Early Miocene soricids (Insectivora, Mammalia) from Limagne (Central France): New systematic comparisons, updated biostratigraphic data and evolutionary implications[☆]

Les soricidés miocènes inférieurs (Insectivora, Mammalia) de Limagne (Centre France) : nouvelles comparaisons systématiques, mises à jour des données biostratigraphiques et implications évolutives

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Abstract

In the Early Miocene lacustrine strata of Limagne (Allier, France), three soricids were described long ago: *Oligosorex antiquus*, *Oligosorex ambiguus* and *Crocidosorex piveteaui*. The lack of precise descriptions of, and comparisons among, these fossils – the type specimens of both species of *Oligosorex* having disappeared – on the one hand, and the lack of accuracy in their biostratigraphic positions on the other, led to long debates about possible synonymies among these species and genera. Many of these controversies are solved by new descriptions, comparisons and better illustrations of the specimens, and recent advances in biostratigraphical attributions. Work along these lines has led to the recognition of *Crocidosorex* and *Oligosorex* as independent genera. An additional taxon can be distinguished among the material previously found at Montaigu-le-Blin: this taxon closely matches Pomel's "*Sorex*" *ambiguus* but is here ascribed to *Meingensorex* nov. gen.

Résumé

Dans les niveaux lacustres du Miocène inférieur de Limagne (Allier, France), plusieurs Soricidae furent nommés dès les années 1850 : *Oligosorex antiquus*, *Oligosorex ambiguus*, puis *Crocidosorex piveteaui*. Le manque de description et de comparaisons entre ces fossiles – les spécimens-types des deux espèces d'*Oligosorex* ayant disparu – ajouté à l'absence de biostratigraphie précise, conduisirent à de longs débats sur les synonymies de ces genres et espèces. La redescription, des comparaisons et une meilleure illustration des spécimens ainsi qu'un cadre biostratigraphique plus précis apportent beaucoup à la résolution de ces controverses. Finalement, plusieurs caractéristiques font de *Crocidosorex* et *Oligosorex* des genres indépendants. Parmi le matériel trouvé précédemment à Montaigu-le-Blin, un taxon supplémentaire peut être reconnu ; il correspond bien au « *Sorex* » *ambiguus* de Pomel mais ses caractères le font attribuer à un nouveau genre : *Meingensorex* nov. gen.

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1. Introduction

In the so-called Limagne, which is the basin of the river Allier (French Massif Central), many soricids were discovered as early as the 1850s; subsequently, their status was often

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debated and contradictory positions were adopted, particularly concerning the synonymy of the genera *Crocidosorex* and *Oligosorex* and the creation of the subfamily Crocidosoricinae (Reumer, 1987; Rzebik-Kowalska, 1998). van den Hoek Ostende (2001), in a comprehensive survey of the literature, reviewed all these problems: he retained the subfamily Crocidosoricinae as valid, and *Crocidosorex* and *Oligosorex* as independent genera. It appears, however, that the problems have been due in large part to a lack of precise comparisons among the relevant fossils on the one hand, and a lack of knowledge of their respective ages on the other. Over the last decades, a better knowledge of the soricids from these levels (Crochet, 1975; Ziegler, 1989), and progress in biostratigraphy, have made it possible to assign them to more precise biostratigraphic positions and to better elucidate their potential relationships.

1.1. Historical background

In his "Catalogue des Vertébrés fossiles du bassin de la Loire et de l'Allier", Pomel (1853) gave diagnoses for two new species of *Sorex* (*Corsira*) [*Corsira* is now considered a junior synonym of *Sorex* (Hutterer, 2005: 282)]: *Sorex* (*Corsira*) *antiquus* Nob. and *Sorex* (*Corsira*) *ambiguus* Nob. These two species came from the locality "Terrain tertiaire à Langy, près Saint-Gérand-le-Puy". They were neither described nor figured and, unfortunately, Pomel's specimens were lost subsequently.

The area of Saint-Gérand-le-Puy/Langy was intensively excavated after being discovered and mentioned in a publication by Geoffroy Saint-Hilaire (1833). Excavations for lime and cement were soon abandoned at Langy and Saint-Gérand-le-Puy, but have continued to the present roughly five kilometres eastwards in the same formations near the locality Montaigu-le-Blin (Fig. 1). Researchers from Lyon, Basel and elsewhere collected intensively at Montaigu-le-Blin at the beginning of the twentieth century. In 1929, Viret became the first to ascribe fossil material to *S. antiquus* and to describe and illustrate a skull, considering *S. ambiguus* to fall within the range of variation of *S. antiquus*. Stehlin (1940) described and figured well-preserved material that he also ascribed to *S. antiquus*. Although he noticed that "antemolar 2 seems to be missing" in one mandible (NMB Ph. 2255), his opinion was that probably only one species was present in the strata in question and that other previously named species (i.e., *S. ambiguus* Pomel from Langy and *Sorex pusillus* von Meyer from Weisenau – the latter species considered a *nomen nudum* by Storch, 1988) were synonyms of *S. antiquus*. Kretzoi (1959) created the new genus *Oligosorex* and selected *S. antiquus* Pomel as its type species. Later on, Crochet (1975: 633) designated the mandible NMB Ph. 12, figured by Stehlin, as the neotype of the species *S. antiquus*, but ascribed this species to the genus *Crocidosorex* rather than *Oligosorex*.

Lavocat (1952) described and figured *Crocidosorex piveteaui* nov. gen., nov. sp. from Marcoin, near Volvic (Puy-de-Dôme) on the basis of a very incomplete mandible retaining p4-m3 (in fact a minute p3 [= a3?] exists under p4 but was hidden by matrix) but lacking the anterior part and ramus. He differentiated it from *Mysarachne picteti* Pomel, 1848 – a taxon with five antemolars from Les Chaufours (Puy-de-Dôme; MP 29) that very likely represents a soricid but was neither described nor figured, and moreover lacks an existing holotype – but did not consider the soricids from Montaigu at all despite the fact that Stehlin (1940) had given a good description of these fossils. As a result the diagnostic characteristics of *Crocidosorex piveteaui* were insufficient and no differential diagnosis was provided.

(Repenning (1967: 29–30), without seeing any material, considered *Oligosorex* a junior synonym of *Crocidosorex* but admitted that "study of the specimens could well lead to the conclusion that the two genera are distinct". The same author
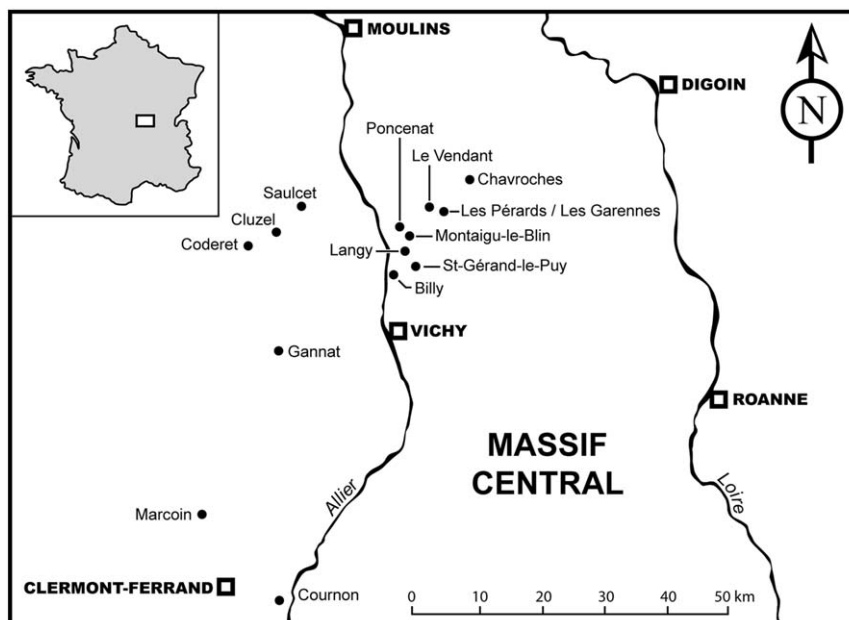

Fig. 1. Map of the Limagne basin indicating the main cities (open squares) and fossil localities (black dots).

gave a diagnosis for the genus *Crocidosorex* essentially based on the characteristics of *Oligosorex*, which was more complete than *Crocidosorex* in that the lower incisor and ramus were known. Later Repenning's point of view was followed by most authors till van den Hoek Ostende's thorough review (2001) gave arguments for the validity of both genera – in agreement with Hugueney (1974) – and ascribed them to Reumer's subfamily Crocidosoricinae (1987). Last, Furió et al. (2007), taking into account the diversity of the Crocidosoricinae, re-established and redefined older subdivisions and divided the Crocidosoricinae into three tribes: Myosoricini Kretzoi, 1965, Crocidosoricini Reumer, 1987 and Oligosoricini, Gureev, 1971.

1.2. Stratigraphic and biochronologic background

When Stehlin (1940) and Viret (1929) described the first soricids from Limagne, the ages of the localities were not precisely known, but progress in biostratigraphy made during the last twenty years now makes it possible to determine their respective ages with greater precision (e.g., de Bruijn et al., 1992; BiochroM'97, 1997; Hugueney, 1997). The Early Miocene level MN2 is subdivided into a lower level (MN2a = Montaigu-le-Blin) and an upper level (MN2b = Laugnac). With regard to Montaigu-le-Blin (the reference locality of MN2a), Hugueney et al. (2006) demonstrated that eomyids from the historical and recent collections from the Montaigu-le-Blin quarries are not identical due to a slight difference in stratigraphic age. Indeed, recent excavations have yielded slightly older faunas than the previously known ones, remaining however within the limits of the MN2a level. This difference in age can be explained by the fact that the excavations go deeper and deeper and so reach older levels of the lacustrine deposits. The soricid fossils described by Stehlin (1940), which were gathered in 1933/1934, seem to come from the uppermost levels of the quarries. The locality Saulcet is near the base of MN2a. The locality Marcoin pertains also to MN2a but is a little more recent than Montaigu: the lagomorph *Marcuinomys roquesi* Lavocat, 1952 from this locality is derived from *Titanomys*, a genus known from Montaigu (López Martínez, 1989). The age of Marcoin is equivalent to that of La Chaux (Switzerland) or Cetina de Aragon (Spain). The fauna of Le Vendant is just a little older. Bouzigues 1 pertains to the level MN2b (Escarguel and Aguilar, 1997), and is perhaps a little more recent than Laugnac (Table 1).

As well as describing new genera and species from the late Oligocene/Early Miocene of France and Germany, Crochet (1975) and Ziegler (1989, 1998) emphasized the diversification of soricids during this period. However, as outlined above, the complex history of successive studies together with the problem of imprecise dating makes it difficult to understand the diversification process of this family and the phylogenetic relationships between their fossil and extant representatives. In the first place, a re-examination and a better characterisation of the taxa *Oligosorex antiquus* and *Crocidosorex piveteaui* are necessary in order to solve the systematic problems related to these two genera. To do so, we present here SEM photographs and better illustrations of these minute specimens, and we compare them in detail with other soricid taxa. We examine here the Montaigu quarry specimens from the NMB collection on which Stehlin (1940) based his description of *Oligosorex* in order to solve the enigma of Pomel's second species, which is described here as belonging to a new genus: *Meingensorex* nov. gen.

2. Material and methods

2.1. Material and collections abbreviations

The classification used in this paper follows Furió et al. (2007); the nomenclature and measurements follow Jammot (1983) and Reumer (1984). For dental formulae we follow the method of Dannelid (1998) counting 'upper/lower' incisors, antemolars, premolars and molars (e.g., genus *Sorex* 1,5,1,3/1,1,1,3). Upper teeth are indicated in capitals and lower teeth in lower case. Measurements are in millimetres. L = maximal length, W = maximal width, Trw = trigonid width, Taw = talonid width. The specimens studied here are preserved in different institutions: collection of the University Lyon-1 (FSL); Museum of Lyon (ML); Natural History Museum of Paris (MNHN); University of Utrecht collections (MU); Naturhistorisches Museum of Basel (NMB).

Table 1

List of soricid localities in the Limagne and Aquitaine basins, and in the Languedoc region. The ages of the localities are given according to the Neogene continental biochronological scale as modified by de Bruijn et al. (1992) for the Early Miocene.

			Crocidosorex piveteaui	*Meingensorex ambiguus*	*Oligosorex antiquus*	*Oligosorex thauensis*	*Soricella discrepans*	*Clapasorex bonisi*	*Clapasorex sigei*	*Carposorex sylviae*
Early Miocene	MN2b	Bouzigues 1				*			*	
		Laugnac								*
	MN2a	Marcoin	*							
		Montaigu-le-Blin		*	*					sp.
		Cluzel			+					
		Poncenat			+					
		Chavroches			+		+			sp.
		Saulcet			+					
	MN1	Paulhiac						*		sp.

+: present; *: type locality.

2.2. Data and Parsimony analysis

The 15 taxa included in this study have been coded into a matrix of 27 morphological characters (Tables S1 and S2). In this study, only characters showing little intraspecific variability have been used. The characters coded concern the morphology of the skull and mandible (six characters), the number of teeth (two characters), and the morphology of the teeth (19 characters). Pigmentation of the teeth can be observed for some extant and fossil species. However, the pigmentation of the fossil taxa may have been affected by diagenesis; we consequently excluded this character from the analysis. Of the ten multistate characters in the analysis, seven are ordered and three are unordered (Table S1). The matrix of characters was processed using the cladistic analysis software PAUP* 4.0, using the heuristic 'stepwise' search method. The Eocene nyctitheriid *Saturninia gracilis* was chosen as the outgroup for the parsimony analysis because of its stratigraphic position and its primitive morphology compared to all late Oligocene and Neogene soricids. *S. gracilis* was successfully used as the outgroup in Ziegler's (2009) previous analysis of phylogenetic relationships among heterosoricines. The consistency index (CI) and homoplasy index (HI) were computed to assess the overall reliability of the cladogram, and unambiguous morphological innovations (i.e., morphological changes occurring one time without reversion in the phylogeny) were counted for each branch.
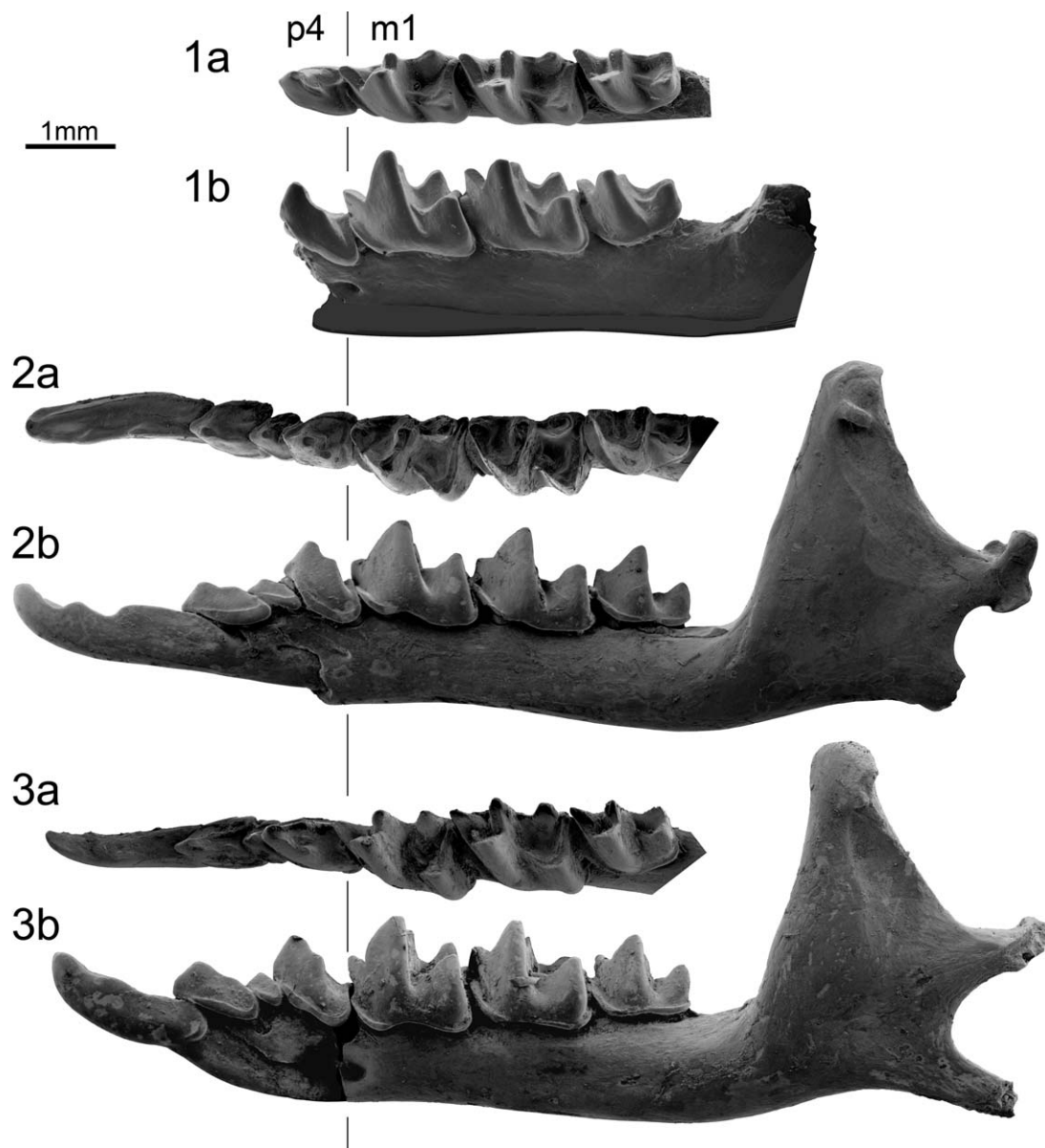

Fig. 2. Crocidosoricine mandibles from Limagne. SEM pictures in (a) occlusal view and (b) labial view. **1**. *Crocidosorex piveteaui* Lavocat, MNHN Cr.39: left mandible with a3-m3, holotype. **2**. *Oligosorex antiquus* (Pomel), NMB Ph.12: left mandible with i-m3, neotype. **3**. *Meingensorex ambiguus* (Pomel) nov. comb., NMB Ph.2255: right mandible (reversed) with i-m3, neotype.
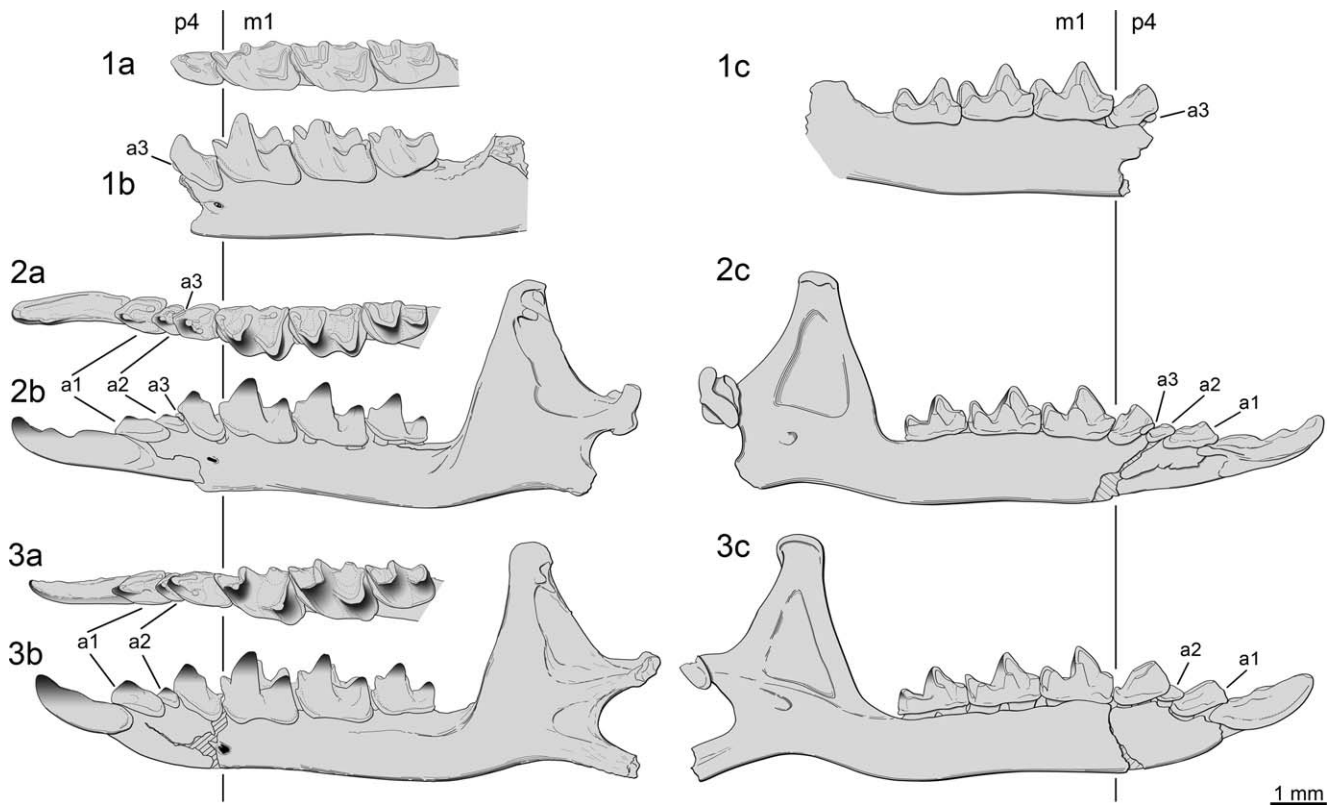
Fig. 3. Sketch drawings of crocidosoricine mandibles from Limagne, in (a) occlusal view, (b) labial view and (c) lingual view. **1**. *Crocidosorex piveteaui* Lavocat, MNHN Cr.39, holotype. **2**. *Oligosorex antiquus* (Pomel), NMB Ph.12: left mandible with i-m3, neotype. **3**. *Meingensorex ambiguus* (Pomel) nov. comb., NMB Ph.2255, right mandible (reversed) with i-m3, neotype.

3. Systematic paleontology

Order SORICOMORPHA Gregory, 1910
Family SORICIDAE Fischer, 1814
Subfamily CROCIDOSORICINAE Reumer, 1987
Tribe CROCIDOSORICINI Reumer, 1987
Genus *Croscidosorex* Lavocat, 1952
Crocidosorex piveteaui Lavocat, 1952
Figs. 2(1) and 3(1)

Holotype: Mandibular fragment with p3-m3 and alveolus of at least one additional antemolar. The anterior and posterior part of the mandible are both broken away just before and also a little behind m3. MNHN, Cr. 39 (coll. Croizet).

Locus typicus: Marls of Marcoin, near Volvic (Puy-de-Dôme, France). Upper MN2a.

Distribution: Restricted to the type-locality; no other species included.

Measurements: See Table S3.

Original diagnosis [Translated from french]: Soricid with unpigmented teeth and simplified p4 as in *Crocidura*, m3 with bitubercular heel as in *Sorex*.

In a brief description, Lavocat added that m3 has a long talonid, two well-developed tubercles (hypoconid and entoconid), and no basal rim on the three molars except along the paraconid. Later, Crochet (1975) added: m1 and m2 subequal in width (Lm1-m3 = 3.77 mm); dental formula: 1,3(?),1,3. Contrary to Repenning's diagnosis – which is mainly founded on the characteristics of *Oligosorex* – the number of antemolars anterior to the minute p3 is unknown and it is not possible to see if p4 is single-rooted; moreover, the well-developed entoconid crest is not low.

Differential diagnosis: *Crocidosorex* is distinguished from all other Early and Middle Miocene soricids by the following unique combination of characteristics: p4 with only a postero-labial crest and minute p3 included in its anterior part, molars devoid of labial cingulum, m1 and m2 sub-equal in length, trigonid and talonid of m1-2 sub-equal in width, m3 with clearly developed entoconid, and teeth unpigmented. The incompleteness of the mandible prevents further comparisons with other species.

Description: Medium-sized soricid (Lm1-3 = 3.70 mm), with at least two antemolars anterior to p4: a minute p3 with a well-developed root situated in line with the other roots and, anteriorly, an alveolus perpendicular to the ramus for an additional antemolar. p4 has a unique postero-labial crest and an elongated talonid, and also a large foramen mentale under its posterior part. m1-3 each have a strong antero-cingulid that disappears on the labial face of the tooth. m1-2 are roughly the same size with respect to both length and maximal width. The trigonid of m1 is widely open, but the trigonid is narrower in m2 and m3. The talonids of all three molars are elongated. The hypoflexid opens close to the base of each molar. The oblique cristid is sub-parallel to the labial border of m1 and nearly perpendicular to the hypolophid, but ends more and more

lingually on m2 and m3. It ends high on the posterior wall of the trigonid. The hypolophid of m1 and m2 bends posteriorly but does not reach the lingual border. The entocristid is relatively long and high with a distinct entoconid.

Remarks: Evolutionary trends are rather difficult to follow in the early soricids, and indeed *Crocidosorex* shows a combination of features that seem primitive because they are present in *Saturninia gracilis* (such as the absence of a labial cingula in m1-m2, and a developed entoconid in m3) and seemingly derived features such as the presence on p4 of an external crest as in the extant species *Sorex araneus*. As discussed below, these morphological characters might constitute homoplasies in the evolutionary history of soricids.

Tribe OLIGOSORICINI Gureev, 1971
Genus ***Oligosorex*** Kretzoi, 1959

Original diagnosis: *Oligosorex* is proposed for Late Oligocene and Miocene soricids of small dimensions, retaining three unicuspids between p4 and the relatively small and primitive front incisor in the lower jaw. *Sorex antiquus* Pomel is selected as type of the genus – differing from *Miosorex* holotype: *Sorex pusillus* race *grivensis* Depéret, 1892 – which retains but two unicuspids like *Myosorex*.

Included species: *Oligosorex antiquus* (Pomel, 1853); *Oligosorex thauensis* Crochet, 1975; *Oligosorex reumeri* van den Hoek Ostende, 2001.

Oligosorex antiquus (Pomel, 1853)
Figs. 2(2) 3(2), 4(1) and 5(2)
1853. *Sorex antiquus* - Nob. Pomel, pp. 13–14.
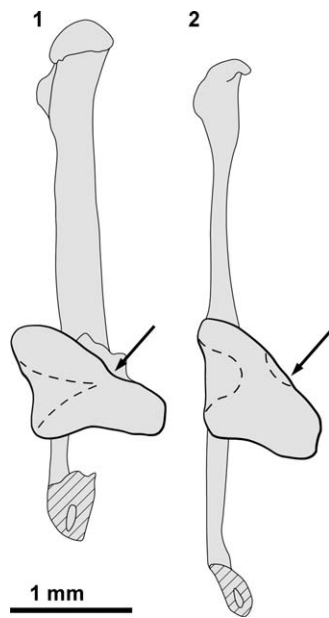1967. *Crocidosorex antiquus* (Pomel) - Repenning, p. 29.

Fig. 4. Sketches of crocidosoricine condyles from Limagne. **1**. *Oligosorex antiquus* (Pomel), NMB Ph.12, left mandible with i-m3, neotype. **2**. *Meingensorex ambiguus* (Pomel) nov. comb., NMB Ph.11: right mandible with i-m1, reversed.

Neotype: (designated by Crochet, 1975: 633): NMB Ph.12, left mandible with i-m3 and complete ramus, except tip of angular process, figured in Stehlin (1940: figs. 1b, 2b, 3).

Locus typicus: Montaigu-le-Blin (Allier, France; MN2a).

Material: From Montaigu: left mandible with p4-m3, condyle (NMB Ph.7); left mandible with p4-m2 (NMB Ph.8); right mandible with i-m3, condyle (NMB Ma.7589); left mandible with m1-m3, condyle (NMB Ma.7592); fragmentary skull, consisting of left maxillary with A4-M3 and right maxillary with A3-M3 (NMB Ma.5274) illustrated by Stehlin (1940: figs. 4b, 5b); fragmentary skull with right and left P4-M3 (ML StG 838). From Le Vendant: left mandible with m1-3 (FSL 98191); two right mandibles, one with m1 (FSL 98192) and one with p4-m3 (FSL 98193).

Measurements: See Tables S3 and S4.

Original diagnosis [Translated from French]: a little smaller than *S. vulgaris*, this species has more cylindrical mandibular condyle, the coronoid process is shorter and its apex isn't thickened. The second intermediate lower tooth has a slightly expanded talonid.

Differential diagnosis: The two other species of *Oligosorex*, *O. thauensis* Crochet from Bouzigues and *O. reumeri* van den Hoek Ostende from Keseköy (Turkey; MN3) show the same lower dental formula but they are more recent and differ from *O. antiquus* in being characterized by smaller size, smaller alveoli for the antemolars, and continuous cingulids on the lower molars. *Clapasorex* from Bouzigues shows the same characteristics as *O. antiquus* but is much smaller and has five cuspules on the lower incisor, a long posterolingual crest on p4, and a short entocristid on each lower molar (further details in Ziegler, 1989; Ziegler et al., 2007). *Lartetium* Ziegler, 1989 from Sansan (MN6) has the same number of antemolars but a smaller rostral part of the mandible, and antero-posteriorly compressed molars with a conical entoconid and reduced entocristid. Moreover P4, M1 and M2 are wider, with narrow hypoconal flanges, and the posterior rim of the infra-orbital foramen is oblique.

The Oligocene genera *Srinitium* and *Ulmensia* have small and crescent-like lower incisors, and more massive molars with thick cingulids. *Srinitium* also has more antemolars, and in m1 of *Ulmensia* the postero-labial edge of the protoconid forms a crest joining the midpoint of ectocingulid. This is also the case in *Aralosorex* Lopatin, 2004 from the Late Oligocene of Kazakhstan, *Taatsiinia* and *Tavoonyia* Ziegler et al., 2007 from the Oligo-Miocene of the Mongolian Lake district, and *Carposorex* from Laugnac. The early Oligocene *Suevosorex* Ziegler, 2009 is only known from a few isolated teeth, but is much larger. The teeth show strong cingula, and M2 has a divided mesostyle and a faint hypoconal flange lacking a cuspulate hypocone.

Among genera with a reduced number of antemolars, *Florinia* Ziegler, 1989 from Wintershof-West (MN3) and *Miosorex* Kretzoi, 1959 from La Grive are generally unpigmented. *Paenelimnoecus* Baudelot, 1972 from Sansan differs in lacking entoconids and *Soricella* Doben-Florin, 1964 from Wintershof-West (Germany; MN3, but also known in Chavroches) differs in that its hypolophid directly joins the entoconid.
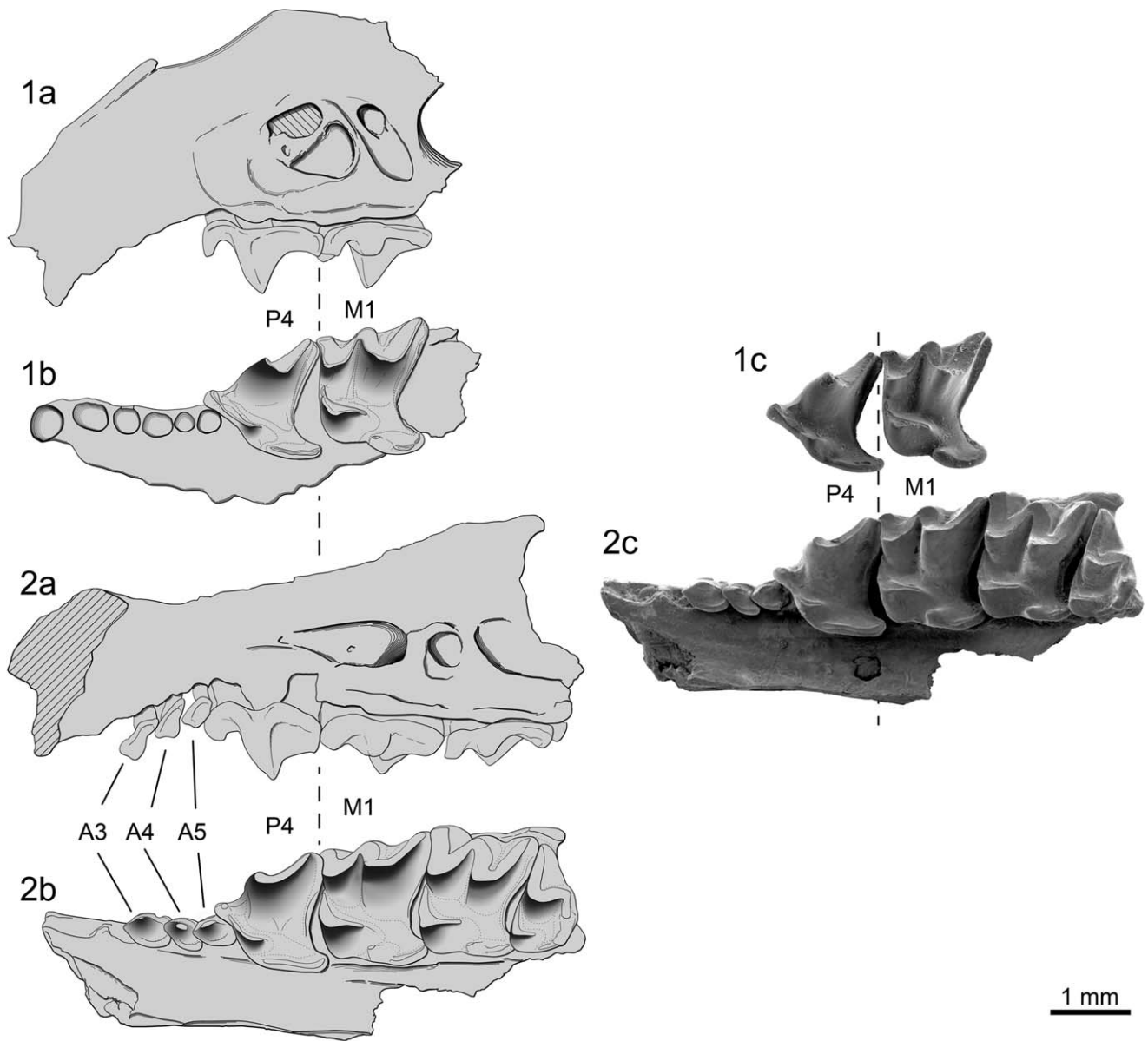
Fig. 5. Crocidosoricine maxillaries from Limagne, in (a) labial view, (b) occlusal view, (b, c) occlusal views. **1**. *Meingensorex ambiguus* (Pomel) nov. comb., NMB 2219, left maxillary with P4-M1. **2**. *Oligosorex antiquus* (Pomel), NMB Ma.5274, left maxillary with A3-M3.

Description: Medium-sized soricid (Lm1-3 range = 3.47–3.65 mm) with three single-rooted antemolars anterior to the double-rooted p4, the minute a3 being hidden under p4; dental formula = 1,5,1,3/1,3,1,3; pigmented teeth.

The mandible has a narrow horizontal body, undulating in the area of m1-2 and the ramus. The ramus is triangular and slightly oblique posteriorly, with an anterior rectilinear rim and slightly inflated labial face (height of the coronoid process ranges from 3.55–3.73 mm). The external tip of the coronoid process is slightly rounded with an anteriorly placed and hooked coronoid spicule, a marked external temporal fossa, and a faint oblique crista. On the lingual face, the internal temporal fossa is well developed and triangular; its base, a little above the level of the molar base, is faintly oblique. The mandibular foramen is located below the posterior part of the internal

temporal fossa. The upper part of the condyle is visible in lingual view, with a marked pterygoid spicule. In caudal view, the condyle is trapezoidal with an enlarged base, and the higher labial part is slightly excavated with a labially extended upper tip; lingually, the tip is compressed. Articular facets are not well defined.

The lower incisor is bicuspid and horizontally elongated, and the labial edge is longer than the lingual one (one specimen with ext. L = 2.35 mm; int. L = 1.93 mm). The posterior cuspid is far from a1.

p4 is short, and the minute alveolus of its anterior root is associated with an antero-lingually placed alveolus for a3. p4 is triangular with curved lateral borders; its crests diverge from the anterior main cusp in a Y-shaped pattern (in the neotype, the lingual crest is shorter than the labial one, which ends in a

cusplet). A proportionally wide cingulid borders the tooth (except anteriorly) and forms a very short talonid with a median cusplet. A small mental foramen is present below the posterior root of p4.

m1-m2 have sharp labial tubercles; the talonid of m1 is wide, whereas m2 is more rectangular; the m1 trigonid opens largely lingually and has a low paralophid, while the m2 trigonid is a little shorter. The hypolophid is well developed and nearly rectilinear, ending lingually far from the entoconid and a little above a faint cingulid; the entocristid is curved between the metaconid and the entoconid. In labial view the sinusid deepens from m1 to m3; the cingulid is strong anteriorly and thinner labially, and is interrupted under the sinusid on m1. m3 bears a small basin-shaped talonid, without a visible entoconid.

The maxillary has five single-rooted antemolars; the tips of these teeth are pigmented. The length of the whole P4-M3 serie ranges from 4.10–4.30 mm, and that of M1-3 from 2.99-3.05 mm. As in the case of *Meingensorex* nov. gen., *in situ* upper incisors are unknown for *O. antiquus* in the NMB and ML collections. The alveoli of the antemolars range in length from 2.05 to 2.25 mm. The alveoli decrease in length from a1 to a5, a1 being conspicuously larger than the others.

P4 has a massive parastyle, well separated from a massive paracone; the protocone is V-shaped. The hypoconal flange is not expanded, but bears a marked ridge and a moderate posterior emargination; no hypocone is present. M1 is a little larger than M2; M1 and M2 are massive, with hypocones that do not protrude lingually. The protocone and hypocone are nearly aligned, and the anterior arm of the protocone continues lingually below the paracone. The teeth have no cingulum around the protocone and anterior area. M3 has a smaller posterior part, but the hypocone is distinguishable. In labial view, the infra-orbital foramen ends above the midpoint of M1 and its posterior rim is perpendicular to the base of the maxillary; the posterior part of the bridge over the canalis infraorbitalis ends posteriorly above the paracone of M2. The large, high lacrimal foramen has a thick antero-dorsal rim.

Remarks: *Oligosorex* might have been present in Europe as early as the Late Oligocene (MP28) based on putative specimens from Cournon (Brunet et al., 1981), but the material is so poor that the generic attribution is doubtful. *O. antiquus* is usually characteristic of MN1-2 levels in Europe (Rzebik-Kowalska, 1998, 2009), especially in the Limagne basin. In this basin, however, the material from the older levels is of smaller size. *O. thauensis* from the MN3 Miocene levels of Spain (van den Hoek Ostende, 2003) shows antero-posteriorly compressed molars that recall the genus *Lartetium*. Later citations of *Oligosorex* are generally doubtful (Rzebik-Kowalska, 1998).

Tribe Incertae sedis
Genus *Meingensorex* nov. gen.
Derivatio nominis: Dedicated to all the members of the Mein family (latin: *gens*) – who helped over a period of years to collect, wash and pick fossils, and to edit and illustrate papers – in recognition of their contribution to vertebrate palaeontology.

Type species: *Sorex ambiguus* Pomel, 1853 (Type specimen lost).

Locus typicus: Montaigu-le-Blin (Allier, France; MN2a, Early Miocene).

Repartition: So far restricted to the type-locality, no other species included.

Diagnosis: Medium-sized soricid with the tips of the teeth darkly pigmented. The lower incisor is crescent-shaped and bicuspulate; the root is not aligned with the crown and the lingual face is nearly as long as the labial face. The mandible displays four aligned alveoli for two antemolars and a large double-rooted p4 with an elongated talonid. p4 has two subequal crests and its anterior root is well developed. m1 is a little longer than m2. The lower molars show sharp tubercles, and the talonids are wider than the trigonids; the cingula are narrow, generally continuous and externally undulating. The labial end of the sinusid is relatively high. m3 has a two-cusped talonid basin. The mandible is slender and faintly curved under m1, and the mental foramen is located below the area between the midpoint of p4 and the posterior part of m1. The ramus is high (range 3.98–4.07 mm). The coronoid process is a little constricted antero-posteriorly near the dorsal end, and the coronoid spicule is rounded and not well formed. The condyle does not protrude labially, its facets are not well delimited, and its bone attaching to the ramus is very thin. There is no pterygoid spicule. The internal temporal fossa is large and triangular, and its lower edge is very oblique. The mandibular foramen is a little posterior to the midpoint of the internal temporal fossa. The angular process bears an internal pterygoid fossa well delimited by a lower oblique rim. One maxillary with subequal alveoli for five upper antemolars is attributed to the same genus. P4 and M1 are each characterized by a deep posterior emargination and by a hypoconal flange that protrudes strongly in the lingual direction; P4 has no hypocone; in M1 an anterior arm of the protocone joins the base of the paracone.

Differential diagnosis: *Meingensorex* differs from *Crocidosorex* in having a double-crested p4 without an included antemolar, well-marked labial cingulids upon the molars, and a smaller talonid of m3. It differs from *Oligosorex* in the following features: crescent-like lower incisor, absence of a minute included a3, better marked labial cingulids on lower molars, and differently shaped mandibular ramus and condyle. Moreover, *Meingensorex* shows more antero-posteriorly compressed upper teeth and a different type of infra-orbital foramina. (cf. description below).

Meingensorex also differs from most *Miosorex* species in having a crescent-like lower incisor with a marked angle between the crown and the root, in having a relatively large second antemolar well separated from a1 and p4, and in lacking an antemolar hidden under p4. It also differs from *Miosorex* in that the bone attach of the articular condyle to the mandibular ramus is very thin. Finally the hypoconal flanges of the upper molars of *Miosorex* do not protrude lingually. It is also noteworthy that *Meingensorex* has pigmented teeth, in contrast to *Crocidosorex* and most *Miosorex*.

Florinia possesses many characters that distinguish it from *Meingensorex*, such as: slightly smaller size; heavier mandible; straight elongated lower incisor with posterior part of crown ending under a2; short single-rooted p4, hollowed for a2; m1-2

with thick cingulids, short and high entoconids; short m3 with smaller talonid. *Carposorex* differs from *Meingensorex* in having rough enamel and in that the disto-labial edge of each lower molar joins the labial cingulid.

The genus *Paenelimnoecus* and the species *M. pusilliformis* (being moreover very small) both differ from *Meingensorex* in having only one antemolar, and the genus *Soricella* in having a distinctive talonid morphology. All the other non aforementioned soricid genera differ from *Meingensorex* in having three lower antemolars.

Meingensorex ambiguus (Pomel, 1853) nov. comb.
Figs. 2(3), 3(3), 4(2) and 5(1)
1974. *Oligosorex antiquus* (Pomel) - de Bruijn and Rümke, p. 70, fig. 5.2.

Neotype: NMB Ph. 2255, right mandible with i1-m3 and both ramus and articular process partly broken.

Material: Left mandible with m1-m2, condyle (NMB Ph.9); right mandible with m1 (NMB Ph.10); right mandible with i-m1, condyle (NMB Ph.11); left mandible with m1-m2, condyle (NMB Ma.7593); left mandible with a2-m2 (NMB Ph. 2222); left maxillary with P4-M1 (NMB Ph. 2219).

Measurements: See Tables S3 and S4.

Original diagnosis: *Sorex ambiguus*, Nob. [Translated from French]: Size and shape very similar to the previous species [i.e., *O. antiquus*], it differs by a mandibular coronoid process being narrower at its top, and by the condyle being less expanded and shorter externally.

Description: Medium-sized soricid (Lm1-3 range = 3.39-3.60 mm); dental formula: 1,5,1,3/1,2,1,3; only two single-rooted antemolars and a double-rooted p4, with well-separated roots. All teeth have darkly pigmented tips. The lower incisor is crescent-like, relatively short (labial crown length = 1.93 mm) and faintly bicuspulate; the posterior cuspule is placed just anterior to the anterior part of a1. The postero-labial cingulum is well-marked, and a thin symphysal cingulum runs along the lower border of the base to the incisor tip; the two faces of the incisor are nearly equal in length, but the lingual face is nevertheless a little shorter. The root is a little shorter than the crown, and joins it forming an angle. a1 is faintly bicuspulate and larger than a2; however, the minute a2 has a developed root and is only partly covered by p4. p4 is elongated and forms a well-differentiated talonid; the anterior cuspid shows an abrupt anterior edge and two relatively long posterior crests that end in a tubercle, the postero-lingual crest being a little lower than the labial one. A marked labial cingulid surrounds nearly the whole base, but vanishes anteriorly where the base is not hollowed; a minute tubercle is situated on the midpoint of the postcingulid. m1 and m2 show sharp tubercles and relatively compressed trigonids, and m2 is a little shorter than m1. The m1 trigonid is largely open lingually, with a high paralophid; it is clearly narrower than the prominent talonid; in m2 the difference between the trigonid and the talonid is less marked, but the talonid is generally still larger than the trigonid. The crista obliqua ends relatively high on the posterior wall of the trigonid. The long hypolophid ends near the entoconid base and sometimes curves toward it. On m1, the crista obliqua and

hypolophid meet the hypoconid nearly perpendicularly. The labial sinusid opens relatively high above the labial cingulid on m1, but in a lower position on the other two molars. The cingula are well developed around the whole tooth, but thinner under protoconids. The labial bases of the molars undulate markedly below the labial tubercles, and the edges of the protoconids are not as oblique as in *C. piveteaui* and *O. antiquus*. m3 is proportionally short, with a talonid smaller than in *C. piveteaui* and *O. antiquus* in both length and width. The crista obliqua is more lingually shifted than on m1-2 (more and more lingually shifted from m1 to m3); the hypolophid extends downward to the minute entoconid; cingulids are well developed as on m1-2.

The horizontal branch of the mandible is relatively narrow, with its base undulating slightly below m1-2 and undulating more below the ramus. The mental foramen is rounded and relatively large; it is located between the posterior parts of p4 and m1. The ramus is triangular but contracted just below the rounded tip of the coronoid process. The coronoid spicule is neither prominent nor well delimited, and is rounded posteriorly. The external temporal fossa is anteriorly limited by a sinuous rim aligned perpendicular to the axis of the mandible. On the lingual face, a posteriorly projecting flange characterizes the tip of the upper coronoid process; the internal temporal fossa is short, and its base lies strongly oblique to the axis of the mandible. The mandibular foramen is posterior to the fossa but close to its base. In caudal view, the outline of the articular condyle is trapezoidal with a basal enlargement; the interarticular area is not emarginated lingually, and its base is high above the upper border of the horizontal ramus. The articular facets are not well delimited and a pterygoid spicule is lacking.

On the maxillary, the total P4-M1 length is similar to that of *Oligosorex antiquus*, but the antemolar is shorter in *M. ambiguus* nov. comb. (LA1-A5 = 1.80 mm). The shorter antemolar series could be related to the evident reduction in the number of lower antemolars and perhaps a general shortening of the muzzle; it supports the assignment of this maxillary to the same taxon as the mandibles. P4 has an acute parastyle that is well-separated from the high paracone. There is no V-shaped protocone but only a slightly inflated crest, at the level of the protocone. The expanded hypoconal flange lacks a hypocone and bears a marked ridge, and the posterior emargination strongly notches the posterior side of the tooth. M1 bears a tuberculated hypocone merging with the enlarged posterior cingulum on the postero-labial side. The hypocone and the hypoconal flange protrude labially beyond the level of the protocone (a characteristic reminiscent of Nyctitheriidae). In M1 the anterior arm of the protocone fuses with the paracone ridge; there is no cingulum either at the protocone base or on the anterior side of the tooth. In labial view, the infra-orbital foramen opens above the M1 mesostyle and its posterior rim is oblique; the bridge over the canalis infra-orbitalis is relatively large, and parallel-sided; the lacrimal foramen shows a faint rim and is situated relatively high above the posterior part of M1. The nasal is not inflated by the incisor root.

Remarks: Despite being very short, Pomel's diagnosis (1853) fits the mandibles of the second species from Montaigu

so well that we think we can ascribe them to the species *S. ambiguus* described by this author. de Bruijn and Rümke (1974) figured an incisor from Montaigu-le-Blin (MU 502) and ascribed it to an upper incisor of *Oligosorex antiquus*; in fact this tooth is a better match for a lower incisor of *Meingensorex*-type.

Variations in the number of unicuspids have been noted in various soricid species (Meester, 1955; Hausser and Jammot, 1974; Ziegler, 1989) but at Montaigu the mandibles with only two antemolars are always associated with a crescent-shaped incisor and/or a distinctive p4 or a typical ramus and condyle; this confirms that the absence of a3 is not due to either poor preservation or intra-specific variability, but does indicate the presence of another taxon. However, as noted by Engesser (2009) for the genera *Lartetium* and *Miosorex,* this form is not easy to distinguish from *Oligosorex* in the absence of well-preserved material, and isolated teeth are certainly difficult to ascribe to any particular genus.

Furió et al. (2007) stated that the tribe Myosoricini was characterized by, among other features, a lower incisor with a straight crown/root alignment and an m3 with a relatively small talonid. *Meingensorex ambiguus* nov. comb. also has a crescent-like incisor. However, this incisor has an angle between the crown and the root, and furthermore the fact that the talonid of m3 is not notably small does not match the diagnosis of the tribe. We here consider *Meingensorex* nov. gen. as belonging to an undetermined tribe, but it might also represent an earlier evolutionary stage of the tribe Myosoricini.

4. Discussion

4.1. Evolutionary trends

Reassessment of the original material of *Crocidosorex* and *Oligosorex* leads to a better knowledge of their distinctive features. Concerning *Oligosorex*, if all attributions to this genus are correct, it would range from the Late Oligocene (MP 28) to the late Early Miocene (MN3 or even later). However,

assessment of evolutionary trends within the genus is not easy because *O. antiquus* seems to grow larger from MN1 to MN2a, at least in the Limagne basin. However, a more precise age attribution for *O. thauensis* (MN2b) – its size being a little smaller than that of *O. antiquus* from Montaigu while its age is more recent – points to a reversal of this trend. So the relationships of the Bouzigues taxon are difficult to trace back, particularly with respect to the possible affinity between *O. thauensis* and *O. antiquus*.

The precise age attribution of *Crocidosorex* (MN2a, but later than *Oligosorex* from Montaigu; Table 1) is important because *Crocidosorex* shows characteristics that are not in accordance with evolutionary trends widely recognized in Soricidae. Indeed, the particular combination of characters seen in *Crocidosorex* suggests that an ancestor/descendant relationship between *Oligosorex* and *Crocidosorex* is unlikely, as is also demonstrated below based on the tentative phylogeny. This conclusion results from the fact that some characters display previously unrecognized homoplasy in the evolutionary history of the family.

In this context, the newly defined genus *Meingensorex* is interesting because it shows some incipient myosoricine characteristics (reduction of the number of lower antemolars, development of labial cingulum on m1-2, reduction of the entoconid on m3). The Early Miocene of Europe does record a rapid diversification of the soricids (Rzebik-Kowalska, 1998; Ziegler, 2006). However, so far, we do not know enough to follow the evolution of the soricids on a regional scale. It is consequently difficult to distinguish between elements of this diversification resulting from local evolution and those resulting from migrations within Eurasia.

4.2. Phylogenetic implications

The phylogenetic analysis resulted in four most parsimonious trees, each having a length of 61 steps. The 50% majority-rule consensus tree (Fig. 6) is characterised by a consistency index of 0.672 and a homoplasy index of 0.328. As indicated by
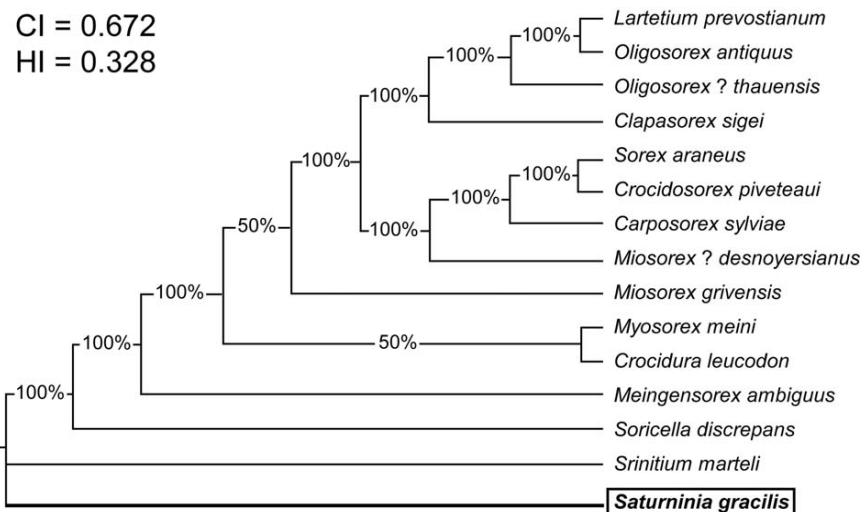

Fig. 6. Majority-rule consensus of four most parsimonious trees, including fossil and extant soricid taxa. The outgroup is indicated in bold characters in a box. CI: consistency index; HI: homoplasy index.

the relatively high homoplasy index, a substantial proportion of characters are homoplasies that seem to have changed independently in different clades during the evolutionary history of Soricidae. *Srinitium marteli* shows the most plesiomorphic association of characters, but its phylogenetic relationships to other soricids remain unclear. However, the six unambiguous changes between *Saturninia gracilis* and *S. marteli*, compared to only three between *S. marteli* and the rest of soricids, support the inference that *S. marteli* is clearly differentiated from the outgroup and rather belongs to the Soricidae, as already stated by previous authors (Reumer, 1987; Ziegler, 2009). Apart from *S. marteli*, *Soricella discrepans* and *Meingensorex ambiguus* nov. comb. retain several plesiomorphies. The analysis identifies a single unambiguous apomorphy (triangular P4) for *M. ambiguus* nov. comb. The two taxa *Myosorex meini* (this species is Late Pliocene in age but the genus *Myosorex* still exists today) and *Crocidura leucodon* (an extant species) are sister taxa in 2/4 most parsimonious trees, and are differentiated from other soricids by one unambiguous apomorphy (less than five antemolars before the P4). This supports the results of Dubey et al. (2007), who demonstrated that Crocidurinae and Myosoricinae are closely related. *Miosorex grivensis* forms an isolated branch with an intermediate phylogenetic position in 2/4 most parsimonious trees; however, this branch is supported by no unambiguous character state changes.

All other soricids are grouped together on a branch supported by one unambiguous change (base of internal temporal fossa slightly instead of strongly oblique). Within this group, *Miosorex desnoyersianus*, *Carposorex sylviae*, *Crocidosorex piveteaui* and *Sorex araneus* form a clade, with *M. desnoyersianus* retaining the most plesiomorphic combination of characters. In this phylogeny *Miosorex* appears paraphyletic (*M. grivensis* being the type species of the genus). Indeed six characters differ between *M. desnoyersianus* and *M. grivensis* (Table S2) indicating that *Miosorex desnoyersianus* could be assigned to another genus. The last clade is composed of *Clapasorex sigei*, *Oligosorex thauensis*, *O. antiquus* and *Lartetium prevostianum*. These four species share one unambiguous synapomorphy (three lower antemolars before p4). In this consensus tree *Oligosorex* appears paraphyletic, both species differing from each other by their labial cingulum on m1-2 and their entoconid on m3, but the lack of information about the evolution of the genus in Central France does not allow any further interpretation of their phylogenetic relationships.

Based on this tentative phylogeny of soricids, the subfamily Crocidosoricinae *sensu* Reumer (1987) is reassessed as paraphyletic, and seems to be something of a wastebasket filled with taxa whose phylogenetic positions are uncertain, as suggested by Furió et al. (2007). With respect to extant species, the position of *Sorex araneus* in this phylogeny compared to *Crocidura* and *Miosorex* supports the hypothesis that the Crocidurinae and Myosoricinae form the sister clade of Soricinae (Dubey et al., 2007 *contra* Quérouil et al., 2001). In the present phylogeny, the position of *S. araneus* also implies an early differentiation of Soricinae from Crocidurinae and Myosoricinae, the closest taxa associated with soricines being Early Miocene in age. So far, the oldest probable soricine material is known from the Early Miocene of Germany (Stubersheim 3, MN3: Ziegler, 1989). The fossil record supports the statement made by Dubey et al. (2007) that the most recent common ancestor of Crocidurinae, Myosoricinae and Soricinae was probably Eurasian. Our results also support an early Miocene differentiation of Soricinae, and more generally a rapid diversification of all soricids as early as the Early Miocene, as previously suggested by Crochet (1975) and Ziegler (2006: table 7).

Appendix A. Supplementary data

Supplementary data Tables S1–S4 associated with this article can be found, in the online version.

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