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Heissigia bolligeri gen. et sp. nov.: a new enigmatic dormouse (Gliridae, Rodentia) from the Miocene of the Northern Alpine Foreland Basin.

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With 4 figures and 1 table

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Abstract: We describe a new genus and species (*Heissigia bolligeri* gen. et sp. nov.) with a highly unusual dental pattern from the early Middle Miocene (middle MN5) of the locality Affalterbach (Germany, Bavaria). This taxon is also present in the late Early Miocene (MN4) of Switzerland (Tägernaustrasse-Jona). The phylogenetic relationships of this new taxon are discussed. According to the present state of knowledge an immigration of *Heissigia* in MN4 from unknown origins is assumed.

Key words: Northern Alpine Foreland Basin, Germany, Rodentia, Gliridae, Glirinae , Miocene.

1. Introduction

The Northern Alpine Foreland Basin (NAFB) extends along the Alpine front from Lake Geneva in the west to the eastern termination of the Alps in Austria. With more than 200 Miocene vertebrate localities (Böhme & Ilg 2003) the basin contains one of the richest Miocene records for Gliridae.

The fossil locality Affalterbach is located in the northern part of the NAFB (Figure 1) southeast of the Landshut-Neuötting fault. The sand pit producing the fossils is situated 800 m northwest from the church of the village Affalterbach. Medium-sized gravels probably belonging to the early part of the upper "Nördliche Vollschotter" (see Abdul-Aziz et al. 2007: Fig. 2) crop out between 435 and 440 meters above sea level. These gravels are overlaid by four meters of homogenous marls, containing the fossil horizon, which are topped by a thin gravely sand followed by a lacustrine marl (Heissig, personal communication).

The biochronologic age of Affalterbach, established on the basis of the evolutionary stage of large-sized *Megacricetodon* aff. *bavaricus* (Heissig 1990: Fig. 5), corresponds to the top of the local biostratigraphic unit C+D (middle part of the European mammal unit MN5, Heissig 1997, 2006, Böhme et al. 2001, Abdul Aziz et al. 2007). Therefore, Affalterbach is younger than the localities of Puttenhausen and Sandelzhausen, but older than Mohrenhausen and the reference locality of MN5 Pontlevoy-Thenay, which both contain the more evolved *M. lappi*. According to the bio-magnetostratigraphic results of Abdul-Aziz et al. (2007) an absolute age of ~16 Ma could be suggested for Affalterbach, which is near the base of the Middle Miocene.

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Fig. 1. Geographic map of southern Germany showing the position of the Affalterbach locality.

In addition to the new taxon described in this paper, the dormouse fauna of Affaltenbach contain six species of Gliridae (Table 1) from evolutionary stages corresponding well to populations described from Puttenhausen and Sandelzhausen (Mayr 1979; Wu 1990).

The Affalterbach material, including all specimens described in this report, is stored in the Bavarian State Collection for Palaeontology and Geology in Munich (reference number: BSP 1987-XX). All measurements are given in mm, and nomenclature of the cheek teeth follow Freudenthal & Martín-Suárez (2006). All teeth in the figures are show in the left orientation.

2. Systematic palaeontology

Rodentia Bowdich, 1821
Gliridae Thomas, 1897
Glirinae Thomas, 1897

Heissigia gen. nov.

Etymology: In honour of Kurt Heissig for his 65th birthday and his intensive work on mammal palaeontology in the Bavarian part of the Molasse Basin.

Diagnosis: Same as for the type species.

Type species: *Heissigia bolligeri* gen. et sp. nov.

Differential diagnosise: *Heissigia* nov. gen. differs from all other Glirinae (sensu Daams & de Bruijn 1995) in having the combination of the following characters: I) mesially-convex meta-, centro-and mesolophid on the m/1 and m/2, II) mesolophid and posterolophid are connected

Table 1. Gliridae from Affalterbach.

Miodyromys aff. *aegercii* (Baudelot, 1972)

Glirulus diremptus (Mayr, 1979)

Microdyromys cf. *complicatus* de Bruijn, 1966

Prodryomys satus Mayr, 1979

cf. *Bransatoglis* sp.

Muscardinus cf. *sansaniensis* (Lartet, 1851)

Heissigia bolligeri gen. et sp. nov.

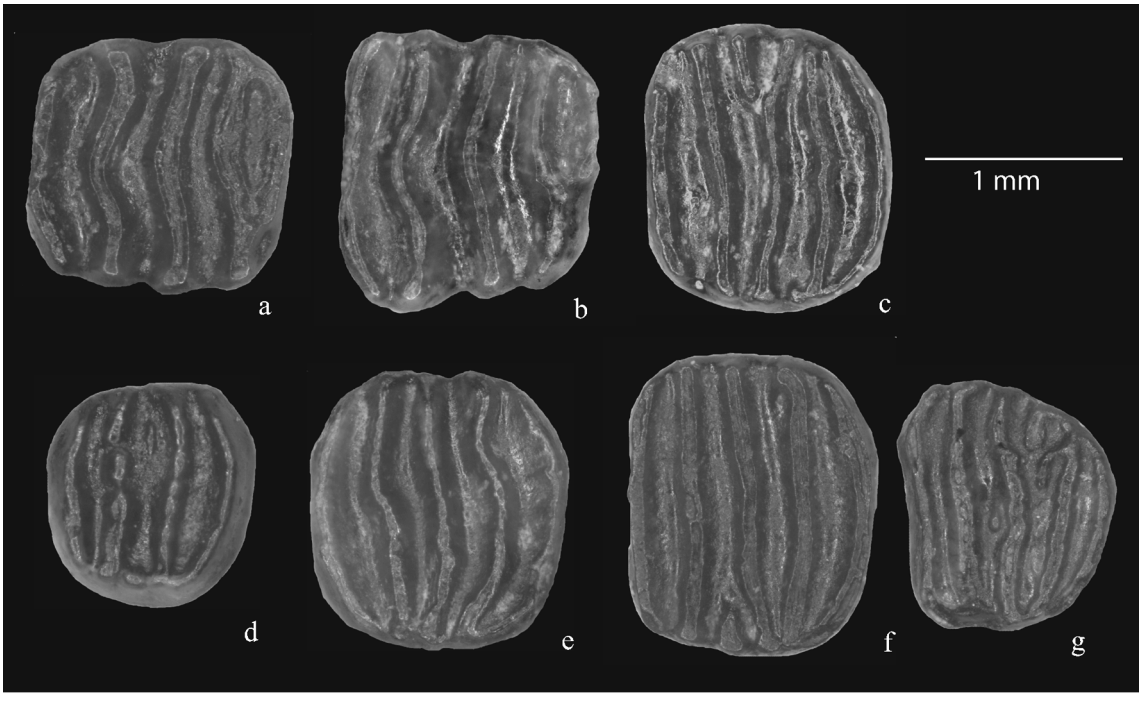


Fig. 2. *Heissigia bolligeri* gen. et sp. nov. from Affalterbach. All teeth in occlusal view. **a.** Holotype, right m/1 (invers., BSP 1987-XX-1). **b.** Right m/2 (invers., BSP 1987-XX-2). **c.** Left M2/ (BSP 1987-XX-8). **d.** Right P4/ (invers., BSP 1987-XX-4). **e.** Left M1/ (BSP 1987-XX-5). **f.** Right M2/ (invers., BSP 1987-XX-6). **g.** Right M3/ (invers., BSP 1987-XX-10).

before the lingual and labial borders on the first two lower molars, III) a reduced morphology of molars with all main crests perpendicular to the longitudinal axe, and IV) rounded M1/ and M2/.

Heissigia bolligeri gen. et sp. nov..
Fig. 2 a-g

1992 Gliridae gen. et spec. indet. – Bolliger, p. 129, fig. 63 (NMB TÄ 13-20).

Etymology: In honour to Thomas Bolliger who first described teeth of this new taxon.

Holotype: Right lower first molar (BSP 1987-XX-1), Fig. 2 a; measurement: 1.35 x 1.28.

Paratypes: (BSP 1987-XX-2 to 10): 1 left and 1 right m/2 (damaged; 1.28 x 1.40), right P4/ (1.03 x 1.07), link M1/ (1.26 x 1.40), 2 right and 2 left M2/ (1.22 x 1.50; 1,21 x 1.42; ~1.14 x ~1.37; damaged), right M3/ (1.05 x ~1.25).

Type locality: Affalterbach (coordinates 11.5333 E, 48.5667 N), 4.5 km north of Pfaffenhofen an der Ilm (Bavaria).

Type horizon: Early Middle Miocene, MN5 (top of OSM C+D).

Diagnosis: Simple Glirinae with an absolute flat occlusal surface, and (with exception of M3/) crests perpendicular to the longitudinal axis; m/1 and m/2 with five main crests, mesially-convex meta-, centro-and mesolophid, and connections of mesolophid and posterolophid before the lingual and labial borders of the molars; rounded M1/ with five complete transversal crests; M2/ with five complete tranversal crests and a reduced lingual or labial pre-or postcentroloph.

Description of the holotype: Antero-, meta- and centrolophid isolated on lingual and labial sides; short posterolophid connected to mesolophid before lingual and labial borders of tooth; meta-, centro- and mesolophid mesially-convex, perpendicularly directed to the longitudinal axis; valleys become deeper on lingual side; number of roots unknown.

Description of the paratypes: m/2: General organisation of crests do not differ from m/1; anterior side enlarged; anterior and posterior valleys less deep than two others valleys; two roots.

P4/: Four main crests and one isolated, centrally placed, small crest; distally-convex posteroloph; anteroloph separated from endoloph; three roots.

M1/: Rounded outline; five crests that trend to connect on lingual side; arched antero-, and posteroloph; mesially-convex metaloph; posteroloph and metaloph lingually

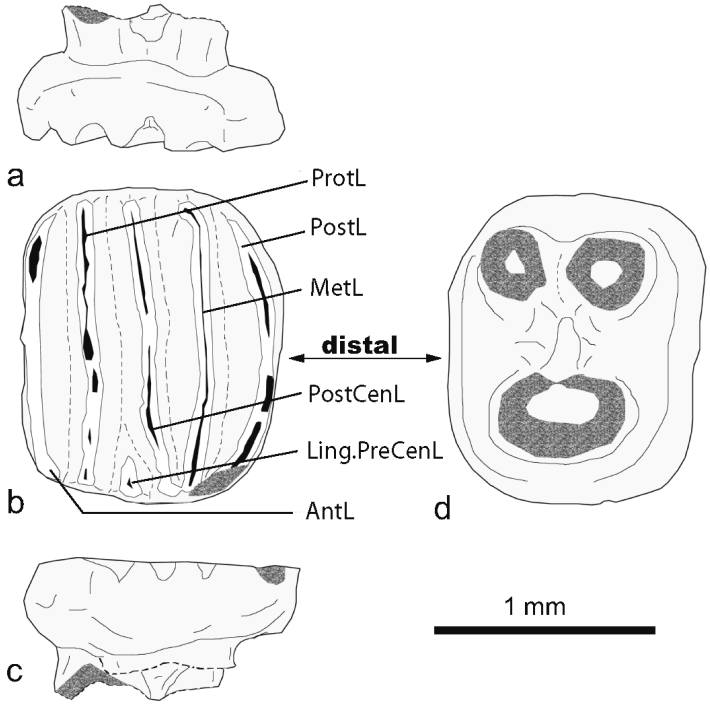


Fig. 3. Orientation and nomenclature of the M2/ (invers., BSP 1987-XX-6) of *Heissigia bolligeri* gen. et sp. nov. from Affalterbach. **a.** Lingual view. **b.** Occlusal view. **c.** Labial view. **d.** View from roots. AntL: anteroloph; Ling.PreCenL: lingual precentroloph; MetL: metaloph; ProtL: protoloph; PostCenL: postcentroloph; PostL: posteroloph.

connected; all valleys of same deep; number of roots unknown.

M2/: Rounded outline, though less rounded than in M1/; five complete crests and a reduced centroloph; reduced labial postcentroloph on two teeth, with a trend to connect the precentroloph, forming an Y-like structure; complet postcentroloph and reduced precentroloph on the two other specimens, on one molar lingual, on other labial; posteroloph and metaloph lingually connected; both root-bearing teeth show three roots.

M3/: In addition to the five complete crests, reduced labial postcentroloph and two small extra crests between protoloph and precentroloph and between postcentroloph and metaloph; damaged lingual border but highly probable connection of the crests; number of roots not observable.

Discussion: The flat occlusal surface of the teeth, in addition to the indistinct main cusp(ide)s places *Heissigia bolligeri* near to the subfamily Glirinae. However, the derived morphology of the species makes the orientation of the molars difficult, and therefore the proposed determination of the crests has to be discussed.

Orientation of the upper molars. – On the M2/, an arched crest surrounds a broad syncline, whereas on the other tooth side the molars are margined by a straight crest. Regarding the M3/, where mesio-distal orientation is evident due to the reduced posterior part of the teeth, the arched crest of the M2/ is interpreted as posteroloph and the straight one as anteroloph. As this morphology is unusual when compared to the other species of Gliridae, where the anteroloph is usually arched and the posteroloph is straight, additional morphologic characteristics are still needed to confirm our interpretations. The comparison of the contact surfaces between the upper molars agrees with this proposal, as on the M2/ this surface is clearly better developed on the straight crest, confirming its relationship with the M1/. This orientation is also indicated by the labial roots, where the anterior one is usually forward-directed by the Gliridae. Roots are very useful in determinating the labial and lingual borders of the molars, as there are two roots on the labial side and only a single broad root on the lingual side. Regarding the well preserved M2/ with roots (BSP 1987-XX-6), the reduced crest is found on the lingual border (Fig. 3), which is unusual as such reduced crests are normally labial. Even more surprising is the fact that this crest is found on the second M2/ specimen with preserved roots (BSP 1987-XX-7) on the labial border, therefore this crest can not be used to determinate the orientation of the other unrooted M2/. However, the orientation of teeth lacking preserved roots could be determined by the lingual connection of the meta- and posteroloph as well as the morphology of the teeth in lateral view as the crown is higher on the lingual border and the synclinals are less deep (Fig. 3a, c). The orientations of the M1/ and M3/ were deduced using these features.

Nomenclature of the upper and lower molars (Fig. 3). – We assume that all crests represent main cusp(ide)s and, regarding the general morphology of the Gliridae, the central crest of the upper molars is interpreted as centroloph. On the M1/ the central crest represents a midcentroloph, whereas on the M2/ two centrolophs are

developed, which we describe using the terms pre- and postcentroloph. In addition, the lingual or labial position of the reduced centroloph have to be specified, so that for reduced centrolophs of *Heissigia* a lingual and labial position for both pre- and postcentrolophs is possible. Since this characteristic is unusual in Gliridae we can not exclude the possibility, due to our limited material, that the M2/ with lingual centroloph represent an aberrant morphotype. On the lower molars (Fig. 4, a1) the distal crest is interpreted as reduced posterolophid. An alternative interpretation is discussed below (paragraph phylogenetic relationships).

Additional evidence of *Heissigia* in the fossil record. – It was BOLLIGER (1992: fig. 63, Gliride indet. 2, NMB TÄ 17-19) who first described five teeth, from Tägernaustrasse-Jona (Switzerland), belonging to the new taxon. The p/4 (NMB TÄ 20), unknown in Affalterbach, with four crests perpendicular to the longitudinal axis corresponds well to the general morphology of other specimens of *Heissigia.* The biostratigraphy of Tägernaustrasse-Jona, based on the presence of *Megacricetodon* aff. *collongensis* and *Ligerimys florancei*, points to a MN4 age (KÄLIN 1997; REICHENBACHER et al. 2005), which is in agreement with the Bavarian local biostratigraphic unit A, that is significantly older than Affalterbach.

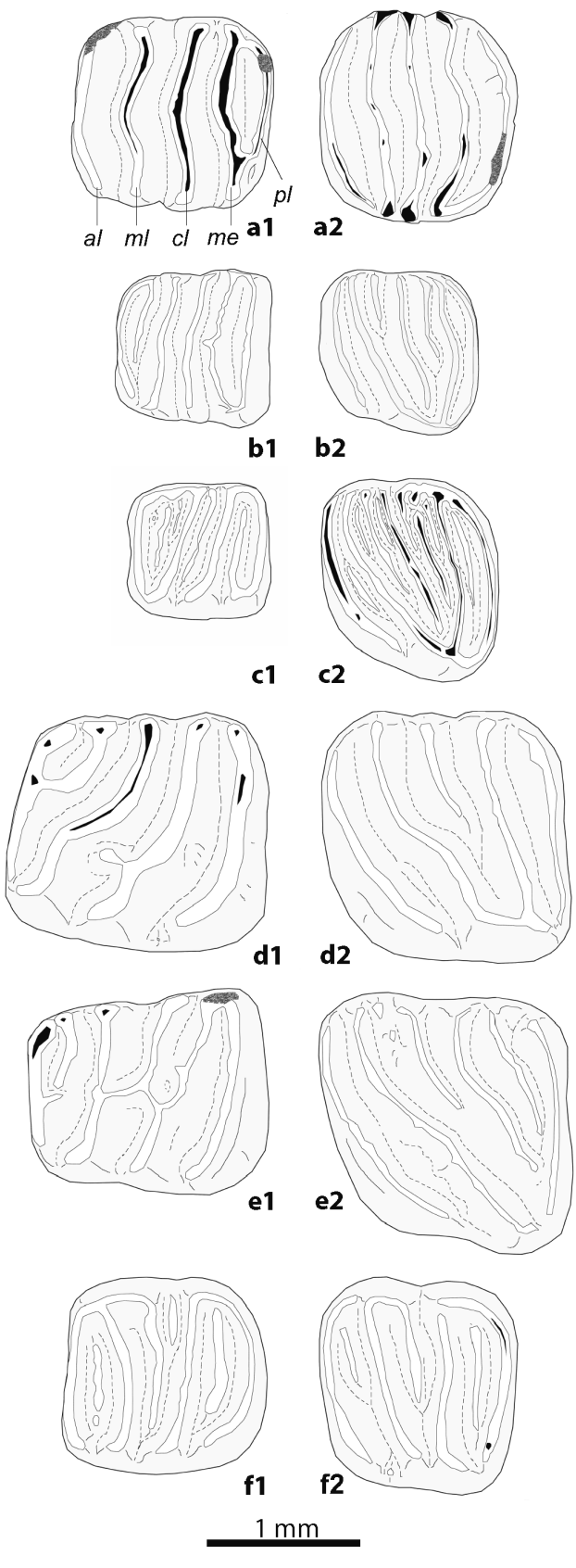
3. Systematic position and phylogenetic relationships

The evolutionary centre of the family Gliridae is, based on the palaeontologic evidence, Western Eurasia (DAAMS 1999) and the European fossil record of this group is remarkably rich. However, the derived morphology of *Heissigia* makes its phylogenetic interpretation very speculative. Moreover, this is not the only case within fossil Glirinae that a group with unusual dental pattern appears suddenly in the fossil record without showing close relationships to contemporaneous taxa (DAAMS & DE BRUIJN 1995). To identify the phylogenetic relationship of *Heissigia* we compare the new taxon with members of the subfamily Glirinae.

Comparison with *Glis* BRISSON, 1762 (Fig. 4f). – The only morphologic feature connecting *Heissigia* with *Glis* are the more or less perpendicular crests in respect to the longitudinal axis, making the possibility of *Glis* as being an ancestor unlikely. The genus *Glis* has a long history in Western Eurasia since its First Occurrence (FO) in the Middle Oligocene of Turkey (ÜNAY 1989). However, in Germany the genus is a rare element before MN9 with the only reported incidence coming from the fissure filling Weißenburg 6 (earliest Miocene, MN 1, MAYR 1979).

Comparison with the *Myoglis* BAUDELOT, 1965 – *Heteromyoxus* DEHM, 1950 group (Fig. 4d, 4e). – *Heteromyoxus* (stratigraphic range MN3-MN4, DAAMS & DE BRUIJN 1995) is traditionally interpreted as a descendant of *Myoglis* (FO Lower Miocene, AGUILAR 1974), and these two genera can be distinguished by the presence of first longitudinal crests on the lower molars. The morphology of the antero-and posteroloph(id)s of these genera show some similarities with *Heissigia.* Furthermore, a highly reduced crest can be present on the distal wall of the posterolophid of the m/1 and m/2 of *Myoglis* and *Heteromyoxus,* leading one to hypothesise that the distal crest of the first two lower molars of *Heissigia* is an extra ridge, and for this reason we distinguish between the crests using the terms antero-, meta-, meso- and posterolophid and distal extra ridge. However, this proposal is morphologically not supported by the mesially-convex fourth crest of *Heissigia,* which is hardly comparable to a posterolophid. In addition, if a phylogenetic relationship between these genera is proposed, *Heissigia* would not be predicted to be an ancestor of *Myoglis* due to its derived morphology. However, the seemingly unlikely possibility that these genera have a common ancestor cannot at present be excluded.

Comparison with the *Glirudinus* DE BRUIJN, 1966 – *Muscardinus* KAUP, 1829 group (Fig. 4b, 4c). – Based on the morphology of the dental crests and the outline of the teeth the genus *Muscardinus* shows by far the closest affinities to *Heissigia,* providing the hypothesis of the origin of *Heissigia* from a primitive *Muscardinus* stock. The oldest representative of *Muscardinus* is believed to come from the Spanish locality of Valdemoros 3E (DAAMS 1985), which is recently dated to 14.53 Ma (VAN DAM et al. 2006). However, in the NAFB this genus is present in the middle part of MN5 in Vermes 1 (ENGESSER et al.1981) and Puttenhausen classic (WU 1990), the latter correlate to the later part of chron C5Cr around ~16.8 Ma (ABDUL-AZIZ et al. 2007). Even earlier occurrences are indicated by a few teeth from localities of Schönenberg and Eitensheim (MAYR 1979), which both belonging to an early MN5. The presence of *M.* cf. *sansaniensis* in the fissure filling Petersbuch 2 (MN4) is interpreted by WU (1993: 47) as a mixed element. The genus is also recorded in the French fissure filling Blanquatère 1 biostratigraphically correlate with the transition from MN4 to



MN 5 (Aguilar & Lazzari 2006). The highly diversified glirid fauna from this locality (16 species) is comparable to Petersbuch 2 (19 species) and the rare specimens of *Muscardinus* in Blanquatère could possibly also be interpreted as mixed elements. Therefore, at the present state of knowledge, the oldest unequivocal records of *Muscardinus* are younger than the first occurrence of *Heissigia* in Tägernaustrasse. Since *Muscardinus* is a descendant of the genus *Glirudinus* (Daams & de Bruijn 1995; Wu 1993), the descent of *Heissigia* from this latter genus is at least possible, although very speculative. Interestingly though, recent findings of *Glirudinus* from the French Quercy (Itardies, MP 23) do document a long evolutionary history of the genus (Vianey-Liaud 2003).

4. Conclusions

The highly derived dental morphology of *Heissigia* nov. gen. makes its phylogenetic relationships difficult to interpret. While the most morphologically related Glirinae, *Muscardinus,* has a similar FO (early MN 5 or MN 4/5) to *Heissigia* (MN 4) allowing the speculation that both taxa share a common ancestor, the sudden appearance of this new taxon does point to the possibility of an evolutionary advance outside of the well studied European basins. Therefore, at the present state of knowledge an immigration of *Heissigia* in the NAFB in MN4 is assumed. The high specialisation of the new genus is supported by its derived dental morphology and the rare occurrence in fossil assemblages of the NAFB.

Fig. 4. The first lower and upper molars of Glirinae (sensu Daams & de Bruijn 1995). [The genus *Stertomys* Daams & Freudenthal, 1985 was recently removed from the Glirinae (Freudenthal & Martín-Suárez 2006)]. 1: m/1; 2: M1/. **a.** *Heissigia bolligeri* gen. et sp. nov. from Affalterbach (a1: invers., BSP 1987-XX-1; a2: BSP 1987-XX-5). **b.** *Muscardinus* aff. *sansaniensis* (Lartet, 1851) from Kleineisenbach (b1: invers., BSP 1972-XVI-1159; b2: BSP 1972-XVI-1160). **c.** *Glirudinus undosus* Mayr, 1979 from Petersbuch 2 (c1: invers., BSP 1976-XXII-1297; c2: BSP 1976-XXII-1223). **d.** *Myoglis antecedens* Mayr, 1979 from Petersbuch 2 (d1: invers., BSP 1976-XXII-5804; d2: BSP 1976-XXII-5796). **e.** *Heteromyoxus schlosseri* Dehm, 1950 from Petersbuch 2 (e1: BSP 1980-XXXII-3122; e2: BSP 1980-XXXII-3110). **f.** *Glis apertus* Mayr, 1979 from Weißenburg 6 (f1: BSP 1961-XII-689; f2: BSP 1961-XII-683). al. anterolophid, ml. metalophid, cl. centrolophid, me. mesolophid, pl. posterolophid.

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