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The Erinaceidae from the late Oligocene of Coderet-Bransat and Peublanc (Allier, France; MP 30): new data on *Amphechinus pomeli* (Schlosser, 1925-1926) and *Galerix minor* (Filhol, 1880)

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Abstract

The late Oligocene faunas from central France are often rich and provide crucial information for understanding the evolution of mammals during the Oligocene-Miocene transition. The locality of Coderet-Bransat, where *Amphechinus arvernensis* was so far the only known hedgehog, yielded new specimens hitherto identified as *Galerix minor* and *Amphechinus pomeli*. The new specimen of *Amphechinus pomeli,* together with a new study of the type specimens from Peublanc, confirm the previously questioned validity of this species, the smallest of all hedgehogs. The similarities between the faunal lists of Coderet-Bransat and Peublanc indicate a very close age (MP30), whereas some aquatic taxa only found in Peublanc suggest a slightly different palaeoenvironmental context compared to Coderet-Bransat.

Keywords

Eulipotyphla, Erinaceidae, Central France, late Oligocene.

1. INTRODUCTION

Several localities from central France (Allier Dpt.) and covering the Oligocene-Miocene transition yielded rich mammalian fossil assemblages: e.g. Coderet-Bransat (MP30), Peublanc (MP30), Saulcet (MN1) and faunas near St-Gérand-le-Puy such as Montaigu-le-Blin and Langy (MN2a) (see Hugueney, 1997 for a review). Despite their diversified mammalian fauna they yielded a relatively poor record of fossil hedgehogs.

Schlosser (1925-1926) described the material from different localities from central France (Allier Dpt.), purchased 30 years before by the "Münchner Paläontologie Sammlung". This material is part of a larger collection initially gathered by Féningre at the end of the 19th century in France. An interesting remark of Schlosser is that the Féningre's collection contains a number of very small teeth and bones as if this material had been collected by wet washing and precisely picked out; if so Féningre was certainly one of the first palaeontologists to use this method and Schlosser highlighted that his name was to be remembered as a precursor in using modern palaeontological sampling methods.

Among other fossil faunas, Schlosser (1925-1926) published the mammalian fauna from Peublanc (situated around 20 km of the well-known localities of Coderet-Bransat, MP30, and St-Gérand-le-Puy, MN1/2). It is unclear where the material of St-Gérand-le-Puy to which Schlosser (1925-1926) refers comes from, considering that no carry or outcrops are known in the town of St-Gérand-le-Puy. Nowadays the two localities of Montaigu-le-Blin (MN2a) and Langy (MN2a) represent what we know of the "St-Gérand-le-Puy" fauna. The conclusion of Schlosser's study was that the assemblage of Peublanc noticeably differed from that of St-Gérand-le-Puy due to both occurrences of different species (e.g. in cricetids) and unknown taxa never observed in St-Gérand-le-Puy (e.g. Theridomyidae, *Rhizospalax*). Among the Eulipotyphlans, he found a minute hedgehog and described it as "*Erinaceus pomeli* n. sp." despite the material being very poor and badly preserved: a reduced mandibular fragment with m2-3 (SNSB-BSPG 1896 VII 47, Fig. 1A-E) and an edentate maxillary (SNSB-BSPG 1896 VII 561, Fig. 1F).

Later, in the nearby Coderet-Bransat locality (Allier, MP 30), Viret (1928-1929: pl. 28, figs 1-3) describes a single

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erinaceid, *Palaeoerinaceus arvernensis* Filhol, 1879 (now referred to the genus *Amphechinus* Aymard, 1850 which has priority). *A. arvernensis* has overall approximately the same size as *A. edwardsi* from St-Gérand-le-Puy (MN1) but differs by the shape and relative proportions of its molars and premolars (more transverse form of the upper teeth, large P2, and M1 notably larger than M2). Additionally, concerning *A. arvernensis,* Viret (1938) concluded that "if the molars of the Oligocene hedgehog remind that of the extant one, its skull is very different and its anterior incisors are stronger […] even if close to *Erinaceus* Linnaeus, 1758 it is not its ancestor" [translated from French]. Viret (1928-1929) also notices that in Coderet-Bransat no specimen corresponds to the minute "*Erinaceus" pomeli* published by Schlosser and even suspects that the maxillary referred by Schlosser to this species does not display the characteristics of an erinaceid, thus casting doubts on validity of this species for the first time (although he did not detail this statement). Later, Butler (1948) provided a detailed study of *Amphechinus* and considers that "*Erinaceus" pomeli* (Schlosser, 1925-1926) could be identical to *A. arvernensis*, thus also questioning the validity of the species. However, the specimens have never been studied again since their first description by Schlosser (1925-1926).

In the 1960s, tons of sediment from Coderet-Bransat were sampled and screen-washed that yielded a rich mammalian assemblage (Hugueney, 1969). Among the numerous specimens discovered, and additionally to the already described *A. arvernensis* (Viret, 1928-1929), two rare fossil hedgehogs' taxa were found but remained unpublished, including a very small and incomplete erinaceid mandible with p4-m2, which can be referred to the species "*Erinaceus" pomeli*. These new specimens are described and illustrated below including a study and comparison with the type specimens of "*Erinaceus" pomeli*; the other small taxon is also described here and can be referred to the genus *Galerix* Pomel, 1848.

2. MATERIAL AND METHODS

2.1. Terminology

Anatomical terminology and methods of measurement of the teeth follow Ziegler (1983): the length of the upper molars is measured along the anterior part and the width perpendicularly. All the dimensions are given in millimetres.

Abbreviations: L = maximal length, W = maximal width, width, H = height, I/i = upper/lower incisor; C/c = upper/lower canine; M/m = upper/lower molar; P/p = upper/lower premolar.

Institutional abbreviations: UCBL-FSL = University Claude Bernard of Lyon, LGL-TPE, Villeurbanne, France (former 'Faculté des Sciences de Lyon'); SNSB-BSPG = Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; MJSN = Jurassica Museum, Porrentruy, Switzerland (former 'Musée Jurassien des Sciences Naturelles')

Chronologic framework: The present study focuses on the European fossil record. Localities considered in the study range from the late Oligocene to the early Miocene, biochronological units ranging from MP30 (Palaeogene, reference level) to MN2 (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 (Aguilar *et al.,* 1997; Mein, 1999).

3D reconstruction: The specimen images were produced using the Bruker Skyscan 2211 CT scanner at the CT Imaging Laboratory of the University of Fribourg, Switzerland. The specimens were CT-scanned, using beam energy of 70 kV, a flux of 600 µA, a 360° rotation with a step size of 0.2° and an aluminium filter. The final image resolution is of 4.5 µm per pixel. Three-dimensional reconstructions were produced in Amira 6.0.

Material: The new specimens from Coderet-Bransat are hosted in the collections of the University Claude Bernard of Lyon.

3. SYSTEMATIC PALAEONTOLOGY

Family Erinaceidae Fischer, 1814
Subfamily Erinaceinae Fischer, 1814
Genus *Amphechinus* Aymard, 1850

Type species: *Erinaceus arvernensis* Blainville, 1839.

Diagnose of *Amphechinus* from Butler (1956): "Primitive Erinaceinae in which I1 and i2 are greatly enlarged; the root of i2 terminates below p4; the cheek teeth are displaced backward in the skull so that P4 stands partly under the orbit, and the molars are reduced in size."

***Amphechinus pomeli* (Schlosser, 1925-1926)**
Figs 1A-E, 2 and 3

Synonymies:

1925-26. *Erinaceus pomeli* Schlosser, pl. 11, fig. d-e.
non 1925-26. *Erinaceus pomeli* Schlosser, pl. 11, fig. a-c.

Type locality: Peublanc (Allier, France; MP 30).

Lectotype from Peublanc: left mandible fragment with incomplete m2 and complete m3, SNSB-BSPG 1896 VII 47 (Fig. 1A-E); figured in Schlosser (1925-1926: pl. 11, fig. d-e). Length of m2-3 (length of the broken m2 estimated) = 3 mm.

Material and measurements from Coderet-Bransat: left mandible with p4-m2 UCBL-FSL-218087 (Figs 2, 3). Length of tooth row (based on alveoli due to missing

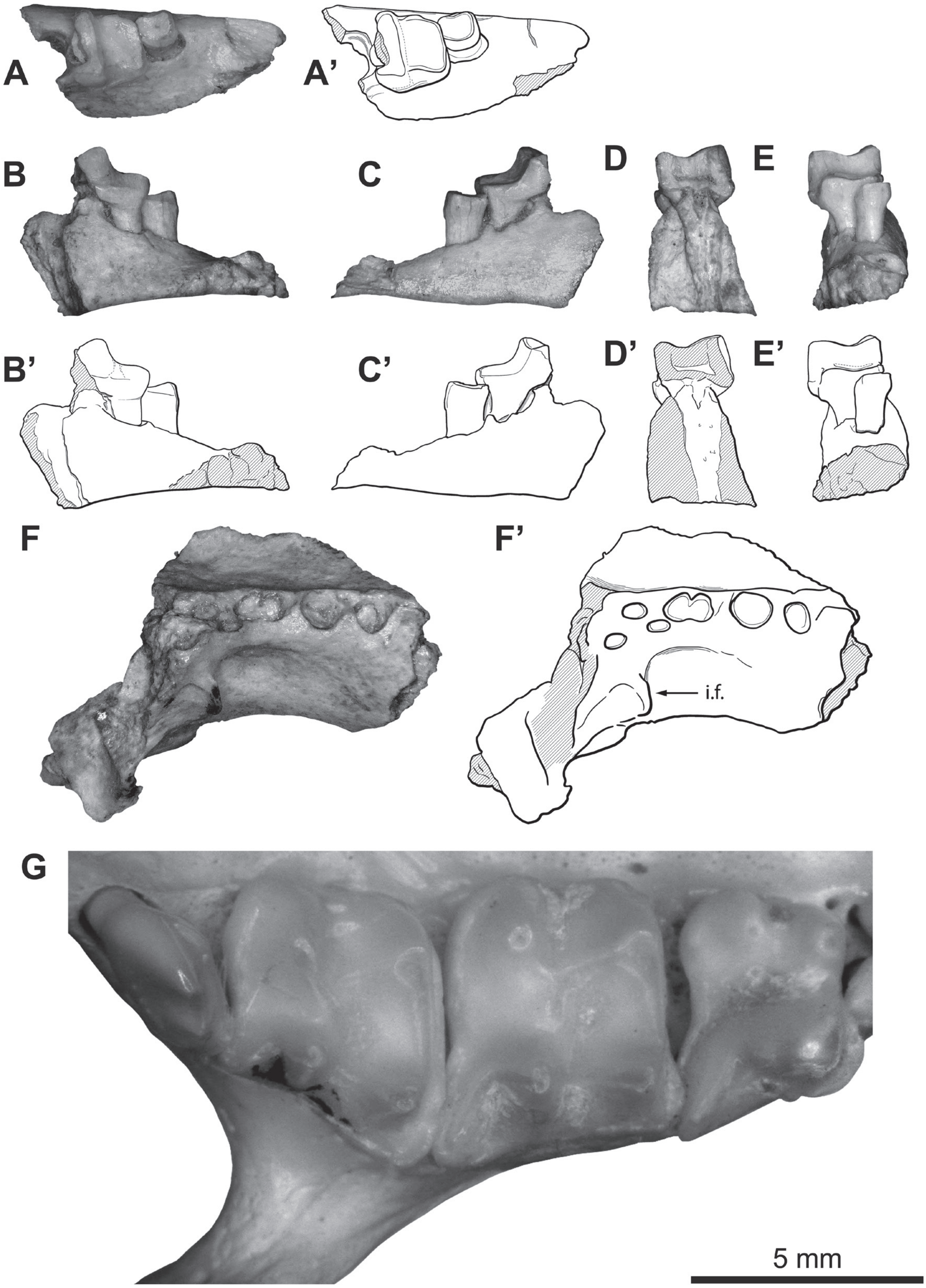

Fig. 1: Specimens from Peublanc initially referred to *Erinaceus pomeli* by Schlosser (1925-1926) and comparison of the maxillary fragment with the maxillary of an extant hedgehog. **A, B, C, D, E**: *Amphechinus pomeli*, left mandible fragment with m2-3 (Lectotype), SNSB-BSPG 1896 VII 47 (figured in Schlosser, 1925-1926: pl. 11, fig. d-e); **F**: Mammalia indet., left edentate maxillary fragment, SNSB-BSPG 1896 VII 561 (figured in Schlosser, 1925-1926: pl. 11, fig. a-c); **G**: *Erinaceus europaeus*, left maxillary and premaxillary with full upper dentition, MJSN-OS-75. **A, F, G**: occlusal views (i.f.=infra-orbital foramen); **B**: labial view; **C**: lingual view; **D**: anterior view, **E**: posterior view. **A' to F'**: line-drawings of the respective photos. Scale bar = 5 mm.

premolars) = 13 mm; p4: 2.2 × 1.5 mm; m1: 3.7 × 2.2 mm; m2: 3.2 × 1.6 mm; m3 alveolus: 1.0 × 1.2 mm; length of p4-m3 = 10 mm; length of m2-3 = 3 mm.

New description of the mandible from Peublanc (SNSB-BSPG 1896 VII 47):

Mandible (Fig. 1A-E): the specimen is broken anteriorly at the level of the m2, of which anterior part is missing, and posteriorly to the m3 at the base of the coronoid process. Although the coronoid process is not preserved it is possible to observe that it starts just below the level of the tooth row.

m2 (Fig. 1A-E): The trigonid of the m2 is mostly broken but it is possible to see that it is higher than the talonid, its posterior arm (protolophid) is transverse and extends to the metaconid branch. The trigonid depression is deep, extending nearly to the base of the crown. The posterior arm of the hypoconid joins transversely the entoconid. A short and slender cingulum is present on the labial side between the protoconid and the hypoconid.

m3 (Figs 1A, B, C, E): The tooth is very small compared to the m2, almost squared, and single rooted. Its morphology is very simple with none of the cuspid distinguishable: a continuous crest surrounds the smooth central depression.

Description of the mandible from Coderet-Bransat (UCBL-FSL-218087):

Mandible (Fig. 2): The horizontal ramus is relatively high (H = 5 mm) with a reduction in height of the ramus below the diastema between the p4 and the anterior end of the mandible. The teeth are close without diastema in between; the mandible shows a median groove between the two roots of the biradiculate teeth which is characteristic of both Erinaceinae and Galericinae. The large mental foramen is situated just before the anterior root of the p4. The posterior end of the jaw is poorly preserved, however the mandibular foramen is well preserved and located on the ascending coronoid process just below the level of the tooth row. The anterior part of the mandible is also damaged but, anteriorly to the p4 and above the large horizontal alveolus of the incisor, four rounded alveoli are visible (the anterior-most alveolus being broken, see Fig. 2B). The tooth row is dominated by the p4 and the m1 which are both higher and larger than other teeth.

p4 (Fig. 3A): The crown of the biradiculate p4 is constituted almost entirely by the trigonid which displays three marked tubercles. The paraconid is located slightly lingually and is very high and sharp compared to the other cuspids; the paraconid is also a little curved oriented posteriorly at its top. The protoconid is more massive and located labially, its top also bends backwards. Due to the wear, the protoconid seems to merge with the lower, and not well defined, metaconid. The posterior part of the tooth is not reduced and is underlined by a transverse marked cingulum, separated from the main cuspids by a furrow. A faint labial cingulum, almost discontinuous between paraconid and protoconid, reaches the posterior cingulum. No labial cingulum can be observed.

m1 (Fig. 3B): The trigonid of the m1 is much longer and higher than the talonid, and largely open lingually. The acute protoconid is the highest cuspid. Its anterior arm is high and stretches horizontally in the direction of the paraconid. The posterior arm of the trigonid (protolophid) is transverse and extends to the metaconid branch, but it is interrupted in its middle. The trigonid depression is deep, extending nearly to the base of the crown. The posterior arm of the hypoconid joins transversely the entoconid. An irregularly slender cingulum runs on the whole labial base of the tooth but no cingulum is visible on the lingual side.

m2 (Fig. 3C): It is shorter and lower than the m1 but its pattern is otherwise similar with a dominating trigonid. However, the width of the talonid is reduced compared to the m1.

m3: It is not preserved but possesses a strong unique root based on the posterior-most alveolus of the mandible.

Remarks on the identification of the specimens:

As far as the dentition of *Amphechinus* is concerned, the biradiculation of the P2 as figured by Schlosser is not an exception. Indeed, Viret (1928-1929) also mentioned the biradiculate P2 of *A. arvernensis*. This character is consequently not characteristic of one species but rather seem to be a common feature among some *Amphechinus* species. However, Butler (1948) notices that in the Erinaceinae most species retain a characteristic triangular shape of the P3, as in *Erinaceus*, whereas other genera of the subfamily (such as *Amphechinus*) display a more oval outline. These teeth being unknown so far for *A. pomeli*, it doesn't help referring this species to a genus. Nevertheless, considering the age of Coderet-Bransat, and until more material of *A. pomeli* is found, we choose to refer this small species to the contemporaneous genus *Amphechinus* rather than *Erinaceus*.

The upper dentition remains totally unknown. The only fragment of left maxilla (SNSB-BSPG 1896 VII 561) referred to "*Erinaceus" pomeli* by Schlosser (1925-1926) is indeed missing teeth. However as already suggested by Viret (1928-1929), the morphology of this maxilla is noticeably different from hedgehogs' morphology (see Figs 1F and 1G for comparison). Indeed, the re-examination of the specimen first reveals that the illustration provided by Schlosser (1925-1926) is inaccurate. Not only the specimen has been broken since its first publication (posterior part missing), but the specimen also shows a nicely preserved start of zygomatic root and large infraorbital foramen visible in occlusal view, which are neither illustrated nor described in Schlosser (1925-1926). Additionally, the specimen shows six root cavities as opposed to the seven illustrated by Schlosser (1925-1926). The three anterior cavities are confirmed, but the four-rooted posterior tooth is in fact three-rooted (one anterior and two posterior). The three anterior aligned

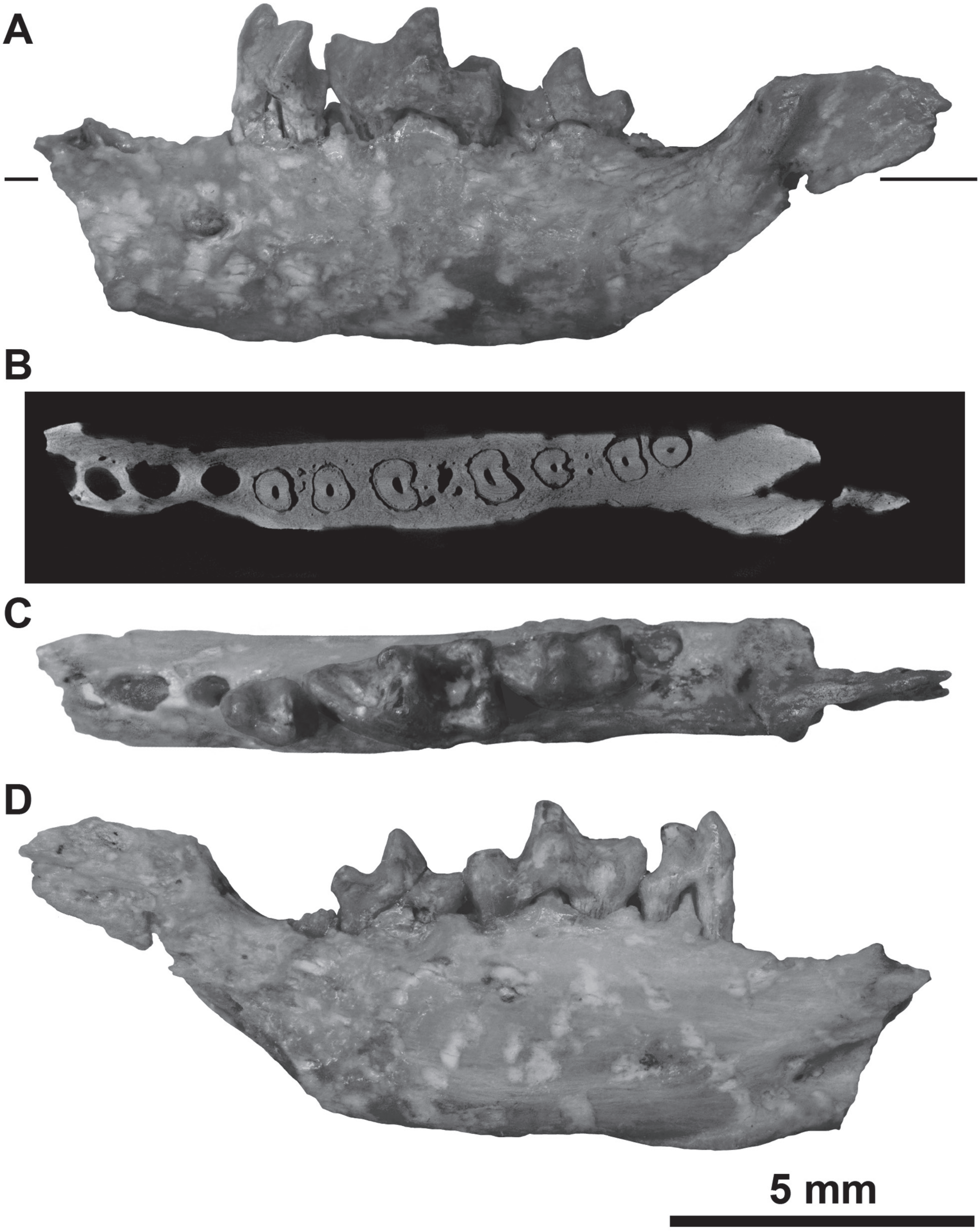

Fig. 2: Left mandible of *Amphechinus pomeli* with p4-m2 from Coderet-Bransat, UCBL-FSL-218087. **A**: labial view; **B**: transversal section as indicated in a.; **C**: occlusal view; **D**: lingual view. Scale bar = 5 mm.

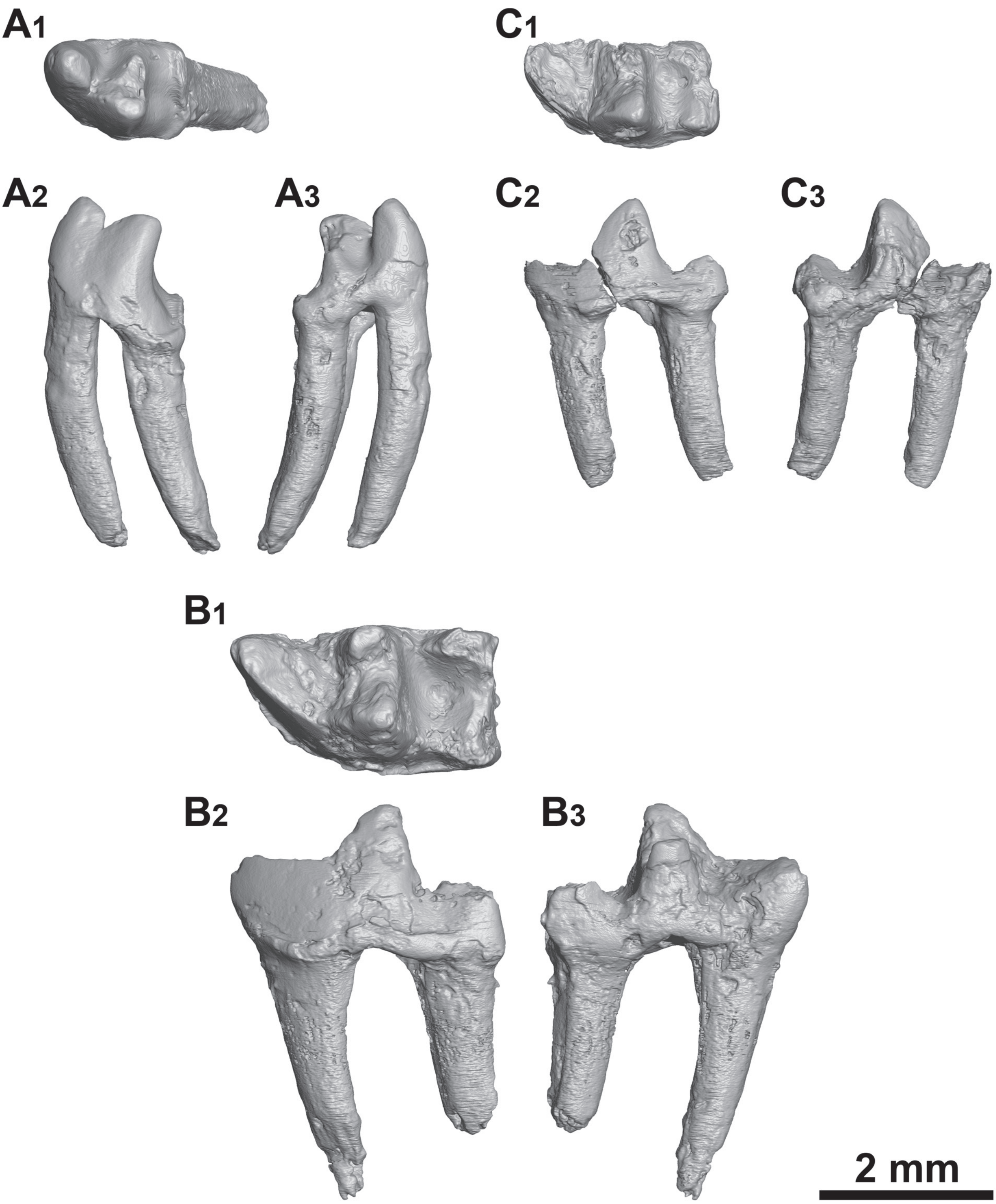

Fig. 3: 3D reconstruction (using microtomography) of the teeth of the mandible of *Amphechinus pomeli* from Coderet-Bransat, UCBL-FSL-218087. **A**: left p4 (**A1**: occlusal view, **A2**: labial view, **A3**: lingual view); **B**: left m1 (**B1**: occlusal view, **B2**: labial view, **B3**: lingual view); **C**: left m2 (**C1**: occlusal view, **C2**: labial view, **C3**: lingual view). Scale bar = 2 mm.

cavities likely correspond to double-rooted premolars whereas the three posterior cavities correspond to a three-rooted P4 (unlike the four-rooted P4 in Erinaceids). The zygomatic root starting at the level of the P4 and the infraorbital foramen visible in occlusal view strongly differ from the morphology of *Erinaceus* (Fig. 1G). For those reasons, and in agreement with Viret (1928-1929), the fragment of maxilla referred to *"Erinaceus" pomeli* by Schlosser (1925-1926) is not an Erinaceidae at all. Identifying this specimen is consequently beyond the point of this study, however, it is worth noticing that a zygomatic arch starting at the level of the P4 is rare among mammals and mostly observed in carnivorans. Likewise, the low position of the infraorbital foramen and the three-rooted P4 are also frequent in carnivorans.

Discussion:
Schlosser (1925-1926) noticed that the morphologies of the m2 and the m3 of his new species "*Erinaceus*" *pomeli* are similar to the corresponding teeth of *Erinaceus europaeus* Linnaeus, 1758 and display features characteristic of Erinaceinae: i.e. biradiculate m2 with high trigonid and talonid and uniradiculate m3 reduced to a trigonid. Schlosser also stated that the genus *Tetracus* Aymard, 1850, of which the m3 displays a trigonid followed by a true talonid, is in contrast noticeably different from *A. pomeli*. Schlosser (1925-1926) also compared *A. pomeli* with *Amphechinus edwardsi* Filhol, 1879 from "St-Gérand-le-Puy" (MN1/2) (referred to *Palaeoerinaceus* at the time), which was twice larger. Due to many similarities, he hypothesized that it could have evolved from *A. pomeli*. As explained above, the precise origin of this *Amphechinus edwardsi* from "St-Gérand-le-Puy" is unclear since it has never been noticed in Montaigu-le-Blin or Langy but only in other localities in the vicinity such as Chavroche. However, in Coderet-Bransat (MP30), *Amphechinus arvernensis* which is of approximately the same size as *A. edwardsi* but with a biradiculate P2 is considered since Viret (1928-1929) as the ancestor of *A. edwardsi*. In Coderet-Bransat, *A. arvernensis* is abundant and it cohabits with the *A. pomeli*, thus questioning the hypothesis proposed by Schlosser (1925-1926) of a direct phylogenetic relationship between *A. pomeli* and *A. edwardsi*.

In Coderet-Bransat, the small p4 of *A. pomeli* resembles those of *A. arvernensis*, *A. edwardsi* and *E. europaeus* but the two anterior cuspids seem to be more bulbous and the talonid more developed transversally with a marked furrow. Additionally, the strong and very high anteroconid seems to dominate the protoconid which is not the case in *Amphechinus* and *Erinaceus* and could be a characteristic of *A. pomeli*. The new specimen from Coderet-Bransat corresponds well to *A. pomeli* from Peublanc based on both the morphology and the size. It confirms the validity of the species which in turn is the smallest hedgehog known so far including both extinct and fossil species.

Subfamily Galericinae Pomel, 1848
Genus *Galerix* Pomel, 1848
Type species: *Viverra exilis* Blainville, 1839

Galerix minor **(Filhol, 1880)**
Figs 4, 5

Material from Coderet-Bransat:
Right mandible with only p2 (UCBL-FSL-218088); partly broken left mandible with p3-m1 (UCBL-FSL-218089); partly broken right mandible with p3-4 and m2 (UCBL-FSL-218090); left mandible with p4-m3 (UCBL-FSL-218091); 6 edentated mandibles (UCBL-FSL-218099 a-f); 1 m2 (UCBL-FSL-218092); 4 M1s (UCBL-FSL-218093+218097 a-c); 5 M2s (UCBL-FSL-218094-95+218098 a-c); 1 M3 (UCBL-FSL-218096). For measurements see Tables 1 and 2.

Table 1: Measures of the mandibles of *Galerix minor* (UCBL-FSL-218088 to 218091, and edented mandibles UCBL-FSL 218100 to 218105). * Measures based on the position of alveoli.

	p4-m3	m1-m3	Under m1
	L	L	H
UCBL-FSL-218088	10.2*	7.3*	4.0
UCBL-FSL-218089	11.7*	9.5*	4.0
UCBL-FSL-218090	10.0*	7.5*	5.0
UCBL-FSL-218091	10.0	8.0	4.0
UCBL-FSL-218100	8.9*	8.0*	4.4
UCBL-FSL-218101	10.0*	8.5*	4.0
UCBL-FSL-218102	-	8.3*	4.0
UCBL-FSL-218103	-	8.0*	4.3
UCBL-FSL-218104	-	7.8*	4.3
UCBL-FSL-218105	-	7.5*	4.0
N	6	10	10
Min	8.9	7.3	4.0
Mean	10.1	8.0	4.2
Max	11.7	9.5	5.0

Description of the material:
Mandibles (Fig. 4): The mandibles are characterized by the presence of a complete dentition: three incisors anteriorly, four premolars with an uniradiculate p1, biradiculate p2 to p4. The m3 is also biradiculate, its roots being distinctly smaller than for the other molars. The corpus mandibulae is fully preserved on some specimens, it is slender and rectilinear. The coronoid process is narrow

Table 2: Measurements of the teeth of *Galerix minor* from Coderet-Bransat (in mm).

		Length			Width		
	N	min	mean	max	min	mean	max
M1	4	2.9	3.0	3.0	3.2	3.3	3.5
M2	5	2.4	2.5	2.7	2.7	2.9	3.1
M3	1	-	1.8	-	-	2.1	-
p2	1	-	1.6	-	-	0.9	-
p3	1	-	1.5	-	-	1.1	-
p4	2	2.3	-	2.5	1.5	-	1.7
m1	1	-	3.1	-	-	2.1	-
m2	2	2.7	-	2.8	1.8	-	2.1
m3	1	-	2.5	-	-	1.5	-

with a rather rectilinear anterior margin drawing an angle of 118° to the occlusal plane. The dental foramen is located approximately at the level of the tooth row. The triangular and rounded condyle is a little oblique and high above the tooth row. The foramen mentale is the largest one; it is located under the p3. Two other smaller foramina are also present, the anterior one being much smaller and located under the p2, the posterior one located under the p4. The symphysis extends back to a point lateral to the middle of the p2.

Incisors and canine: No incisor or canine is preserved, but the alveoli of the roots provide some information. The alveolus of the second incisor is larger than the two others and all are a little compressed antero-posteriorly. A large and rounded root represents the canine and, on four mandibles where the anterior part is preserved, only one shows a faint diastema between the canine and the p1.

Lower dentition:

p1: No p1 has been found, but based in the single alveolus, the root is about the same size as that of the other premolars.

p2 (Fig. 4A): The two roots of p2 are as long or perhaps a little longer than those of p3, the p2 present on the complete mandible shows a flat triangle shape with two conulids, a sharp one anteriorly and lower one posteriorly.

p3 (Figs 4B, C; 5B): The shape of the p3 is similar to the p2 but p3 is a little wider posteriorly. As opposed to the p2, the p3 has no metaconid, the anterior conulid is smaller, and the heel is minute.

p4 (Figs 4B, C; 5A, B): The p4 is much longer than the p3. It has a trigonid with a well-developed paraconid but a less distinct metaconid. The principal cusp reaches the same height as m1. The long posterior cingulum shows a marked furrow.

m1 (Figs 4B; 5A, B): The trigonid is slightly higher than the talonid whereas they are about the same width. A cingulum follows the whole labial side and continues on the posterior side where it ends at a middle point between the hypoconid and the entoconid.

m2 (Figs 4C; 5A, C): The m2 is similar to the m1, but a little bit smaller.

m3 (Fig. 5A): It shows a talonid nearly as long as the trigonid but with a particularly stretched entoconid.

Upper dentition (only isolated teeth):

M1 (Fig. 5D): This quadrangular tooth, broader than long, is only a little stretched at the metacone level. Its anterior border is rectilinear with a faint protoconule whereas the posterior border is constricted at the level of the metaconule. The paracone and the metacone are rounded. A complete crest joins the rounded paracone and the metacone, and continues to the labial border of the tooth. The metaconule shows a pyramid shape with a rounded base and short crests, one directed to the protocone posterior crest and the two others to the base of the metacone without reaching the postero-labial corner. The hypocone anterior crest and the protocone posterior crest both connect at the base of the metaconule. A faint cingulum surrounds the tooth but disappears on the lingual border.

M2 (Figs 5E-F): This tooth is nearly triangular; it is convex and wide anteriorly whereas it is a little narrower posteriorly due to the reduction of the hypocone. Its morphological pattern resembles that of the M1 but the metaconule is more rounded at the base of the paracone. Like in M1, the hypocone anterior crest and the protocone posterior crest both connect at the base of the metaconule. A basal cingulum begins on the anterior side at the level of the protocone and continues along the labial side where it ends at the level of the metaconule. The protocone anterior crest ends at the base of paracone; it can be interrupted by a paraconule in three cases out of five.

M3 (Fig. 5G): Only one tooth can be referred to this species. It has only three tubercles. The paracone and the

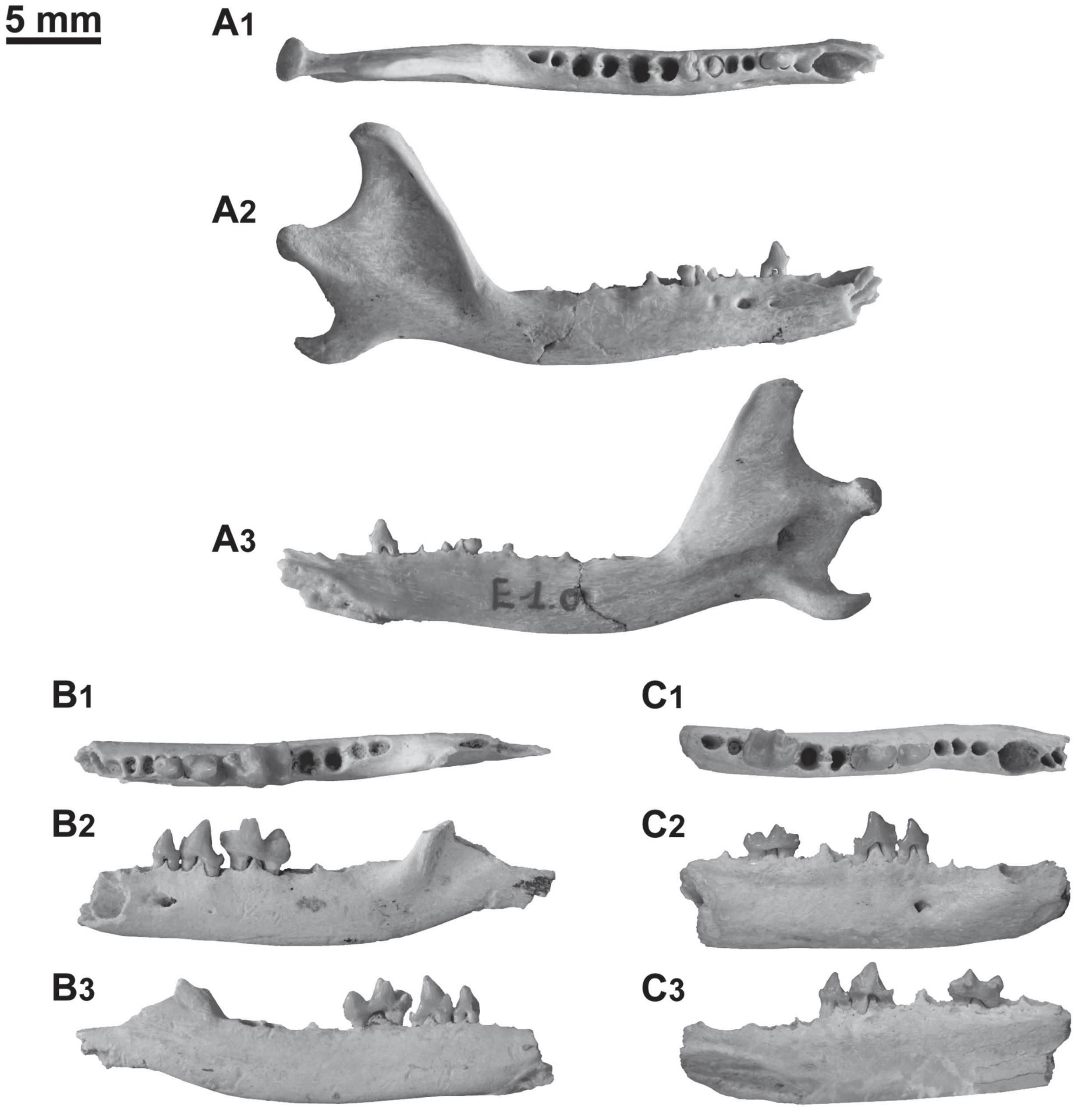

Fig. 4: Mandibles of *Galerix minor* from Coderet-Bransat. **A**: right mandible with p2, UCBL-FSL-218088 (**A1**: occlusal view; **A2**: labial view; **A3**: lingual view); **B**: left mandible with p3, p4 and m1, UCBL-FSL-218089 (**B1**: occlusal view; **B2**: labial view; **B3**: lingual view); **C**: right mandible with p3, p4 and m2, UCBL-FSL-218090 (**C1**: occlusal view; **C2**: labial view; **C3**: lingual view). Scale bar = 5 mm.

metacone are similar to their homologues in the other teeth but the hypocone and metacone are much reduced. The anterior and posterior arms of the protocone end at the base of paracone and metacone respectively. A minute cingulum almost surrounds the entire base of the tooth except near the protocone.

Discussion:

In Coderet-Bransat, this species noticeably differs from *A. arvernensis* by the gracility of its mandible and the shape of the coronoid process, although the alveolar length is not very different. Indeed, the mandible is slender, the coronoid process is more rectilinear anteriorly and the angle of elevation of the anterior edge (118°) is greater than in *Amphechinus* (70-80°; see Butler, 1948 and Engesser, 2009). Additionally, the number of alveoli shows a complete dentition indicating that it belongs to the subfamily Galericinae rather than Erinaceinae.

Among Oligocene Galericinae, the genus *Tetracus* also resembles our material. However Butler (1948) and

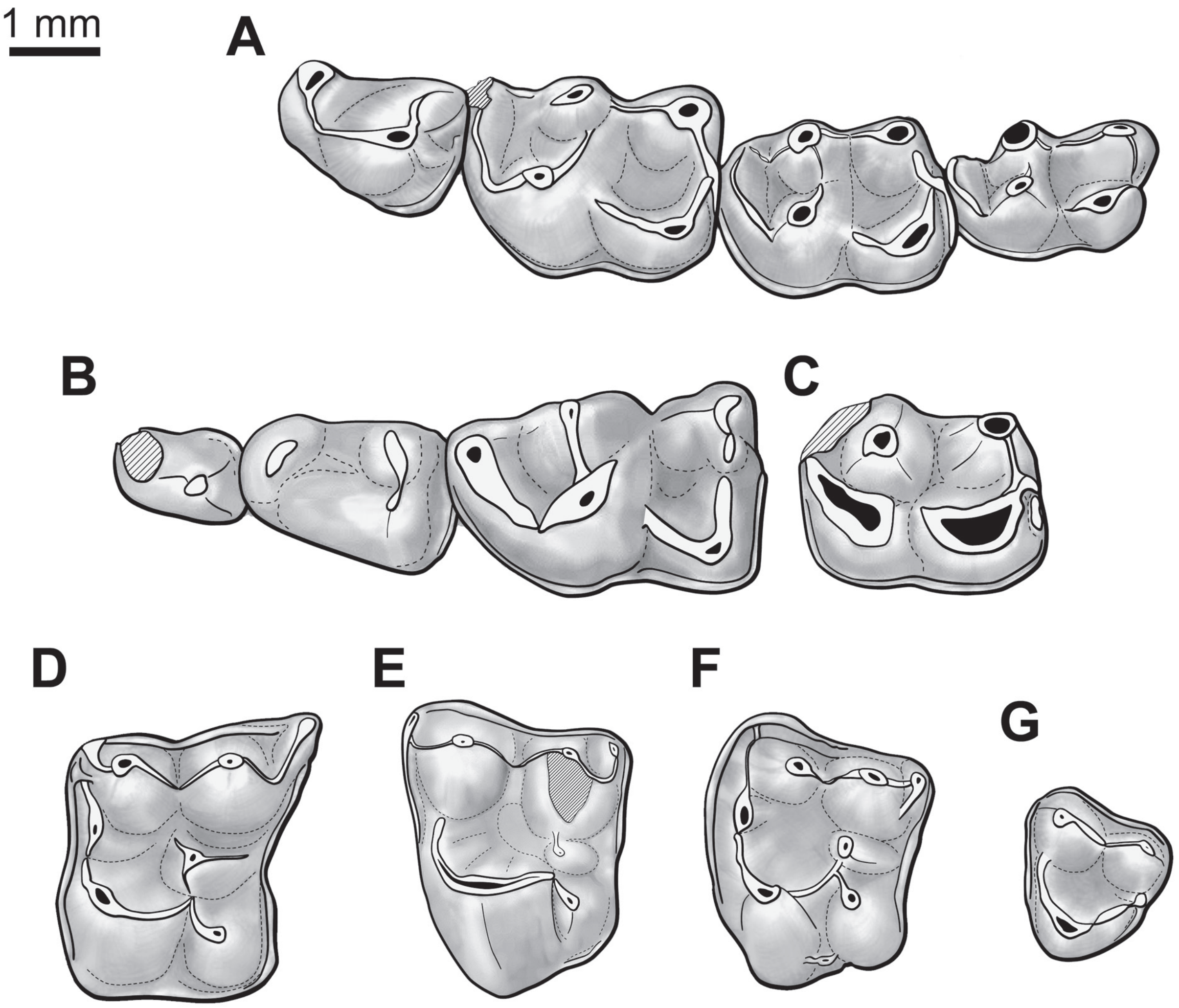

Fig. 5: Cheek teeth of *Galerix minor* from Coderet-Bransat in occlusal view. **A**: lower left tooth row with p4 to m3, UCBL-FSL-218091; **B**: lower left tooth row with p3 to m1 of the mandible UCBL-FSL-218089; **C**: right m2 (strongly worn out), UCBL-FSL-218092; **D**: left M1, UCBL-FSL-218093; **E**: left M2, UCBL-FSL-218094; **F**: right M2 [reversed], UCBL-FSL-218095; **G**: right M3 [reversed], UCBL-FSL-218096. Scale bar = 1 mm.

Crochet (1973) provided characteristic morphological features for *Tetracus* that differs from the specimens of Coderet-Bransat: the foramen mentale located under the p4 (whereas is it more anteriorly located under the p3 in Coderet-Bransat, as also in the holotype of *Galerix exilis* de Blainville, 1839 in Engesser, 2009); the lower molars of *Tetracus* have no hypoconulid (whereas it is present on the lower molars from Coderet-Bransat).

Butler (1948) described an Oligocene galericine mandible from Quercy hosted in the British Museum collection, previously referred to *Neurogymnurus minor* Filhol, 1884 by Lydekker (1885). However Butler (1948) noticed several morphological characters that differ from *Neurogymnurus* Filhol, 1877 of which characters are considered plesiomorphic after Ziegler (2005): the complex p4 with a well-developed paraconid (whereas is not distinct in *Neurogymnurus)*; a well-developed metaconid (whereas it is very small or absent in *Neurogymnurus)*; the row of lower premolars shorter than the molar rows (whereas it is the other way around in *Neurogymnurus)*; and a connection between the protocone and the hypocone of upper molars (whereas they are independent in *Neurogymnurus)*. These differences led Butler to transfer the Quercy mandible into the genus *Galerix* and refer it to *G. minor*. These morphological features are also characteristic of the above described mandibles from Coderet-Bransat. Hoek Ostende (2001, 2003), Hoek Ostende & Doukas (2003) and Ziegler (2005) stated that the p2 longer than the p3 is a diagnostic character for the genus *Galerix*. However, it is not the case for the mandibles described by Butler (1948) nor it is the case in the specimens from Coderet-Bransat based on the alveoli, making this diagnostic feature questionable. Otherwise, the upper molars of Coderet-Bransat show a well-developed metaconule which is characteristic of the genus *Galerix*. The dentition of the specimens from Coderet-Bransat and the morphology of the mandibles correspond well to Butler's description although the specimens from Coderet-Bransat are slightly larger. We consequently refer the specimens from Coderet-Bransat to *G. minor*.

The Oligocene-Miocene transition in Europe is characterized by noticeable changes in the occurrences of Erinaceidae in the fossil record. The Galericinae were hitherto unknown in European faunas during a period extending from MP 26 to MN3. MN2 additionally corresponds to an "Erinaceid vacuum", before the onset of *Galerix* success from MN3 onward (Hugueney & Adrover, 2003; Ziegler, 2006). The occurrence of *G. minor* in the rich Coderet-Bransat locality indicates that it was present earlier but perhaps extremely rare.

4. CONCLUSIONS

New record of hedgehogs

The already rich locality of Coderet-Bransat yielded two additional erinaceids besides the previously known *Amphechinus arvernensis*. However, *A. arvernensis* remains noticeably more abundant than *Amphechinus pomeli* and *Galerix minor*. Even if the material of the two newly recovered species is poor, it makes possible to definitively accept *Amphechinus pomeli* as a valid species and to document the presence of *Galerix minor* earlier than previously known. *Amphechinus pomeli* appears to be a very rare species as it is only known in Peublanc and Coderet-Bransat; curiously it is also the only hedgehog found in Peublanc. Based on the mensuration of the teeth, *A. pomeli* is also to date the smallest hedgehog among both extant and fossil species.

Biochronology

Progress in the stratigraphic succession of mammalian faunas led to choose the locality Coderet-Bransat as European reference level for the final mammalian biochronological unit of the Oligocene: MP 30. As early as 1928, Viret already stated an identical age between the localities Coderet-Bransat and Peublanc. Based on its faunal composition it is now possible to formally refer Peublanc to the MP 30 mammalian level. Indeed, the faunal list of Peublanc contains several characteristic taxa which are also known in Coderet-Bransat (Hugueney, 1997: *Caenotherium geoffroyi, Amphitragulus feningrei, Amphechinus pomeli, Geotrypus antiquus, Rhizospalax poirrieri* and *Archaeomys arvernensis*) and also in the other contemporaneous Swiss locality Küttigen for *Rhizospalax poirrieri* (Engesser & Mödden, 1997). *Archaeomys* and *Rhizospalax* both indicate a late Oligocene age for Peublanc as for Coderet-Bransat. It is worth keeping in mind that all theridomorphs and *Rhizospalax* disappear at the end of the Oligocene (Engesser & Mayo, 1987), for instance not found in the rich locality Paulhiac (reference locality for MN1 biozone), their records from Peublanc and Coderet-Bransat are therefore among the last ones in Europe.

Palaeoenvironment

The faunal list of Peublanc, with only 17 mammal species (Hugueney, 1997) plus *Ptychogaster* indet., Lacertilien indet., *Palaeobatrachus* indet. and *Chelotriton* indet., doesn't allow to apply a method of reconstruction of the palaeoenvironment such as the cenograms (Legendre, 1986). Nevertheless, as discussed above, Peublanc is very close both geographically and chronologically from Coderet-Bransat on which this method was applied by Legendre (1987). We can consequently assume generally similar environmental conditions for Peublanc; the conclusion of Legendre (1987) for Coderet-Bransat being high mean annual temperatures associated with a relatively arid climate and open vegetation. However, Peublanc also yielded a few taxa that are absent from Coderet-Bransat such as the otter *Potamotherium valetoni* living near river or lakes, and the amphibians *Palaeobatrachus* and *Chelotriton* which require freshwater and shadow (Böhme *et al.*, 2006). *P. valetoni* is known later in some early Miocene localities such as Saulcet and Langy (Hugueney, 1997) but is unknown in Coderet-Bransat, as well as the amphibians. Although the climatic condition must be the same as in Coderet-Bransat, these occurrences might suggest slightly more closed vegetation and the presence nearby of a large body of freshwater. Moreover, in Peublanc, Schlosser (1925-1926) indicates that a mineralogical analysis of sediment found inside the shaft of the bones makes it possible to recognize volcanic dust with augite, olivine, volcanic glass and particles of basic feldspaths indicating, in the vicinity, a nearby volcanic activity that might also have impacted, at least locally, the environmental conditions (see Table 3 for a summary of all the localities and taxa mentioned above).

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Table 3: Summary of the late Oligocene and early Miocene localities, mentioned herein, that yielded fossil erinaceids. * = type locality.

Age / Locality	Bioch.	Erinaceid taxa	Other significant taxa	References
Early Miocene				
Langy (FR)	MN2a	*Amphechinus edwardsi ?*	*Oligosorex antiquus** *Meingensorex ambiguus**	=St-Gérand-le-Puy; Hugueney (1997); Hugueney & Maridet (2011)
Montaigu-le-Blin (FR)	MN2a	*Amphechinus edwardsi** *Dimylechinus bernouillii*	*Titanomys visenoviensis* *Eucricetodon gerandianus*	=St-Gérand-le-Puy; Hugueney (1997)
Chavroche (FR)	MN2a	*Amphechinus edwardsi* *Dimylechinus bernouillii*	*Titanomys visenoviensis* *Eucricetodon gerandianus*	Hugueney (1997)
Paulhiac (FR)	MN1	*Amphechinus arvernensis*	*Titanomys visenoviensis* *Eucricetodon collatus* *Rhodanomys schlosseri*	Ziegler (1983)
Saulcet (FR)	MN1	*Amphechinus edwardsi* *Dimylechinus bernouillii**	*Titanomys visenoviensis* *Eucricetodon gerandianus* *Rhodanomys schlosseri*	Hugueney (1997)
Late Oligocene				
Coderet-Bransat (FR)	MP30	*Amphechinus arvernensis* *Amphechinus pomeli* *Galerix minor*	*Piezodus branssatensis** *Eucricetodon longidens** *Issiodoromys bransatensis** *Archaeomys laurillardi* *Rhizospalax poirrieri* *Geotrypus antiquus* *Amphitragulus feningrei*	This study; Hugueney (1997)
Peublanc (FR)	MP30	*Amphechinus pomeli**	*Archaeomys laurillardi* *Rhizospalax poirrieri* *Geotrypus antiquus* *Amphitragulus feningrei* *Potamotherium valetoni* *Palaeobatrachus* indet. *Chelotriton* indet.	This study; Hugueney (1997)
Küttigen (CH)	MP30	*Amphechinus* cf. *arvernensis*	*Eucricetodon collatus* *Archaeomys laurillardi* *Rhizospalax poirrieri* *Rhodanomys hugueneyae*	Engesser & Mödden (1997)
Quercy (FR)	MP ?	*Galerix minor*	-	Locality unknown; Butler (1948)

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