-marnes de Montchernot and the earliest Neustrian "argile à lignite" and "Marnes à rognons". This hiatus would correspond to the top of NP8 and NP9 in marine successions (Dupuis *et al.* 1998). The new Rivecourt Sand Member introduced by Smith *et al.* (2014) is a lignitic sand tentatively correlated with the "Sables ligniteux supérieurs" (Upper lignitic sands) evidenced in boreholes, including Le Tillet (Blondeau *et al.* 1968, 1976). Unlike the classical Sparnacian facies of lignitic marls and sands (Graves 1847), the Rivecourt Sand Member has not yielded any amber remains suggesting that the tree producing amber appeared during the PETM (De Franceschi & De Ploëg 2003). The proposed correlation of the paleosol at the top of the Bracheux sands in the Therdonne section with the unconformity identified in several boreholes (Cuisela-Motte, Le Tillet, Sailly-1) suggests that the Therdonne fauna is older than that of Rivecourt.

Comparisons with the late Paleocene Holarctic faunas – Intercontinental biochronologic correlations

Presently, the Therdonne fauna documents nine species of mammals based on approximately 45 dental specimens. The main feature of the fauna is the relative diversity of its rodents, previously attested in the MP6b faunas by incisor fragments that are not taxonomically diagnostic (Smith *et al.* 2014). The rodent molars represent *c.* 20% of the dental specimens recovered at Therdonne, allowing recognition of three different taxa that make their first occurrence in Europe: the ischyromyoid *Ailuravus*, previously known from several earliest Eocene faunas of Europe (Escarguel 1999; Missiaen *et al.* 2013), the basal theridomorph *Sparnacomys* and a tiny microparamyine? ischyromyid both so far unknown before the base of the Eocene (Escarguel 1999). The Albas fauna of southern France, dated to a few thousand years before the CIE, has yielded two species of ischyromyid rodents, including *Acritoparamys atavus* known in the Clarkforkian-1 in North America (Tabuce *et al.* 2025).

The artocyonid *Landenodon* sp. is the most abundant species in the Therdonne assemblage, being represented by 30% of the recovered specimens. *Landenodon* belongs to the core archaic Paleocene fauna of Europe, and its stratigraphic range straddles the Paleocene-Eocene boundary (Godinot 1980). The louisinid *Paschatherium* is another taxon endemic to Europe which is generally abundant (>60% of total specimens) in the PETM faunas (López-Martínez *et al.* 2006). At Therdonne, the number of diagnostic teeth referable to *Paschatherium* in our sample does not exceed 25%, suggesting that Therdonne is not in the *Paschatherium* acme which has been interpreted as a macro-evolutionary response to the transient global warming (López-Martínez *et al.* 2006). The pseudorhyncocyonid *Phakodon* is another member of the core endemic fauna of Europe and it may be the last representative of a Paleocene lineage of pseudorhyncocyonids that went extinct during the Paleocene-Eocene transition (Hooker 2013).

Carnivorous "miacids" represent 14% of the fossils reported here, and they document the FAD of the carnivoraform *Dormalocyon* in Europe. Miacids are otherwise represented by *Vassacyon prieuri* from Rivecourt and *Gracilocyon* sp. from the MP6b locality of Jibou in Romania, which previously were the earliest occurrences of carnivoraforms in Europe and are two index taxa of the MP6b biozone (Solé *et al.* 2016). *Dormaalocyon latouri* is the third basal carnivoraform known in Europe during the late Thanetian, a group that first appeared in the Clarkforkian 2 in North America (Anemone *et al.* 2024). While basal carnivoraforms are represented in North America by the sole genus *Uintacyon*, they show an unexpected late Paleocene diversity in Europe with three genera (*Dormaalocyon*, *Gracilocyon* and *Vassacyon*), which represent three distinctive morphologies and ecomorphs (Solé *et al.* 2016).

It is worth noting that *Uintacyon*, which is a common element of the Cf-2 faunas in North America, dispersed to Europe by PE-III (Hooker 1996) while *Dormalocyon* never dispersed to North America. The presence of *Dormalocyon* in the late Paleocene of Europe is consistent with an Asian origin of this genus (Solé *et al.* 2016), thus involving faunal exchanges through the Turgai Strait (Hooker & Dashzeveg 2003) prior to the PETM.

Among the unexpected findings at Therdonne, the lower molar referred to *Aletodon*, a genus so far restricted to North America, confirms faunal exchanges between North American and Europe, and further constrains the Paleocene age of the Therdonne fauna. The latter is however still incompletely sampled since it lacks several taxa that are fairly common in the Rivecourt fauna such as plesiadapiforms and pleuraspidotheriids. This absence may be related to a taphonomic bias or it may reflect a distinct paleoenvironment, knowing that paralic flat landscapes can change rapidly with sea level rise or fall.

If the MP6b biozone is characterized by the first occurrence of rodents and "miacid" carnivoraforms in Western Europe, the rest of the Clarkforkian elements (tillodonts, apatotherians, cimolestids, and *Coryphodon*) are missing so

far, suggesting a strong filtering effect for the faunal exchange along the Thulean route between North America and Western Europe during the late Paleocene. Conversely, the Clarkforkian faunas in North America lack elements of the core "archaic" Paleocene fauna documented in Cernay-Berru, notably including the pleuraspidotheriids and louisiniids. This unidirectional and selective pathway for intercontinental dispersals seems to have persisted until the end of the Paleocene as attested by the Albas fauna of southern France, dated several thousand years before the CIE, and where the the Clarkforkian elements (tillodonts, apatotherians, cimolestids, and *Coryphodon*) are also missing (Tabuce *et al.* 2025). It is worth noting that *Coryphodon* and tillodonts are still missing in those latest Paleocene faunas of Europe, and they are known so far exclusively from the MP7. Interestingly, the uppermost part of the Sables d'Ostricourt in the northern Paris Basin have yielded remains of *Coryphodon* (Malaquin 1899; Lucas 1986), and those fluvial sands correlate with the Bois-Gilles Sand Formation which is considered as latest Thanetian (Mégnien 1980; Steurbaut 1998). If these pre-PETM occurrences of *Coryphodon* are confirmed, it would reinforce the MP6b biozone as an equivalent of the Clarkforkian-2 as defined by Anemone *et al.* (2024).

The enhanced fossil data recently published from the late-latest Paleocene of Europe (Smith *et al.* 2014; Tabuce *et al.* 2025) suggest that the North American fauna is the main source of the MP6b immigrant taxa although Asia appears as a plausible geographic center of origin for several taxa like artiodactyls, carnivoraforms (Solé *et al.* 2016), and some rodents (Godinot & Lapparent de Broin 2003).

CONCLUSION

The new late Paleocene mammal fauna reported here from Therdonne (Oise) provides a snapshot of the mammalian community that inhabited the Paris Basin during an interesting pre-PETM interval. The immature paleosol yielding the mammalian fossil assemblage was deposited during the late Thanetian regressive trend and is stratigraphically situated on top of the Bracheux sands Formation which is dated to the NP9 nannoplankton biozone (Steurbaut 1998; Aubry *et al.* 2005). Moreover, the identification of the parasequences exposed in the Therdonne LF section, and regional correlations with relatively close boreholes in the Paris Basin indicate an age for the Therdonne mammal fauna between the base of the nannoplankton zone NP9a (i.e., 57.2 Ma, Speijer *et al.* 2020) and the age of the maximum flooding surface (T3) which is recognizable in that part of the basin (Oise) and dated to 56.9 Ma (Briais *et al.* 2016).

The Therdonne LF currently comprises nine taxa and indicates a mixture of European endemic taxa known exclusively in the Paleocene (*Phakodon*) or during the Paleocene-Eocene transition (*Landenodon* and *Paschatherium*), and cosmopolitan taxa which made their first appearance in Western Europe during the late Paleocene (MP6b biohorizon for rodents, and "miacids" carnivoraforms). Although still incompletely known, the Therdonne fauna appears to be close in age to the Rivecourt fauna, which was previously the only known MP6b fauna of the Paris Basin. While only documented by an incisor at Rivecourt, the rodents are relatively well diversified in Therdonne, and they document the earliest occurrence of European endemic Theridomorpha, and the presence of Ischyromyoidea which are present during the Clarkforkian of North America, suggesting faunal exchanges with Europe during the late Paleocene. Although poorly documented, the presence of *Aletodon*, a genus restricted to the Paleocene of North America marks the first record of Apheliscidae in Europe, thus indicating further faunal exchanges between Europe and North America during the late Paleocene (Tabuce *et al.* 2025).

The Therdonne LF reinforces the evidence of a "European Clarkforkian" proposed by previous authors (López-Martínez & Pelaez-Campomanes 1999; Smith *et al.* 2014), marked by the first occurrence of rodents and miacid carnivores. The age of the Therdonne LF inferred from sequence stratigraphy and biostratigraphy provides an age for MP6b which is consistent with of the Cf-2 proposed by Anemone *et al.* (2024). If "miacids" associated with rodents are present in Europe during the late Thanetian and thus attest for a Cf-2 equivalent biozone in Europe, the Cf-1 equivalent may be still missing in Europe even if the transition between the endemic Cernaysian fauna and the late Paleocene faunas with modern taxa may not be similar to the pattern observed in North America between Tiffanian and Clarkforkian NALMAs. The image of the latest Paleocene fauna of Europe is still incomplete and certainly skewed. For example, large and medium-sized taxa remain poorly documented for the MP6b interval.

Currently, there is no published chemostratigraphic record for the Paleocene-Eocene sequence exposed in the Mont de Bourguillemont. Likewise, dinoflagellate cyst biostratigraphy may refine the age of the Therdonne sequence with respect to the PETM, and pre-PETM carbon excursions that are recorded in several sections in North America (Bowen *et al.* 2015), and southern Europe (Tabuce *et al.* 2025). Further sampling of the Therdonne fauna will also provide important data to better understand macro-evolutionary patterns (such as provincialism or intercontinental dispersals) that occurred during the Paleocene-Eocene transition in the Holarctic region.

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