BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE SCIENCES DE LA TERRE, 74-SUPPL.: 165-175, 2004
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN AARDWETENSCHAPPEN, 74-SUPPL.: 165-175, 2004

Primitive Equoid and Tapiroid mammals: keys for interpreting the Ypresian-Lutetian transition in Belgium

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SMITH, T., DE WILDE, B. & STEURBAUT, E., 2004. — Primitive Equoid and Tapiroid mammals: keys for interpreting the Ypresian-Lutetian transition in Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **74 Supplement**: 165-175, 1 pl., 5 figs., Bruxelles-Brussel, December 15, 2004 – ISSN 0374-6291.

Abstract

Terrestrial mammal teeth, pertaining to the primitive horses *Hallensia louisi* and *Propachynolophus levei* and the tapiroid *Lophiodon remensis*, have been discovered at the base of the marine Lede Formation in the Oosterzele and Balegem sandpits, 10 km southeast of Gent. According to its calcareous nannofossil NP15 dating, the basal Lede Formation in that area belongs to the Middle Lutetian. Comparison with in situ records in the Paris Basin suggests a latest Ypresian origin for the mammals (reference-level MP10) and consequently reworking. The Oosterzele and Balegem specimens most probably originate from erosion of the continental Aalterbrugge Lignitic Horizon (uppermost Ypresian), which is cropping out nearby. The additional reworked faunal and lithological components at the base of the Lede Formation suggest that also the Aalter Formation (top NP13-base NP14) and the overlying Brussel Formation (NP14), or certain parts of these, were deposited but subsequently eroded in that area. The depositional history of the Lede Formation, resulting from the interplay of tectonic uplift and eustatic sea-level changes, is detailed.

Key words: Mammals, Perissodactyla, reworking, Ypresian-Lutetian transition, Belgium.

Résumé

Des dents de mammifères, appartenant aux chevaux primitifs *Hallensia louisi* et *Propachynolophus levei* ainsi qu'au tapiroïde *Lophiodon remensis*, ont été découvertes à la base de la Formation de Lede dans les sablières d'Oosterzele et Balegem, situées à 10 km au sud-est de Gand. L'analyse des nannofossiles calcaires indique que la base de la Formation de Lede dans cette région appartient à la biozone NP15 et est donc d'âge Lutetien moyen. La comparaison des dents de mammifères avec des spécimens in situ du Bassin de Paris suggère que celles-ci sont remaniées de l'Yprésien terminal (niveau-repère MP10). Les spécimens mammaliens d'Oosterzele et Balegem sont donc très probablement originaires de l'érosion de l'Horizon continental lignifère d'Aalterbrugge (Yprésien terminal) qui affleure dans la région. Les autres composants fauniques et lithologiques remaniés à la base de la Formation de Lede suggèrent que la Formation de Aalter (NP13 sommital-NP14 basal) ainsi que la Formation de Bruxelles sus-jacente (NP14), ou certaines parties de celles-ci, ont été déposées et érodées par la suite dans cette région. L'histoire du dépôt de la Formation de Lede, résultant de l'interaction des mouvements tectoniques et des changements eustatiques du niveau de la mer, est discutée.

Mots-clefs: Mammalia, Perissodactyla, remaniement, transition yprésienne-lutétienne, Belgique.

Introduction

Terrestrial mammal remains have been rarely preserved in the Early Palaeogene of Belgium because of its essentially marine content and erosion of continental strata during subsequent marine transgressions. The famous early Selandian Hainin mammal fauna (GODFRIAUX & THALER, 1972; STEURBAUT, 1998; SMITH & SMITH, 2003) and the earliest Eocene Dormaal mammal fauna (TEILHARD DE CHARDIN, 1927; SMITH & SMITH, 1996; STEURBAUT et al., 1999; SMITH, 2000), which figure among the internationally accepted mammal reference levels (the so-called MP-levels), are the only exceptions, being buried at the edges of the basin. Discoveries of terrestrial mammal remains in marine settings are extremely important in light of the very incomplete mammal record of these environments and the potential of precise dating of the mammal finds. Some of these, even isolated teeth, have allowed exact positioning of poorly dated continental vertebrate sites (e.g. the classic sites from the Paris Basin) into well-calibrated stratigraphic frameworks and the integrated time scale of BERGGREN et al. (1995) (HOOKER, 1996; SMITH & SMITH, 2003).

Isolated cheek teeth of middle-sized and large terrestrial mammals have recently been discovered at the base of the marine Middle Eocene Lede Formation in two sandpits south of Gent, East-Flanders (Fig. 1). The majority of the material (9 teeth and 3 tooth fragments) was collected in the Scheurbroek sand quarry at Oosterzele (map-sheet 22/6; x = 111.950; y = 181.075). It was found in a badly sorted 50-cm thick basal interval, together with sandstone pebbles, lamniform and carchariniform shark teeth, *Pristis* rostral teeth, terebratuloid brachiopods, isolated valves of the bivalve *Megacardita planicosta* and very rare crocodile and turtle remains. One complete premolar was recovered from the classic Verlee quarry at Balegem (map-sheet 22/6; x = 110.800, y = 179.100). This quarry is now almost completely filled in. A new quarry has recently been excavated a few hundred meters southward.

Fig. 1 — Location of Oosterzele and Balegem where the mammal teeth have been discovered.

Lithology and stratigraphical interpretation

The Scheurbroek sand quarry at Oosterzele

A seven-meter thick section, of which the lithological description is given in Fig. 2, is exposed at the hamlet of Scheurbroek, 1.5 km southeast of the Oosterzele village centre and about 2.5 km northeast of the Verlee quarry at Balegem. The middle part of the section, sandwiched between the cross-bedded medium-sand of the Vlierzele Sand Member below and the Quaternary loamy sands above, corresponds to the Lede Sand Formation. Its stratigraphy is very complex and is discussed in detail. The Lede Sand Formation can be subdivided into three units, clearly separated by omission surfaces.

Unit A

The lower unit A is highly fossiliferous and contains numerous nests of reworked medium-grained glauconite. Its lower junction is sharp and marked by intense bioturbation into the underlying Vlierzele Sand Member. Unit A presents a fining-upward trend in which several distinct layers can be identified. The lowermost 20 cm are somewhat coarser and poorly calibrated, consisting of a layer of flat sandstone pebbles and large shark (*Pristis*) teeth at the extreme base and, dispersed into the sandy matrix, rolled sandstone fragments and isolated *Megacardita planicosta* valves, always in convex-up position. The larger sandstone fragments and the *M. planicosta* valves are no longer present in the overlying 15 cm thick fossiliferous fine sand. Between 35 cm and 50 cm above the base of the Lede Formation the sandstone pebbles reappear, in association with concentrations of shark teeth and intact brachiopods. This layer is locally cemented into sandstone blocks and laterally into an irregular sandstone layer. Above this layer occurs a 70 cm thick, rather well calibrated and bioturbated fossiliferous fine sand, rich in small bivalves, ray teeth and tiny *Nummulites variolarius*.

Unit B

An irregular, undulating surface separates unit B from the underlying unit A. Its lowermost 10 cm consist of fossiliferous very fine sand, locally slightly obliquely laminated, rich in small ray teeth, *N. variolarius* and brachiopods. This sand, which is sporadically burrowed into the underlying unit, is overlain by a 30 cm thick continuous fossiliferous sandstone bed and by 70 cm of bioturbated rather well calibrated fine sand.

Unit C

The base of unit C is marked by an undulating surface, without obvious burrows. This unit consists of whitish bioturbated very fine sand with concentrations of *N. variolarius* at base and top.

A very detailed calcareous nannofossil investigation was carried out in order to assess the age of the different units identified. The co-occurrence of *Nannotetrina quadrata* (Bramlette & Sullivan, 1961) Bukry, 1973 and *Blackites gladius* (Locker, 1967) Varol, 1989 allows the Lede Formation at Oosterzele to be attributed to calcareous nannofossil zone NP15 of Martini (1971; see also Perch-Nielsen, 1985) and to zone CP13 of Okada & Bukry (1980), which are of middle Lutetian age. The marker species *N. quadrata* seems to be restricted to the lower 20 cm of unit A, whereas *B. gladius* has only been observed in unit C, enabling a further biostratigraphic subdivision of the Lede Sand Formation. The following biostratigraphic useful taxa are found throughout the Formation: *Lanternithus minutus* Stradner, 1962, *Braarudosphaera stylifera* Troëlson & Quadros, 1971 and *Discoaster wemmelensis* Achuthan & Stradner, 1969. The underlying and overlying units appeared to be carbonate-free and could not be dated on the basis of micropaleontological criteria.

The Verlee sand quarry at Balegem

Jacobs & Sevens (1994) investigated the lithology and stratigraphy of this currently abandoned sand quarry. They recognised the following units (in ascending order and with local maximum thickness): the Vlierzele Member (7 m), the Lede Sand Formation (7.5 m) and the Maldegem Formation, including the Wemmel Sand Member (2 m) and the Asse Clay (4 m) (see Fig. 5 for an overview of the stratigraphy). Only the Lede Sand Formation, as observed in the old quarry, will be discussed here.

The lower boundary of the Lede Sand Formation is complex and marked by an irregular and undulating but

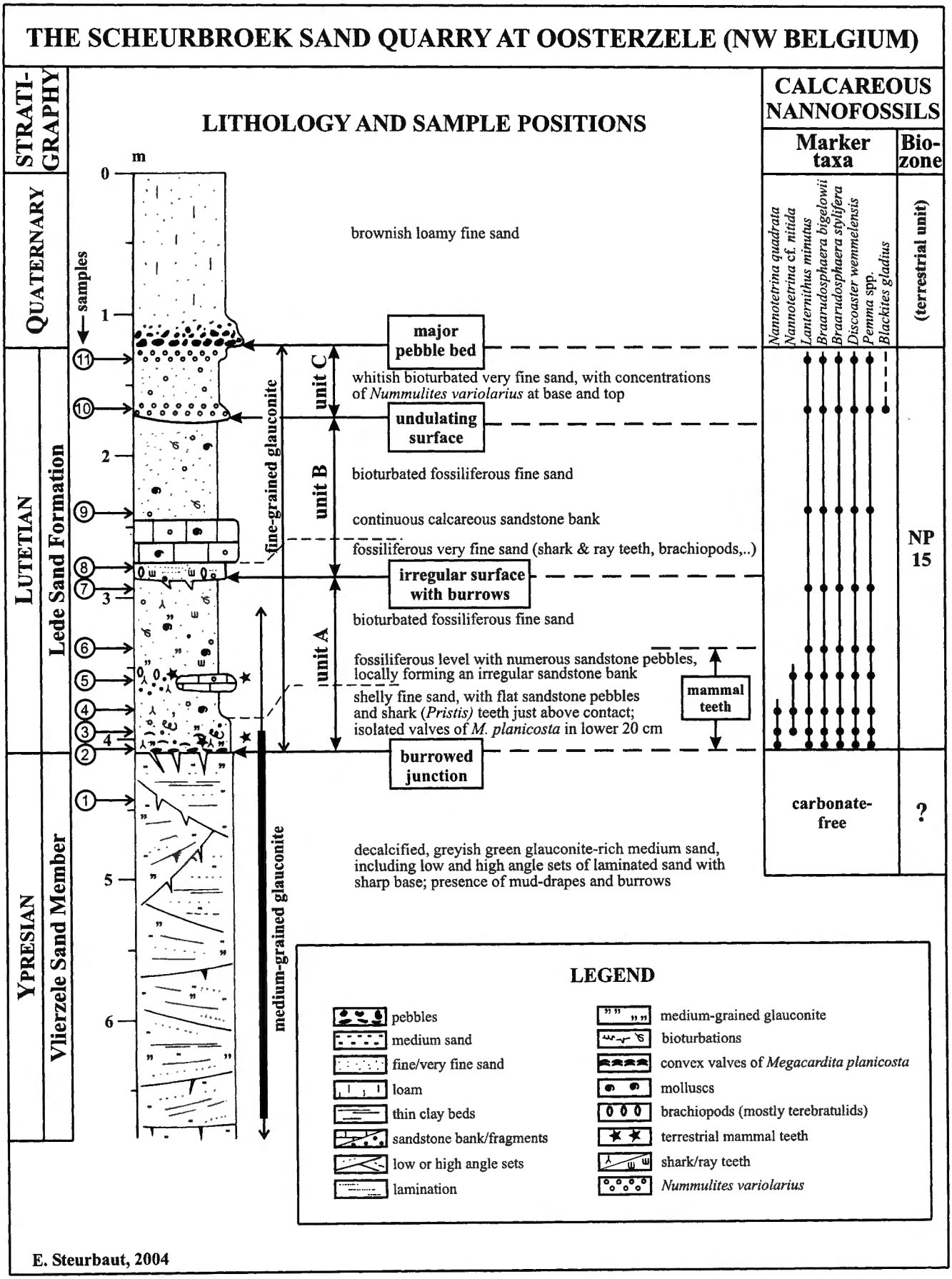

Fig. 2 — Lithostratigraphy of the Scheurbroek sand quarry at Oosterzele.

sharp surface. It is overlain by a 10-cm thick heterogeneous package of fine calcareous sands, containing well-rounded calcareous sandstone pebbles, abundant *Nummulites variolarius* and (at the base, in broad shallow gullies) shell grit concentrations of transported *Megacardita planicosta* specimens, typical for the Aalter Formation. It is overlain by 70 cm fossiliferous fine sand. The lower 30 cm of this 80 cm thick unit is locally cemented forming an irregular sandstone bank (FOBE, 1986; NOLF & STEURBAUT, 1990). About 80 cm above the base of the Lede Formation occurs a second sharp boundary, underlined by a lag of small calcareous sandstone pebbles with shell grit and shark teeth. In the overlying 6 to 7 m thick calcareous fine sands occur 3 thin sandstone layers of which the uppermost is often laterally replaced by a layer of coarse sand. The topmost part of the Lede Formation is locally leached and consists of white fine pure quartz sands and brown iron staining (oxidation) with clay infiltration. It is intensely bioturbated and sometimes mixed with glauconitic fine sand of overlying Wemmel Sands.

The Lede Sand Formation in the Balegem quarry is fairly rich in macrofossils, among which are molluscs, shark teeth (essentially in the two lowermost gravel beds), and fish otoliths (NOLF, 1974). HOOYBERGHS investigated the planktonic (1984) and the benthic foraminifera (1985). Calcareous nannofossil investigation was carried out by one of the authors (ES) in the late 1980s using a set of samples collected by NOLF in 1972. The marker species *Nannotetrina quadrata* was not found, because the basal 30 cm of the Lede Formation was not sampled, being cemented in the sampled quarry front. The first *Blackites gladius* were recorded in a shell bed at about 3 m above the base, similar to its position in the Oosterzele quarry. *B. gladius*, *L. minutus*, *B. stylifera* and *Discoaster wemmelensis* remain consistenly present up to the top of the 7 m thick Lede Sand Formation, allowing its attribution to Zone NP15 and Zone CP13.

Abbreviations

IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles.
MNHN: Museum National d'Histoire Naturelle, Paris, France.
MSNL: Museum des Sciences Naturelles, Lyon, France.
GMH: Geiseltalmuseum, Halle an der Saale, Germany.

Systematic palaeontology of the mammals

Class Mammalia LINNAEUS, 1758
Order Perissodactyla OWEN, 1848
Suborder Hippomorpha WOOD, 1937
Superfamily Equoidea GRAY, 1821
Family indet.
Genus *Hallensia* FRANZEN & HAUBOLD, 1986
Type species *Hallensia matthesi* FRANZEN & HAUBOLD, 1986

Hallensia louisi HOOKER, 1994

Plate 1, Figures 1-2

HOLOTYPE
Left M^1 or M^2 from the Argiles à Lignites d'Epernay, Mutigny (Marne, France), MP8-9, Early Eocene.

NEW MATERIAL
Left M_3 (specimen IRSNB M 1861), right P_4? (specimen IRSNB M 1862) from the Scheurbroek sand quarry at Oosterzele (NW Belgium).

DESCRIPTION AND DISCUSSION
The M_3 presents a weak development of the hypoconulid and of the hypolophid, which is typical for the genus *Hallensia*, the most primitive equoid perissodactyl (HOOKER, 1994; FROEHLICH, 1999, 2002). The M_3 from Oosterzele is much smaller than these of *Hallensia matthesi* FRANZEN & HAUBOLD, 1986 from the Lutetian of Geiseltal (specimen GMH XIV/1731, unteren Unterkohle, MP11, Germany; FRANZEN & HAUBOLD, 1986, pl. 3, fig. 3) and *H. parisiensis* FRANZEN, 1990 from the "Sables à Unios et Térédines" of Monthelon (MP10, Marne, France). It is similar in morphology to these of the species *H. louisi* known from several late Ypresian localities of the Paris Basin. However, the M_3 from Oosterzele is slightly smaller than the M_3 of *H. louisi* from Avenay (specimen MNHN Av-65519, SAVAGE et al., 1965, fig. 4g; MP8+9, France), and the postentocristid and posthypocristid show a slight difference in morphology. This could result from intraspecific variability and/or from the wear of the tooth crests. The worn P_4 is here provisionally referred to *H. louisi* by its size, the rounded outline of the tooth in occlusal view, and the presence of two distinct cusps on the talonid (entoconid and hypoconid). This determination is tentatively made by comparison with the P_4 of *H. matthesi* because no complete P_4 of *H. louisi* has been described until now.

Family Palaeotheriidae BONAPARTE, 1850
Genus *Propachynolophus* LEMOINE, 1891
Type species *Propachynolophus gaudryi* (LEMOINE, 1878)

Propachynolophus levei HOOKER, 1994

Plate 1, Figures 3-8

HOLOTYPE
Left maxilla with P^3-M^3 from the Sables de Cuise, Condé-en-Brie (Aisne), France; MP8-9, Early Eocene.

NEW MATERIAL
Left M_1 (specimen IRSNB M 1863), fragment of right M_3 (specimen IRSNB M 1864), right M_3 (specimen IRSNB M 1865), right M^1 (specimen IRSNB M 1866), right upper molar broken labially (specimen IRSNB M 1867), fragment of left upper molar (specimen IRSNB M 1868) from the Scheurbroek sand quarry at Oosterzele (NW Belgium).

DESCRIPTION AND DISCUSSION

This species belongs to the equoid family Palaeotheridae on the basis of its typical tooth morphology, marked by the important development of the hypoconulid on M_3, by the preparaconule crista on the upper molars that is directed towards the preparacrista but not joining it; by the centrocrista forming a ridge labially; and by the well-developed parastyle. The completely worn lower molar can be attributed to an M_1 by its moderate size. It shows a rectangular outline in occlusal view, which is different from the contemporaneous genus *Hallensia*. Several characters allow identifying this species as belonging to the genus *Propachynolophus* LEMOINE, 1891, which is considered as one of the most primitive palaeothere taxa according to the most recent phylogenetic analyses of the early perissodactyls (HOOKER, 1994; FROEHLICH, 1999, 2002). The M_3 hypoconulid basin is larger than in the other palaeotheres, but the hypolophid is moderate. The morphology of the centrocrista on the upper molars, which is devoid of a mesostyle is much less derived than in the more lophodont and dilambdodont palaeothere genera *Pachynolophus* POMEL, 1847, *Lophiotherium* GERVAIS, 1852, *Propalaeotherium* GERVAIS, 1849, *Plagiolophus* POMEL,1847, *Anchilophus* GERVAIS, 1852, and *Palaeotherium* CUVIER, 1804. The metaconule is less developed and more integrated in the metaloph than in the basal palaeothere *Hyracotherium leporinum* OWEN, 1841. The specimens from Oosterzele are attributed to the species *Propachynolophus levei* HOOKER, 1994, which is only known from the French locality of Condé-en-Brie (specimen CB 16165, MP8+9, Paris Basin), indicating a late middle to early late Ypresian age. This identification is based on the small size of the species in comparison with the type species *P. gaudryi* (LEMOINE, 1878) from the latest Ypresian of the Epernay area (MP10, Marne, France), and on the slightly developed dilambdodonty in M^1 without mesostyle.

Suborder Ceratomorpha WOOD, 1937
Superfamily Tapiroidea GRAY, 1825
Family Lophiodontidae GILL, 1872
Genus *Lophiodon* CUVIER, 1822
Type species *Lophiodon tapiroides* (CUVIER, 1812)

***Lophiodon remensis* LEMOINE, 1878**
Figures 3-4

NEOTYPE

Right maxilla with P^2-M^3 from the ''Sables à Unios et Térédines'', Epernay area, France, MP 10, Early Eocene.

NEW MATERIAL

Left M_3 (cast IRSNB M 1869), left DP^3 (specimen IRSNB M 1870), fragment of right M^1 or M^2 (specimen IRSNB M 1871), right M^3 (specimen IRSNB M 1872) from the Scheurbroek sand quarry at Oosterzele; right P_2 (specimen IRSNB M 1873) from the Verlee sand quarry at Balegem (NW Belgium).

DESCRIPTION AND DISCUSSION

The large lophodont M_3 and M^3 found at Oosterzele indicate the presence of a large ceratomorph tapiroid perissodactyl belonging to the typical genus *Lophiodon*. The teeth are small in comparison with most of the species of this genus well represented in the Middle Eocene. The small size and the non-labially salient paracone in occlusal outline on the M^3 allow attribution to the species *Lophiodon remensis* LEMOINE, 1878 as diagnosed by SAVAGE et al. (1966). This species, which is the smallest and the most primitive of the genus, is only known from latest Ypresian (MP10) localities of the Paris Basin and Central France. The size and morphology of the upper deciduous premolar refer to a DP^3 of *L. remensis*.

The only complete mammal tooth at Balegem represents a P_2 of *L. remensis* on the basis of the lens-shaped occlusal outline with a prominent centro-anterior protoconid slightly curved toward the back of the tooth. It is similar in morphology and proportion to the P_2 of the specimen MSNL-1932 (fig. 20, SAVAGE et al., 1966) from the ''Sables à Unios et Térédines'' of the Epernay area, except that the French specimen is slightly larger.

Discussion

Palaeohabitat of the mammal taxa encountered

All the mammal teeth collected at the base of the Lede Formation belong to perissodactyls. They vary between 6.5 mm and 32.0 mm in length. Following the allometric relation between the dimensions of the molars and the weight of the animal (see LEGENDRE, 1989), the three species correspond to large mammals for that time (between 8 to 250 kilograms). *Lophiodon*, probably the largest mammal of its time, was a leaf-eating swamp dweller, whereas the two horses probably preferred the surrounding areas. The study of a well-preserved specimen of *Hallensia matthesi* from Messel (specimen IRSNB M1465, MP11, Germany) showed the presence of numerous stem fragments and sand particles, but only few leaves in the gut content (FRANZEN, 1990). *Propalaeotherium*, the closest palaeothere to *Propachynolophus*, ate essentially leaves (FRANZEN, 1976, 1992). Skeletons of more than 70 individuals of *Propalaeotherium* have been excavated at Messel, whereas only one skeleton of *Lophiodon* is known from this locality. A size limitation for finds of land mammals, which did not live close to the border of the lake of Messel has been postulated (FRANZEN, 1992). On the other hand, several skeletons of *Lophiodon* have been found together with numerous specimens of *Propalaeotherium* in the Geiseltal. STORCH and SCHAARSSCHMIDT (1988) have considered the Geiseltal as a kind of peat bog swamp vegetation. From the point of view of palaeo-environment, *Lophiodon*, *Hallensia* and *Propachynolophus* may have coexisted in the Oosterzele-Balegem area, suggesting that they have been reworked from a palaeohabitat relatively similar to that of the Geiseltal.

The mammal finds and their time frame

The three mammal species found at the base of the Lede Formation are known from several Early Eocene localities of the Paris Basin. *Hallensia louisi* and *Propachynolophus levei* are known from the MP8+9 reference level, which is of late middle Ypresian to early late Ypresian age (SMITH & SMITH, 2003). A few specimens referred to as *Propachynolophus* aff. *maldani* are present at Prémontré, a locality of reference-level MP10 (DÉGREMONT et al., 1985). These specimens are smaller than *P. gaudryi* (MP10, Marne, France) and have a size close to that of *P. maldani*, although their morphology is quite different. As a consequence, the specimens from Prémontré could belong to the species *P. levei* or to a new small species of the genus *Propachynolophus*, extending the small-sized forms into reference level MP10. *Lophiodon remensis* is restricted to reference-level MP10. All representatives of *Propachynolophus* disappeared, in contradiction to *Hallensia* and *Lophiodon*, before reference-level MP11. Faunas from the early (not basal) Lutetian reference-level MP11 (untere Unterkohle from the Geiseltal and Messel, Germany) are already very different from those of the latest Ypresian MP10 (localities of Grauves and Prémontré). Most of the species are different, which suggests a relatively important time-span between the two reference-levels. To conclude, the ranges of the taxa encountered at Oosterzele and Balegem may argue for reworking from a single stratigraphical unit, most closely related to reference-level MP10.

Other discoveries of terrestrial mammal teeth have been linked to the Ypresian-Lutetian transition of Belgium. RUTOT (1881) mentioned a few perissodactyl teeth from the basal gravel of the "Laekenian" at St Gilles (Brussels), now equated with the base of the Lede Formation. Other small teeth of perissodactyls have been described from the base of the Lede Sand, overlying the Brussel Sand, at Uccle, Forest and St Gilles (Brussels) and one tooth of *Lophiodon* has been described from the Brussel Sand at Uccle (DEPÉRET, 1912). The genus *Hallensia* has also been recorded at the base of the Brussel Formation at Hoegaarden (SMITH & HOOKER, 1996). These records suggest that at least two continental phases may have occurred during the latest Ypresian and early Lutetian in Central Belgium. The first phase, obviously predating the deposition of the Brussel Formation, occurred in the latest Ypresian. The continental to marginal marine Aalterbrugge Lignitic Horizon, which is well documented in the stratigraphical record (outcrops and boreholes around Gent), probably formed during this phase. The second, post-dating the deposition of the Brussel Formation, is not represented by sediments, but only known through erosion products (terrestrial mammal teeth) at the base of overlying units (generally the Lede Formation). This phase is within the Lutetian.

Depositional history of the Oosterzele-Balegem area

The stratigraphic succession in the Oosterzele quarry, discussed in this paper and that from the Balegem quarry, based on 10 to 30 years old observations, is quite similar, suggesting uniform depositional conditions in the area. This is not surprising seen the short distance (only 2.5 km) between the quarries.

The depositional history as demonstrated by the exposures started with the accumulation of successive low and high angle sets of glauconite-rich, laminated and cross-bedded sands, referred to the Vlierzele Sand Member and indicating a tidally-influenced high energy estuarine deposition regime. These sands are believed to be deposited around 50 Ma, according to their biostratigraphically based calibration with the integrated time-scale of BERGGREN et al., 1995 (STEURBAUT et al., 2003). The calcareous nannofossil dating of the base of the overlying Lede Formation (lower part of NP15) witnesses the incompleteness of the sedimentological record in the area. According to the Biochron boundary dates of BERGGREN et al. (1995) the missing record approximates 3 m.y. (see Fig. 5). However, the presence of reworked *Megacardita planicosta* at the base of the Lede Formation allows partial reconstruction of the depositional history during this interval. *In situ* records of this bivalve are known from many outcrops and boreholes in Belgium (e.g. at Aalter, STEURBAUT & NOLF, 1989) and N France (Mont-de-Récollets, NOLF & STEURBAUT, 1990), and always restricted to the lower part of the Aalter Sand Formation.

The rounded and flattened fossiliferous sandstone pebbles in the same basal layer are believed to be reworked too. The form of the pebbles, suggesting substantial long erosion, as well as the absence of the tiny *Nummulites variolarius*, exclude in situ cementation. Some of these pebbles yield fine-grained glauconite, while others almost none, excluding reworking from the Vlierzele Member (its sandstones always contain medium-grained or coarse-grained glauconite). As the Aalter Formation does not contain solidly cemented sandstones, they must be derived from another source. The Brussel Sand Formation with its numerous sandstone banks seems to be the only remaining candidate. Evidence to support this may come from the study of the dinoflagellate cysts, preserved in the pebbles (work in progress).

The presence of terrestrial mammal teeth in a marine context can be explained through reworking or to almost contemporaneous taphonomic processes such as stranding and subsequent decay of carcasses on a river inlet or beach shortly after their death (with or without fluviatile transport). The second seems to be the less plausible, as the mammal remains at the base of the Lede Formation belong to different taxa only represented by isolated teeth. Other arguments in favour of reworking are based on the time frame during which the mammal taxa lived. According to their *in situ* distribution patterns in the Paris Basin, the taxa encountered at Oosterzele and Balegem probably lived during the latest Ypresian (see above). Continental strata of this age have recently been identified in the area by one of us (ES), 4 km north of the Oosterzele quarry (map-sheet; x = 112.325; y = 185.225). The temporarily exposed white clean sands and black organic rich clays, essentially reflecting alluvial plain

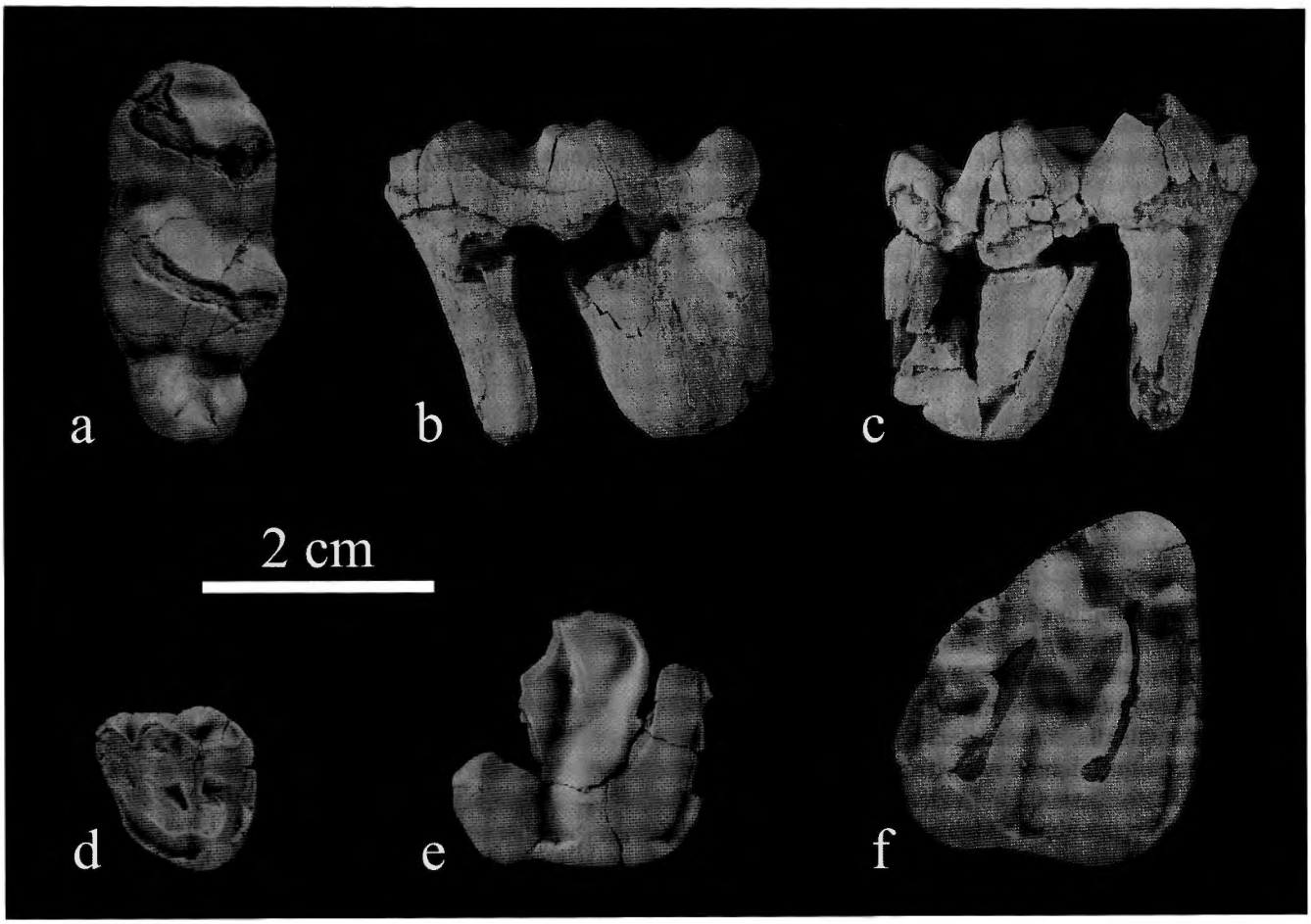

Fig. 3 — *Lophiodon remensis* LEMOINE, 1878 from Oosterzele (Belgium). a-c: Left M_3, cast IRSNB M 1869, occlusal (a), labial (b), lingual (c) views. d: Left DP^3, specimen IRSNB M 1870, occlusal view. e: Fragment of right M^1 or M^2, specimen IRSNB M 1871, occlusal view. f: Right M^3, specimen IRSNB M 1872, occlusal view. Specimens coated with ammonium chloride.

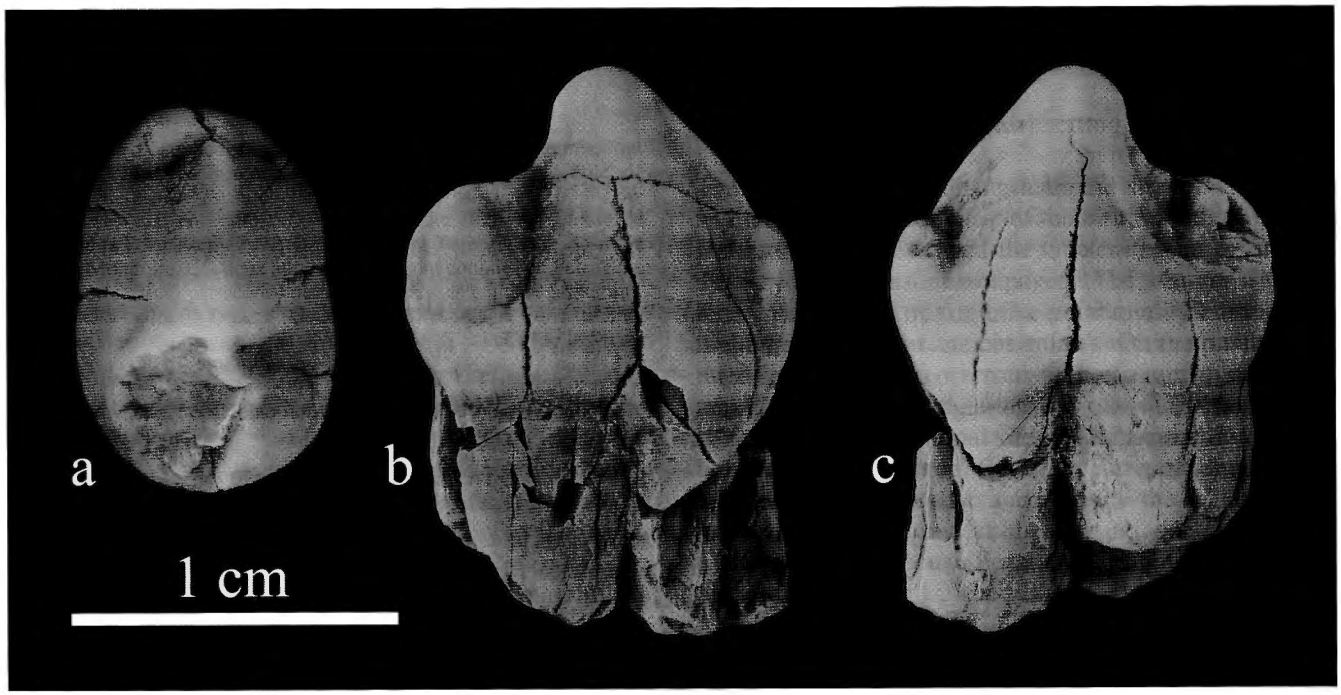

Fig. 4 — *Lophiodon remensis* LEMOINE, 1878 from Balegem (Belgium). a-c: Right P_2, specimen IRSNB M 1873, occlusal (a), labial (b), lingual (c) views. Specimen coated with ammonium chloride.

sedimentation, are tentatively attributed to the Aalterbrugge Lignitic Horizon. The study of the palynomorphs, which is in progress, may confirm the stratigraphic position and palaeo-environment of these organic-rich clays.

According to the reworked faunal and lithologic components at the base of the Lede Formation, the Aalterbrugge Lignitic Horizon, the overlying Aalter Sand Formation (top NP13-base NP14) and the Brussel Sand Formation (NP14), or part of it, must have been deposited in the area and were subsequently eroded. Removal of quite thick packages during a marine transgression suggests major uplift of the sedimentation area, which can keep pace with the sea-level rise. The accumulation of these large pebbles, perforated by marine molluscs, reworked bivalves and mammal teeth results from winnowing in a high-energy coastal environment (lower part unit A). It represents a stabilisation of the relative sea-level change, allowing organisms to burrow into the underlying Vlierzele Sand. As the sea transgressed, and the palaeo-environment became somewhat deeper, bioturbated fine sand accumulated (upper part unit A). Afterwards the sea retreated, allowing winnowing and concentration of shells, shark and ray teeth. It deepened again, from foreshore facies passing into shoreface (parallel lamination) and offshore-transition facies (bioturbated fine sand) (= unit B). The undulating surface at the base of unit C indicates submarine channelling, due to a major storm event or to small relative sea-level changes. Shallow marine conditions prevailed throughout the remainder of the Lede Sand Formation, as shown in the disused Balegem quarry. However, its exact sedimentation history cannot be detailed because of lack of sufficient information and of non-preservation in the Oosterzele quarry and the new Balegem quarry.

Acknowledgments

The authors are very grateful to Pascal TASSY and Claire SAGNE for providing access to mammal collections at the Museum National d'Histoire Naturelle (Paris); to Jérôme THOMAS (Université de Lyon) for giving photographic documents and comments on *Lophiodon*; to Richard SMITH for making casts of the material; to Gino MARIEN, Pieter DESCHUTTER, Guy VAN DEN EECKHOUT, Joop TAK, and Dirk NOLF for the gift of the material to the RBINS; to Theo LAMBRECHTS for helping in the fieldwork at Oosterzele. At the RBINS, Wilfried MISEUR produced the photographs and Hugo DE POTTER assisted in making the stratigraphical figure. Finally, we would like to express our gratitude to Jerry HOOKER (Natural History Museum, London) and Jens FRANZEN (Germany) for discussions about basal horses. Chris KING (Greenwich University, UK) and Jens FRANZEN (Germany) are thanked for reviews

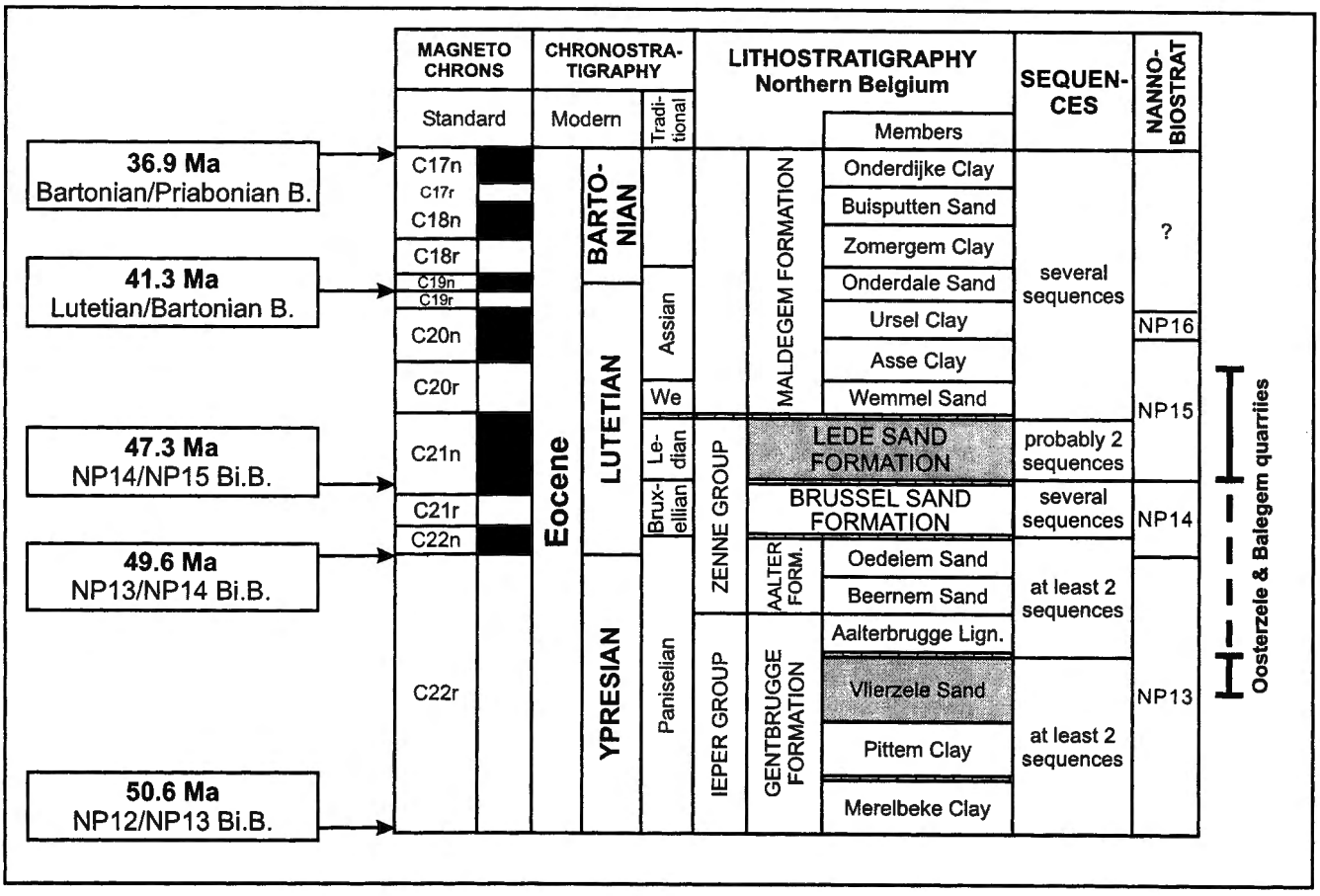

Fig. 5 — Lithostratigraphy of the Ypresian-Lutetian transition in Belgium and its calibration with the integrated time scale of BERGGREN et al., 1995 (after STEURBAUT et al., 2003). Bi.B.: Biochron boundary; We: Wemmelian.

improving the manuscript. This paper is a contribution to Research Project MO/36/011 financially supported by the Belgian Federal Science Policy Office. It is dedicated to Pierre BULTYNCK (RBINS) for initiating and promoting the "Evolution of Mesozoic and Cenozoic mammals" as one of the main axes in the research programme of the RBINS.

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Typescript submitted: 15 December 2003
Revised typescript received: 29 August 2004

Explanation of Plate 1

Hallensia louisi HOOKER, 1994 from Oosterzele (Belgium). Specimen coated with ammonium chloride.
Fig. 1 — Left M_3 in occlusal view (specimen IRSNB M 1861).
Fig. 2 — Right P_4 in occlusal view (specimen IRSNB M 1862).

Propachynolophus levei HOOKER, 1994 from Oosterzele (Belgium). Specimens coated with ammonium chloride.
Fig. 3 — Left M_1 in occlusal view (specimen IRSNB M 1863).
Fig. 4 — Fragment of right M_3 in occlusal view (specimen IRSNB M 1864).
Fig. 5 — Right M_3 in occlusal view (specimen IRSNB M 1865).
Fig. 6 — Right M^1 in occlusal view (specimen IRSNB M 1866).
Fig. 7 — Right upper molar (broken labially) in occlusal view (specimen IRSNB M 1867).
Fig. 8 — Fragment of left upper molar in occlusal view (specimen IRSNB M 1868).

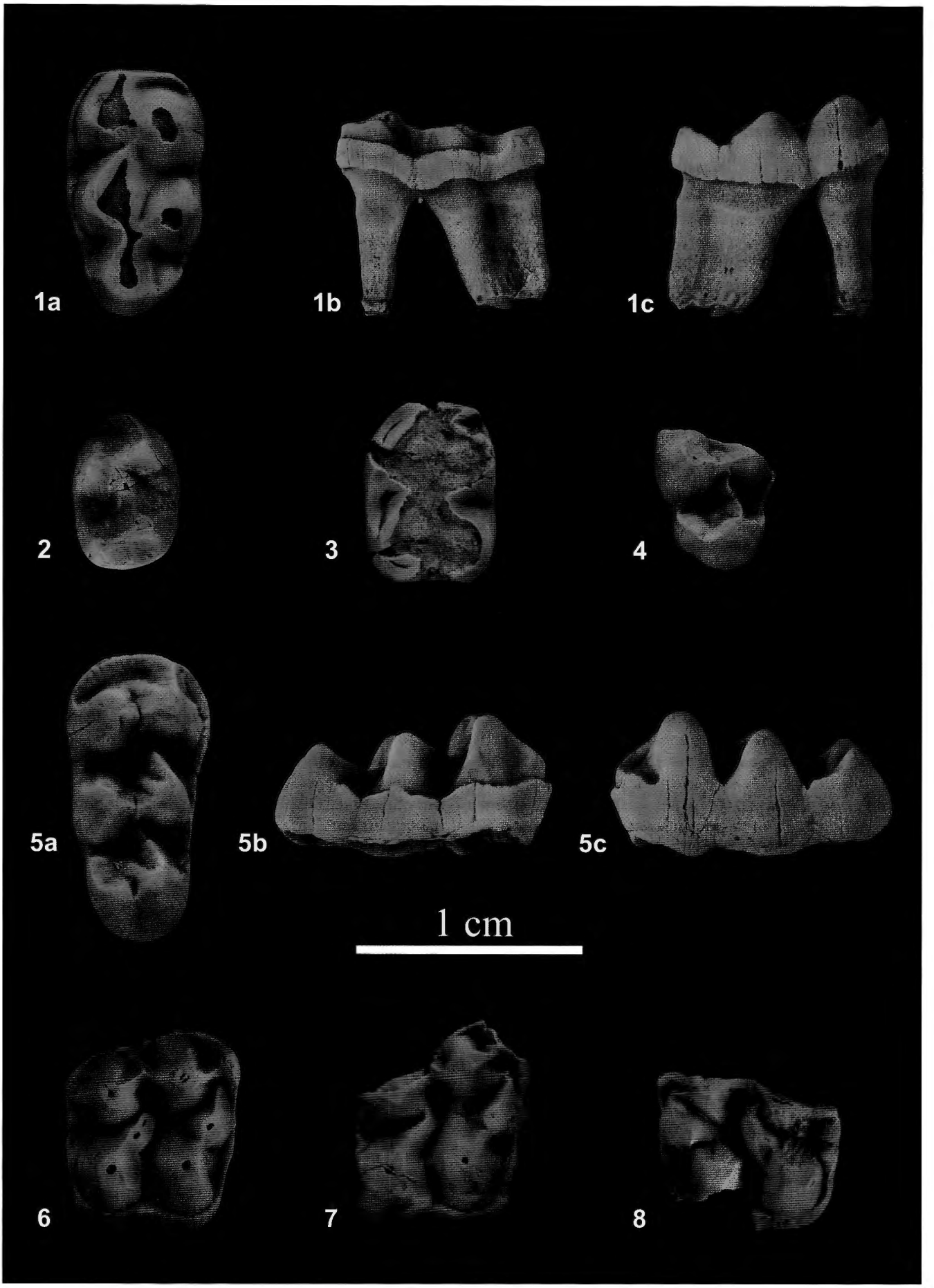

PLATE 1