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## Evolution of Oligo-Miocene talpids (Mammalia, Talpidae) in Europe: focus on the genera *Myxomygale* and *Percymygale* n. gen.

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### ABSTRACT

New material recovered in the Oligocene locality St-Martin-de-Castillon (Vaucluse, France; MP24) provides a better knowledge of the characteristics of the species *vaclusensis* in its type-locality, hitherto assigned to the genus *Myxomygale* (Talpinae, tribe Urotrichini). In Europe, the species assigned to *Myxomygale* range from Late Eocene/Early Oligocene to the end of the Middle Miocene (MN 7/8). However noticeable differences can be observed in mandibles of these taxa, sometimes even coexisting in the same localities. We propose for the plesiomorphic branch (including *M. vaclusensis* and *M. minor*) a new genus, *Percymygale*, closely related to *Myxomygale*. *Percymygale* is consequently also assigned to the tribe Urotrichini. Today, the tribe Urotrichini (American and Japanese shrew-moles) is composed of terrestrial, semi-fossorial species, not well adapted to digging but able to climb small bushes, and foraging in grasslands, forests and covered landscapes. As a result, their limbs protrude laterally from the body (unlike in moles) and their humeri are usually longer with very limited adaptations to digging. Humeri are poorly known for *Myxomygale* and only fragmentary humeri are known for *Percymygale* n. gen. making comparisons difficult. However the muzzle development in *Percymygale* and *Myxomygale* suggests that *Myxomygale* was perhaps a better burrower than *Percymygale*.

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### KEYWORDS

Talpidae; *Myxomygale*;  
*Percymygale* n. gen.; Europe;  
Oligocene/Miocene;  
systematic

### Introduction

Talpids arrive in Europe just before the beginning of the Oligocene but are generally rare in the Oligocene fossil record, badly preserved, often only represented by isolated teeth and crushed bones. Talpids are consequently not well known and their evolutionary history is difficult to decipher. The tribe Urotrichini – now only represented by three genera: one north-american and two japanese – was present in the Oligocene and Miocene with the genus *Myxomygale*. Paradoxically, even if also rare in the fossil record, *Myxomygale* extends on the whole Europe (Austria, Czech Republic, Serbia, Greece and especially Germany); more frequent and abundant in northern Europe (Ziegler 2003, 2006, 2012). It extends even to Spain during the Early/to Middle Miocene (Ruiz-Sanchez et al. 2012; van den Hoek Ostende et al. 2016), possibly linked to the extension of humid environments (Daams et al. 1988). New studies in the last fifty years made it possible to better understand the phylogenetic relationships between the different taxa, especially at generic level (Schwermann & Thompson 2015). New findings of the genus *Myxomygale* extends its record in Europe and it is now known during the entire Oligocene and can be found up to the end of the Middle Miocene (Ziegler 2012).

*Myxomygale* was created by Filhol (1890) on the basis of a unique mandible from the old collections of Quercy (unknown locality and age). It remained for long time the only specimen

known of this taxon. Huguene (1972) referred a poor dental talpid material from St-Martin-de-Castillon (Vaucluse, MP 24, 18 teeth) to the genus *Myxomygale* (as *M. cf. antiqua*) on the basis of dental similarities, even though the dental formula of this material was unknown and the posterior mental foramen absent below m1. This generic attribution was followed by other authors but Crochet (1995) created a new species, *M. vaclusensis*, on the basis of material from Huguene (1972) and choose the mandible with m1-3 from St-Martin-de-Castillon C (figured by Huguene 1972, Figure 27, p. 54 and here) as holotype of his new species.

Later on, new excavations in the St-Martin-de-Castillon localities yielded more material (Maridet et al. 2010). The discovery of some fragments of the mandibular horizontal ramus of *Myxomygale* in St-Martin-de-Castillon makes it possible to precise the diagnostic characteristics of *M. vaclusensis* in its type locality and to compare them to the rich material of the basal Oligocene levels of South Germany (MP 21-22; Ziegler 2012).

### Material and methods

*Terminology*: Anatomical terminology follows Hutchison (1968, 1974), but the length of M1-M2 is measured along the labial margin and the width perpendicular to the length (= L1 × W1 in Prieto et al. 2015; Figure 2). All measurements are in millimetres.

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**Figure 1.** Comparison of *Myxomygale antiqua* and *Percymygale vauclusensis* mandible morphologies. (a) *M. antiqua*, holotype (cast with broken ascending ramus), right mandible with p4-m2, MNHN QU 8682 (a1: occlusal view; a2: labial view); (b) *P. vauclusensis*, St-Martin de-Castillon: right mandible with m1-3, FSL 99318 (labial view).

Note: Scale bar: 2 mm.

*Abbreviations:* *L* = length, *W* = maximal width, *Wtr* = trigonid width, *Wta* = talonid width, *I/i* = incisors; *C/c* = canine; *M/m* = molar; *P/p* = premolar (respectively for Upper/lower teeth).

*Institutional abbreviations:* FSL = Lyon 1 University (former 'Faculté des Sciences de Lyon'); MNHN = Paris Museum.

*Chronologic framework:* The present study focuses on the European fossil record. Localities considered in the study range from the Late Eocene to the Middle Miocene, biochronological units ranging from MP20 (Palaeogene, reference level) to MN7/8 (Neogene, biozone). The units are defined for the European faunas on the basis of associations, first appearances and evolutionary stages of some diagnostic mammal species with large geographical ranges (Biochron'97 1997; Mein 1999).

### Systematic paleontology

Family TALPIDAE Fischer, 1814

Tribe Urotrichini Dobson, 1883

Genus *Myxomygale* Filhol, 1890

*Myxomygale antiqua* Filhol, 1890

(Figure 1(a))

*Type species:* *Myxomygale antiqua* Filhol, 1890

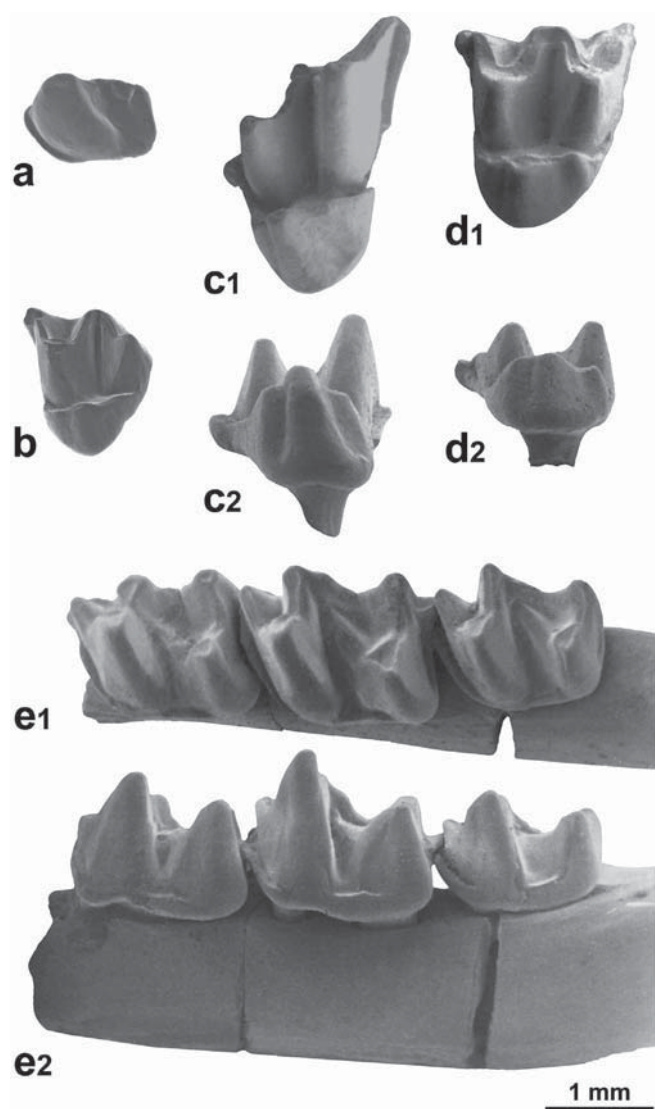
*Original diagnosis:* Translated from Filhol (1890)

'Insectivores seemed to be numerous, as well at generic and specific levels, on the Quercy up-land, when extensive masses of lime phosphate deposited. I had already the opportunity to make known several of them and my last prospectations have yielded the lower maxillary of an animal pertaining to this order which seems to have not yet been noticed.

The size of our animal was very small and the total length of the lower mandible, measured from posterior part of the condyle to alveolus of internal incisor, was 0.015. Dental formula: Incisors. 3 – Canine. 1 – Premolars. 4 – Molars. 3.

Fourth premolar and molars are the only teeth preserved on our specimen. Incisors seem, judging from their alveoli, to possess approximately the same volume. They were inserted along an antero-posterior line. Canine was single-rooted and its alveolus was larger than that of the third incisor. The three first premolars were single-rooted and their alveoli increased very slightly in volume from the first to the third. Alveolus of the first premolar was more reduced than that of the canine. Fourth premolar was double-rooted and its shape can be compared to that of the corresponding tooth from *Mygale*. Molars decrease in size from

the first to the last, characteristics which can also be found in water-moles and are missing in *Talpa*, where the second molar is larger. The cusps were less sharp, less compressed antero-posteriorly than in *Mygale* and are more similar to those of *Talpa*.



**Figure 2.** *Percymygale vaclusensis* (Crochet 1995). (a) left p4, FSL 99319, occlusal view; (b) left M3, FSL 99320, occlusal view; (c) left M1, FSL 99321 (c1: occlusal view, c2: lingual view); (d) left M2, FSL 97410 (d1: occlusal view, d2: lingual view); (e) left mandibular fragment with m1-m3, holotype, FSL 97405, ex '*Myxomygale cf. antiqua*' (e1: occlusal view, e2: labial view).

Note: Scale bar: 1 mm.

The ascending ramus displays very clear characteristics. It is noticeably developed as in *Desmana*; the angular process was separated and lengthened behind as a long thorn.

In *Talpa* the angular process is huge whereas in *Desmana* it is short and thicker. The coronoid process was high, wide at the base and its top was bent backwards. In *Mygale*, it is very slender and projects upwards and forwards.

If we sum up the characteristics, this fossil insectivore differs from *Talpa* in the single-rooted p1, in the posterior decrease of the molars and in the pattern of the ascending ramus; it differs

from *Mygale*, with which it shows more affinities, by the thicker cusps of its molars, by the pattern of the angular and coronoid processes.

**Size of mandible:** Length of the lower maxillary from incisor margin to end of the condyle, 0.0150 mm; Length of dental row, 0.0100 mm; High of the mandible at the canine level, 0.0015 mm; High of the mandible before the first molar, 0.0020 mm; High of the mandible behind the last molar, 0.0024 mm; High of the tip of the coronoid process above the lower border of the maxillary, 0.0068 mm; Horizontal distance between the posterior part of the condyle and the anterior edge of the ascending ramus, 0.0050 mm; Distance between the posterior part of the condyle and the posterior part of the alveolus of the last molar, 0.0070.

I designate this new mammal genus, which will be figured in another communication, as *Myxomygale antiqua*. (Translated from French)

**Holotype and measurements:** unique Quercy specimen hitherto referred to this species (Crochet 1974): right mandible with p4-m2 and damaged ascending ramus, MNHN QU 8682, (Figure 1(a)). p4:  $L = 1.33$ ,  $W = 0.84$  mm; m1:  $L = 1.99$ ,  $W = 1.24$  mm; m2:  $L = 1.91$ ,  $W = 1.18$  mm (notice decreasing size of molars distally).

**Other species included:** *M. hutchisoni* [(Ziegler, 1985); previously *Palurotrichus* n. g., junior synonym; MN 4], *M. engesseri* Doukas, 1986 (MN4), *M. minor* Ziegler, 1990 (MP 21-MN 3), *M. vaclusensis* Crochet, 1995 (MP 24-25), *M. gracilis* Ziegler, 2003 (MN 7/8). *M. asiaprima* Lopatin, 2004 (Late Oligocene, Kazakhstan) and the Late Eocene North-American *Oreotalpa florissantensis* Lloyd and Eberle, 2008 are also attributed to *Myxomygale* by Ziegler (2012); as non European species, these two last species are not considered here.

**Biochronologic distribution:** from MP 23/24 to MP 30 for *M. antiqua*, from MN3 to MN7/8 for *M. hutchisoni* and *M. gracilis*. *M. engesseri* cannot be assigned to *Myxomygale* with certainty.

**Description:** The holotype is from an old individual with heavily worn teeth rendering the morphologic characteristics difficult to observe. Crochet (1974) noticed and figured a faint mandibular branch with anterior mental foramen between p3 and p2 and posterior mental foramen below the talonid of m1, and seven alveoli before p4. Double-rooted p4 is as high as molars; the major cuspid displays a posterolingual crest joining a transverse talonid; a cingulid surrounds the talonid, the buccal side and ends anteriorly in a faint tubercle. p4 and molars are partly superposed and difficult to measure. The talonid of m1 is a little wider than the trigonid; on m2 they are similar. Protoconid and hypoconid form with the transverse crests very sharp angles. The oblique cristid joins the middle of the protoconid on m1 but is longer on m2 and joins nearly the metaconid. A marked cingulid surrounds the buccal side of the molars and ends in a marked entostylid.

**Remarks:** Filhol (1890) created this new talpid taxon from a unique mandible and interpreted the dental formula of this small insectivore as complete: 3.1.4.3. The mandible displays three anterior alveoli of nearly identical size for incisors, a slightly larger alveolus for the canine and three alveoli for anterior pre-molars increasing in size posteriorly. The alveolus of p1 is slightly smaller than that of the canine. Filhol notices that the morphology of the two-rooted p4 is similar to that of *Mygale* (former name for *Desmana*). In addition, Filhol noticed that the molars decrease in size from m1 to m3 as in *Desmana* whereas in *Talpa*

m2 is larger than m1 and that the molar morphology is more similar to that of *Talpa*. As differential diagnosis Filhol summed up the characteristics as: 'this insectivore differs from *Talpa* in the single-rooted p1, in the posterior decrease of the molars and in the pattern of the ascending ramus; it differs from *Mygale* by its thicker molar cusps, by the pattern of the mandibular angular and of the coronoid processes' (translated from French).

Crochet (1974) proposed several interpretations for the anterior lower dental formula of *Myxomygale*. Later, Crochet (1995) and Sigé and Crochet (2006) referred the type-mandible to the level MP 28 and proposed a completely different dental formula 2.1.3.3, with only two incisors, the first being enlarged, a minute canine, and two double-rooted premolars before p4. We have to remark, however, that this pattern does not correspond to the type mandible where the first incisor is not enlarged, as emphasised by Filhol (1890) 'incisors alveoli seem to possess approximately the same volume' (Translated from French) (see also Figure 1(a2)). Moreover, Ziegler and Storch (2008) figured a mandible from the German Cyrena Beds (MP 23-25) that corresponds well to that of *Myxomygale antiqua* and precise that 'the dentary preserves seven alveoli mesial to p4; three small ones for the procumbent incisors, one for the canine and three for the premolars anterior to p4'; they add that 'there is no indication of an enlarged incisor or canine'. As a matter of fact, this mandible corresponds well to *Myxomygale antiqua* and the fact that the p4 is larger could be due to difficulties for measuring the p4 of the type, its talonid being partly covered by the trigonid of m1. It is noteworthy that the age of the Cyrena Beds may correlate with many Quercy levels.

#### **Genus *Percymygale* n. gen.**

*Derivatio nominis*: in honour of Percy M. Butler; *-mygale* was a former name for desman used by Filhol and recalls the similarities between this new genus and *Myxomygale*.

*Type species*: *Percymygale minor* (Ziegler, 1990) from Ulm (MN2)

*Holotype*: left M1

*Type-locality*: Ulm-Westtangente (Germany)

*Species included*: *P. minor*, *P. vaucclusensis*.

*Biochronologic distribution*: MP 20 to MN3 for *P. minor*, MP 21 to MP 25 for *P. vaucclusensis*.

*Remarks*: the Czech locality Merkur-North yielded a very complete material (teeth and bones) of this species.

*Generic diagnosis*: small- to medium-sized talpid (a little smaller than *Myxomygale antiqua*) with slender mandible often tapering anteriorly, anterior mental foramen below anterior root of p2, posterior mental foramen below anterior root of p4; complete dental formula with double-rooted p1-p4. Pattern of the molars without clear differences with other species; m1 with curved paracristid, talonid wider than trigonid and oblique cristid joining the middle of the protocristid between protoconid and metaconid. Both m2 and m3 more rectangular with compressed trigonid and longer oblique cristid directed to the metaconid with more or less developed metacristid; marked cingulids vanishing under main labial tubercles. P4 has well-individualised protocone and parastyle and oblique metastyle. Upper molars triangular to more or less rectangular, strong dominating protocone, often with two lateral furrows corresponding to the well

marked protoconule and metaconule. In M1, the anterior arm of the protoconule joins the parastyle and the metaconule sends a posterior cingulum (partly broken on Figure 2(c)) to the base of the metastyle. The mesostyle is generally undivided. M2 is more symmetrical, protoconule is higher than metaconule, cingulum anterior and posterior less developed than on M1. The metacone of M3 is reduced. Humeri are slender with, apparently, some variations between the different species.

*Differential diagnosis*: *Percymygale* is compared to other small talpids which have modified and generally reduced antemolar part of the jaws; the number of antemolars and their number of roots is complete or nearly complete only in few genera. Many small talpids have slender humeri. We first compare with fossil genera generally ascribed, as *Myxomygale*, to the tribe Urotrichini: *Paratalpa*, *Tenuibrachiatum*, *Urotrichus*, *Dymecodon* and *Neurotrichus*, extant genera of this tribe, display reduced anterior premolar part of the mandible. However the systematic position of many fossil talpids within the family Talpidae is often under discussion.

- *Myxomygale* (all species) differs from *Percymygale* in having a reduced antemolar part of the jaw (7 alveoli anterior to p4), and posterior mental foramen below the talonid of m1. Humerus is unknown in the type-species.

- *Paratalpa* Lavocat, 1951 from the Late Oligocene/Early Miocene (MP 28-MN 1-2; France, Germany; Ziegler 1990; = *Teutonotalpa* Hutchison 1974; junior synonym) differs by its clear urotrichine affinities with very reduced antemolar part (only two lower incisors, no canine and from two to one premolar before p4, p3 being two-rooted or uniradicate or even absent). The posterior mental foramen varies from below the anterior root of m1 to between the two roots of p4; the anterior one from between the two roots of p4 to between the two roots of p2. Upper molars shows a triangular protocone, more or less divided mesostyle and continuous posterior cingulum. Humerus is relatively slender (Ziegler 1999, Figure 5.6).

*Desmanodon* Engesser, 1980 differs from *Percymygale* by the reduction of antemolars anterior to p4, by the pattern of the molars and particularly by its humerus better adapted to burrowing.

- *Tenuibrachiatum* Ziegler, 2003 from Petersbuch 31 (upper part of the Middle Miocene, MN7) differs from *Percymygale* by its very small size, the posterior mental foramen under m1, a less reduced antemolar part of the jaw than *Myxomygale* (9 alveoli anterior to p4) and only two incisors of different size. Slender humeri are very small and gracile with clear urotrichine affinities.

- *Mygatalpa arvernensis* from the late Oligocene (Hugueney 1972) differs from *Percymygale* by its mandible more thickened under i1-p3, with posterior mental foramen below anterior root of m1, by its m2 and m3 with a lower and more labial oblique cristid and the sinusid more largely open lingually; upper molars are more rectangular lingually, with clearly divided mesostyle and posterior cingulum often interrupted. Shaft of the humerus is slender (Hutchison 1974, Figure 13).

- *Asthenoscapter* Hutchison, 1974 from Late Oligocene (*A. zieglerei* Engesser and Storch, 2008) displays a mandible with posterior mental foramen below p4 or the anterior root of m1, lengthening of the anterior part from c to i1, p4-p2 double-rooted but p1 with one or two roots. Talonids of lower molars are long and oblique cristids of m2-3 ends low at the base of metaconid;

cingulids are labially massive and continuous. On M1-M2, lingual tubercles are aligned longitudinally, protoconule and metaconule are strong and a distinct postcingulid forms a posterior extension of the lingual border. In the type species, *A. meini* from the Middle Miocene of La Grive L7, the shaft of humeri is extremely slender (Hutchison 1974, Figure 11).

- *Desmanella* Engesser 1972 shows a complete lower dental formula but all teeth anterior to p4 have one root except p3 which has one or two roots (7/8 alveoli anterior to p4); the posterior mental foramen is below m1.

- *Theratisκος* van den Hoek-Ostende, 2001 from the Early Miocene of Anatolia displays a mandible with a complete lower dentition but posterior mental foramen below anterior root of m1, with double rooted p1-p4, p2 being larger than p3; m1 and m2 are of the same length with not very reduced m1 trigonid; the oblique cristid ends near the middle of the protoconid-metaconid crest or just a little more lingually; entocristid is well developed, but metacristid rare. Upper molars display faint protoconules but well developed metaconules. The shaft of humeri is extremely slender.

- *Talpa tenuidentata* Ziegler, 1990/*T. minuta* Blainville, 1838 show a mandible with some variations in the position of foramina mentale (under m1 and p2/p3) and four double-rooted premolars but p1 is enlarged. It differs mainly from *Percymyrgale* by humeri with a much thicker and robust shaft, a morphology that indicates a strong burrowing adaptation (Engesser 2009).

**Remarks:** In St-Martin-de-Castillon (Vaucluse, France; MP24), the type-locality of *P. vaclusensis*, this form is the only talpid of medium size and upper and lower teeth are homogeneous; the size of the fragments of humeri correspond to what is known for this taxon in other localities. As exemplified by the diagnosis and differential diagnosis of *Percymyrgale*, the differentiation from *Myxomyrgale* and *Percymyrgale* can not be made on isolated molars only. Consequently, *M. engesseri* Doukas, 1986 which is known from isolated molars can not be referred to any of these genera with certainty. We propose however to keep the original assignation to *Myxomyrgale* until more material is known.

Hooker (2010) assigned to *Myxomyrgale* cf. *antiqua* a small sample of 21 isolated teeth – no mandibular fragments showing alveoli – from post Grande-Coupure upper Hamstead Member of the Isle of White (England). He stated that their characteristics were nearer to the Quercy species, but recognised that ‘in these circumstances, judging intraspecific variation and therefore what defines a particular species is difficult’. A particularity of this material is however important: the teeth identified as p1 and p3 are double-rooted. This characteristic would rather support an assignation to the genus *Percymyrgale*, and the material could

rather be referred to the species *Percymyrgale vaclusensis* considering the similar size (see below).

### ***Percymyrgale vaclusensis* (Crochet, 1995) (Figures 1(b), 2(a)–(e))**

**Holotype:** mandible with m1-3, FSL 97405 (figured in Hugueneay 1972 Figure 27, p. 54 and here Figure 2(e)).

**Type-locality:** St-Martin-de-Castillon level C (Vaucluse, south-eastern France).

**Referred specimens:**

- Material figured in Hugueneay 1972 as *Myxomyrgale* cf. *antiqua* from St-Martin-de-Castillon level C: FSL 97406 to FSL 97410: right p4 (FSL 97406, Fig. 28, p. 55); left P4 (FSL 97407, Fig. 29, p. 55); right M3 (FSL 97408, Fig.30, p. 55); left M1 (FSL 97409, Figure 31, p. 55); left M2 (FSL 97410, Figure 32, p. 58).

**New material and measurements:** Measurements are given in Table 1

- Figured material: FSL 99318, right mandible with m1-3, Figure 1(b); FSL 99319, left p4, Figure 2(a); FSL 99320, left M3, Figure 2(b); FSL 99321, left M1, Figure 2(c).

- Referred material: 1 P4 (FSL 99322); 2 M1 (FSL 99323a-b); 5 M2 (FSL 99324a-e); 2 M3 (FSL 99325a-b); 8 p4 (FSL 99326a-h); 4 m1 (FSL 99327a-d); 5 m2 (FSL 99328a-e); 4 m3 (FSL 99329a-d); damaged bones (FSL 99330).

**Description:**

**Mandible:** it is slender and tapers anteriorly; it displays a complete dental formula with double-rooted p1-p4 and posterior mental foramen below the anterior root of p4, the anterior one being below the anterior root of p2. The symphysis extends in St Martin to the posterior part of p2. Ten alveoli exist before the double-rooted p4: three more or less identical (the first being a little damaged) for the incisors, one larger and a little elongated for the canine and six for double-rooted p1-p3; p1 displays larger alveoli than p2 and p3, the anterior one being shifted more labially. The teeth anterior to p4 are unknown.

**p4:** it displays a triangular main cusp rounded anteriorly and concave posteriorly, with a transverse talonid. An anterior cingulid exists labially and a little one lingually. A posterior cingulid borders the talonid. One tooth shows a faint metaconid near the postero-lingual crest (Figure 2(a)).

**Lower molars:** The lower molars (Figure 2(e)) are massive with large cingulids anteriorly and posteriorly, continuing a little lingually under the paraconid but disappearing under the main cusps.

**m1:** the width of the trigonid is reduced and the paralophid is curved; the oblique cristid ends on the posterior wall of the

**Table 1.** Measurements of *Percymyrgale vaclusensis* (Crochet, 1995) in mm.

	N	L			Min	Wtr		Min	W/Wta		Mean
		Min	Max	Mean		Min	Max		Min	Max	
P4	1	–	–	1.63	–	–	–	–	–	–	1.21
M1	2	1.91	1.97	1.94	–	–	–	1.46	1.67	–	1.56
M2	5	1.49	1.68	1.59	–	–	–	1.74	1.94	–	1.83
M3	2	0.96	1.15	1.05	–	–	–	1.45	1.58	–	1.51
p4	8	1.06	1.35	1.17	–	–	–	0.70	0.75	–	0.76
m1	4	1.64	1.67	1.65	0.98	1.05	1.13	1.14	1.23	–	1.19
m2	5	1.72	1.81	1.76	1.10	1.35	1.19	1.13	1.21	–	1.16
m3	4	1.28	1.54	1.41	–	–	–	0.87	1.04	–	0.95

Note: L = Length, W = maximal width, Wtr = trigonid width, Wta = talonid width.

trigonid between the protoconid and the metaconid. Trigonid and talonid are widely open lingually.

*m2 and m3*: they are similar but in the *m3* the talonid is narrower than the trigonid; they have straight paralophids; the oblique cristid is long and nearly reaches the metaconid; a meta-cristid is generally developed. Otherwise *m2* is the largest tooth and *m3* has a faint posterior cingulid.

*P4*: it shows an anterior labial main cusp, a well marked paraconule and a lingually detached protocone, with thin cingulum.

*Upper molars*: they display a more or less rounded and symmetrical protocone; protoconule, metaconule and parastyle generally marked (Figure 2(b)–(d)). No unworn tooth could show a division of the mesostyle. Anterior and posterior cingula are present but there is no posterior cingulum on *M3*.

*Postcranial elements*: Some fragments of humeri are so damaged (broken shaft and extremities partly crushed) that they are difficult to interpret. However, the fragments show at least that the humerus shaft is slender.

*Remarks*: In its type-locality, *Percymygalé vaclusensis* displays many resemblances with the rich material referred to this species in the basal Oligocene levels of South Germany (MP 21–22; Ziegler 2012). *Percymygalé vaclusensis* long maintains the same plesiomorphic mandibular characteristics and size until at least MP 24/25, but no published material is known later. Considering that both *P. minor* and *P. vaclusensis* have a very similar morphology and as *Percymygalé minor* exists since MP 20 (Upper Eocene) and even co-exists with *Percymygalé vaclusensis* in Möhren 13 (Ziegler 2012), their specific differentiation must predate the Oligocene as they already constitute two independent lineages at the beginning of the Oligocene in Europe.

It is also noteworthy that the *Percymygalé minor* lineage persists in Europe until the Early Miocene also with a very conservative morphology. Indeed *Percymygalé minor* (Ziegler 1990) displays until MN3 (Mercur-North; van den Hoek Ostende and Fejfar 2003) the same mandibular characteristics as *Percymygalé vaclusensis* during the Oligocene, although it is conspicuously smaller.

## Discussion

In the diverse species hitherto referred to *Myxomygalé* the posterior mandibular mental foraminae appear in two different positions that remain stable during several millions years: the posterior mental foramen is either under *m1* as it is the case for the type-species *M. antiqua* or under the roots of *p4*, as in species hitherto also assigned to *Myxomygalé*, *M. vaclusensis* or *M. minor* (van den Hoek-Ostende and Fejfar 2003; Ziegler 2012). In all dentaries with posterior mental foramen below *p4*, *p1*–*p3* are double-rooted while the postero-mental foramen below *m1* is linked to less developed roots for the lower premolars (only seven alveoli before *p4*).

Compared to the pattern known in the specimens now referred to *Percymygalé* n. gen., *P. vaclusensis* and *P. minor*, the typical pattern of *Myxomygalé antiqua* with reduced number of alveoli and more posterior mental foramen can be interpreted as apomorphic. The age of the type mandible of *Myxomygalé antiqua* is not precisely known (old collections from Quercy), but Sigé and Crochet (2006), apparently on the basis of unpublished material from Les Chauffours level (MP29; Puy-de-Dôme,

France), assign *M. antiqua* to this level but as MP28 (even if Les Chauffours locality is normally correlated to MP 29; Escarguel et al. 1997).

As previously shown Ziegler and Storch (2008) assigned to *M. aff. antiqua* a mandible from the Cyrena beds of Offenbach (Germany, Hesse), so the typical *Myxomygalé antiqua* morphology (with already reduced anterior denture) is testified in Europe around the MP 23/24 levels, *i.e.* later than the beginning of the Oligocene.

In the Late Oligocene Engesser and Storch (2008) referred one *M1* (2.34 × 1.98 mm) and one *M2* (1.76 × 2.06 mm) to *M. cf. antiqua*. These two teeth are larger than all the other known species and, as the lower molars of *M. antiqua* are also proportionally large, these teeth could well represent the last presence of this species at the end of the Oligocene.

In the Early and Middle Miocene the same apomorphic pattern exists with two successive species, *M. hutchisoni* (MN3/4) and then *M. gracilis* (MN 7/8), which is a little smaller. *M. hutchisoni* (MN4, Ziegler 1985; MN3, Wintershof-West, Ziegler 1994 and Petersbuch 28, Klietmann et al. 2014) displays the same dental formula as *M. antiqua*. The dental formula of *M. gracilis*, from the end of the Middle Miocene, is unknown even if the posterior mental foramen is below *m1* as in *M. antiqua*.

Considering that *Myxomygalé antiqua* displays, without change, the same large-sized and apomorphic features during the Oligocene, and that *Percymygalé* (*P. vaclusensis* and *P. minor*, which arrived earlier at the beginning of the Oligocene) also displays the same plesiomorphic features across the Oligocene and Early Miocene, it is logical to assume that both groups were already differentiated before their arrival in Europe. If they certainly derive from a common ancestor, they constitute two evolutionary long separated and independent groups, which can occasionally coexist in the localities. Even if isolated teeth are almost indistinctive (in the absence of knowledge on individual variation), the above described morphological differences (position of foramina mentale, number of roots of antemolars), justify to separate the plesiomorphic species from the apomorphic ones and to group the less derived ones in a new genus, *Percymygalé vaclusensis* and *Percymygalé minor* (Table 2).

The differences between the two genera (the number of antemolars and their roots) and the different patterns of the anterior part of the mandibles imply that the anatomy of their muzzle differed noticeably. Hutchison (1968, p. 57) notice a general relationship between the reduction in rostrum length and increasing fossoriality. In this case, the semifossorial genus *Percymygalé*, with its long muzzle, would have not been well adapted to digging, but rather to foraging in grasslands, forests and covered landscapes and suggests that *Myxomygalé* was a better burrower and had a noticeable different ecology. Unfortunately the material of humerus for the species of both genera is either absent or too fragmentary to further compare the burrowing abilities of the different species. The only observation that can be made is that the humerus of *P. minor* from Mercur-North (van den Hoek-Ostende & Fejfar 2006) seems more gracile than the fragments of *P. vaclusensis* from St-Martin-de-Castillon which also indicate different burrowing abilities within the genus *Percymygalé*. In addition, the size differences between the different species of *Myxomygalé* and *Percymygalé* also indicate that they had differentiated life history traits. In turn, despite the overall similar morphology, all these

**Table 2.** Stratigraphic distribution of species of *Myxomygale* and *Percymygale* n. gen. in the main European localities.

		<i>Percymygale</i>		<i>Myxomygale</i>
		Double-rooted p1-p3		Single-rooted teeth anterior to p4
		10 alv. before p4		7 alv. before p4
		posterior mental foramen below p4		posterior mental foramen below m1
		<i>Small size</i>		<i>Medium size</i>
Miocene	MN 7/8			<i>M. gracilis</i> Petersbuch 10 <sup>a</sup>
	MN 6			<i>M. hutchisoni</i> Sandelzhausen
	MN 5			<i>M. sp.</i> Pico del Fraile 2
	MN 4/5			<i>M. cf. hutchisoni</i> Karydia
				<i>M. hutchisoni</i> Petersbuch 2 <sup>a</sup>
	MN 4			<i>M. hutchisoni</i> Oberdorf
				<i>M. hutchisoni</i> Erkertshofen 1-2
				<i>M. engesseri</i> Aliveri <sup>a</sup>
				<i>M. engesseri</i> Snegotin
		MN 3	<i>P. minor</i> Merkur-North	
				<i>M. hutchisoni</i> Stubersheim 3
				<i>M. hutchisoni</i> Petersbuch 28
				<i>M. cf. hutchisoni</i> Ramblar 1
	MN 2	<i>P. minor</i> Ulm-Westtangente <sup>a</sup>		
	MN 1			
Oligocene	MP 30	<i>P. minor</i> Oberleichtersbach		<i>M. antiqua</i> Oberleichtersbach
		<i>P. minor</i> Eggingen-Mittelhart 1-2		
	MP 29			
	MP 28			
	MP 27			<i>?M. antiqua</i> Quercy <sup>a</sup>
	MP 26			
	MP 25			
				<i>P. vaclusensis</i> Garouillas
				<i>P. vaclusensis</i> Rigal-Jouet
				<i>P. vaclusensis</i> Escoufle
			<i>P. vaclusensis</i> St Vincent-de-Barb.	
			<i>P. vaclusensis</i> Les Matelles	
	MP 24		<i>P. vaclusensis</i> St Martin de Castillon <sup>a</sup>	
	MP 23/24			<i>M. aff. antiqua</i> Cyrena beds
	MP 22	<i>P. aff. minor</i> Möhren 13	<i>P. vaclusensis</i> Möhren 13	
		<i>P. aff. minor</i> Ehrenstein 12	<i>P. vaclusensis</i> Ehrenstein 8, 10, 11, 12	
			<i>P. vaclusensis</i> Herrlingen 7	
	MP 21	<i>P. aff. minor</i> Möhren 19	<i>P. vaclusensis</i> Liptingen 17, 1A	
			<i>P.?vaclusensis</i> Hamstead	
			<i>P. vaclusensis</i> Haag 2	
			<i>P. vaclusensis</i> Möhren 12, 19	
Eocene	MP 20	<i>P. aff. minor</i> Möhren 20	<i>P. vaclusensis</i> Möhren 20	

<sup>a</sup>Type locality of the species.

differences reduce the competition between the different species of *Myxomygale* and *Percymygale* and can explain how similar species have long coexisted in the same regions by the partitioning of the available ecological niches.

## Conclusion

Among the different species previously assigned to the genus *Myxomygale*, two groups coexisting across the Oligocene and Early Miocene differed by their antemolar morphologies. Some species have a reduced antemolar region (considered to be apomorphic) whereas others have complete antemolar pattern (considered to be plesiomorphic). Despite these morphological differences, the two groups are overall morphologically similar, indicating a close phylogenetic relationship.

The reduced pattern is that of the type-species *Myxomygale antiqua* (with single-rooted p1-p3 and posterior mental foramen below m1), which is only known in Europe since the

Early Oligocene (MP 23/24). The complete pattern (with double-rooted p1-p4 and posterior mental foramen below p4) is known earlier since the latest Eocene (MP20). In some regions the two types coexist. The differentiation of these two types, as well in morphology as in time, led to consider them as long separated groups and to assign the complete pattern to a new genus *Percymygale* that includes *P. minor* (Ziegler, 1990) and *P. vaclusensis* (Crochet, 1995). *P. minor* is chosen as type-species of the new genus, as more teeth and bones are known (van den Hoek-Ostende & Fejfar 2006; Ziegler 2012).

The new material of *Percymygale vaclusensis* from the type-locality (St-Martin-de-Castillon, MP 24) demonstrates the similarities in morphology and size with the German Early Oligocene material referred to this species (Möhren 13, MP 22: Ziegler 2012). These observations illustrate that the morphology and size remain stable during the Oligocene. Identical stability exists also for the minute *P. minor* known from the latest Eocene to the Miocene level MN 3. *P. vaclusensis* and *P. minor* show

identical plesiomorphic characteristics of the mandible and represent two different-sized lineages. The fossil record indicates that the differences in the anterior part of the mandible could predate the arrival of these forms in Europe and justify the creation of a separate genus beside the genus *Myxomygale*. In addition, burrowing ability of the two genera could have been different based on the length of the muzzle (Hutchison 1968).

In the genus *Myxomygale*, morphological evolution of the teeth seems to be hardly discernible and it is certainly difficult to distinguish species by means of isolated teeth. In addition, the above comparison between *Myxomygale* and *Percymygale* shows that the lower molars and the upper dentition bear no diagnostic feature allowing the distinction between the two genera. As far as the post-cranial material is concerned, the new material from St-Martin-de-Castillon unfortunately yielded no complementary information on the pattern of the humerus that could be compared with the few humeri known for *Myxomygale*. More complete material from different levels is necessary to better understand the evolutionary history of these generally very rare talpids.

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No potential conflict of interest was reported by the authors.

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