Geobios 45 (2012) 581–589

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Original article

Primitive Anourosoricini and Allosoricinae from the Miocene of Germany☆

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ARTICLE INFO

Article history:
Received 16 March 2011
Accepted 30 March 2012
Available online 27 September 2012

Keywords:
Insectivora
Soricidae
Crusafontina
Anourosoricini
Allosoricinae
Miocene
Germany

ABSTRACT

The origin of the peculiar and highly specialized shrew tribe Anourosoricini is poorly known. The oldest known genera, *Crusafontina* Gibert and *Darocasorex* van Dam, first occur in Europe and North America around the Middle-Late Miocene transition (12-11 Ma), with the extremely rare cf. *Crusafontina* sp. from Anwil (Switzerland) extending the age of the oldest fossils back to at least 13 Ma. Here, new material of the oldest named *Crusafontina* species, *C. exculta* (Mayr and Fahlbusch), is described from the German localities Hammerschmiede (layers 1 and 3) and Hillenloh. The primitive nature of this species is confirmed. Apart from the unnamed specimens from Anwil, it is considered to be the oldest representative of a lineage leading to *C. endemica* Gibert and *C. kormosi* (Bachmayer and Wilson). Furthermore, the status of the extinct Allosoricinae Fejfar as a separate subfamily is well accepted, but opinions differ whether *Paenelimnoecus* Baudelot and/or "*Allosorex*" *gracilidens* (Viret and Zapfe) should be included in this subfamily. Here we propose to include only the latter form, after describing dental material from the locality of Giggenhausen. We assign three isolated M1-2 to this species, which we regard as the oldest known upper molars of Allosoricinae *sensu* Repenning. Anourosoricini and Allosoricinae show parallel and coeval evolution towards carnivore-like adaptation in their dentition, including the development of carnassial teeth and the reduction of third molars.

1. Introduction

Although represented in the recent fauna by the Southeast Asian and Indian mole-shrew *Anourosorex*, the peculiar and highly specialized tribe Anourosoricini was much more common and diverse during the Late Neogene in Europe, Asia and North America (van Dam, 2004). Recent advances in molecular phylogeny suggest a split of Anourosoricini from the Nectogalini-Notiosoricini clade, just after the onset of the radiation of the earliest Soricinae into three clades (Dubey et al., 2007):

- Anourosoricini-Nectogalini-Notiosoricini;
- Soricini;
- Blarinini/Blarinelli.

This result is largely consistent with the fossil record. The estimated origin of the Anourosoricini can be dated at 17-18 Ma combining molecular phylogenetics with data on fossil Soricidae (van Dam, 2010). Until now, the oldest Anourosoricini fossils are at least 13 Myr old (Anwil, North Alpine Foreland Basin, Switzerland; Engesser, 1972; van Dam, 2004).

Rare shrew specimens excavated from the almost contemporary late Middle Miocene German locality Giggenhausen (Bavaria, Germany) share some morphological features with Anourosoricines, but actually belong to a different clade of shrews, the Allosoricinae. The parallel evolution towards carnivore-like dentitions in Anourosoricini and Allosoricinae will be discussed in the light of the rich *Crusafontina* material (Anourosoricini) from the German locality Hammerschmiede.

2. Fossil localities

2.1. Giggenhausen

The locality is situated 1 km north of Giggenhausen, 7 km south-west of Freising (Bavaria: N48.3655, E11.6482), and described in Fahlbusch (1964: p. 109) and Böhme and Ilg (2003). It is no longer accessible. Mammals and vertebrates have been reported by Black (1966), Fahlbusch (1964, 1975), Mayr (1979), de Bruijn et al. (1993), Böhme (2003), Eronen and Rössner (2007), and Prieto (2007, 2010, 2012). The floodplain deposits from

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0016-6995/$ – see front matter © 2012 Elsevier Masson SAS. All rights reserved.
http://dx.doi.org/10.1016/j.geobios.2012.03.001

Giggenhausen belong to the upper series of the Upper Freshwater Molasse of the North Alpine Foreland Basin.

The fauna is biostratigraphically correlated to the Assemblage Zone of Anwil (*sensu* Kälin et al., 2001) or *Deperetomys hagni* taxon range zone (*sensu* Kälin and Kempf, 2009; ~13.8-~13.2 Myr), corresponding to MN7-8. The fauna lacks *Megacricetodon germanicus* (for taphonomic or biostratigraphic reasons), a species which belongs to a lineage characterized by molar size increase that has been used for relative age estimation (Kälin et al., 2001; Prieto and Rummel, 2009a). Nevertheless, the fauna can be reasonably dated because it is biochronologically close to that of the rich Swiss locality Anwil (Engesser, 1972; Prieto, 2007), the age of which is estimated 13.3 Ma (Kälin and Kempf, 2009).

2.2. Hammerschmiede

The localities are situated 300 m west of Hammerschmiede, 6 km north of Kaufbeuren (Bavaria: N47.9258, E11.080; Fahlbusch and Mayr, 1975; Böhme and Ilg, 2003). Layer 3 is accessible. See for Hammerschmiede 1: Mayr and Fahlbusch (1975); and for Hammerschmiede 1 and 3: Prieto and Rummel (2009b). Mammal fossils have been described by Fahlbusch (1975), Fahlbusch and Mayr (1975), Mayr and Fahlbusch (1975), Mayr (1979), Bolliger (1996), Kretzoi and Fejfar (2005), Prieto and Rummel (2009b), van Dam (2010), Prieto et al. (2011), and Prieto (2012). Fluviatil freshwater molluscs were recently reported by Schneider and Prieto (2011).

Based on the presence of *Microtocricetus molassicus*, the locality Hammerschmiede is traditionally correlated to the base of the Late Miocene (MN9). This correlation is challenged on the basis of the evolutionary grade of the rodent *Collimys*, which is primitive with regard to the Sarmatian (Middle Miocene) species from Hungary (Prieto and Rummel, 2009b; Prieto et al., 2010: 432). Furthermore, Prieto et al. (2011) propose that Hammerschmiede, which includes the re-appearance of *Galerix* cf. *exilis*, should be contemporaneous or pre-dates the last occurrence of the gymnure in Spain (Nombrevilla 2, Zone G3, Middle Miocene, 11.7 Ma; Garcés et al., 2003). Therefore, the age of Hammerschmiede can only be approximated as "Middle to Late Miocene boundary".

2.3. Hillenloh

This locality is situated 2 km south of Markt Rettenbach (Bavaria: N47.94, E10.00; Schaefer and Berlinger, 1954; Prieto and Rummel, 2009b; Böhme and Ilg, 2003) and not accessible anymore. Small mammals have been described by Bolliger (1996), Prieto and Rummel (2009b), and Prieto (2012).

Based on the evolutionary stage of *Collimys dobosi*, Hillenloh can be assumed to be slightly younger than Hammerschmiede (Prieto and Rummel, 2009b). Like Hammerschmiede, correlation and absolute dating of the locality are difficult, and it cannot be assessed whether the locality has a Middle or Late Miocene age.

3. Methods

The measurements and dental terminologies are presented in van Dam (2004). The specimens are stored in the *Bayerische Staatssammlung für Paläontologie und Geologie* in Munich (abbreviated BSPG) under the reference numbers 1980 XXVIII (Hammerschmiede 3), 1973 XIX (Hammerschmiede 1), and 1952 XIV (Giggenhausen). SEM and digital photos have been made at the Biogeology and Applied Paleontology laboratory and the Terrestrial Palaeoclimatology work group of the Eberhard Karls University in Tübingen, respectively.

Abbreviations: L: length; LL: lingual length; BL: buccal length; W: width; AW: anterior width; PW: posterior width; H: height; LT: talon length; PE: length to posterior emargination (not to be confused with PE-index); sd: standard deviation.

4. Systematic paleontology

Order SORICOMORPHA Gregory, 1910
Family SORICIDAE Fischer, 1814
Subfamily SORICINAE Fischer, 1814
Tribe ANOUROSORICINI Anderson, 1879
Genus **Crusafontina** Gibert, 1975

Type species: *Crusafontina endemica* Gibert, 1975.

Other species: *Crusafontina exculta* (Mayr and Fahlbusch, 1975), *C. kormosi* (Bachmayer and Wilson, 1970) (see comments on *Amblycoptus vicinus* Kretzoi, 1954 in Mészáros, 1998: p. 149), *C. magna* (Hutchison and Bown, 1980), *C. minima* (Hutchison and Bown, 1980), *C. fastigata* van Dam, 2004, *C. vandeweerdi* van Dam, 2004.

Emended diagnosis: see van Dam (2004).

Crusafontina exculta (Mayr and Fahlbusch, 1975)
Figs. 1 and 2

Material and measurements: Ham1 and Ham3: see Table 1 (the material includes new fossils and the specimens described by van Dam, 2010, which, in turn, includes a large part of the specimens described by Mayr and Fahlbusch, 1975 - part of the latter material is lost). Hillenloh: 2 fragmentary I1, 1 P4 (W: 1.73, PE: 1.31), 2 M2 (LL: 1.21, PE: 0.99; LL: 1.25, PE: 1.04), 1 fragmentary i1, 1 m2 (1.60 × 0.98), 1 m3 (1.38 × 0.84).

Type locality: Hammerschmiede 1 (Germany), referred to as Hammerschmiede in previous publications.

Age: not precisely known, but considered to be Middle to Late Miocene transition.

Emended diagnosis (van Dam, 2010): small-sized Anourosoricini. Anterior broadening of buccal cingulum of I1 less than in *C. endemica*. Buccal cingulum without cusp. A1 shorter, with paracone less robust and less extending posteriorly than in *C. endemica*. Protocone of P4 protruding from the anterior border instead of being situated in a more anterolingual position at the meeting point of the straight lingual and anterior borders, as in *C. endemica*. Length/width ratio in M1 and M2 smaller than in *C. endemica*. Posterior emargination weaker, not showing a sharp angle, as in *C. endemica*. M1 with small parastyle. Tendency for uninterrupted surrounding crest on M3, in contrast to the crest in *C. endemica*, which is posteriorly interrupted thereby tending to form a small hypocone. Lower first antemolar (a1) slightly asymmetric bucco-lingually, but without strong posteriorly extending wing as in *C. endemica*. All three lower molars differing from *C. endemica* in the direction of the oblique crests, being truly oblique and not sub-parallel to entoconid crests. Trigonids of m1 and m2 less stretched longitudinally compared to other *Crusafontina* species.

Description: for a detailed description of the original material from Hammerschmiede 1, see Mayr and Fahlbusch (1975) and van Dam (2010). In the following, only new characters observed in the Hammerschmiede (1 and 3) and Hillenloh samples are described.

Mandible: the mental foramen is positioned somewhat half the height of the mandible under the buccal emargination on the crown of the m1. The mandibular foramen is situated underneath the round internal temporal fossa. The pterygoid fossa is deep and triangular. The condyle shows a lingual emargination. The interarticular area is relatively narrow, and the condyle is L-shaped in distal view.

The lower incisor has two distinct cuspules on its dorsal edge, the anterior one being projected relatively buccally. A narrow cingulid is present on the bucco-dorsal part of the enamel. The lingual furrow extends to about the middle of the root. Two a1