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Plesiosoricids from early Oligocene fissure fillings in South Germany, with remarks on plesiosoricid phylogeny

REINHARD ZIEGLER



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The plesiosoricids from two fissure fillings from Möhren on the Franconian in South Germany are described. All belong to *Butselia biveri*. Möhren 12 correlates with the early Oligocene standard level Soumailles, corresponding to the Paleogene mammal unit MP 21, and Möhren 13 with the standard level Villebramar, which corresponds to MP 22. These occurrences represent the first record of the genus *Butselia* in Germany. A review of the known plesiosoricid species and a cladistic analysis of *Butselia* and *Plesiosorex* are presented. It shows the basal position of *Butselia* with respect to *Plesiosorex*, and the basal position of *Plesiosorex soricinoides* with respect to the other *Plesiosorex* species.

Key words: Mammalia, Lipotyphla, Plesiosoricidae, *Butselia*, cladistic, systematics, Germany.

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Introduction

The plesiosoricids (see Table 1) are a widespread insectivore family of mammals with an early Eocene to late Miocene temporal range, recorded from Asia, Europe and North America. The number of genera included in the Plesiosoricidae is a matter of some debate. The genera are briefly discussed in taxonomic order, beginning with the oldest unambiguous genus *Butselia*, followed by *Plesiosorex*, the most speciose, and by the taxa with doubtful plesiosoricid affinities.

Butselia biveri was first described by Quinet and Misonne (1965), on the basis of two upper molars from Hoogbutsel in Belgium, as a new genus of the new family Butseliidae. Later it was included in the family Plesiosoricidae Winge, 1917 by Butler (1972). Two lower molars, identified by the authors of this monotypic genus as indeterminate zalambdodonts (*Zalambdodontes* gen. et sp. indet.), obviously belong to *Butselia*. Smith (2004: pl. 1: 7) reported on new material from Boutersem TGV near the type locality, which includes two jaw fragments and 32 isolated teeth, of which he figured one upper molar. The new site was discovered during the railway construction of the rapid train TGV (Train a grande vitesse) near the village Boutersem. However, beyond the figured specimen, Smith (2004) did not provide any details. In faunal lists, Hooker (1987, 2005 and Hooker et al. (2004) mention occurrences from similar-aged strata in the English Hampshire Basin (Isle of Wight) and one tooth predating the "Grande Coupure" from the same island. But so far no details have been published on any of the material of *Butselia* from the Isle of Wight. Only Butler (1972: fig. 1) figured a left M2, a right p4 trigonid, right m1 trigonid, and an m2 from the Isle of Wight.

Plesiosorex Pomel, 1848, was described by Pomel with the type species *P. talpoides* from Cournon, France. This species is a junior synonym of *Erinaceus soricinoides* Blainville, 1838 from Chaufour in the Limagne, France. Pomel (1853) classified it with *Plesiosorex*. Hence, *Plesiosorex soricinoides* is the type species. *Plesiosorex* is the most speciose genus of the plesiosoricids, with a temporal range from the late Oligocene to late Miocene, and the only genus known from Europe, Asia and North America.

Meterix Hall, 1929, with the only species *M. latidens* Hall, 1929 from the late Miocene or early Pliocene of Nevada, was originally identified as a hedgehog. The similarity between the European *Plesiosorex* and *Meterix* was soon recognised (Dietrich 1929; Stromer 1940). Both genera belong to the Plesiosoricidae without any doubt, but there are differences which some authors consider sufficient to warrant generic separation (e.g., Wilson 1960; McKenna and Bell 1997). I agree with Green (1977), who formally placed it in synonymy with *Plesiosorex*. Hence, the correct name is *Plesiosorex latidens* (Hall, 1929).

Hibbarderix Martin and Green 1984, with the only species *Hibbarderix obfuscatus* from the Hemingfordian (early Miocene) Rosebud Formation in South Dakota, was classified as an erinaceine by the authors but synonymised with *Plesiosorex* by Mc Kenna and Bell (1997). Gunnell et al. (2008) listed *Plesiosorex obfuscatus* among included species of *Plesiosorex*. Martin and Green (1984) persuasively differentiated *Hibbarderix* from *Plesiosorex*. *Hibbarderix obfuscatus* is, without doubt, an erinaceine and thus is not discussed further herein.

Ordolestes Lopatin, 2006 is a monospecific genus from the lower Eocene of Mongolia. The only species is *O. ordi-*

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natus Lopatin, 2006, which is represented by the holotype, an isolated left m1, another left m1 and a dentary fragment with m2–m3.

Pseudoneurogymnurus Gureev, 1979 is known by two species from the early Oligocene of eastern Kazakhstan, the genotype *P. shevyrevae* Gureev, 1979 and *P. zhchikvadzei* Gureev, 1979. The genus has been referred to the Galericinae by Gureev (1979) and Lopatin (2006), but was assigned to the Plesiosoricidae by McKenna and Bell (1997). The P4 and the M2 of P. *zhchikvadzei* figured in Gureev (1979: fig. 61b) suggest galericine affinities of this species: more labial position of paracone and metacone, absence of labial stylar cusps in the M2; the well-developed parastyle, the marked protocone and the small, if present hypocone in the P4. However, the holotype M1 (Gureev 1979: fig. 1a) of the genotype *Pseudoneurogymnurus shevyrevae* more closely represents a plesiosoricid, as indicated by the large and projecting parastyle and the lingually shifted paracone and metacone. Hence, this species is better classified as a plesiosoricid.

Pakilestes lathrius Russell and Gingerich, 1981, the only species of the genus, is known from three isolated teeth—p4, a presumed m1 (holotype) and a trigonid of ?m2—from the early–middle Eocene of Pakistan. It was classified as a genus of a family incertae sedis of the order Proteutheria (?) by Russell and Gingerich (1981) and referred to the Plesiosoricidae by McKenna and Bell (1997). The teeth preserve too few characters for certain familial allocation. At best they represent presumed plesiosoricids and can be referred to the ?Plesiosoricidae.

Ernosorex Wang and Li, 1990 with its only species *E. jilinensis* Wang and Li, 1990, from the middle Eocene Huadian Formation from Northeast China was classified as a soricid by the authors. It has been referred to the Changlelestidae Tong and Wang, 1993 by the authors of the family based on the serrated incisor, which is more reminiscent of nyctitheriids than of *Plesiosorex*. This allocation was adopted by Storch et al. (1998), but not by McKenna and Bell (1997), who included it in the Plesiosoricidae. In the present study, the allocation of Tong and Wang (1993) to Changlelestidae is accepted.

The plesiosoricids presented here represent the earliest occurrences in Germany. Although widespread, plesiosoricids only occur in small numbers, and so these new fossils merit acknowledgement. The relationships between the genera and between the species are poorly understood. Here I try to elucidate the phylogenetic relationships in a cladistic analysis.

Instutional abbreviation.—BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany.

Other abbreviation.—Hum1, height of the dentary lingually under the middle of m1; L, length; m, arithmetic mean; n, number of specimens; R, range of measurements; W, width. Lower case letters refer to lower teeth (e.g., m1 = first lower molar), upper case to upper teeth (e.g., M1 = first upper molar).

Geological setting

The Möhren quarry is situated in the Treuchtlingen area about 20 km west of Eichstätt, Germany (see topographic map 1 : 25000, sheet 7031 Treuchtlingen), and has been well-known for many years (Fig. 1). It has yielded many fossiliferous fissure fillings, excavated by Kurt Heissig in the 1970s. He made known the fissure fillings, presented faunal lists and their stratigraphic correlations in several contributions (e.g., Heissig 1973, 1978, 1987). The Möhren 12 fissure filling correlates with the early Oligocene standard level Soumailles, which corresponds to the Palaeogene mammal unit MP 21; and Möhren 13 correlates with the standard level Villebramar, which corresponds to MP 22. Thus far only the rhinocerotids and the nyctitheriids have been published in more detail (Uhlig 1999; Ziegler 2007).

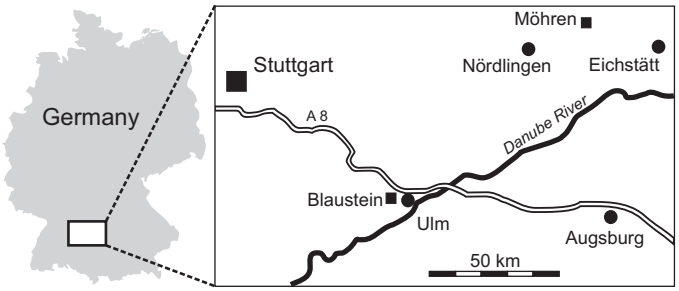


Fig. 1. Sketch map with the location of the Möhren site.

Methods

Dental terminology follows that of Van Valen (1966: fig. 1). The measurements of the teeth follow those presented by Schötz (1989: fig. 1, p4 according to fig. 8). All measurements are given in mm. In Table 2, the usual biometric parameters are presented.

Systematic palaeontology

Order Lipotyphla Haeckel, 1866

Suborder Soricomorpha Gregory, 1910

Family Plesiosoricidae Winge, 1917

Genus *Butselia* Quinet and Misonne, 1965

Type species: *Butselia biveri* Quinet and Misonne, 1965.

Type locality and age: Hoogbutsel, Belgium; early Oligocene, standard level Soumailles, Palaeogene mammal unit MP 21.

Butselia biveri Quinet and Misonne, 1965

Fig. 2.

Material.—Left dentary fragment with alveoli of i2-c and p2, p1 and p3–m3 (BSP 1971 XXX 60, Möhren 12). Two right edentulous dentary fragments, left dentary fragment with p3–

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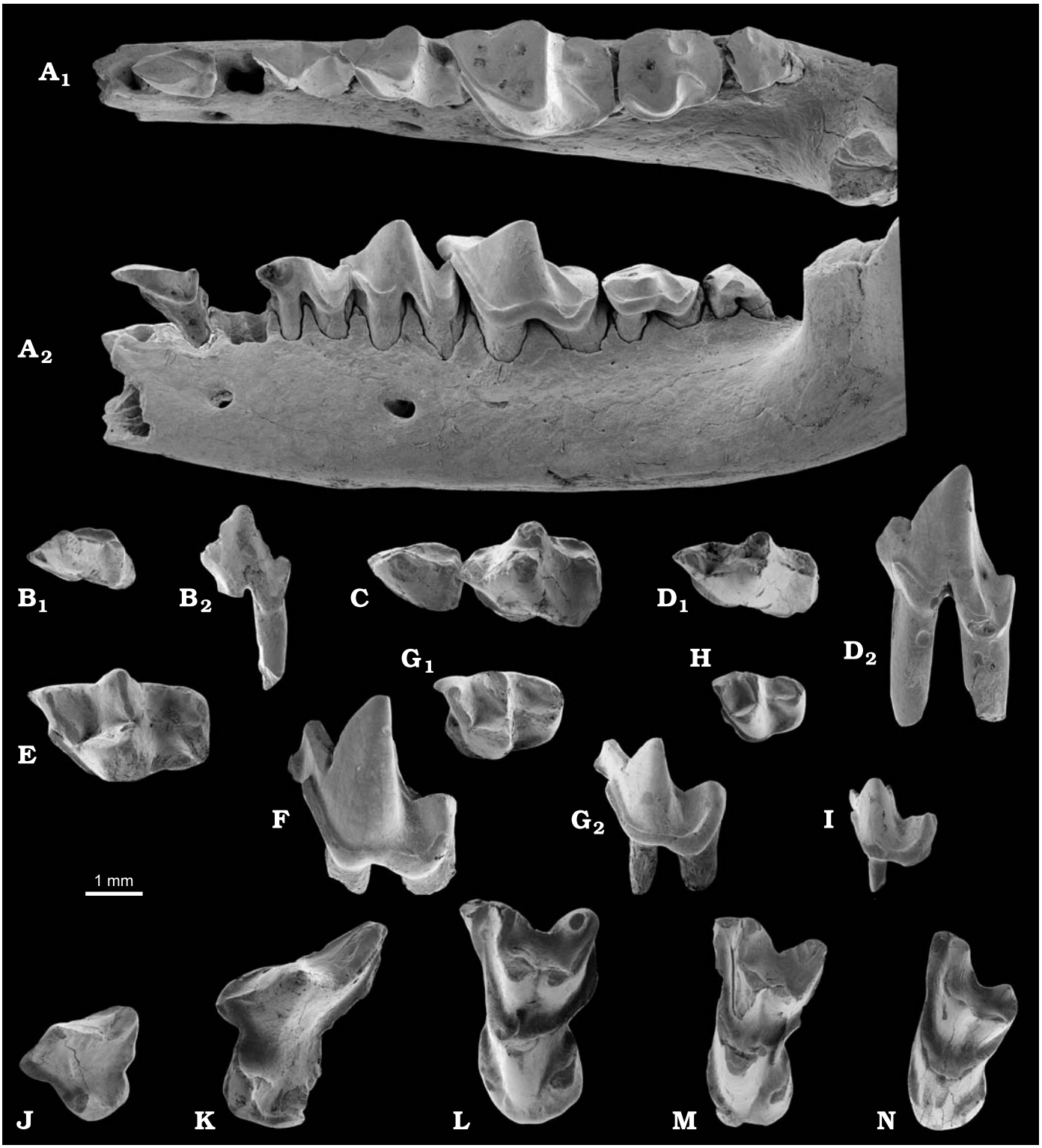


Fig. 2. Plesiosoricid mammal *Butselia biveri* Quinet and Misonne, 1965 from the Möhren Quarry (early Oligocene, southern Germany). **A**. Left dentary fragment with p1 and p3–m3, in occlusal (A_1) and labial (A_2) views, Möhren 12, BSP XI 1971 XXX 60. **B**. Left p2, in occlusal (B_1) and labial (B_2) views, Möhren 13, BSP 1972 XI 5908. **C**. Left dentary fragment with p3–p4 , in occlusal view, Möhren 13, BSP 1972 XI 239. **D**. Left p4, in occlusal (D_1) and labial (D_2) views, Möhren 13, BSP 1972 XI 225. **E**. Left dentary fragment with m1, in occlusal view, Möhren 13, BSP 1972 XI 5604. **F**. Left m1, in labial view, Möhren 13, BSP 1972 XI 228. **G**. Right m2, reversed, in occlusal (G_1) and labial (G_2) views, Möhren 13, BSP 1972 XI 229. **H**. Left m3, in occlusal view, Möhren 13, BSP 1972 XI 5909. **I**. Right m3, reversed, in labial view, Möhren 13, BSP 1972 XI 5599. **J**. Left P3, in occlusal view, Möhren 13, BSP 1972 XI 217. **K**. Left P4, in occlusal view, Möhren 13, BSP 1972 XI 218. **L**. Left M1, in occlusal view, Möhren 13, BSP 1972 XI 220. **M**. Left M2, a. in occlusal view, Möhren 13, BSP 1972 XI 223. **N**. Left M3, in occlusal view, Möhren 13, BSP 1972 XI 243.

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Table 1. List of known plesiosoricid species and their stratigraphic range.

Geography	Species	Stratigraphy
Europe	*Plesiosorex roosi* Franzen, Fejfar, and Storch, 2003	Late Miocene
	Plesiosorex evolutus Ziegler, 2006	Late Miocene
	Plesiosorex schaffneri Engesser, 1972	Late middle Miocene
	Plesiosorex germanicus Seemann, 1938	Middle Miocene
	Plesiosorex styriacus Hofmann, 1893	Middle Miocene
	Plesiosorex soricinoides De Blainville, 1838	Late Oligocene–early Miocene
	Plesiosorex martinii Engesser and Storch, 2008	Latest Oligocene, MP 30
	Butselia biveri Quinet and Misonne, 1965	?Late Eocene–early Oligocene
Asia	*Plesiosorex aydarlensis* Kordikova, 2000	Early/middle Miocene
	Pseudoneurogymnurus shevyrevae Gureev, 1979	Early Oligocene
	Pakilestes lathrius Russell and Gingerich, 1981	Middle Eocene
	Ordolestes ordinatus Lopatin, 2006	Early Eocene
North America	*Meterix latidens* Hall, 1929	Late Miocene
	Plesiosorex donroosai Green, 1977	Middle Miocene
	Plesiosorex greeni Martin and Lim, 2004	Early Miocene
	Plesiosorex coloradensis Wilson, 1960	Early Miocene

p4, left dentary fragment with m1, and 24 isolated teeth (BSP 1972 XI 217–243, 5599–5605, 5908–5909, Möhren 13). See Table 2 for specimens and measurements.

Description

Dentary.—Only fragments of the horizontal ramus are preserved. The most complete specimen from Möhren 12 includes the lowermost part of the ascending ramus with the cylindrical condyle high above the level of the tooth row and a strong, ledge-shaped mylohyoid ridge. Directly below this ridge the mandibular foramen opens posteriorly. The mental foramina lie under the anterior roots of p4 and p2, respectively. In one edentulous fragment from Möhren 13, there are three mental foramina: under the posterior root of p4, and under each of the roots of p3. Another fragment, which is broken anterior to p3, preserves one mental foramen under the posterior root of p4.

Lower dentition.—Based on the alveoli, there are at least three single-rooted teeth anterior to the p1. One small alveolus is for the obliquely implanted canine, another small alveolus housed a more obliquely implanted i3, and a procumbently oriented alveolus housed a large i2. The possible presence of i1 is suggested by the remnant of what appears to have been a very small alveolus. The single-rooted p1, which is preserved in the Möhren 12 dentary, is heavily worn. It has a lingual cingulid, a posterior cuspule and a straight posterior margin. The p2 has two perpendicular roots, a crested main cusp, a tiny anterior cuspule, a somewhat larger posterior cuspule, and a broad postero-lingual cingulum. The p3 differs from the p2 in its larger size and a more anteriorly directed taper. The p4 has a blade-like paraconid, a metaconid attached to the lingual face of the protoconid, a posterior cuspule and marked precingulid. The lower molars are strongly graded in size. Morphologically all are rather similar in the trigonid, being distinctly wider than the talonid. Anterior to the paraconid is a vertical bar. The paraconid is blade-like, at best a slightly pointed extremity of the paralophid, which is notched. All lower molars have a well-developed precingulid. The protolophid is also deeply notched. The talonid is reduced in size, with an entoconid more or less fused in the entocristid.

Upper dentition.—All upper teeth are isolated. One double-rooted tooth (no. 5603) with an ovoid occlusal outline, a crested main cusp and a posterior cuspule, is probably a P2. The P3 (no. 217; Fig. 2J) is triple-rooted with a lingual talon. The paracone is crested and the parastyle is only an anterior cingular projection. The protocone is a small cusp. The ectocingulum is interrupted above the paracone. The lingual part of this tooth, from the parastyle to the metastyle, is bordered by a cingulum. In the triple-rooted P4 the parastyle is a small, anterior and slightly cuspidate projection. There is a large talon with an anteriorly situated protocone and without a hypocone. Though the posterior part of the talon is broken the missing part is too small to have housed a hypocone. A cingular swelling may be interpreted as a vestigial (or incipient) hypocone. The most conspicuous feature of the P4 is the expanded, postero-labially directed metastylar blade. The crown base is surrounded by a lingually interrupted cingulum. The M1 and M2 are morphologically indistinguishable. An upper molar from the type locality was determined as M1/2 by Quinet and Misonne (1965). The new material—a dentary fragment with p4–m1, a maxillary fragment with P3–P4 and 32 isolated teeth—was included in Smith (2004) but were not described in detail. There are no upper molars in situ but in the Möhren 13 sample there are two size classes of morphologically identical teeth. The larger ones are considered to be the M1, the smaller ones the M2. The upper molars are extremely short with respect to their width. The paracone is the highest cusp, followed by the protocone. The metacone is adjacent and posterior to the paracone and is distinctly smaller. On the labial side there is an expanded stylar shelf.

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Table 2. *Butselia biveri* Quinet and Misonne, 1965, sample statistics of the teeth. Abbreviations: m, arithmetic mean; n, number of specimens; R, range of measurements.

Locality	Measurements	n	R	m
Möhren 12	Hum1	1		3.90
Möhren 13	Hum1	3	4.00–4.27	4.13
Möhren 12	Lp4–m3	1		8.25
Möhren 12	Lm1–m3	1		6.43
Möhren 13	Lm1–m3(a)	3	6.12–7.09	6.55
Möhren 12	Lp1	1		1.52
	Wp1	1		0.90
Möhren 13	Lp2	1	1.64	1.64
	Wp2	1	0.98	0.98
Möhren 12	Lp3	1		1.85
	Wp3	1		1.00
Möhren 13	Lp3	1		1.73
	Wp3	1		1.18
Möhren 12	Lp4	1		2.30
	Wp4	1		~1.25
Möhren 13	Lp4	2	2.50–2.66	2.58
	Wp4	3	1.20–1.50	1.40
Möhren 12	Lm1	1		3.29
	Wa	1		2.09
	Wpm1	1		1.59
	Wa*100/L	1		63.5
Möhren 13	Lm1	3	2.98–3.20	3.09
	Wam1	6	1.82–2.12	1.97
	Wpm1	3	1.35–1.71	1.53
	Wa*100/L	3	57.2–68.6	62.3
Möhren 12	Wam2	1		1.69
Möhren 13	Lm2	1		2.38
	Wam2	1		1.66
	Wpm2	1		1.49
	Wa*100/L	1		69.7
Möhren 12	Wam3	1		1.24
Möhren 13	Lm3	2	1.65–1.75	1.70
	Wam3	2	1.27–1.28	1.28
	Wa*100/L	2	73.1–77.0	75.1
Möhren 13	LP2	1		1.60
	WP2	1		0.96
Möhren 13	LP3	1		2.30
	WP3	1		1.87
Möhren 13	LP4	2	2.98–3.21	3.10
	WP4	2	3.60–3.67	3.64
Möhren 13	LM1	2	2.58–2.87	2.73
	WaM1	3	4.09–4.39	4.28
	Wa*100/L	2	153.0–158.5	155.7
Möhren 13	LM2	2	2.28–2.47	2.38
	WaM2	2	3.73–3.86	3.80
	Wa*100/L	2	156.3–163.6	159.9
Möhren 13	LM3	4	1.60–1.97	1.83
	WaM3	3	3.22–3.60	3.46
	Wa*100/L	3	191.4–201.3	194.7

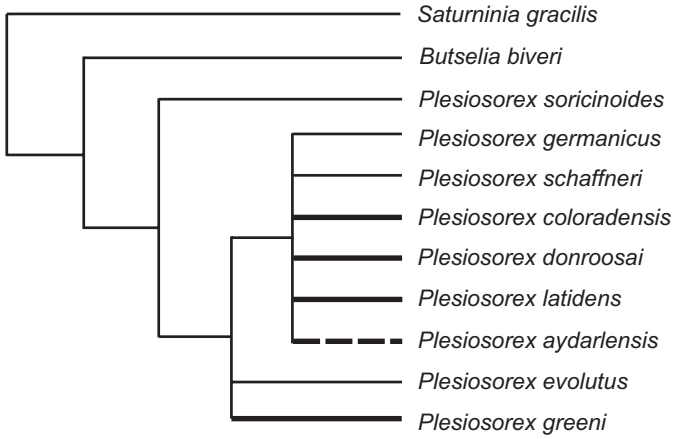


Fig. 3. Strict consensus of the 96 most parsimonious trees resulting from the analysis of the data matrix given in Table 2. Only the 10 ingroup-species with character completeness of >35% are included in the analysis; 26 characters. Tree length = 33, consistency index (CI) = 0.8788, rescaled consistency index (RC) = 0.7030, CI excluding uninformative characters = 0.8000, retention index (RI) = 0.8000. Thin lines = European taxa; bold lines = North American species; dashed line = Asian species.

The stylar cusps labial to the paracone and metacone are well developed but distinctly lower than the paracone and metacone, respectively. The parastyle and hypocone are the lowest cusps. The preprotocrista is continuous with the paracingulum; the postprotocrista joins the metacingulum. These crests converge at an acute angle towards the protocone. Slight constrictions on the preprotocrista and postprotocrista, respectively may indicate a vestigial paraconule or metaconule. The precingulum and postcingulum are also well-developed. The hypocone is either an inconspicuous swelling of the postcingulum (as on M3) or is slightly cuspidate (on M1 and M2). The M3 differs from the M2 in its smaller size and in its reduced postero-labial part, which results in an oblique labial margin.

Discussion.—Without doubt the specimens under study belong to *Butselia*. The characteristic morphology of the short upper molars, with their reduced posterior heel and poorly developed hypocone, differentiates them from any other plesiosoricid known by upper molars. The specimens herein compare well with *Butselia biveri* from the type locality, Hoogbutsel, Belgium, in the extremely short upper molars, in the absence of a marked hypocone, the size of the stylar cusps, in their degree of zalambdodonty and in the reduced talonid of the lower molars. The size differences are expected to lie within the normal size range of a population.

Quinet and Misonne (1965) placed *Butselia* in its own family, Butselidae, in the insectivoran suborder Zalambdodonta because of its semi-zalambdodont molars. Butler (1972) was the first to include it in the family Plesiosoricidae. Recently the plesiosoricid affinities of *Butselia* were questioned by Hooker (2005). He identified an isolated astragalus from the Isle of Wight as that of *Butselia*, which is unlike that of any lipotyphlan, but he did not publish further details. So far postcranials of plesiosoricids are unknown. Hooker (2005) presented two alternatives: either the Plesiosoricidae are not

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lipotyphlans or *Butselia* is not a plesiosoricid. Given the poor record, another alternative seems to be more probable (i.e., that the astragalus does not belong to *Butselia*). At present, there is no reason to exclude *Butselia* from the Plesiosoricidae.

Hooker (1987) and Hooker et al. (2004) also reported on the first pre-Grande Coupure record of *Butselia*, again from the Isle of Wight. This extended the range of the genus to the late Eocene. To date, all other pre-Oligocene plesiosoricids are Asian. However, as discussed earlier, the Chinese *Ernosorex* is not a plesiosoricid, and the familial allocation of the Pakistan *Pakilestes* is somewhat questionable. Hence *Ordolestes ordinatus* from the early Eocene of Mongolia is the only record which, though being sparse, may be attributed with some certainty to the plesiosoricids. *Ordolestes* is only known from some lower molars. They share with *Butselia* the narrow talonid, but differ from it in the strong ectocingulid below the hypoconid, and in the smaller entoconid. Given their sparse pre-Oligocene record, the origin of the plesiosoricids remains obscure.

Stratigraphic and geographic range.—*Butselia biveri* is recorded from England (Isle of White), from Belgium, and from Möhren in South Germany. The sites correlate with the late Eocene and the the early Oligocene.

Cladistic analysis of Plesiosoricidae

The sparseness of the fossil record severely impedes understanding of the phylogenetic relationships between the species. We have to rely solely on dental material. Many species—*Plesiosorex soricinoides*, *P. styriacus*, *P. roosi*, *P. greeni*, *P. donroosai*, *Ordolestes ordinatus*, and *Pakilestes lathrius*—are only known from their lower dentitions, and *Pseudoneurogymnurus shevyrevae* only from an M1. All characters are described below:

Characters of the dentary and the lower dentition

1 dental formula: complete (0), reduced (1)
2 p3: double-rooted (0), single-rooted (1)
3 p2: double-rooted (0), single-rooted (1)
4 i2: cuspulate (0), acuspulate, caniniform (1)
5 anterior mental foramen: absent (0), present (1)
6 posterior mental foramen below: p3 (0), p4 (1), m1 (2)
7 coronoid process: inclined posteriorly (0), perpendicular (1), anteriorly (2)
8 p4, base of labial crown: ± horizontal (0), bent upwards (1)
9 m1/2 hypoconulid: well-developed (0), rudimentary or absent (1)
10 m1 precingulid: present (0), absent (1)
11 m1 paralophid: carnassial notch absent (0), present (1)
12 m1/2 cingulid under hypoconid: present (0), absent (1)
13 m3 talonid: narrower than trigonid (0), ± as wide as or wider than trigonid (1)

Characters of the upper dentition

14 P3: occlusal outline triangular (0), trapezoidal (1)
15 P4: metacone present (0), absent (1)
16 P4: hypocone absent (0), present (1)
17 P4 postprotocrista: long (0), absent (1)
18 M1/2 paracone and metacone: situated labially (0), shifted lingually (1)
19 M1/2 ectoflexus concave: slightly (0), distinctly (1)
20 M1 antiparacone (cusp labial to paracone): absent (0), smaller than paracone (1), higher than paracone (2)
21 M1 antimetacone (cusp labial to the metacone): absent (0), present (1)
22 M1 precingulum: present (0), absent (1)
23 M1/2 hypocone: cingular swelling (0), well-developed (1)
24 M1 postprotocrista: continuous (0), short (1)
25 M2 antimetacone: absent (0), present (1)
26 M1/2: relatively wide (0), less wide (1)

The data matrix (Table 3) was analysed using the PAUP portable version 4.0b10 for Microsoft Windows. In the analysis 26 characters and ten ingroup taxa were considered. The polarity was determined with the nyctitheriid *Saturninia gracilis* as outgroup taxon. The nyctitheriid ancestry of Plesiosoricidae is evident, for stratigraphic as well as for morphologic reasons. The nyctitheriid *Saturninia gracilis* is less derived in all characters than any plesiosoricid. The analysis was performed in the heuristic and branch-and-bound modes. All characters were ordered, because the outgroup is well known and its plesiomorphic state is no matter of discussion. As there are only few multistate characters there are no significant differences between the analysis with ordered and unordered characters. Only species with character completeness of more than 35% are included in the analysis. Hence, *Plesiosorex martini*, *P. styriacus*, *P. roosi*, *Ordolestes ordinatus*, *Pakilestes lathrius*, and *Pseudoneurogymnurus shevyrevae* were omitted from the analysis. Autapomorphic characters have been ignored as they are irrelevant for interspecies relationships.

Table 3. Data matrix of character states analysed here. For explanation see text. In the matrix *Meterix latidens* and *Plesiosorex greeni* are synonymised. From Table 1 only the species with a character completeness > 35% are included in the analysis.

Character no./ completeness	12345678910	12345678910	12345678	%
Saturninia gracilis	0000000000	0000000000	000000	100
Butselia biveri	110?111110	1101101111	101101	96
Plesiosorex soricinoides	1111111110	110???????	??????	46
Plesiosorex germanicus	1111?12111	1111111111	102001	96
Plesiosorex schaffneri	1??1?2?111	111?111111	10110?	79
Plesiosorex evolutus	???????110	1111111101	101011	68
Plesiosorex coloradensis	0111122111	11??111112	11210?	86
Plesiosorex doroosai	1111122?11	11????????	??????	43
Plesiosorex latidens	11111?2110	11?????112	11211?	71
Plesiosorex aydarlensis	????????1?	?11????11?	11100?	39

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Although much of the cladogram is unresolved, it does show the clear separation of *Butselia* from the remaining plesiosoricids. *Butselia* differs from all other plesiosoricids in four unambiguous synapomorphies, the double-rooted p2 (character 3) and the absence of a hypocone on P4 (character 16), the absence of a well-developed hypocone on M1/2 (character 23), and in the width of upper molars (character 26). The sister-group relationship between *P. soricinoides* and the other *Plesiosorex* species is supported by two unambiguous synapomorphies (characters 6, 7), and by one homoplasy (character 13). The other *Plesiosorex* species are largely unresolved. The clade encompassing *P. germanicus* to *P. aydarlensis* is supported by one unambiguous synapomorphy (character 10).

Among the analysed taxa *Butselia* is the most primitive and the oldest species, and *P. soricinoides* is the oldest and most primitive species of that genus. The clade encompassing *P. germanicus* to *P. aydarlensis* includes European, Asian and North American, and early to late Miocene species. It seems to be an artificial grouping. The basal position of *Butselia* within the plesiosoricids argues in favour of their subdivision into two subfamilies, the Butseliinae Quinet and Misonne, 1965 and the Plesiosoricinae Winge, 1917, as suggested by Lopatin (2006).

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