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The creodonts (Mammalia, Ferae) from the Paleocene-Eocene transition in Belgium (Tienen Formation, MP7)

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ABSTRACT. Study of the dental remains of creodont mammals from the Paleocene-Eocene transition in Belgium (Tienen Formation, reference-level MP7) allows seven species to be recognized, four of which belong to the family Hyaenodontidae and three to the Oxyaenidae. The four hyaenodontid species, which are new to science, present numerous symplesiomorphic characteristics. They represent the oldest hyaenodontids of northern Europe and are shown to be the most primitive representatives of the sub-family Hyaenodontinae known so far. They are closely related to the oldest North American species but the morphological differences between them demonstrate that they are not vicariant species. Thus, the Belgian species could be at the origin of the American hyaenodontid lineages or belong to lineages already distinct but recently differentiated from common ancestors slightly older than both of these species groups. As for oxyaenids, their dental morphology shows that they could originate from the North American Paleocene lineages, although their small size does not support this hypothesis. The smallest Belgian creodont, *Prototomus minimus* n. sp. is remarkable in that it may present sexual dimorphism in mandibular morphology.

KEY WORDS: mammals, creodonts, Paleocene-Eocene transition, MP7, Belgium.

INTRODUCTION

At the Paleocene-Eocene transition, about 55 million years ago, most of the placental mammal orders of modern type appear simultaneously in western Europe, North America and central Asia. The most typical groups are the rodents, euprimates, perissodactyls, artiodactyls, bats, miacid carnivorans and hyaenodontid creodonts. On the other hand, persisting archaic type groups from the Paleocene begin to decline, such as condylarths, arctocyonids, plesiadapiform "primates", cimolestids, viverravid carnivores and oxyaenid creodonts.

The mammal faunas from the outcrop sections of Dormaal, Orp-le-Grand and Hoegaarden in the Brabant province, and those of Erquelinnes and Leval in the Hainaut province, belonging all to the Tienen Formation (Upper "Landenian", Landen Group), representing the Paleocene-Eocene transition in Belgium, have been the subject of detailed study (SMITH, 1999, 2000). Among these, the important Dormaal fauna (see SMITH & SMITH, 1996; STEURBAUT et al., 1999) was specified for reference-level MP7 of the mammalian biochronological scale for the European Paleogene (SCHMIDT-KITTLER, ed., 1987).

In this first part of the study we analyse the order Creodonta, which is classified with the Carnivora and the Cimolesta in the grand-order Ferae Linnaeus, 1758 (MCKENNA & BELL, 1997). The creodonts form a group of carnivorous mammals that persisted from the Middle Paleocene to the Late Miocene (60-10 million years ago). They are characterised by the presence of at least two pairs of shearing carnassial teeth (generally M1/ and M/2, M2/ and M/3), whereas the carnivorans have only one pair of shearing carnassial teeth (P4/ and M/1). Two large families are included in the creodonts: the oxyaenids and the hyaenodontids. The oxyaenids, which are known from the Paleocene to the Middle Eocene, have two molars per half-jaw. The hyaenodontids, which appear at the beginning of the Eocene and persist to the Late Miocene, present three molars per half-jaw.

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MATERIAL AND METHODS

For the sake of homogeneity, the mammal systematic classification in this work is that proposed by McKenna & Bell (1997). The terminology of the dental cusps and crests used here (see Smith, 1996, fig. 1) is based on that defined by Van Valen (1966) to describe the tribosphenic tooth of the therian mammals.

ABBREVIATIONS

Institutions:

AMNH: American Museum of Natural History, New York.
BMNH: Natural History Museum, London.
IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles.
MNHN: Muséum National d'Histoire Naturelle, Paris.
UC (MP): University of California (Museum of Paleontology), Berkeley.
UM (VP): University of Michigan (Vertebrate Paleontology), Ann Arbor.

Localities and collections:

AC: Meudon, collections of the MNHN.
Al, ARP: Argiles à lignites du Soissonnais, collections of the MNHN.
CL: Dormaal, collection J-C. Lepage (IRSNB).
D: Dormaal, general collection of the IRSNB.
DIRS, DIIARS, DIICRS, DIIIRS: Dormaal, collection R. Smith.
DMG: Dormaal, collection M. Girardot (R. Smith).
DC, DD, DL: Dormaal, collection D. Delsate (IRSNB).
Do: Dormaal, general collection of the IRSNB; numbering of P. Gigase.
DoPG: Dormaal, collection P. Gigase.
Eq: Erquelinnes, general collection of the IRSNB.
IRSNB M: Mammals, collection of types and figured specimens of the IRSNB.
L, Louis: Collection P. Louis (MNHN).
Mu: Mutigny.
RI: Rians, collection of the MNHN.
TS: Dormaal, general collection of the IRSNB, numbering of T. Smith.
WL: Dormaal, collection G. Wouters (IRSNB).

SYSTEMATIC PALAEONTOLOGY

Order CREODONTA Cope, 1875
Family HYAENODONTIDAE Leidy, 1869
Subfamily HYAENODONTINAE Leidy, 1869

Genus *Prototomus* Cope, 1874
Type species *Prototomus viverrinus* Cope, 1874

Prototomus minimus n. sp.

(Figs 1 and 2)

1927: Créodontes indéterminés; Teilhard de Chardin, p. 20, figs. 16c-d, pl. V, figs. 1, 6, 11, 12.
1927: Miacidés; Teilhard de Chardin, p. 21, fig. 18d.
1966: Proviverrinae, Cat. I.; Quinet, p. 37, pl. V, figs. 7-9.
1966: Proviverrinae, Cat. II.; Quinet, p. 37, pl. V, figs. 10-11.
1966: Proviverrinae, Cat. III.; Quinet, p. 37, pl. V, figs. 12-13.
1978: cf. *Prolimnocyon*; Godinot et al., p. 1273.
1987: *Prolimnocyon* sp.; Lange-Badré *in* Godinot et al., p. 275.

Material

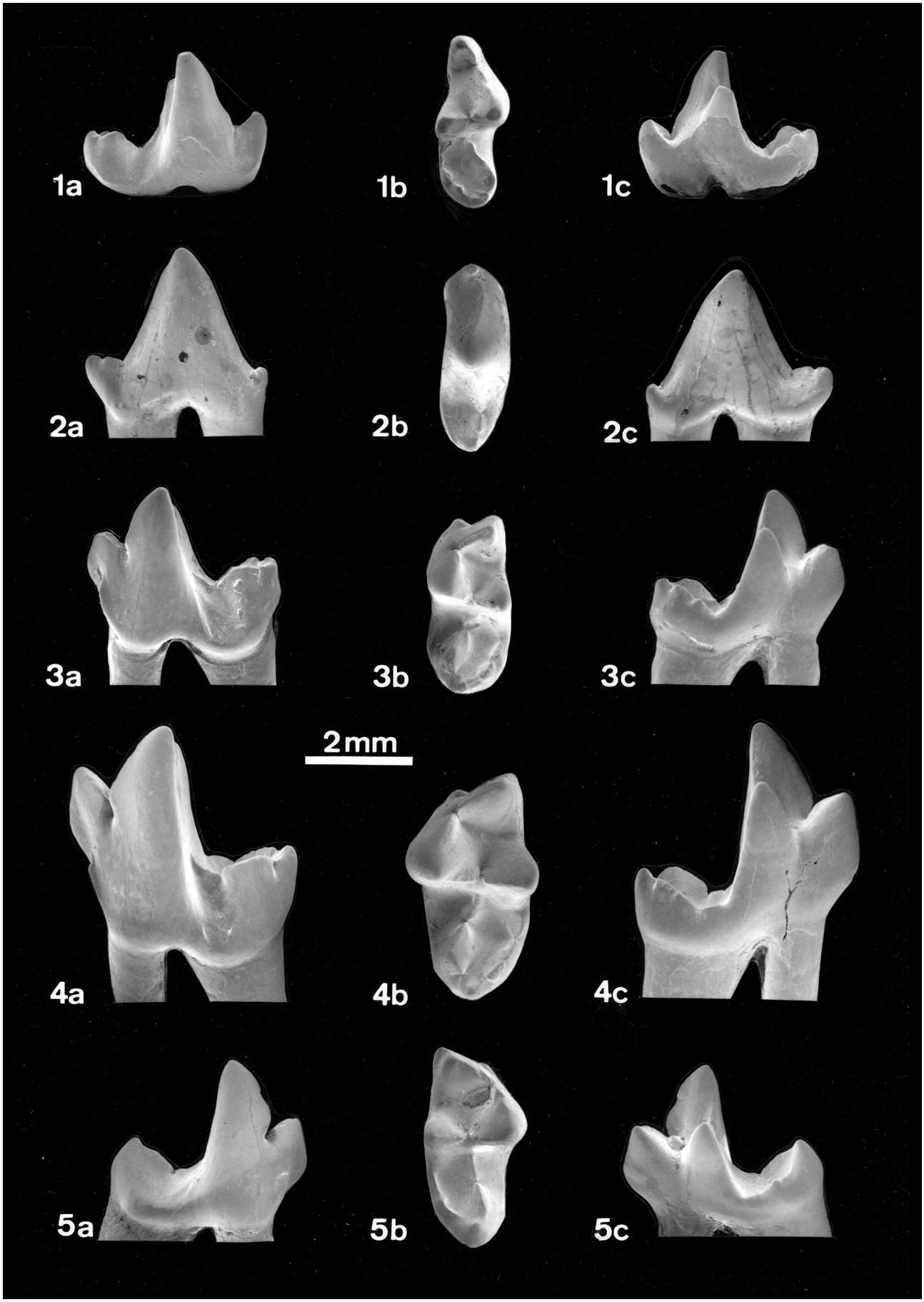
Holotype: IRSNB M1287, LM/1.

Paratypes: IRSNB M1285, RDP/4; IRSNB M1286, RP/4; IRSNB M1288, LM/2; IRSNB M1289, RM/3; IRSNB M1356, RDP4/; IRSNB M1290, LP4/; IRSNB M1291, LM1/; IRSNB M1292, RM2/; IRSNB M1293, LM3/; IRSNB M1294, edentulous fragment of left mandible; IRSNB M1295, edentulous fragment of left mandible.

Referred material: DI1471RS, RP/3?; DIIC1389RS, RDP/4; TS5, RDP/4; TS6, LDP/4; Do1713PG, RDP/4; DIIA2296RS, RP/4; CL706, RP/4; TS7, RP/4; TS8, LP/4; TS9, RP/4; IRSNB M919, RM/1; DI1429RS, LM/1; DIIC1681RS, LM/1; DIII325RS, RM/1; DIII80RS, RM/1; DIIC1574RS, LM/1; DIII82RS, RM/1; TS10, LM/1; TS11, RM/1; TS12, LM/1; TS13, LM/1; DIII258RS, LM/1; WL167, LM/2; WL158, LM/2; CL102, LM/2; TS14, LM/2; TS15, RM/2; TS16, LM/2; TS17, RM/2; TS18, LM/2; DIII81RS, LM/2; DIII264RS, RM/2; DIII79RS, RM/2; DIIA1910RS, RM/2; DIII364RS, LM/2; IRSNB M917, RM/3; TS19, RM/3; TS20, RM/3; CL379, LDP4/; DIIC624RS, RDP4/; DIIC625RS, RDP4/; DIIC1557RS, LDP4/; DIIA1912RS, LDP4/; TS21, RDP4/; IRSNB M72, RM1/; IRSNB M80, LM1/; DIII363RS, LM1/; TS22, LM1/; TS23, RM1/ (broken); TS24, LM1/ (broken);

Legend to the figures (see opposite page)

Fig. 1. – *Prototomus minimus* n. sp. – 1. IRSNB M1285, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1286, RP/4. a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1287, LM/1 (holotype). a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1288, LM/2. a: labial view, b: occlusal view, c: lingual view. – 5. IRSNB M1289, RM/3. a: labial view, b: occlusal view, c: lingual view.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DIII312RS, RM2/ (broken); DIII72RS, LM2/ (broken); DIIA1782RS, RM3/; TS25, RM3/; TS26, RM3/ (broken); TS29, edentulous fragment of right mandible.

Type locality

Dormaal.

Diagnosis

Smallest species of the genus, differing from all the other species, except maybe *P. giraroti*, by M/3 smaller than M/2 (the ratio M/3:M/2 length is 0.87) and proportionally smaller M3/, and by M2/ with more labially oriented parastyle and with a pronounced ectoflexus.

Etymology

The name refers to the extremely small size of this species. B. Lange-Badré (Université Paris VI), in her unfinished study of the Dormaal creodonts, intended the name *minimus* for this species, which she believed to belong to the genus *Prolimnocyon*. However, the latter is characterized by developed P/4 and P4/, reduction of M2/, and extreme reduction of M/3 and M3/, which it is not the case in the present taxa. We validate here the species name *minimus* as a tribute to her work.

TABLE 1

Measurements (in mm) of cheek teeth of *Prototomus minimus* n. sp. from Dormaal. L: length; l: width; n: number of specimens; OR: observed range of variation; M: mean; σ: standard deviation; V: coefficient of variation.

		n	OR		M	σ	V
DP4/	L	6	2.95	3.25	3.16	0.11	3.53
	l	6	2.85	3.05	2.94	0.10	3.47
P4/	L	1	2.95		-	-	-
	l	1	3.05		-	-	-
M1/	L	5	3.10	3.65	3.48	0.22	6.31
	l	5	3.60	3.80	3.71	0.08	2.21
M2/	L	1	3.65		-	-	-
	l	1	4.95		-	-	-
M3/	L	3	2.00	2.25	2.12	0.13	5.94
	l	3	2.27	2.95	2.85	0.13	4.64
P/3	L	1	3.10		-	-	-
	l	1	1.25		-	-	-
DP/4	L	5	3.30	3.60	3.44	0.13	3.76
	l	5	1.40	1.55	1.47	0.08	5.16
P/4	L	6	3.45	3.80	3.61	0.13	3.55
	l	6	1.30	1.45	1.37	0.05	3.78
M/1	L	9	3.35	3.90	3.62	0.20	5.57
	l	9	1.65	1.95	1.82	0.12	6.45
M/2	L	15	3.90	4.45	4.12	0.17	4.15
	l	15	2.15	2.6	2.43	0.13	5.21
M/3	L	3	3.45	3.80	3.60	0.18	5.01
	l	3	1.85	2.00	1.90	0.08	3.98

Description

Lower dentition

The trigonid of DP/4 (Fig. 1. 1a-c) is wider than the talonid. The paraconid is narrow and well distinct. The metaconid is slightly posterior to the protoconid. The latter is slender.

The P/4 (Fig. 1. 2a-c) is tall with a simple morphology. A small paraconid is present. The talonid is narrow with a central crest (slightly shifted labially) bearing two small cusps.

The M/1 (Fig. 1. 3a-c) is the same length as P/4. It is also relatively narrow. Trigonid and talonid have about the same width. On some specimens the trigonid is even somewhat narrower than the talonid.

The M/2 (Fig. 1. 4a-c) is much larger than M/1. The trigonid is wide, particularly developed and elevated.

The M/3 (Fig. 1. 5a-c) is a little larger than M/1. The trigonid is not as wide as on M/2. The talonid basin is long and narrow. The hypoconulid is the most developed cusp of the talonid.

Three edentulous fragments of mandible belonging to *Prototomus minimus* n. sp. from Dormaal have been identified by comparison with the mandible UM79612 of *Prototomus deimos*. The alveoli indicate that P/1 was single-rooted. It is worth noting that the fragment of mandible IRSNB M1294 is higher and more elongated than in IRSNB M1295 and TS29, the alveoli for the canine is larger, the diastemata on each side of P/2 are longer and the mental foramina are larger (Fig. 3).

Upper dentition

The parastyle of DP4/ (Fig.2. 1a-b) is wide labio-lingually, and anteriorly developed. Paracone and metacone are labio-lingually compressed. The protocone is relatively anterior. The postmetacrista is short. The two conules present weak postparaconule crista and premetaconule crista.

The P4/ (Fig. 2. 2a-b) is small. The paracone is relatively low and it has a central position. The relatively short metastylar crest is somewhat developed in height. The protocone is weakly developed, as is the entire lingual part of the tooth.

On M1/ (Fig. 2. 3a-b) as on DP4/, the paracone is slightly higher than the metacone. The parastyle is anteriorly oriented. The postmetacrista is of medium length and labio-posteriorly orientated. The paraconule is protruded

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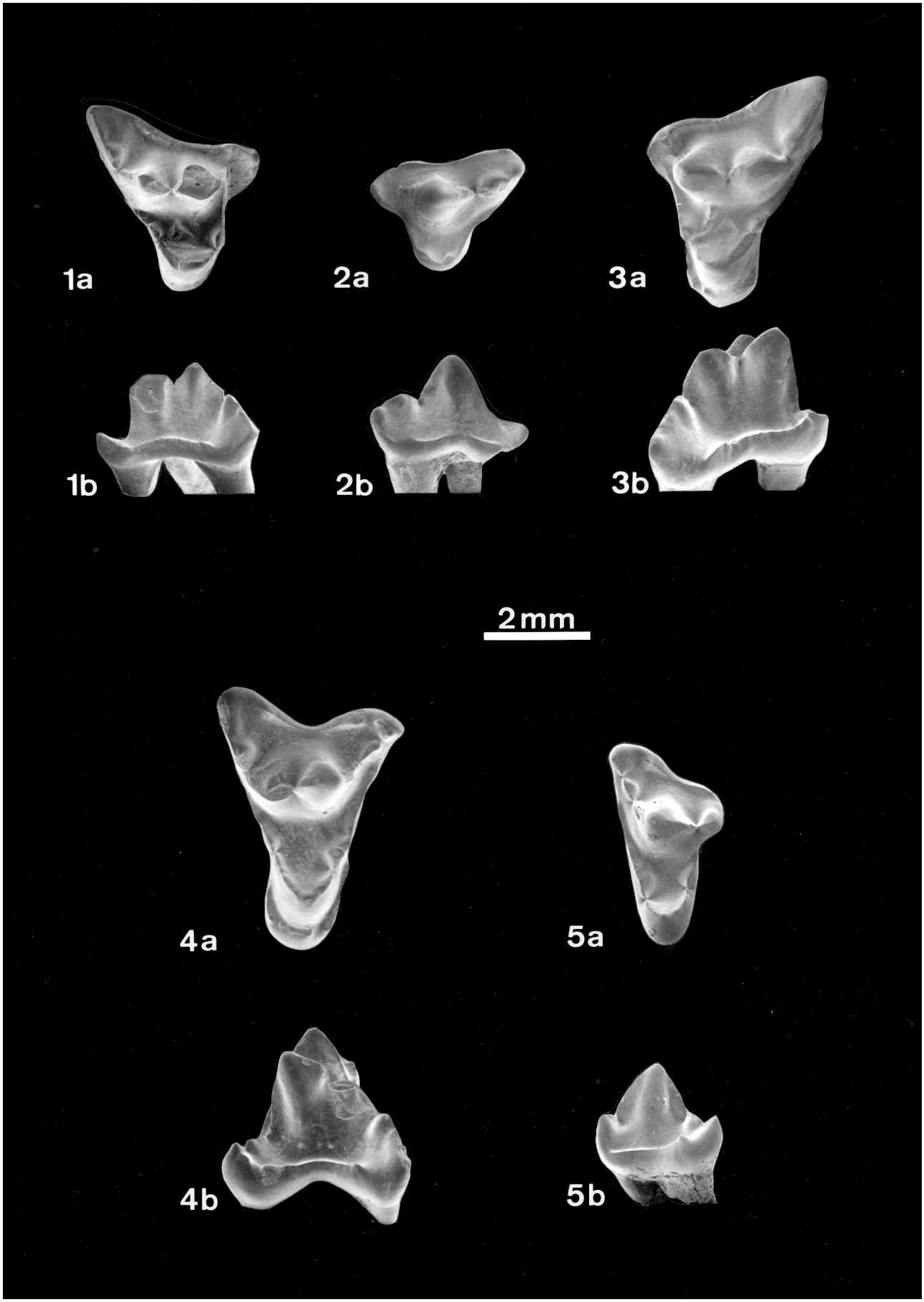
Fig. 2. – *Prototomus minimus* n. sp. – 1. IRSNB M1356, RDP/4. a: occlusal view, b: labial view. – 2. IRSNB M1290, LP4/; a: occlusal view, b: labial view. – 3. IRSNB M1291, LM1/; a: occlusal view, b: labial view. – 4. IRSNB M1292, RM2/; a: occlusal view, b: labial view. – 5. IRSNB M1293, LM3/; a: occlusal view, b: labial view.


1a
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and is connected to the base of the paracone by a postparaconule crista. Weak pre- and postcingula border the protocone. The latter is thicker on M1/ than on DP4/.

The M2/ (Figs. 2. 4a-b) is a wide tooth labio-lingually and larger than M1/. The ectoflexus is pronounced. The paracone and metacone are close to one another. The parastyle is more developed than on M1/ and antero-labially orientated. The postmetacrista is the same length as on M1/ or is slightly shorter. The protocone is nearly median with respect to the paracone and the metacone. The pre- and postcingula are slightly more developed than on M1/ and the protocone is somewhat larger.

The M3/ (Fig. 2. 5a-b) is small in comparison with M2/. It has a small metacone and two conules. The protocone is poorly developed labio-lingually and has no cingula. The preparacrista is present as a labially stretched cusp.

Discussion

The upper molars of this taxon present a series of primitive characters recalling the Paleocene didelphodontid Cimolesta such as *Cimolestes* species: close paracone and metacone, protocone median with respect to the paracone and the metacone (scarcely shifted anteriorly), postmetacrista labially orientated and with little elongation, parastyle anteriorly orientated. However, this taxon corresponds well with hyaenodontid creodonts in the narrow stylar shelf, the different morphology of the P4/ and the poorly developed talonid cusps of the lower molars.

This mammal is the smallest creodont in the Belgian fauna. It belongs to the genus *Prototomus* by having simple P/4 and P4/, narrow lower molars, M/1 and M1/ distinctly smaller than M/2 and M2/, only slightly reduced M/3 and M3/, and the metaconid slightly higher than the paraconid on M/1-2.

The teeth are morphologically close to those of *P. deimos* Gingerich & Deutsch, 1989 (Wa0-3), *P. phobos* Gingerich & Deutsch, 1989 (Wa1-4) and *P. martis* Gingerich & Deutsch, 1989 (Wa2-3), which are the oldest known representatives of the genus in North America. However, the Belgian species differs from the three American species by its clearly smaller size, proportionally shorter P/4 and P4/, and smaller M/3 et M3/ with a hypoconulid less developed on M/3. *P. deimos*, the smallest and oldest species, is, according to its M/1 and M/2 measurements, 20-30% larger than *Prototomus minimus* n. sp. from Dormaal.

The DP4/ of *P. minimus* have been identified by comparison with DP4/ of *P. martis* (UM67138, two fragments of maxilla with DP4/-M1/ and DP4/-M2/). These teeth present a series of plesiomorphies: absence of cingulum around the protocone, considerable development of the parastyle, presence of para- and metaloph.

The postparaconule crista on M1/ (plesiomorphic character) is also present in *P. deimos* (UM46642) and *P. martis* (UM67138). It seems to be absent or strongly attenuated in *P. phobos* (UM74134).

The molars of *Prototomus minimus* n. sp. are fairly similar to those of the smallest North American hyaenodontid, *Acarictis ryani* Gingerich & Deutsch, 1989 (UM79081), but they are slightly smaller. One of the main diagnostic characteristics of the genus *Acarictis*, known from only four specimens, is the singularity of its P3/. However, this tooth (UM86291) more closely resembles a DP3/ by its low length/width ratio, its protruding parastyle, the presence of a protocone and of three roots. The validity of the genus *Acarictis* could therefore be questioned, and the species *A. ryani* should probably be attributed to the genus *Prototomus* or *Prolimnocyon*. An objection to the synonymy *Acarictis*-*Prototomus* could be argued to be the absence of diastema between P/2 and P/3 in *Acarictis*. On the other hand, *Prolimnocyon haematus* Gingerich & Deutsch, 1989 is close in size to *Acarictis ryani* and does not possess a diastema, either. Moreover, both come from the same stratigraphic level.

The respective alveoli of the three edentulous fragments of mandible attributed to *Prototomus minimus* n. sp. have the same dimensions and cannot correspond to the large teeth of *Prototomus girardoti* n. sp. (see following pages). The mandibular variability seems to result from sexual dimorphism comparable to those of the extant red fox *Vulpes vulpes* (GINGERICH & WINKLER, 1979). The more developed mandible (IRSNB M1294) belongs probably to a male individual (Fig. 3).

Among the rare teeth of European Proviverrini, those of *Proviverra palaeonictides* (Lemoine, 1880) from Epernay (MNHN Al5515, MP8+9, upper Ypresian, Champagne) and of *Proviverra eisenmanni* Godinot, 1981 from Rians (RI 400, MP7, Early Eocene, Provence) present a well-developed and individualised entoconid on a relatively large talonid, while the entoconid is reduced and crestiform on the lower molar of *Prototomus minimus* n. sp. This apomorphic character is not shared by *Prototomus* cf. *P. palaeonictides* (RICH, 1971, p. 14) from Grauves (MNHN Louis195, MP10). Moreover, the alveoli of its mandible indicate that P/1 was double-rooted. It is thus justified to consider this last taxon as belonging to the genus *Proviverra* Rütimeyer,

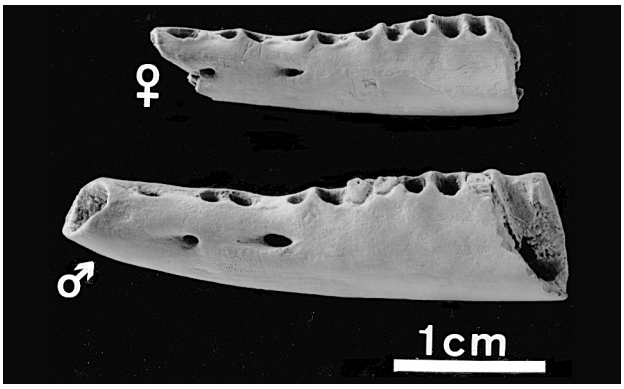


Fig. 3. – *Prototomus minimus* n. sp. – ♀. IRSNB M1294, edentulous fragment of left mandible belonging to a female individual; in labial view. – ♂. IRSNB M1295, edentulous fragment of left mandible belonging to a male individual; in labial view.

1862. On the other hand, the RM3/, named cf. *Proviverra* or *Prototomus* sp. (RICH, 1971, p. 16) from Mutigny (MNHN Mu6464, MP8+9), has two small conules, a somewhat reduced metacone and a marked ectoflexus like that on M3/ of *Prototomus minimus* n. sp. These characters bring these teeth rather closer to the genus *Prototomus*, M3/ of *Proviverra* being clearly more developed.

***Prototomus girardoti* n. sp.**
(Fig. 4)

Material

Holotype: IRSNB M1297, RM/1

Paratypes: IRSNB M1296, RDP/4; IRSNB M1298, RM/3; IRSNB M1299, RP4/; IRSNB M1300, RM3/.

Type locality

Dormaal.

Diagnosis

Species similar in size to *P. deimos* but differing by smaller M/3 (11 to 26 % smaller).

Etymology

Named after Michel Girardot who contributed to the Dormaal collections.

TABLE 2

Measurements (in mm) of cheek teeth of *Prototomus girardoti* n. sp. from Dormaal. Abbreviations as in Table 1.

		n	OR	M	σ	V
P4/	L	1	4.55	-	-	-
	l	1	3.00	-	-	-
M3/	L	1	2.05	-	-	-
	l	1	3.45	-	-	-
DP/4	L	1	4.05	-	-	-
	l	1	1.85	-	-	-
M/1	L	1	4.40	-	-	-
	l	1	2.25	-	-	-
M/3	L	1	4.45	-	-	-
	l	1	2.40	-	-	-

Description

Lower dentition

The trigonid of DP/4 (Fig. 4. 1a-c) is slightly wider than the talonid. The metaconid is posterior to the protoconid.

The M/1 (Fig. 4. 2a-c) also presents a trigonid slightly wider than the talonid. Three small cusps are set in the lingual edge of the talonid.

The talonid of M/3 (Fig. 4. 3a-c) is relatively long and narrow. A small antero-labial cingulum is visible and the trigonid is somewhat closed.

Upper dentition

The P4/ (Fig. 4. 4a-b) has a long and narrow labial part. The relatively tall paracone has a central position. The lingual part of the tooth is weakly developed, and the protocone is insignificant.

The M3/ (Fig. 4. 5a-b) is labio-lingually elongated. It presents a developed metacone and 2 conules. The protocone is relatively massive.

Discussion

The few teeth of this taxon are distinctly larger than those of *Prototomus minimus* n. sp. but relatively similar in morphology. They differ also in having P4/ more anteroposteriorly elongated, the preparacrista of M3/ longer and the protocone more developed. The dimensions are nearly the same as those of *P. deimos* from Wyoming (Wa0-3), only M/3 is here smaller than on the American species.

Genus *Arfia* Van Valen, 1965
Type species *Arfia opisthotoma* (Matthew, 1901)

***Arfia gingerichi* n. sp.**
(Figs 5 and 6)

1982: *Arfia woutersi* n. sp.; LANGE-BADRÉ & GODINOT, p. 295-300, pl. 1, figs. 2-4; *non* pl. 1, fig. 1.
1989: *Arfia junnei*; GINGERICH, p. 36.

Material

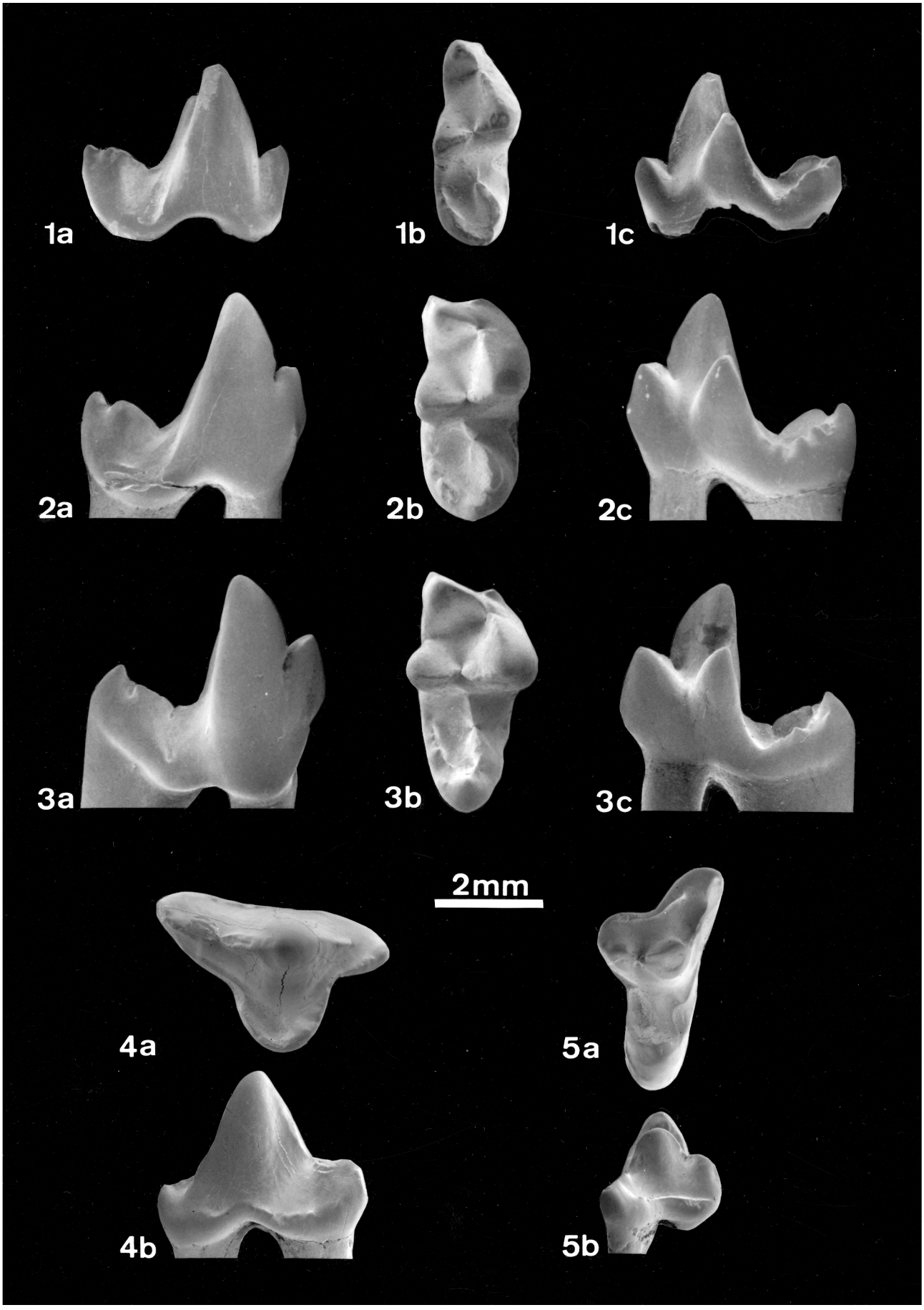
Holotype: IRSNB M1275, RM/3, figured as CL13 by LANGE-BADRÉ & GODINOT (1982; pl. I, fig. 4a-c).

Paratypes: IRSNB M1301, LP/3; IRSNB M1302, RDP/4; IRSNB M1303, RP/4; IRSNB M1304, RM/1 (CL14 in LANGE-BADRÉ & GODINOT, 1982, pl. I, fig. 3b, e, h); IRSNB M1305, RM/2; IRSNB M1306, LM/3;

Legends to the figures (see next pages)

Fig. 4 – *Prototomus girardoti* n. sp. – 1. IRSNB M1296, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1297, RM/1 (holotype). a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1298, RM/3. a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1299, RP4/. a: occlusal view, b: labial view. – 5. IRSNB M1300, RM3/. a: occlusal view, b: labial view.

Fig. 5. – *Arfia gingerichi* n. sp. – 1. IRSNB M1301, LP/3. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1302, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1303, RP/4. a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1304, RM/1. a: labial view, b: occlusal view, c: lingual view. – 5. IRSNB M1305, RM/2. a: labial view, b: occlusal view, c: lingual view.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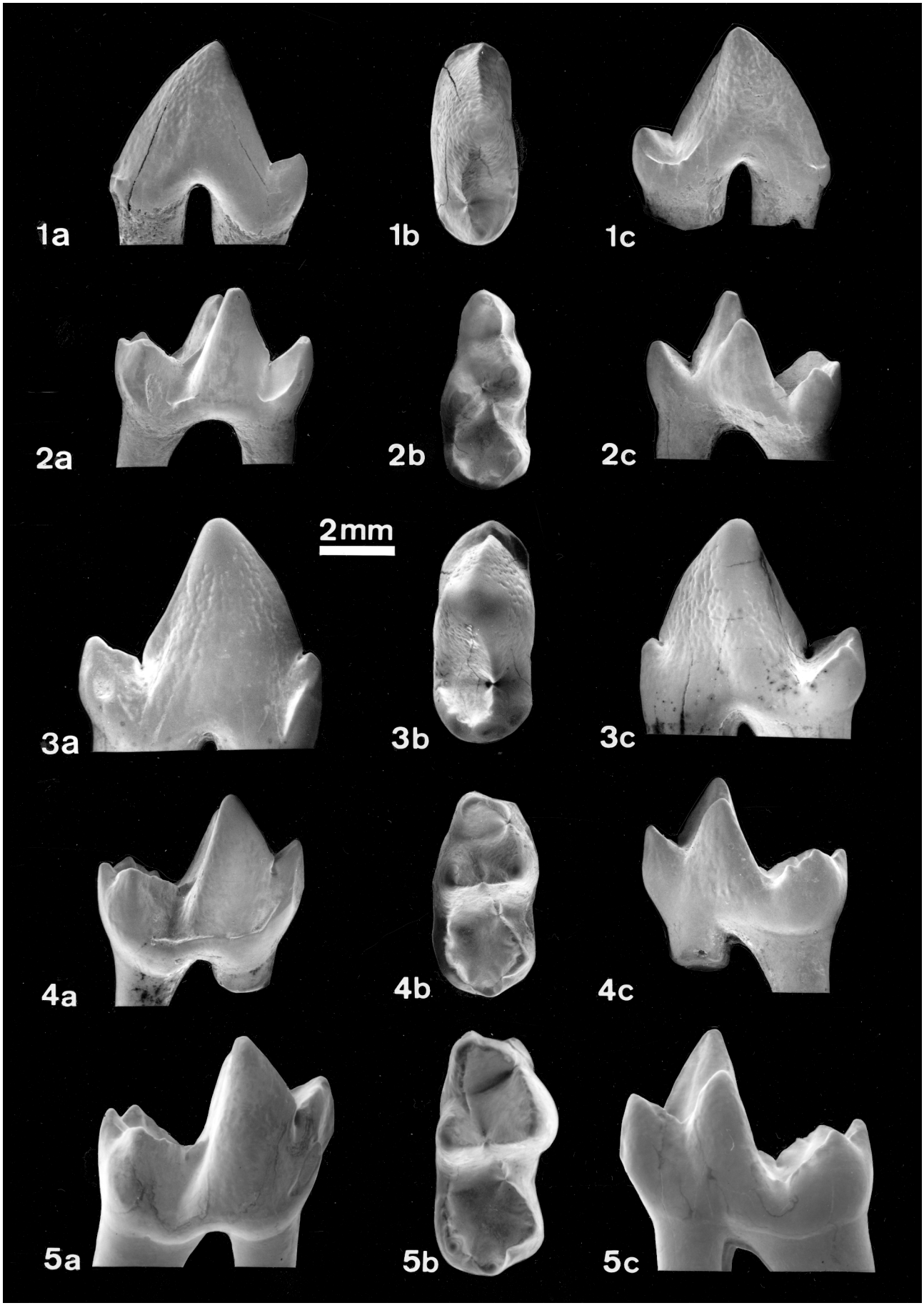

1a
1b
1c
2a
2b
2c
2mm
3a
3b
3c
4a
4b
4c
5a
5b
5c

IRSNB M1307, RP3/; IRSNB M1358, RDP4/; IRSNB M1308, LP4/; IRSNB M1309, RM1/; IRSNB M1310, RM2/ (labial part); IRSNB M1311, LM3/.

Referred material: CL44, LP/3; CL46, LP/3; CL47, LP/3; DIII173RS, RP/3; DIIC643RS, LP/3; TS30, LP/3; TS31, RP/3; TS32, LP/3 (broken); D83, LDP/4 (trigonid); DC143, RDP/4; DIIC641RS, RP/4; DIIC1687RS, LP/4; IRSNB M1276, RM/1 (WL169 in LANGE-BADRÉ & GODINOT, 1982, pl. I, fig. 3a, d, g); IRSNB M1277, LM/1 (CL22 in LANGE-BADRÉ & GODINOT, 1982, pl. I, fig. 3c, f, i); DIII1315RS, LM/1; DIIC250RS, LM/1; TS34, RM/2; TS35, RM/2 (trigonid); TS36, RM/3 (trigonid); DIII177RS, RM/3; DIII261RS, RM/3; TS42, LM/3 (worn); Do1712PG, RM/3 (trigonid); TS37, RP2/?; Do832, LP3/; DI1426RS, LP3/; CL37, LP4/ (labial part); DL1, RM1/; DD8, LM1/; TS39, RM1/ (lingual part); DI1849RS, LM3/; TS41, LM3/; Eq1, LM/3 (trigonid); Eq2, RP/4.

Type locality

Dormaal

Other localities

Erquelinnes, Try (MP7, Early Eocene, Marne, France), Kyson (MP7, Early Eocene, Suffolk, England).

Diagnosis

Smallest species of the genus, differing from all the other species by M/3 with distinctly less developed talonid cusps, by the absence of postcingulum on lower molars, and by proportionally smaller M3/.

Etymology

Named after Prof. Philip Gingerich (University of Michigan, Ann Arbor) who contributed to the knowledge of the Wa0 faunas. He was the first to show the similarities between *A. junnei* from Wyoming and the Belgian species here described (GINGERICH, 1989, p. 33-36).

Description

Lower dentition

As for all the teeth of this new species, the P/3 (Fig. 5. 1a-c) presents a finely crenulated enamel surface. The paraconid is generally absent or reduced to a tiny spherical cusp (CL47). The crest that descends the posterior wall of the trigonid and the central crest of the talonid delimit the labial edge of a slight basin.

The molariform DP/4 (Fig. 5. 2a-c) has well-developed metaconid and talonid cusps. The metaconid is strongly posterior in comparison with the position of the protoconid. The paraconid is prominent. The talonid is relatively high.

TABLE 3

Measurements (in mm) of cheek teeth of *Arfia gingerichi* n. sp. from Dormaal. Abbreviations as in Table 1.

		n	OR		M	σ	V
DP4/	L	1	4.85		-	-	-
	l	1	4.20		-	-	-
P3/	L	2	5.75	5.80	5.78	0.04	0.61
	l	2	2.90	3.10	3.00	0.14	4.71
P4/	L	1	6.75		-	-	-
	l	1	5.80		-	-	-
M1/	L	1	5.45		-	-	-
	l	1	5.90		-	-	-
M3/	L	3	2.95	3.5	3.22	0.28	8.56
	l	3	7.95	8.5	8.32	0.32	3.82
DP/3	L	2	5.05	5.05	5.05	0.00	0.00
	l	2	1.85	1.90	1.88	0.04	1.89
DP/4	L	1	5.50		-	-	-
	l	1	2.50		-	-	-
P/3	L	8	5.55	5.8	5.64	0.09	1.55
	l	8	2.2	2.35	2.29	0.06	2.80
P/4	L	4	5.85	6.90	6.25	0.45	7.24
	l	4	2.65	3.05	2.88	0.17	5.94
M/1	L	4	5.60	6.00	5.89	0.19	3.28
	l	4	3.00	3.25	3.11	0.11	3.56
M/2	L	1	6.90		-	-	-
	l	1	3.45		-	-	-
M/3	L	4	6.35	7.40	6.79	0.47	6.92
	l	4	3.45	3.90	3.65	0.20	5.36

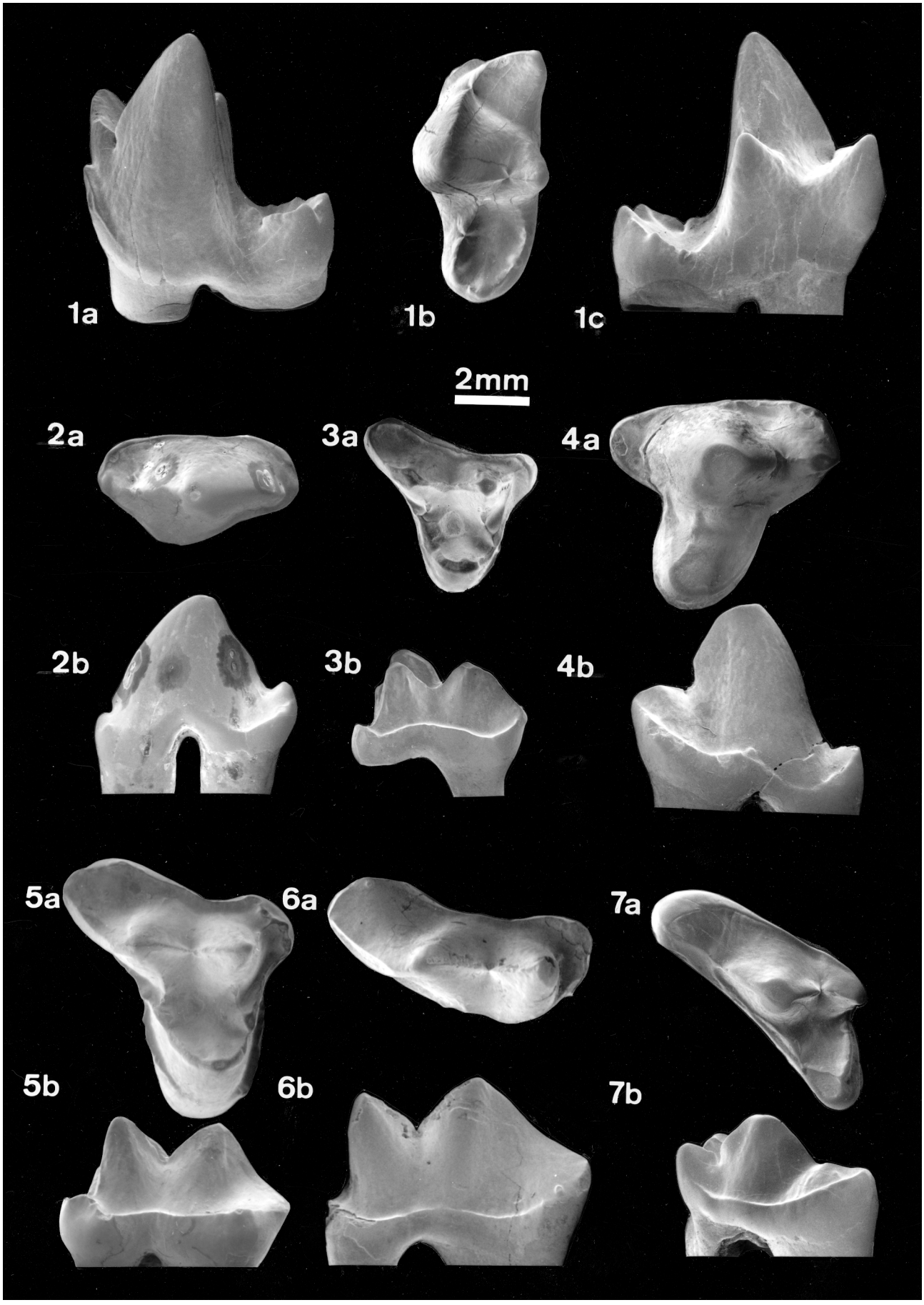
The P/4 (Fig. 5. 3a-c) is large with a massive wide protoconid. An antero-labial cingulum and an antero-lingual fold are situated on either sides of a small paraconid.

The M/1 (Fig. 5. 4a-c) is a little shorter than P/4 and slightly wider. The metaconid is more developed than the paraconid. In addition to the three talonid cusps (hypoconid, hypoconulid, entoconid), an entoconulid is developed on the entocristid. An incomplete labial cingulum is present: the postcingulum is absent. The specimen IRSNB M1277 is slightly larger than the others and shows a somewhat more developed talonid.

The M/2 (Fig. 5. 5a-c) is distinctly larger than M/1. The trigonid is proportionally larger than on M/1. The metaconid is also more developed than the paraconid. Only an antero-labial cingulum is visible, the labial cingulum being absent. A crest descends the postero-lingual edge of the paraconid on specimen IRSNB M1305. This crest is absent on the specimens TS34 and TS35.

Legend to the figures (see opposite page)

Fig. 6. – *Arfia gingerichi* n. sp. – 1. IRSNB M1306, LM/3. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1307, RP3/. a: occlusal view, b: labial view. – 3. IRSNB M1358, RDP/4. a: occlusal view, b: labial view. – 4. IRSNB M1308, LP4/. a: occlusal view, b: labial view. – 5. IRSNB M1309, RM1/. a: occlusal view, b: labial view. – 6. IRSNB M1310, RM2/ (labial part). a: occlusal view, b: labial view. – 7. IRSNB M1311, LM3/. a: occlusal view, b: labial view.


1a
1b
1c
2mm
2a
3a
4a
2b
3b
4b
5a
6a
7a
5b
6b
7b

The M/3 (Fig. 6. 1a-c) is a little shorter than M/2 (except maybe for the specimen IRSNB M1306). The metaconid is more reduced than on M/1 and M/2, but still sub-equal to the paraconid. The protoconid is well developed and taller than on the other molars. The talonid cusps are less differentiated than on M/1 and M/2.

Upper dentition

The P3/ (Fig. 6. 2a-b) is slightly wider anteriorly than posteriorly. It presents an antero-labial bulge and a posterior cusp.

The DP4/ (Fig. 6. 3a-b) presents a parastylar lobe extended anteriorly. The metacone has almost the same height as the paracone.

The P4 / (Fig. 6. 4a-b) is large and its lingual part is particularly developed. The paracone is massive and the metastylar crest is relatively thick.

The M1/ (Fig. 6. 5a-b) and M2/ (Fig. 6. 6a-b) show a considerable development of the metastylar lobe. Their paracone and metacone are approximately of the same height but the paracone is shorter. Although the unique M2/ (IRSNB M1310) is broken, its preserved labial part has a morphology similar to that of M1/ but it is definitely larger.

The parastylar lobe of M3/ (fig. 6. 7a-b) is very elongated antero-labially. The metacone is reduced compared with that of M1/ and M2/. The protocone is short antero-posteriorly.

Discussion

The presence of the genus *Arfia* was announced for the first time in Europe with *Arfia woutersi* from Dormaal (Lange-Badré & Godinot, 1982). Subsequently, three M/1 (IRSNB M1304, IRSNB M1277, IRSNB M1276), among the six teeth described in 1982, were referred to *A. junnei* from the Wa0 of Willwood Formation, Wyoming (Gingerich, 1989). Thus, *A. junnei* was one of the rare species reported on the two continents. The validity of *A. woutersi* was questioned because one of the two syntypes designated by Lange-Badré & Godinot (1982) was recognized by Gingerich (1989) as belonging to a genus other than *Arfia* and he voluntarily selected it as the lectotype of "*A.*" *woutersi* (LM1/, IRSNB M1319). The latter is an oxyaenid creodont; it is described further on.

We have today about 30 teeth collected at Dormaal and Erquelinnes that we attribute to the genus *Arfia*. This material indicates that the Belgian species is indeed closely related to *Arfia junnei* from the Willwood Formation Wa0 (M/1, M1/ and DP4/ are nearly identical). However, it is characterized by the absence of postcingulum on the lower molars and by M/3 probably a little shorter than M/2, a reverse situation to that of *A. junnei* and the other American species (*A. shoshoniensis* Matthew, 1915 and *A. opisthotoma* Matthew, 1901). It should be noted that a similar observation was already made for the M/3 at the time of the comparison of *Prototomus minimus* n. sp. from Dormaal with *P. deimos* from the Wa0. Moreover, the talonid cusps of the lower molars are less differentiated and individualized than in *A. junnei*. It is M/3 that presents the least developed talonid (observation on four complete specimens). This character, which affects preferentially the entoconid, is found to a lesser extent on the specimen AMNH15745 of *A. shoshoniensis*. The protocone of M3/ of *Arfia gingerichi* n. sp. is proportionally shorter than that of *A. opisthotoma* (AMNH99). We could not compare the M3/ with that of *A. junnei*, the M3/ of the latter being as yet unknown.

The Belgian taxon belongs to another species than *A. junnei*. By its incomplete labial cingulum on the lower molars and its less developed M/3, it differs somewhat from the American lineage and is at its origin or close to its origin. At all events, there is no doubt that the two species are very close.

Genus *Galecyon* Gingerich & Deutsch, 1989
Type species *Galecyon mordax* (Matthew, 1915)

Emended diagnosis: hyaenodontid with robust canines, short deep dentary, single-rooted P/1, large and sharp posterior cusp on P/4, short basined talonids on M/1-3 with reduced entoconid and hypoconulid which form a lingual crest, reduced M/3, high metastylar and parastylar crests on P4/, tall cusps and very short postmetacrista on upper molars.

***Galecyon morloi* n. sp.**
(Fig. 7)

Material

Holotype: IRSNB M1314, LM/1.

Paratypes: IRSNB M1312, RDP/4; IRSNB M1313, RP/4; IRSNB M1315, RM/2; IRSNB M916, RM/3; IRSNB M1316, RP4/; IRSNB M1317, LM1,2/.

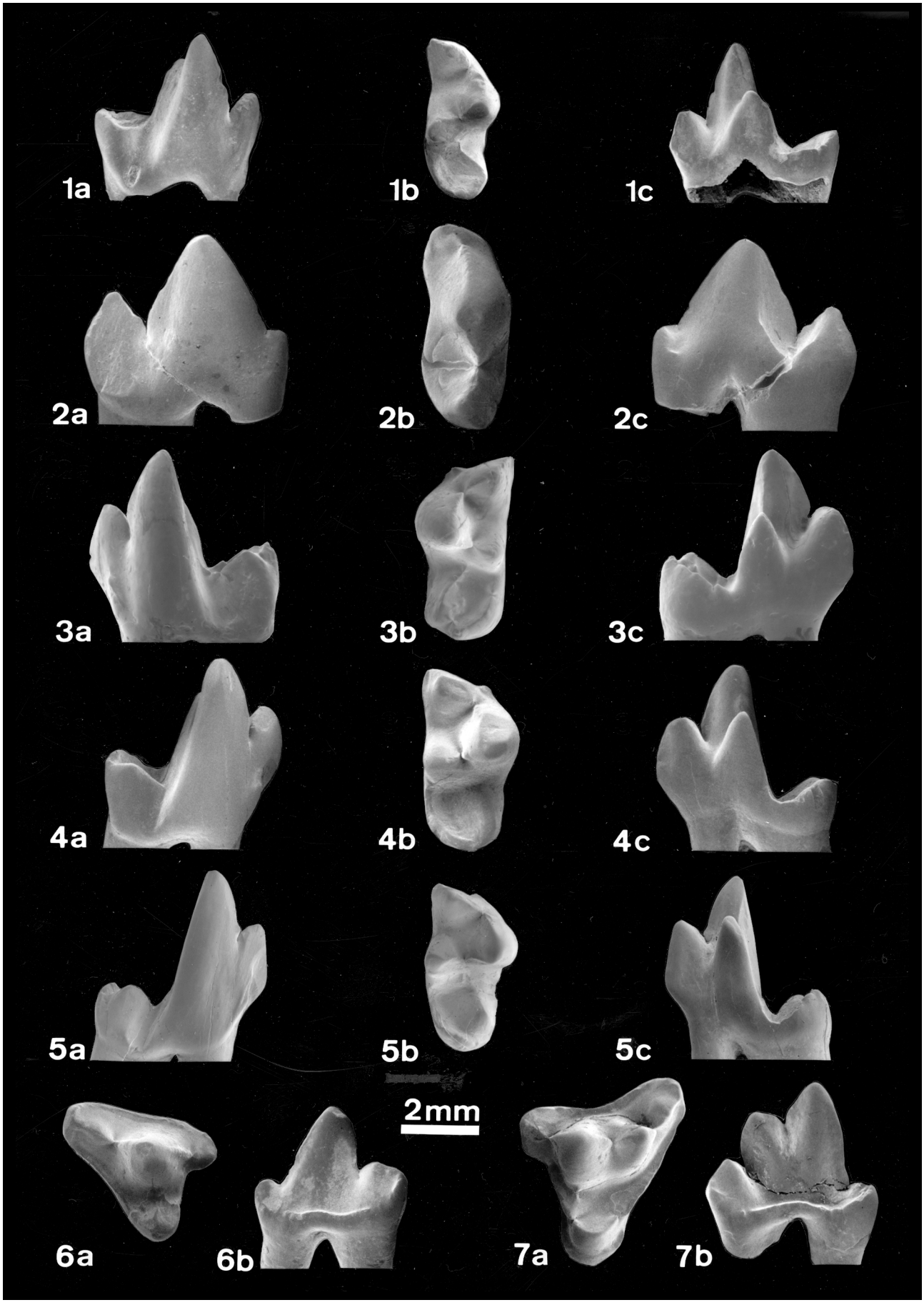
Referred material: DIII175RS, LP/4; D137, LM/1; CL89, RM/1; DIII176RS, LM/1; Do291PG, RM/1; Do306PG, RM/1?; TS44, LP4/ (labial part); DIII478RS, RDP4/?; IRSNB M1357, M1,2/d; CL94, LM1,2/.

Type locality

Dormaal.

Legend to the figures (see opposite page)

Fig. 7. – *Galecyon morloi* n. sp. – 1. IRSNB M1312, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1313, RP/4. a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1314, LM/1 (holotype). a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1315, RM/2. a: labial view, b: occlusal view, c: lingual view. – 5. IRSNB M916, RM/3. a: labial view, b: occlusal view, c: lingual view. – 6. IRSNB M1316, RP4/. a: occlusal view, b: labial view. – 7. IRSNB M1317, LM1,2/. a: occlusal view, b: labial view.


1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c
5a
5b
5c
2mm
6a
6b
7a
7b

Diagnosis

Smallest species of the genus, differing from *Galecyon mordax* in being about 20 % smaller, by the higher ratio M/3:M/2 length (0.93 for *G. morloi*; 0.75 for *G. mordax*), and by the less developed lingual crest of the talonid and hypoconulid.

Etymology

Named after Dr. Michael Morlo (Frankfurt) who has contributed to the knowledge of the hyaenodontid creodonts of Europe.

TABLE 4

Measurements (in mm) of cheek teeth of *Galecyon morloi* n. sp. from Dormaal. Abbreviations as in Table 1.

		n	OR		M	σ	V
P4/	L	1	4.30		-	-	-
	l	1	3.40		-	-	-
M1,2/	L	2	4.60	4.85	4.73	0.18	3.74
	l	2	4.75	4.90	4.83	0.11	2.20
DP/4	L	2	4.50	4.65	4.58	0.11	2.32
	l	2	2.20	2.25	2.23	0.04	1.59
P/4	L	2	5.70	6.15	5.93	0.32	5.37
	l	2	2.55	2.80	2.68	0.18	6.61
M/1	L	4	5,00	5.60	5.36	0.26	4.78
	l	4	2.45	2.75	2.65	0.14	5.11
M/2	L	1	4.85		-	-	-
	l	1	2.65		-	-	-
M/3	L	1	4.50		-	-	-
	l	1	2.60		-	-	-

Description

Lower dentition

The DP/4 (Fig. 7. 1a-c) presents a high and wide paraconid. The trigonid is longer than the talonid, and the metaconid has a posterior position relative to the protoconid.

The P/4 (Fig. 7. 2a-c) is large and its protoconid is massive. The paraconid is relatively extended lingually. A lingual crest delimits a small talonid basin. The central crest of the talonid rises posteriorly to end in a large sharp cusp.

The lower molars (fig. 7. 3-5) have the trigonid longer than the talonid, a developed and massive paraconid and protoconid, a posterior metaconid, as well as a wide talonid basin. The entoconid is absent and is replaced by a crest that extends from the back of the metaconid to the hypoconulid. The M/1 (Fig. 7. 3a-c) differs from the M/2 (fig. 7. 4a-c) in its narrower trigonid. The M/3 (Fig. 7. 5a-c) is shorter anteroposteriorly than M/1 and M/2 and its talonid is narrower.

Upper dentition

The P4/ (Fig. 7. 6a-b) has an oblique labial edge. The lingual part of the tooth is not reduced. The metastylar and parastylar crests are developed in height. The paracone is high. The postcingulum ascends to the tip of the metastyle.

The M1,2/ (Fig. 7. 7a-b) is a robust tooth, relatively narrow labio-lingually. The paracone is much broader and taller than the metacone. The postmetacrista is very short. The protocone is relatively powerful and is surrounded by a weak but complete lingual cingulum. The postcingulum extends to the metastyle as on P4/.

Discussion

Before being attributed to the new genus *Galecyon*, *G. mordax* was referred to *Sinopa* (MATTHEW, 1915; MACINTYRE & GUTHRIE, 1979) and to *Prototomus* (VAN VALEN, 1965). *Galecyon* is indeed close to *Sinopa* according to the fusion of the lingual cusps and the hypoconulid, which form a curved crest delimiting the talonid basin of the lower molars (derived character). It presents also relatively narrow lower molars and an important difference in height between the trigonid and the talonid.

The differences between *Galecyon mordax* Matthew, 1915 (Wa1-3, Willwood Formation, Wyoming) and *Galecyon morloi* n. sp. from Dormaal lie primarily in the larger size of the American species (15-30%), the more developed lingual crest of the talonid and hypoconulid, and the lower length/width ratio of the molars. *G. mordax* is known from only six specimens. Most of them are damaged and they all belong to lower dentitions. However, an upper molar ascribed to *Prototomus martis*, UM86399 from the Wa2 of Willwood Formation (GINGERICH & DEUTSCH, 1989), is quite similar to M1,2/ of *Galecyon morloi* n. sp. Indeed, its thick and very short postmetacrista does not correspond to the genus *Prototomus*. It should probably be referred to *G. mordax*.

On the other hand, the two specimens RI275 and RI276 of *Prototomus* cf. *mordax* from Rians (GODINOT, 1981) belong actually to the genus *Galecyon*. They present 10 to 25% larger lower molars than those of the Belgian species. Moreover, the paraconid of P/4 is clearly less developed than in *Galecyon morloi* n. sp.

The discovery, in Dormaal, of the upper molars of *Galecyon* reveals a very short postmetacrista. This character is particularly primitive for the creodonts. It thus seems that *Galecyon morloi* n. sp. preserves symplesiomorphic characters while already developing some synapomorphic characters, which could give it a position between *Prototomus* and *Sinopa* in the cladogram of the early Hyaenodontidae proposed by POLLY (1996, fig. 12).

Family OXYAENIDAE Cope, 1877
Subfamily OXYAENINAE Cope, 1877
Genus *Oxyaena* Cope, 1874
Type species *Oxyaena lupina* Cope, 1874

***Oxyaena woutersi* (Lange-Badré & Godinot, 1982) comb. nov.**
(Fig. 8. 1-3)

1982: *Arfia woutersi* n. sp.; LANGE-BADRÉ & GODINOT, p. 295-300, pl. 1, fig. 1.; non pl. 1, figs. 2-4.

1989: "*Arfia*" *woutersi*; GINGERICH, p. 36.

Material

Lectotype: IRSNB M1319, LM1/ (or LDP4/?), figured as WL1147 by LANGE-BADRÉ & GODINOT (1982; pl. I, fig. 1a-b).

Referred material: IRSNB M1318, RP/3,4; IRSNB M1320, LM1/.

Type locality

Dormaal.

Diagnosis

Smallest species of the genus. Differs from *Oxyaena transiens* by the shorter postmetacrista on M1/; from *O. krausei* and *O. aequidens* by its lower and spindlier cusps.

TABLE 5

Measurements (in mm) of cheek teeth of *Oxyaena woutersi* (Lange-Badré & Godinot, 1982) from Dormaal. Abbreviations as in Table 1.

		n	OR	M	σ	V
M1/	L	2	6.35 7.00	6.68	-	-
	l	2	8.20 9.45	8.83	-	-
P/3,4	L	1	6.40	-	-	-
	l	1	3.05	-	-	-

Description

Lower dentition

The single lower tooth is a P/3,4 (fig. 8. 1a-c) the surface of the enamel of which is finely crenulated. The paraconid is weak. The central crest of the talonid is very high and its tip is round. A lingual cingulum delimits a weak basin on the talonid.

Upper dentition

Both M1/ (fig. 8. 2-3) have somewhat different dimensions primarily because of labio-lingual shortening of the tooth IRSNB M1319. Paracone and metacone are fairly closely set and have appreciably the same height. The postmetacrista is little extended and the protocone is short antero-posteriorly.

Discussion

GINGERICH (1989) designated the M1/ IRSNB M1319 as the lectotype of "*Arfia*" *woutersi*. The morphology of this tooth agrees not with that of the hyaenodontid *Arfia*, but with that of an oxyaenid. Indeed, the proximity of the paracone and metacone, the relatively short and massive postmetacrista, and the well-developed metacone characterize the Oxyaeninae. The different length/width proportions between IRSNB M1319 and IRSNB M1320 result probably from a simple intraspecific variation but we can not exclude that the lectotype IRSNB M1319 is in fact a DP4/.

The morphology of the P/3,4 confirms the presence, at Dormaal, of a species of Oxyaeninae attributable to the genus *Oxyaena* Cope, 1874 or *Dipsalidictis* Matthew, 1915. *Oxyaena*, a large animal, was considered as ranging through the entire Wasatchian, whereas *Dipsalidictis*, smaller in size, characterized the Clarkforkian and the early Wasatchian. It is to be noted that *D. platypus* Matthew, 1915, the smallest oxyaenine of North America, is still approximately 40% larger than the Belgian species. The characters separating the genera *Dipsalidictis* and *Oxyaena* are poor and some of them are probably related to differences in body size (GUNNELL & GINGERICH, 1991, p. 165). Besides, *Dipsalidictis* was recently included in the genus *Oxyaena* (MCKENNA & BELL, 1997, p. 226). Considering the paucity of the material from Dormaal, it is still difficult to specify the phylogenetic relations of *Oxyaena woutersi*. However, the rather short postmetacrista on M1/ (symplesiomorphic character) distinguishes it from *O. transiens* Matthew, 1915 (Wa0-2). This character is found on the two oldest American species: *O. krausei* (Gunnell & Gingerich, 1991) (Cf1-3) and *O. aequidens* Matthew, 1915 (Cf2-3). *O. krausei* has taller cusps and the teeth of these two species are clearly more massive than those of *O. woutersi*. *O. platypus* (Cf2-Wa1), of a slender aspect, seems to be the closest to the Belgian species. A fragment of the right maxilla with P3/-M2/ (UM66137, Wa0) well shows a relatively short but a little posteriorly tilted postmetacrista.

Among the European Oxyaenidae, *Oxyaena* sp. (LM/1, UCMP83754) from Sinceny (MP10, Aisne, Paris Basin) described by RICH (1971) is similar to *O. transiens* (Wa0-2) from Wyoming (GUNNELL & GINGERICH, 1991). Moreover, for HOOKER (1998) it would belong to the same species as *Oxyaena* sp. (trigonid of LM/1, MNHN AC656) recognized at Meudon (Ypresian, Hauts-de-Seine, France) by GUNNELL & GINGERICH (1991, p. 177). A small species represented by the lingual part of a RM1/ (BMNH15128) and a large species known by a RM/2 (BMNH13778), both from Abbey Wood (lower Ypresian, England) and described by VAN VALEN (1965), were also referred as *Oxyaena* sp. (GUNNELL & GINGERICH, 1991). These authors relate the large species to *O. aequidens* (Cf2-3) from Wyoming, whereas HOOKER (1998) names it *O. gulo* Matthew, 1915 known also from Wyoming (Wa2-3). All these taxa are larger than that from Dormaal. Only that from Meudon could possibly be related to *Oxyaena woutersi* considering its small size. However, owing to the very scarce material currently available, it is difficult, for the time being, to make any more detailed comparisons.

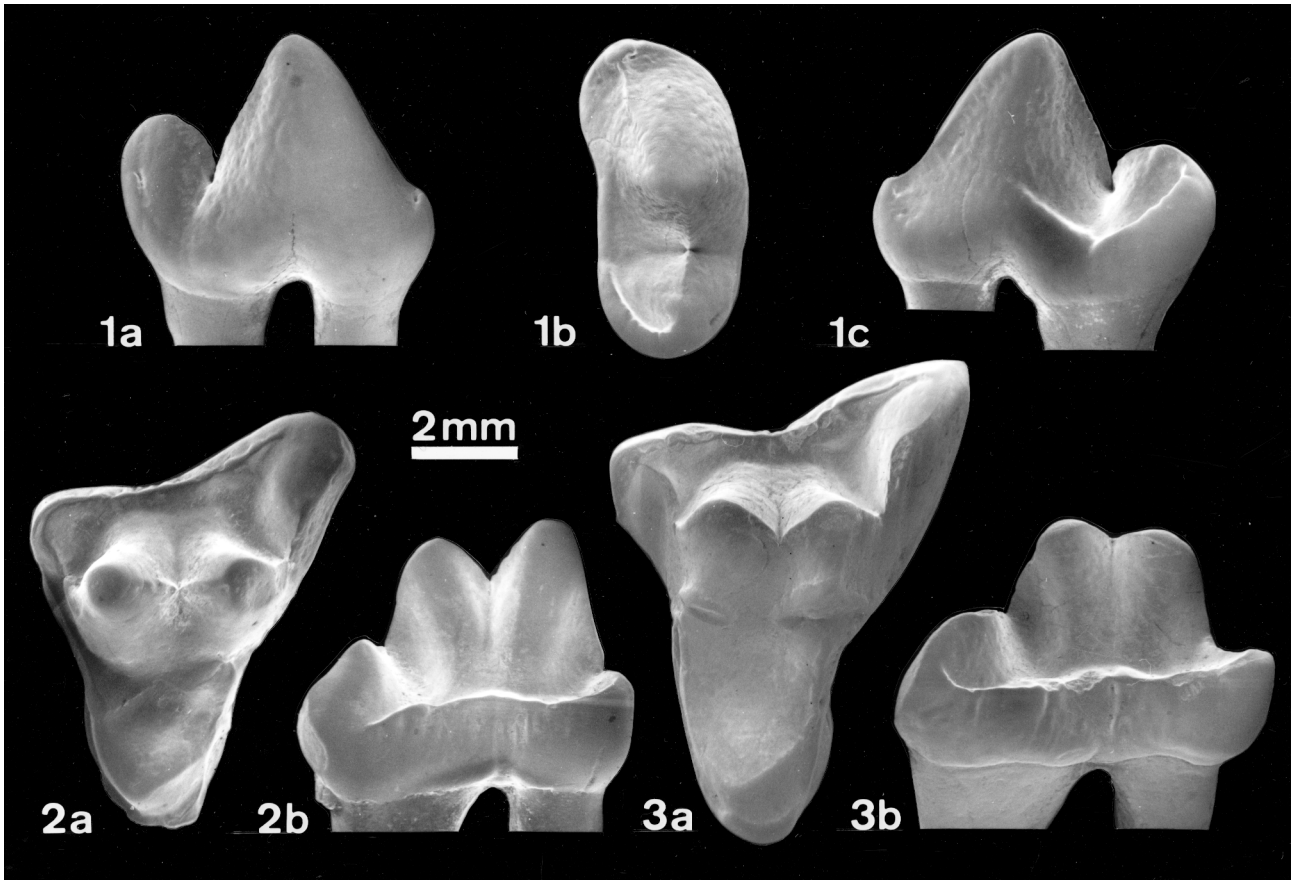


Fig. 8. – *Oxyaena woutersi* (Lange-Badré & Godinot, 1982) – 1. IRSNB M1318, RP/3,4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1319, LM1/ (Lectotype). a: occlusal view, b: labial view. – 3. IRSNB M1320, LM1/. a: occlusal view, b: labial view.

Subfamily AMBLOCTONINAE Cope, 1877

Genus *Palaeonictis* de Blainville, 1842

Type species *Palaeonictis gigantea* de Blainville, 1842

Palaeonictis gigantea de Blainville, 1842

1966: *Oxyaena* (?) *casieri* n. sp.; Quinet, p. 35, pl. V, figs 4-6.
1978: cf. *Palaeonictis*; Godinot et al., p. 1273.
1987: *Palaeonictis gigantea*; Lange-Badré, p. 831.

Material

Syntypes: ARP52, fragment of left mandible with P/3, P/4 (talonid), M/1 (talonid); ARP53, canine; ARP54, upper premolar (Argiles à lignites du Soissonnais).

Referred material: IRSNB M1355, LP/4 (Dormaal); IRSNB M1797, LDP/4 (Hoegaarden).

Type locality

Not specified, area of Soisson (Argiles à lignites du Soissonnais).

Other localities

Dormaal, Hoegaarden, Meudon?

Discussion

No new material can be referred to *Palaeonictis gigantea*. The DP/4 discovered at Hoegaarden was identified by comparison with DP/4 of the American species *Palaeonictis occidentalis* Osborn, 1892 (UM73459, Wa1-4) and *P. peloria* Rose, 1981 (UM65640, Cf3) (Smith & Hooker, 1996). These two species are larger than *P. gigantea* (*P. occidentalis*: 20%, *P. peloria*: 50%). Considering the less reduced M/2 with a larger metaconid, *P. peloria* would be more plesiomorphic than *P. occidentalis,* and would be closer to *P. gigantea* (Rose, 1981). In addition, the holotype of *P. gigantea* shows that P/4 had to be a little larger than the IRSNB M1355, which does not exclude the possibility that the taxon from Dormaal could belong in fact to a new species. In the absence of additional material, we thus refer to the work of Lange-Badré (1987). *P. gigantea* is currently one of the most primitive oxyaenid creodonts of Europe.

Genus *Dormaalodon* Lange-Badré, 1987
Type species *Dormaalodon woutersi*
Lange-Badré, 1987

***Dormaalodon woutersi* Lange-Badré, 1987**

Material

Holotype: IRSNB M1474, RM/1.

Referred material: IRSNB M1466, LM/1 (worn).

Type locality

Dormaal.

Discussion

The state of the knowledge on *Dormaalodon woutersi* remains unchanged because no other tooth has been found since its study by Lange-Badré (1987). This enigmatic species is characterized by many apomorphies: the retreat of the metaconid and its integration in the talonid, the communication between the trigonid basin and the hypoflexid, the relative fusion of the hypoconid and the hypoconulid, the disappearance of the entoconid.

RELATIONSHIPS OF NORTH AMERICAN AND EUROPEAN LATE PALEOCENE AND EARLY EOCENE CREODONTS

The creodonts of the Paleocene-Eocene transition are well represented in Belgium: two families and three subfamilies for six genera. Such an observation is a priori unexpected since, not only are the creodonts rare in the Early Eocene of Europe (Lange-Badré *in* Godinot et al., 1987), but, in addition, they represent in Dormaal one of the first occurrences of this group in Europe.

The hyaenodontid creodonts (Fig. 9) are closely related to those of the Wasatchian Wa0 of the North American Willwood Formation (Wyoming) from which *Arfia* and *Prototomus* can be distinguished primarily by M/3 and M3/. In both Belgian taxa, M/3 and M3/ are proportionally smaller and the talonid of M/3 is less developed, whereas among the various species of *Arfia* and *Prototomus* of the higher Wasatchian levels, the size of M/3 remains at least equal to M/2. P/4 and P4/ of *Prototomus* are less developed in the Belgian species, and the upper molars show primitive evolutionary stages, particularly M2/. Thus, two hypotheses can be drawn from our study. The Belgian species could either be at the origin of the American lineages, or belong already to distinct lineages but of recent differentiation.

The Belgian oxyaenid creodonts (Fig. 10) seem to resemble more the primitive species of the North American Clarkforkian than those already more derived from the Wasatchian. This would indicate that the north European species could be originating from the Paleocene lineages as presently documented by the North-American record. However, this does not explain their very small size as compared to the oxyaenids of the New World.

In conclusion, the phylogenetic relations between the Belgian and North American creodonts of the Paleocene-Eocene transition are narrow and any way relatively recent.

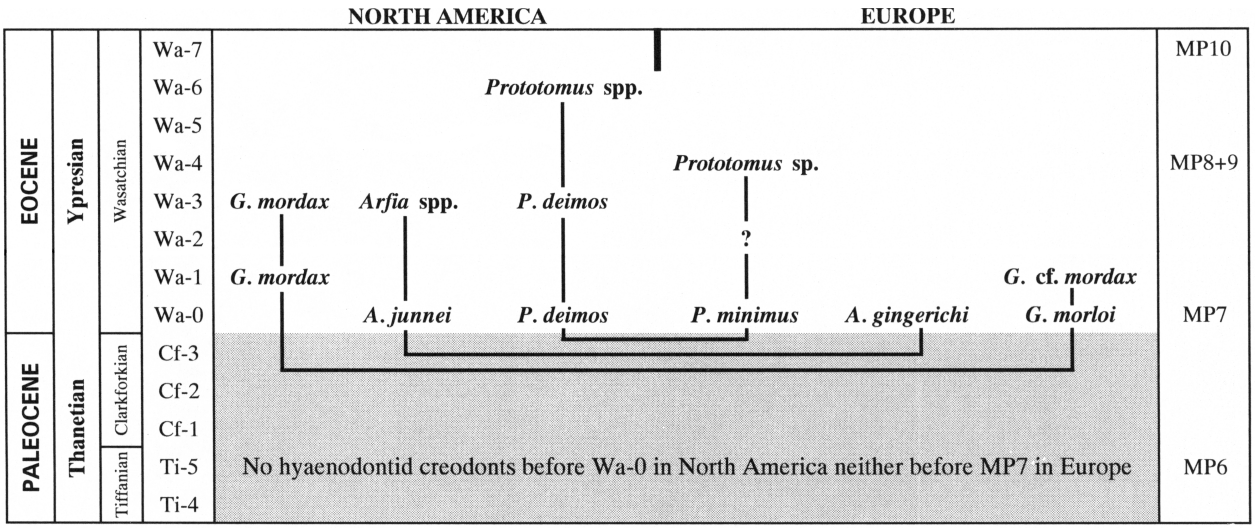


Fig. 9. – Spatial and temporal distribution of hyaenodontid creodonts in Europe and North America that have phylogenetic relationships with those of Belgium (the lines connect the closely related species). The left columns indicate the international stratigraphic scale and the equivalent stages in the continental stratigraphic scale of North America. The right columns indicate the reference levels of the mammalian biochronological scale for the European Paleogene (MP: Mammal Paleogene, MP6 to 10).

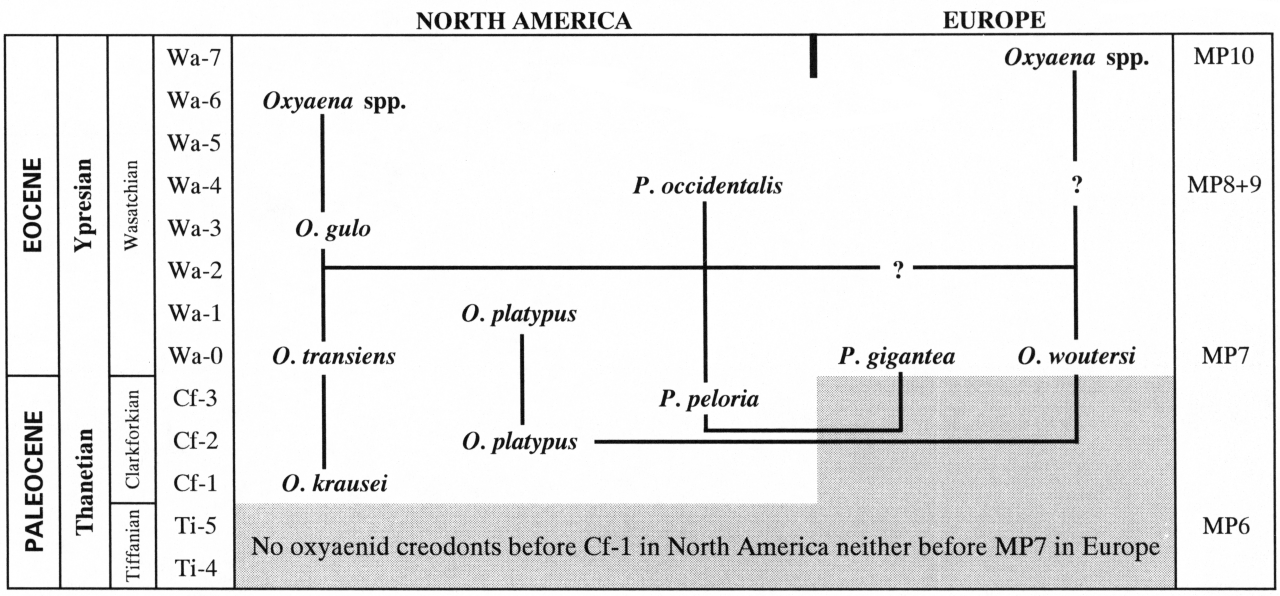


Fig. 10. – Spatial and temporal distribution of oxyaenid creodonts in Europe and North America that have phylogenetic relationships with those of Belgium (the lines connect the closely related species).

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