



The carnivoran-like insectivore *Butselia biveri* Quinet & Misonne, 1965 (Mammalia, Plesiosoricidae) from the lowermost Oligocene of Europe

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ABSTRACT

Plesiosoricidae is a small extinct family of soricomorphan insectivores distributed from the Early Eocene to the Late Miocene on the three continents of the Northern Hemisphere. One of two known plesiosoricid subfamilies is represented by the particular Eurasian subfamily Butseliinae. Here we describe new dental and postcranial elements of *Butselia biveri*, the type-species of the genus *Butselia* from the lowermost Oligocene of Belgium. The specialized anterior dentition shows a strong caniniform i2 while the upper and lower molars show a remarkable convergent evolution with early carnivorans, especially the small Early Eocene miacids. Tarsal bones of *Butselia biveri* are also identified and described, suggesting a closely relationship with Nyctitheriidae but also indicating some convergent features with small scansorial carnivorans.

Keywords: Soricomorpha, Plesiosoricidae, *Butselia*, MP21, Belgium.

RESUMEN

Plesiosoricidae es una pequeña familia extinta de insectívoros soricomorfos distribuidos desde el Eoceno temprano al Mioceno tardío en los tres continentes del Hemisferio Norte. Una de las dos subfamilias plesiosoricidas está representada por la particular subfamilia euroasiática Butseliinae. Aquí describimos nuevos elementos dentales y postcraneales de *Butselia biveri*, la especie tipo del género *Butselia*, del inicio del Oligoceno en Bélgica. La especializada dentición anterior muestra un fuerte i2 caniniforme mientras los molares superiores e inferiores muestran una marcada evolución convergente con los carnívoros basales, especialmente los pequeños miácidos del Eoceno temprano. Los huesos tarsales de *Butselia biveri* también son identificados y descritos, sugiriendo una relación cercana con Nyctitheriidae pero indicando también algunas características convergentes con pequeños carnívoros escansoriales.

Palabras clave: Soricomorpha, Plesiosoricidae, *Butselia*, MP21, Bélgica.

1. INTRODUCTION

Butselia biveri was originally described by Quinet & Misonne (1965) based on two M1 and one M2 (interpreted as M3) from the Lower Oligocene (MP 21) of Hoogbutsel (Belgium). These authors considered *B. biveri* as a zalambdodont insectivore and assigned it to the new family Butselidae. In the same paper, they also described two lower molars that they referred to an unidentified genus and species of zalambdodont insectivore. Later, these lower molars were assigned to *B. biveri* by Butler (1972) who described and figured additional material of *B. biveri* from the Isle of Wight and moved the genus *Butselia* into the family Plesiosoricidae. Later, McKenna & Bell (1997) considered the family Butselidae as a junior synonym of the family Plesiosoricidae in which they included the genera: *Pakilestes* Russell & Gingerich, 1981 from the early Middle Eocene Kuldana Formation of Kohat, Pakistan; *Ernosorex* Wang & Li, 1990 from the Middle Eocene of China; *Butselia* Quinet & Misonne, 1965 (subject of this article); *Pseudoneurogymnurus* Gureev, 1979 from the Late Eocene-Early Oligocene of Eastern Kazakhstan; *Plesiosorex* Pomel, 1848 from the Late Oligocene to the Late Miocene of Europe, North America and Asia; and *Meterix* Hall, 1929 from the Middle Miocene of Nevada (although *Meterix* was regarded as a junior synonym of *Plesiosorex* by Green, 1977). However, Lopatin (2006) proposed to restore the group name Butseliinae as a subfamily of Plesiosoricidae and described the new genus *Ordolestes* from the Early Eocene of Mongolia that he considered as the earliest representative of the subfamily Butseliinae and the family Plesiosoricidae in general. He included *Pakilestes* and *Butselia* in this subfamily and recognized two subfamilies among Plesiosoricidae: Butseliinae Quinet & Misonne, 1965 and Plesiosoricinae Winge, 1917.

Recently, Peigné *et al.* (2009) described *Siamosorex debonisi* from the latest Oligocene of Nong Ya Plong in Thailand. This species that belongs to the Plesiosoricidae and represents a unique example of convergent evolution with true carnivorans may have some relationships with the genus *Butselia* (Peigné *et al.* 2009). The same year, Ziegler (2009) described new dental specimens of *Butselia biveri* from the early Oligocene (MP 21 and MP 22) of Germany. In a phylogenetic analysis Ziegler (2009) showed the basal position of *Butselia* with respect to *Plesiosorex*, and the basal position of *Plesiosorex soricinoides* with respect to the numerous other *Plesiosorex* species.

In this study we describe new dental and postcranial elements of *Butselia biveri* from the lowermost Oligocene of Belgium, including for the first time the incisors and tarsal bones that allow reassessing the phylogenetic positioning of the Butseliinae. The specimens described were collected during a field work by one of the authors

(RS) in September 1999 at the locality of Boutersem, ca. 30 km east of Brussels, Belgium (Fig. 1). The site was a shallow outcrop at km 29,650 along the highway E 40 (A3), temporarily exposed during the High Speed Train (TGV) railway construction. The fossil bed occurred at the base of a fluvio-lacustrine complex, the Boutersem Member that overlies the latest Eocene marine Neerrepn Sands. The Boutersem Member that consists of shell-beds, clayey sands, and shelly sands belongs to the Borgloon Formation that is included in the Tongeren Group (Wouters & Vandenberghe, 1994; Mayr & Smith, 2001). The Boutersem sands contain molluscs (Marquet *et al.*, 2008) and also yielded a rich fauna of vertebrates represented by amphibians (Folie *et al.*, 2010), lizards (Augé & Smith, 2009), birds (Mayr & Smith, 2001), and mammals (Smith, 2003). The mammal fauna is correlated with the reference level MP 21 of the mammalian biochronological scale for the European Paleogene (Aguilar *et al.*, 1997) defined on the fauna of Soumaillies (Aquitaine, France). All the fossils are recorded from the oldest continental levels of the Early Oligocene near the «Grande Coupure» (Stehlin, 1909). The mammals are represented by several insectivorous taxa (see Smith, 2004 a, b, 2006 a, b, 2007; Smith & van den Hoek Ostende, 2006) and among those, many teeth belonging to *Butselia biveri* that allow to reconstitute the dental upper and lower series. Next to the dental remains, several astragalus and calcaneum were easily attributed to *Butselia biveri* based on its size and abundance as only the well-known and abundant rodent *Theridomys* is larger than *Butselia* in Boutersem; all the other species are distinctly smaller than *Butselia*.

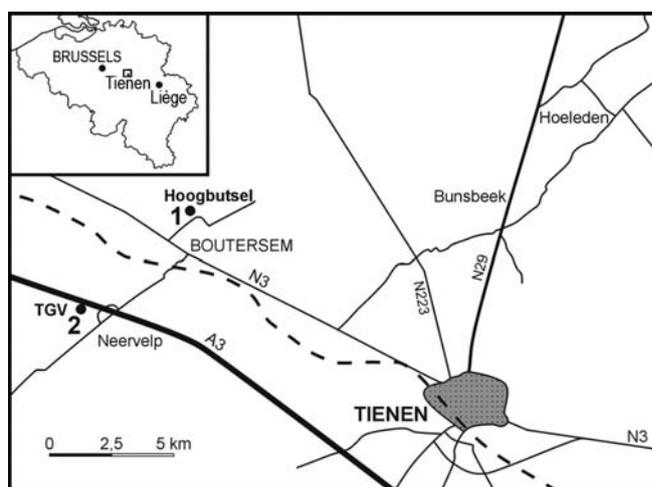


Figure 1. Location of the localities of Hoogbutsel (1) and Boutersem TGV (2).

2. MATERIALS AND METHODS

The mammal systematic classification used here is that proposed by McKenna & Bell (1997). The terminology used for dental crests and cusps is based on that defined by Van Valen (1966), completed for the subfamily Butselinae by Lopatin (2006). The terminology for the tarsal bones is that of Cifelli (1983). The fossils figured in this paper are housed at the Royal Belgian Institute of Natural Sciences (IRSNB). All of them were collected by one of the authors (RS) in the locality of Boutersem-TGV, except IRSNB M2057 which is from the type-locality of Hoogbutsel. The other specimens recorded from Boutersem-TGV are housed in the collection of R. Smith (RS).

Abbreviations

BSP: Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany.

GSP-UM: Geological Survey of Pakistan, Islamabad, Pakistan.

IRSNB : Institut royal des Sciences naturelles de Belgique, Brussels, Belgium.

TGV : Train à Grande Vitesse (High Speed Train).

BOU: Boutersem-TGV.

3. SYSTEMATIC PALAEONTOLOGY

Grandorder LIPOTYPHILA Haeckel, 1866

Order SORICOMORPHA Gregory, 1910

Superfamily SORICOIDEA Fischer, 1817

Family **Plesiosoricidae** Winge, 1917

Subfamily Butseliinae Quinet & Misonne, 1965

Genus *Butselia* Quinet & Misonne, 1965

Type species *Butselia biveri* Quinet & Misonne, 1965

Butselia biveri Quinet & Misonne, 1965

Figs 2-5, Table 1

Holotype: IRSNB M1222 (see Quinet & Misonne, 1965).

Type locality and horizon: Hoogbutsel near Boutersem, Flemish Brabant, Belgium (Glibert & de Heinzelin de Braucourt, 1952; Smith, 2003), lowermost Oligocene, Boutersem Member, Borgloon Formation, Early Rupelian, reference level MP 21 (see Aguilar *et al.*, 1997).

Other localities: Boutersem-TGV, Belgium (see Smith, 2003, 2004 a, b); Yarmouth, Isle of Wight, England, lower Hamstead Member (Butler, 1972; Hooker *et al.*, 2004); Möhren quarry, Germany, MP21-22 (see Ziegler, 2009).

New material: Right dentary with p4 and trigonid of m1: IRSNB M2057; fragmentary left dentary with p4-m1: BOU 365 RS; i1?: IRSNB M2058 (BOU 802 RS); i2: IRSNB M2059 (BOU 804 RS), BOU 805 RS, BOU 806 RS, BOU 807 RS, BOU 808 RS; i3: IRSNB M2118 (BOU 814 RS); p1: BOU 799 RS, IRSNB M2060 (BOU 813 RS); dp4: IRSNB M2061 (BOU 502 RS); p4: IRSNB M2062 (BOU 440 RS); m1: IRSNB M2063 (BOU 92 RS); m2: BOU 81 RS, BOU 194 RS, IRSNB M2064 (BOU 286 RS); m3: IRSNB M2065 (BOU 288 RS), BOU 513 RS, BOU 636 RS; fragmentary right maxilla with P3-P4: IRSNB M2066a-b (BOU 594 RS); P3: BOU 575 RS; DP4: IRSNB M2067 (BOU 626 RS); P4: BOU 408 RS; M1: BOU 93 RS, BOU 95 RS, BOU 113 RS, BOU 231 RS, BOU 353 RS, IRSNB M2068 (BOU 567 RS), BOU 623 RS; M2: BOU 534 RS, IRSNB M2069 (BOU 552 RS), BOU 558 RS, BOU 574 RS, BOU 673 RS, BOU 677 RS, BOU 691 RS; M3: BOU 130 RS, BOU 255 RS, IRSNB M2070 (BOU 424 RS), BOU 621 RS, BOU 678 RS; Astragalus: IRSNB M2071 (BOU 800 RS), BOU 812 RS; Calcaneum: IRSNB M2072 (BOU 801 RS), BOU 809 RS, BOU 810 RS, BOU 811 RS.

Table 1: Measurements (in mm) of cheek teeth of *Butselia biveri* from Boutersem-TGV. 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	1	2.90		-	-	-
	l	1	3.30		-	-	-
P3	L	2	2.30	2.45	2.38	0.11	4.63
	l	2	1.60	1.80	1.70	0.14	8.24
P4	L	2	3.25		-	-	-
	l	2	3.60	3.70	3.65	0.07	1.92
M1	L	7	2.35	3.60	2.51	0.08	3.19
	l	7	3.60	4.00	3.84	0.14	3.65
M2	L	7	1.60	2.05	1.79	0.14	7.84
	l	7	2.45	3.10	2.81	0.24	8.53
M3	L	5	1.00	1.15	1.07	0.07	6.54
	l	5	1.35	1.60	1.52	0.12	7.89
p1	L	1	1.15		-	-	-
	l	1	0.85		-	-	-
dp4	L	1	2.25		-	-	-
	l	1	1.40		-	-	-
p4	L	2	2.10	2.25	2.18	0.11	5.06
	l	2	1.40	1.60	1.50	0.14	9.33
m1	L	2	2.90	3.10	3.00	0.14	4.67
	l	2	2.30	2.30	2.30	0.00	0.00
m2	L	3	2.15	2.30	2.22	0.08	3.61
	l	3	1.80	2.00	1.90	0.10	5.26
m3	L	3	1.45	1.55	1.48	0.06	4.04
	l	3	1.20	1.25	1.23	0.03	2.43

3.1. Dentary

The dentary is slender and elongated anteroposteriorly (Fig. 2). The symphysis is poorly marked but well extended from the tip of the jaw to below the anterior root of p3. The horizontal ramus is slender on the level of the symphysis. It becomes gradually somewhat labiolingually thicker from p4 to m3. The coronoid process is poorly preserved and seems to form a right angle with the horizontal ramus. The lower part of the dentary is relatively convex. There are two mental foramina, a small one below p2 and a larger one below the anterior root of p4 (on IRSNB M2057) or between the two roots of p4 (on BOU 365 RS). Doubling of the anterior foramen is observed in BOU 365 RS with

a second foramen below the posterior root of p3. The posterior part of the dentary BOU 365 RS is broken and does not show much information. The alveoli of the teeth are well preserved on both dentary fragments and attest the presence of at least two incisors, one single-rooted canine, single-rooted p1 and p2 (except on BOU 365 RS on which the alveolus of p2 is double-rooted) and two-rooted p3 to m3. The most anterior partially preserved alveolus is for a large curved incisor, probably i2 and is followed by a very small curved and circular alveolus for i3. The alveolus of i1 is not preserved.

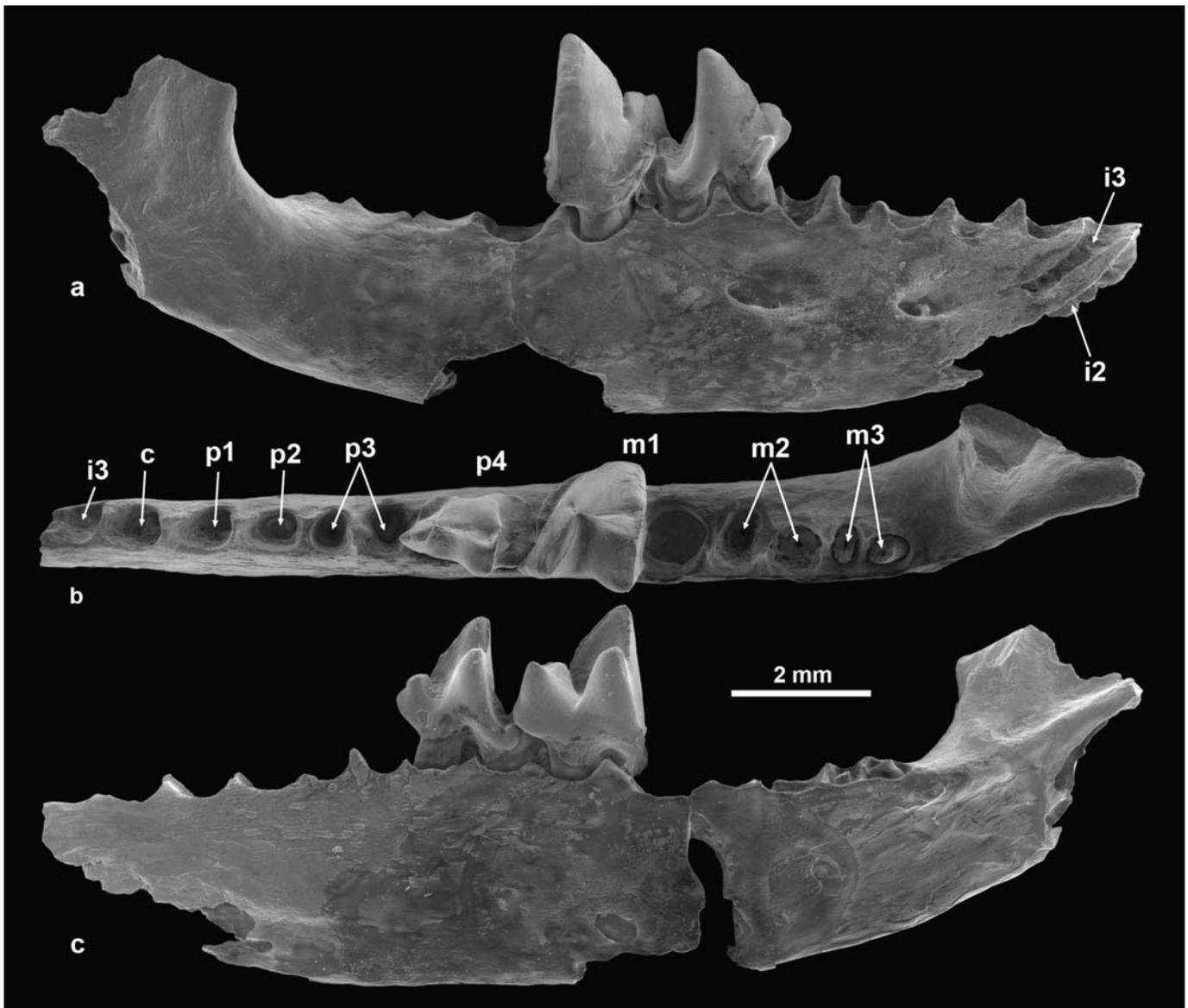


Figure 2. Right dentary IRSNB M2057 of *Butselia biveri* Quinet & Misonne, 1965 with p4 and trigonid of m1 in (a) labial, (b) occlusal and (c) lingual views.

3.2. Lower dentition

The tooth identified as a possible i1 (i1?) is a slightly curved long-rooted tooth that is compressed laterally (Figs 3a-c). The crown is slender with a posterior depression longitudinally divided in two by a thin central ridge. On the lateral side the crown shows a curved lateral ridge with a middle-sized accessory cusp at middle distance of the crown length. The medial ridge is curved, simple and joins posteriorly the lateral ridge. i2 is a large and long curved caniniform incisor with a slender and sharp-pointed crown (Figs 4d-f). The root is about twice the length of the crown and somewhat flattened on its medial side. The postero-lateral depression of the crown is longitudinally divided in two by a strong central ridge.

The i3 is a very small and curved premolariform incisor (Figs 3g-h). The crown is very simple, low, and bears an accessory posterior cusp and a slight bulge on the anterior side.

The teeth increase in size from p1 to p4 and decrease from m1 to m3. p1 is procumbent and single-rooted (Figs 3i-k). The anterior crest of the main cusp is convex and sharp while the posterior crest also sharp is nearly straight and joined a tiny posterolingual accessory cusp. In occlusal view the two crests are aligned and the labial edge extends gradually anteroposteriorly. There is a weakly developed cingulid on the two edges of the tooth. The labial cingulid is longer and somewhat more developed than the lingual cingulid. Between these cingulids and the main cusp a small depression occurs on both sides, narrow on the lingual side and enlarged on the labial side.



Figure 3. Anterior and deciduous teeth of *Butselia biveri* Quinet & Misonne, 1965. **a-c**) left i1? IRSNB M2058 (BOU 802 RS), (a) lateral, (b) posterior, (c) medial views; **d-f**) right i2 IRSNB M2059 (BOU 804 RS), (d) lateral, (e) posterior, (f) medial views; **g-h**) i3 IRSNB M2118 (BOU 814 RS), lateral and medial views; **i-k**) right p1 IRSNB M2060 (BOU 813 RS), (i) labial, (j) occlusal, (k) lingual views; **l-n**) right dp4 IRSNB M2061 (BOU 502 RS), (l) labial, (m) occlusal, (n) lingual views; **o-p**) left DP4 IRSNB M2067 (BOU 626 RS), (o) labial, (p) occlusal views.

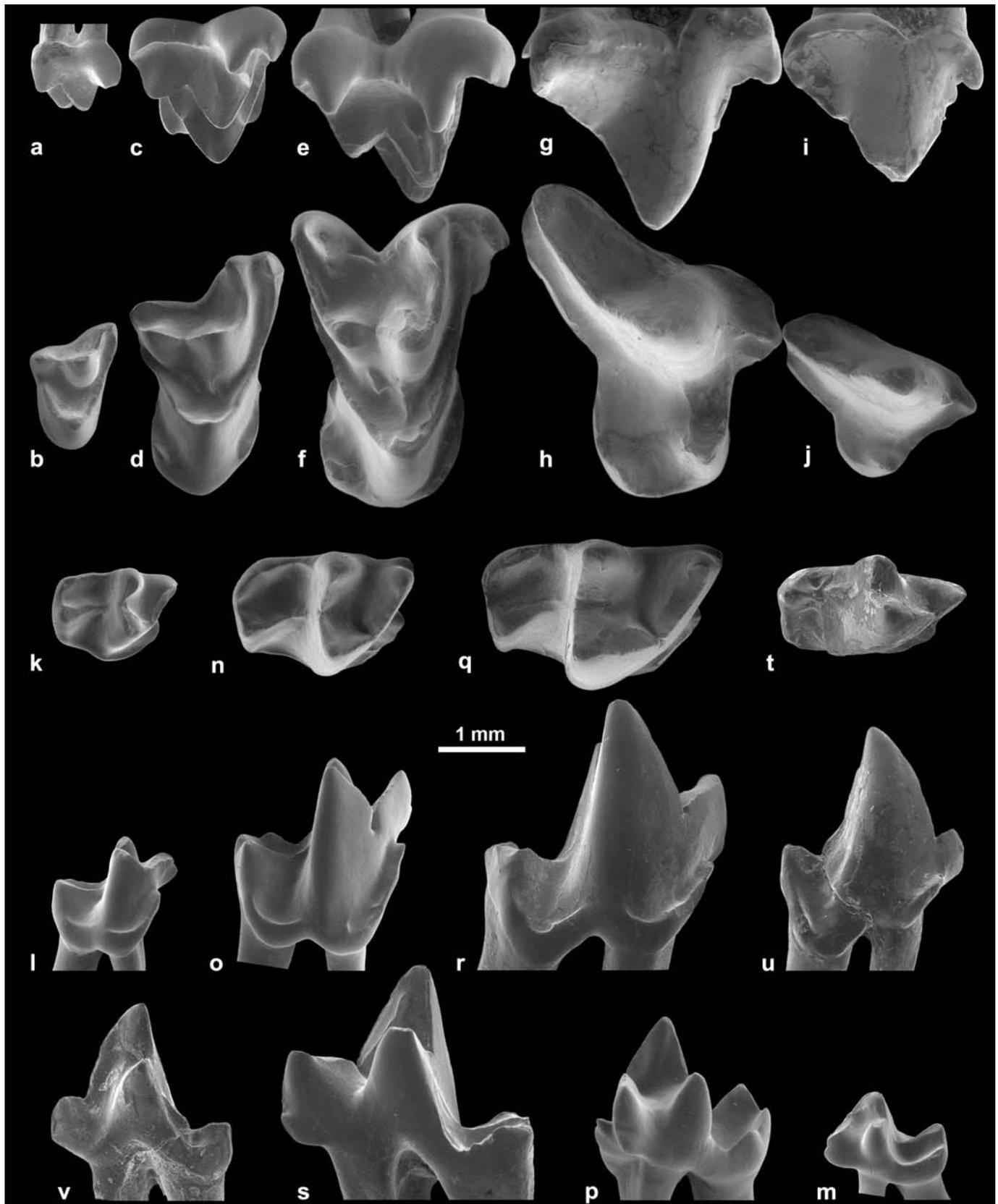


Figure 4. Upper and lower jugal teeth of *Butselia biveri* Quinet & Misonne, 1965. **a-b**) left M3 (reversed) IRSNB M2070 (BOU 424 RS); **c-d**) left M2 (reversed) IRSNB M2069 (BOU 552 RS); **e-f**) right M1 IRSNB M2068 (BOU 567 RS); **g-h**) right P4 IRSNB M2066a (BOU 594 RS); **i-j**) right P3 IRSNB M2066b (BOU 594 RS) in labial and occlusal views; **k-m**) right m3 IRSNB M2065 (BOU 288 RS); **n-p**) left m2 (reversed) IRSNB M2064 (BOU 286 RS); **q-s**) right m1 IRSNB M2063 (BOU 92 RS); **t-v**) right p4 IRSNB M2062 (BOU 440 RS) in occlusal, labial and lingual views.

The dp4 is similar in size to p4 (Figs 3l-n). The trigonid is not high. The protoconid is sharp-pointed. The paraconid is procumbent and very well developed. The protolophid and the paralophid are sharp. The trigonid basin is largely opened lingually. A precingulid is present but its size and aspect are difficult to estimate because the tooth is damaged at this level. The talonid is incurved labially. A small entoconid and hypoconid are separated by a notch. The talonid basin is relatively deep. The entocristid and the cristid obliqua are sub-parallel in occlusal view.

The p4 has a tall trigonid with a particularly high protoconid (Figs 4t-v). The protolophid is long and sharp. The metaconid closely pressed against the protoconid, a little more posterior than it, is only different in its upper part and does not reach its height. The well-developed paraconid is anteriorly projected. A strongly developed precingulid occurs under the base of the protolophid and extends until the base of the protoconid. The extremely reduced prefossilid is largely open lingually. The cristid obliqua reaches the middle height of the metaconid. The low and narrow talonid consists of a single crestiform cusp which is prolonged towards the cristid obliqua. This cusp is separated from the cristid obliqua by a weak notch. The reduced and shallow talonid basin is extremely narrow and lingually displaced. The hypoflexid is prolonged very low on the labial surface of the talonid which strongly goes down on the posterior root of the tooth. A thick cingulum borders all this posterior part.

The m1 is the largest tooth of the dentary (Figs 4q-s). Its trigonid, somewhat higher than that of p4, is much more massive. m1 is also longer and broader. The three trigonid cusps delimit a lingually open basin, definitely more important than that of p4. The paraconid, strongly developed, presents a thickening on the lingual side. The paracristid is strong, shearing, with a narrow deep carnassial notch. The precingulid, more prominent and longer than those of the premolars, nearly joined the postcingulum. The talonid is definitely shorter and narrower than the trigonid. In occlusal view, the lingual edge of the talonid and the cristid obliqua are sub parallel in m1 as in m2 and m3 also. The two m1 specimens present an important wear on the crests of the cusps.

The m2 is smaller than m1 (Figs 4n-p). Its trigonid is shorter than that of m1, the paraconid being smaller, less thick, and closer to the two other cusps. Trigonid and talonid are about equal in length. In labial view, the precingulid joined the postcingulid. The hypoconid is the main cusp of the talonid. The entoconid is less developed than the hypoconulid, these two cusps being close to each other. On the specimen BOU 194 RS which is not worn, they are not distinguishable from the postcristid-entocristid that forms only one long and curved crest. The trigonid and talonid basins are relatively deep.

The m3 is more reduced than m2 and extremely reduced in comparison with m1 (Figs 4k-m). Its paralophid

is somewhat concave in occlusal view and the paraconid is anteriorly prominent. The pre- and postcingulids, are joined and well developed. The talonid has only two cusps, a hypoconid and a presumed hypoconulid.

3.3. Upper dentition

DP4 has a similar size and outline to P4 (Figs 3o-p). The labial edge is also rather similar to that of P4 although a little more sinuous in occlusal view. The paracone is the highest cusp of the tooth. The labial side is concave in lateral view. The paracrista is sharp. The well-developed crestiform parastyle is separated from the paracingulum by a notch open to the anterior side of the tooth. The postparaconule crest connects the top of the protocone. The preprotocrista joins a small paraconule on the anterior side of the tooth. The crestiform metacone is poorly individualized from the paracone. The metacrista is long and relatively sharp. The metastyle is very small. The metastylar lobe presents a thick stylar cusp extended postero-labially. The last is extended by a very fine small crest going up lingually and sub parallel to the metacrista. The two little cusps and the two sub parallel crests form a small basin open in the stylar area. The precingulum is well developed and shows a thin accessory cusp. The well-developed hypocone is well separated from the protocone.

P3 shows a triangular shape in occlusal view (Figs 4i-j). The paracone, the main cusp, is high. The metacone is very light and the centrocrista and metacrista are in the same line giving a blade-like aspect to the metastyle. The labial edge is sub-rectilinear or very slightly concave. The ectocingulum that borders the tooth is weaker in its centre. The parastyle is well developed and separated from the paracrista by a notch. The protocone, relatively low and small, is a little more powerful than the parastyle. There is no hypocone. The shallow profossa, is continued by a gutter parallel to the metacrista and open at its postero-labial extremity.

P4 is definitely larger than P3 (Figs 4g-h). It is the highest tooth of the series. Both teeth are rather comparable in morphology. However, P4 has a more concave labial edge and is more transversally elongated. The metastylar lobe is strongly developed postero-labially. There is no interruption between the centrocrista and the metacrista which form only one long blade-like crest. The well-developed but antero-posteriorly short protocone is separated from a crestiform hypocone by a broad groove. Hypocone and parastyle are of similar size.

M1 is wide. The high paracone and the lesser-developed metacone are separated from the labial edge by a wide stylar shelf. The paracone is connected to a powerful stylocone by a very long paracrista. The stylocone, paracone and protocone are located on the same labio-lingual axis. The stylocone, which is the highest stylar

cusps, is separated from the parastyle by a rather broad and very long paracingulum that is connected to the profossa. The parastylar lobe is much more developed than the metastylar lobe. The metastylar lobe presents a strong styler cusp. The labial edge shows a very deep ectoflexus. The precingulum and the postcingulum, on which a small but well-developed hypocone is present, are nearly connected at the base of the protocone.

M2 is definitely smaller than M1 (Figs 4c-d). The anterior part of the tooth is rather similar to that of M1. The labial edge is dissymmetrical with the parastyle and stylocone present on a strongly developed and labially extended parastylar lobe. The styler shelf, narrower in its posterior part is definitely less important than on M1. The precingulum and postcingulum, as well as the hypocone, are more discrete than on M1.

M3 is extremely reduced (Figs 4a-b). It resembles M2 in miniature and all the morphological characters are attenuated. However it does not show a metastylar lobe nor a precingulum. The postcingulum is vestigial and there is no hypocone.

3.4. Tarsal bones

3.4.1. Calcaneum

The proximal part of the tuber calcanei is medio-laterally compressed and very high dorso-plantarly (Figs 5a-e). There is a strong concavity high on the lateral side just proximal to the ectal facet. The ectal facet is relatively short proximo-distally and is situated a little nearer to the distal border than to the proximal border of the tuber. The long axis of the ectal facet makes an angle of about 40° to the long axis of the tuber calcanei. A small fibular facet seems present but is not very distinct. The sustentacular facet is distally extended until the medio-distal border of the tuber. This distal extension of the sustentacular facet is small in surface. The proximal extremity of the sustentacular facet is situated at the level of the middle of the ectal facet. A nearly distal peroneal tubercle is somewhat laterally extended. The cuboid facet makes an angle of about 70° to the long axis of the tuber in dorsal view and has a L shape in distal view. The plantar tubercle is well developed.



Figure 5. Tarsal bones of *Butselia biveri* Quinet & Misonne, 1965. **a-e**) left calcaneum IRSNB M2072 (BOU 801 RS), (a) dorsal view, (b) plantar view, (c) medial view, (d) lateral view, (e) distal view; **f-k**) right astragalus IRSNB M2071 (BOU 800 RS), (f) dorsal view, (g) plantar view, (h) lateral view, (i) medial view, (j) proximal view, (k) distal view.

3.4.2. *Astragalus*

The trochlea is grooved and of medium width (Figs 5f-k). It represents about 60 % of the bone and makes an angle of 30° with the long axis of the neck. The medial and lateral ridges are parallel and have about the same length giving a square shape to the trochlea in dorsal view with the distal border being especially grooved. Both ridges are high but the lateral ridge is sharper than the medial one. The ectal facet is long, narrow, concave, and extends medio-plantarly. It is obliquely oriented with respect to the long axis of the neck. The neck is relatively strong and short. The fibular facet is vertical in dorsal view. The groove for the flexor fibularis tendon is narrow. There is no astragalar foramen. The sustentacular facet is wide, has a triangular shape and joins medially and laterally the navicular facet but leaves a shallow ovale depression between. The sustentacular facet is separated from the ectal facet by a broad groove. The navicular facet is medio-laterally long and dorso-plantarly narrow. It is nearly perpendicular to the main axis of the trochlea.

4. DISCUSSION

4.1. Comparison of the dental morphology of *Butselia* with that of other Butseliinae

The identification of all upper and lower jugal teeth of *Butselia biveri* at Boutersem-TGV reveals that the upper molar identified by Butler (1972) as M2 (p. 256, fig. 1 A-C) is actually a M1. In the same way, the upper molars BSP 1972 XI 223 identified as a M2 and BSP 1972 XI 243 as a M3 (Ziegler, 2009; fig. 2 M-N) are a M1 and a M2 respectively.

Pakilestes lathrius Russell & Gingerich, 1981 is known from a m1, the trigonid of a m2, and a questionably p4. The m1 GSP-UM 122 is relatively similar in morphology to the m1 of *Butselia* but it is very smaller and thinner than that of *Butselia*. In occlusal view the posterior part of the talonid of *P. lathrius* is rounded whereas that of *B. biveri* is straighter. The protoconid, paraconid and metaconid are proportionally less massive on *P. lathrius* than those of *B. biveri*. On the other hand, the morphology of the p4 of *P. lathrius* is much more different from that of *B. biveri*. The p4 of *B. biveri* is elongated in occlusal view and not short and wide as in *P. lathrius*. The paraconid is reduced, very low and lingually oriented on *P. lathrius* whereas it is well developed and anteriorly oriented in *B. biveri*. The massive protoconid markedly convex in occlusal view on *P. lathrius* is much less developed and straighter on *B. biveri*. The metaconid is larger on *B. biveri* and not so posterolingually situated from the protoconid as on *P. lathrius*. The talonid of *B. biveri* is narrower and not distinctly basined as on

P. lathrius. The hypoflexid that is very deep in *B. biveri* is very weak in *P. lathrius*.

Ordolestes ordinatus Lopatin, 2006 does not show many differences with *Butselia biveri*. The most remarkable difference is for m3. The tooth is more elongated in *O. ordinatus* and shows a hypoconulid that is missing in *B. biveri*.

Siamosorex debonisi Peigné *et al.*, 2009 differs from *B. biveri* by its larger size and in having proportionally lower trigonids on the premolars and the molars. The labial cingulid of m1-3 is complete on *S. debonisi* while it is incomplete at the base of the protoconid on *B. biveri*. The m1-3 show a broader talonid basin and a paraconid more anteriorly directed on *B. biveri*. The cristid obliqua is more labially directed on *S. debonisi*. The discovery of dentary fragments and isolated incisors of the butseliine *Butselia biveri* would indicate that the caniniform tooth of *S. debonisi* would not be a canine but an i2. The i1? of *S. debonisi* is similar to that of *B. biveri* with the accessory lateral cusp being a little more distal.

4.2. Comparison of the tarsal bones of *Butselia* with those of other mammals

The tarsal bones of *Butselia* present several plesiomorphic characters. Those characters are a trochlea not reduced in size and oblique to the neck, and a navicular facet that is oblique to the trochlea on the astragalus; an ectal facet and a cuboid facet that are oblique to the long axis of the tuber calcanei, and the retention of a peroneal tubercle on the calcaneum. However, the bones are also characterized by several apomorphies. Those are a symmetrical trochlea, a particular sustentacular facet on the astragalus, and a sustentacular facet that is distally extended on the calcaneum.

The astragalus of *Butselia* differs from that of amphilemurid erinaceomorphs, rodents and lagomorphs by the symmetrical trochlea with a perpendicular head. The navicular facet of the astragalus is not as elongated and wide proximo-laterally as in the erinaceomorphan *Macrocranion* (Godinot *et al.*, 1996) and *Zinocyon* (Dunn & Rasmussen, 2009). It is also distinguishable from primates by the short neck and from arctocyonids and most of the “condylarth” families by the absence of astragalar foramen and by a dorso-plantarly compressed navicular facet. Such a narrow navicular facet perpendicular to the trochlea axis is also present in the lousinid “condylarth” *Paschatherium* (Godinot *et al.*, 1996) and the miacid *Vulpavus* (Heinrich & Houde, 2006). But *Butselia* has no cotylar fossa and the trochlea is less grooved and asymmetrical than in lousinid condylarths (Godinot *et al.*, 1996; Tabuce *et al.*, 2006) and it differs from *Vulpavus* by the more grooved trochlea and particular shape of the sustentacular facet. Nevertheless, the comparison of the astragalus of *Butselia*

with miacid carnivorans is interesting by the similarities in the proportions, and the medial and lateral ridges that are both high (see Spaulding *et al.*, 2010 for figuration). The trochlea is much smaller than in the living soricomorphan *Sorex* (Hooker, 2001). The astragalus of *Butselia* resembles much that of the nyctitheriid *Cryptotopos?* sp. (Hooker, 2001) by the proportions, the grooved trochlea, the medial and lateral ridges equivalent in length, the absence of an astragalar foramen, the head perpendicular to the trochlea with a dorso-plantarly compressed navicular facet, and the particular shape of the sustentacular facet. However, it differs from *Cryptotopos?* sp. by the shorter neck and the higher medial ridge. These characters suggest an arboreal capability but probably with less mobility than in nyctitheriids.

The calcaneum of *Butselia* also resembles that of the nyctitheriid *Cryptotopos?* sp. (Hooker, 2001) by the proportions, the concavity proximo-lateral to the ectal facet, the inclined cuboid facet, and the distally extended sustentacular facet. However, it is different from *Cryptotopos?* sp. by the peroneal tubercle that is more distal and the ectal facet that is a little more oblique to the axis of the tuber calcanei. The latter is higher dorso-plantarly than in *Cryptotopos?* sp. and in this view resembles more to *Tupaia*. However, the distal peroneal tubercle of *Butselia* is a primitive feature different from *Tupaia*, nyctitheriids, plesiadapiforms, primates and early miacid carnivorans. Nevertheless, the general proportions of the calcaneum are relatively similar to those of early miacids (see Spaulding *et al.*, 2010 for figuration).

5. CONCLUSIONS

The numerous new specimens of *Butselia* from Boutersem-TGV allow to identify all the upper and lower jugal teeth and to complete the dental series of *Butselia biveri*. *Butselia* was probably an insectivore with carnivorous tendencies as previously suggested for the Asian butseliine *Siamosorex* (Peigné *et al.*, 2009). The carnassial-like P4 and m1 associate with a reducing in size of the posterior molars are features known in some modern erinaceid and soricid insectivores (Butler, 1972, 1988) but in a less developed condition. Moreover, in the case of *Butselia*, these features are associated with a strong caniniform incisor that is also in favour of this hypothesis. The discovery and the study of the calcaneum and astragalus of *B. biveri* help in the phylogenetic positioning of the Butseliinae by suggesting a relationship with the no less enigmatic family Nyctitheriidae. Nevertheless, the general proportions of the tarsal bones resemble that of scansorial early miacids and thus confirm the convergent evolution of the Butseliinae with early true carnivorans of small size.

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