

The Genus *Eomyops* Engesser, 1979 (Rodentia, Eomyidae) from the youngest deposits of the German part of the North Alpine Foreland Basin

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Abstract The study of extinct Eomyid rodents represents an important segment of Burkart Engesser's scientific work. To pay tribute to Burkart's work, this paper presents remains of *Eomyops* Engesser, 1979 from the German *Jüngere Serie* localities Kleineisenbach, Giggenhausen, Markt, Hammerschmiede and Hillenloh. Two *Eomyops* species are recorded, i.e. *E. oppligeri* Engesser, 1990 and *E. catalaunicus* (Hartenberger, 1966). A third form, only found at the locality Markt, is retained in open nomenclature. In spite of the richness of the studied material, the time gap separating the individual localities does not allow to assess precisely the relationships between the species recorded.

Keywords Mammal · Eomyidae · Rodent · Miocene · Biostratigraphy · Bavaria

Introduction

Among the wide spectrum of mammalian groups studied by Burkart Engesser (1990) during his scientific career, Eomyid rodents play a particularly important role. One out of many examples for his impressive scientific achievements is his monograph on the Eomyidae from the Swiss part of

the North Alpine Foreland Basin (abbreviated NAFB). After more than two decades, it is still regarded as one of the most important references for the group. Moreover, Engesser (1972, 1979, 1990, 1999) has shown the high potential of the family with regard to biostratigraphy and palaeoecology (Storch et al. 1996). In the context of this special volume, a note on this peculiar extinct family is presented.

Samples of *Eomyops* from several German localities exposing the *Jüngere Serie* (sensu Dehm 1951, 1955) of the NAFB are presented in order to assess the evolution of the genus close to the Middle – Late Miocene transition.

The localities

Giggenhausen (Gig)

Fossils were excavated along a road cutting through a forest in the vicinity of the village of Giggenhausen, 12 km south-west of Freising (see details in Fahlbusch 1964, p. 96). The vertebrate fauna is mainly composed of small mammals and ectothermic tetrapods (Fahlbusch 1964, 1973, 1975; Mayr 1979, Bolliger 1999; Böhme 2003; Böhme and Ilg 2003; Prieto 2007, 2010), but also contains some rare large mammals (Eronen and Rössner 2007); freshwater crabs also have been discovered (Klaus and Prieto, in preparation).

The locality correlates to MN 8 (Middle Miocene) because of its faunal composition that is very similar to that of Anwil (Fahlbusch 1964; Prieto 2007).

Kleineisenbach (KI)

The fauna comes from a closed-down sand/marl pit located near the village of Kleineisenbach, 12 km south-west of

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Freising (see details in Fahlbusch 1975, p. 65), quite close to Giggerhausen. The vertebrate assemblage is dominated by small mammals and ectothermic tetrapods (Black 1966; Mayr 1979; Böhme 2003; Böhme and Ilg 2003; de Bruijn et al. 1993; Prieto 2007, 2010). Large mammals are very rare (Eronen and Rössner 2007). Freshwater crabs have been reported (Klaus and Gross 2010). The fauna differs only in minor details from that of the Giggerhausen and Anwil localities (Prieto 2007).

Markt

The small fauna from Markt (a small town approximately 23 km east of Mühldorf am Inn) represents one of the oldest reported small mammal faunas from the German part of the NAFB (Grimm 1957, around 5 m above the *Südllichen Vollschoeters/Munderfinger Schotter*, see lithologic details therein). Traditionally considered to belong to MN9 because of the presence of *Microtocricetus molasicus*, the vertebrate locality contains small mammals (Black 1966; Fahlbusch 1964, 1973, 1975; Fahlbusch and Mayr 1975) and rare fish remains (Böhme and Ilg 2003). Markt has traditionally been considered older than Hammerschmiede.

Hammerschmiede (Ham)

Hammerschmiede deposits (NNW of Kaufbeuren, see Mayr and Fahlbusch (1975) for details) are widely known for their rich fossil content, dominated by small mammals, ectothermic tetrapods and fishes (Mayr and Fahlbusch 1975; Fahlbusch and Mayr 1975; Mayr 1979; Schleich 1985; Bolliger 1999; Hugueney 1999; Böhme 2003; Böhme and Ilg 2003; Prieto and Rummel 2009; Klembara et al. 2010; Prieto et al. 2011), as well as a rich mollusc fauna (Schneider and Prieto 2011). Large mammals, most of which are remains of carnivores, have sporadically been reported (Mayr and Fahlbusch 1975; Eronen and Rössner 2007). Paleobotanical studies provide insights into the vegetational environment (Meyer 1956; Jung and Mayr 1980; Gregor 1982; Seitner 1987, 2004). The lowermost fossil layer Ham1 is the original layer from Hammerschmiede. A second layer (Ham2), situated above Ham 1 (H. Mayr pers. com. 2008), contains ectothermic tetrapods (Böhme and Ilg 2003), and also yielded small mammals, which are described in this paper for the first time (Böhme and Ilg 2003). Layer Ham 3 of Hammerschmiede is an erosional channel at the top of the sequence that provides a rich small mammal fauna. Most of the fossil bivalves were recently collected from the deposits at the base of a single fluvial channel, just below the top of the sequence that is correlated to Hammerschmiede 3.

Hillenloh (Hil)

The remains were excavated from a pit (now disappeared) near Markt Rettenbach, approximately 14 km west of Hammerschmiede. Bolliger (1999) reports *Anomalomys rudabanyensis* Kordos, 1989 from the locality. Prieto and Rummel (2009) have proposed that the fauna is slightly younger than Hammerschmiede based on the presence of the cricetid rodent *Collimys dobosi*.

Materials and methods

All specimens are deposited in the *Bayerische Staatssammlung für Paläontologie und Geologie* in Munich (BSPG; Hammerschmiede 1: BSPG 1973 XIX; Hammerschmiede 2: BSPG 1980 XXVII; Hammerschmiede 3: BSPG 1980 XXVIII; Hillenloh: BSP 1979 XVIII; Klein-eisenbach: BSP 1972 XVI). Measurements are given in millimeter. The terminology used in the description of molars follows Engesser (1990). SEM images were taken at the Biogeology and Applied Paleontology laboratory of the Eberhard Karls University in Tübingen. To make Figs. 1 and 2 easier to read, locality information is given directly in the figures. All illustrated teeth are shown in left orientation (right molars are reversed). The specimens are figured in occlusal view, some slightly revolved in order to access supplementary morphological information. Because of the uncertainties with regard to the discrimination between the two first upper and lower molars, I have decided not to distinguish them (M1/2 and m1/2).

While it is generally understood today that the MN zones 7 and 8 are in urgent need of regrouping (de Bruijn et al. 1992), some authors still reject this proposal. Under these lines the separation of the MN zones sensu Mein and Ginsburg (2002) is not followed, but MN 7 is defined as in Kálin and Kempf (2009). In their concept, MN 7 is defined by the presence of a *Megacricetodon gregarius*-like species, a taxon with a very a limited stratigraphic range in the NAFB.

Systematic palaeontology

Order: Rodentia Bowdich, 1821

Family: Eomyidae Depéret and Douxami, 1902

Genus: *Eomyops* Engesser, 1979

Diagnosis: Engesser 1979, and see comments in Engesser 1990.

Eomyops and *Leptodontomys* differ principally in mandible and incisor characteristics. Thus the validity of the genera as proposed by Engesser (1979, 1990, 1999) was, and is, not generally followed (e.g. Fahlbusch et al. 1983;

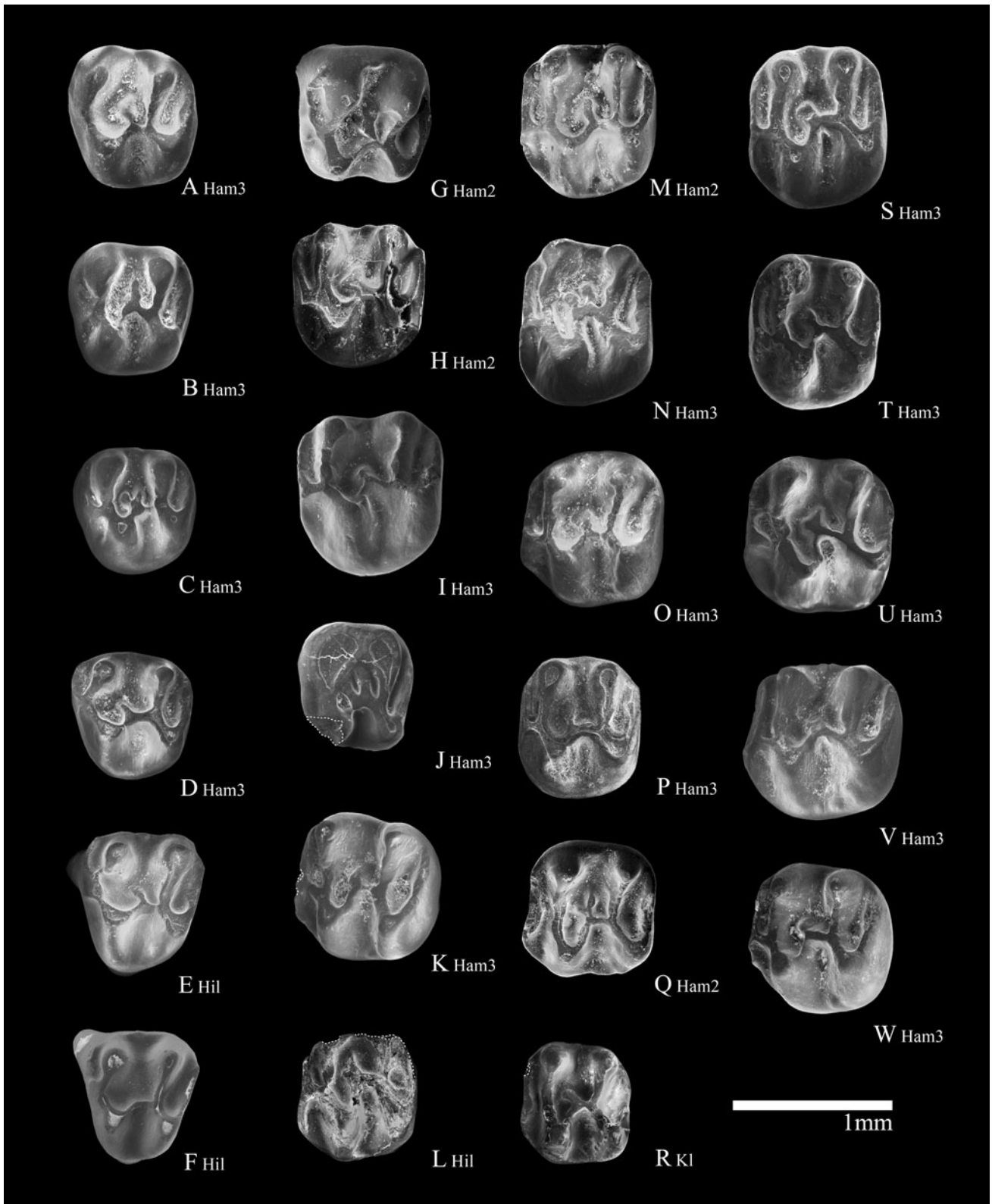


Fig. 1 Upper dentition of *Eomyops catalaunicus* (Hartenberger, 1966) from Hammerschmiede (*Ham*) and Hillenloh (*Hil*), and *E. oppligeri* Engesser, 1990 from Kleineisenbach (*KI*). **a–c** P4, **d–f** D4,

g–w M1,2. Reversed teeth: **a, k, m, p, u** and **w**. *Ham*2 BSPG 1980 XXVII 8–11, *Ham*3 BSPG 1980 XXVIII 328–342, *Hil* BSP 1979 XVIII 89–91, *KI* BSPG 1972 XVI 1765)

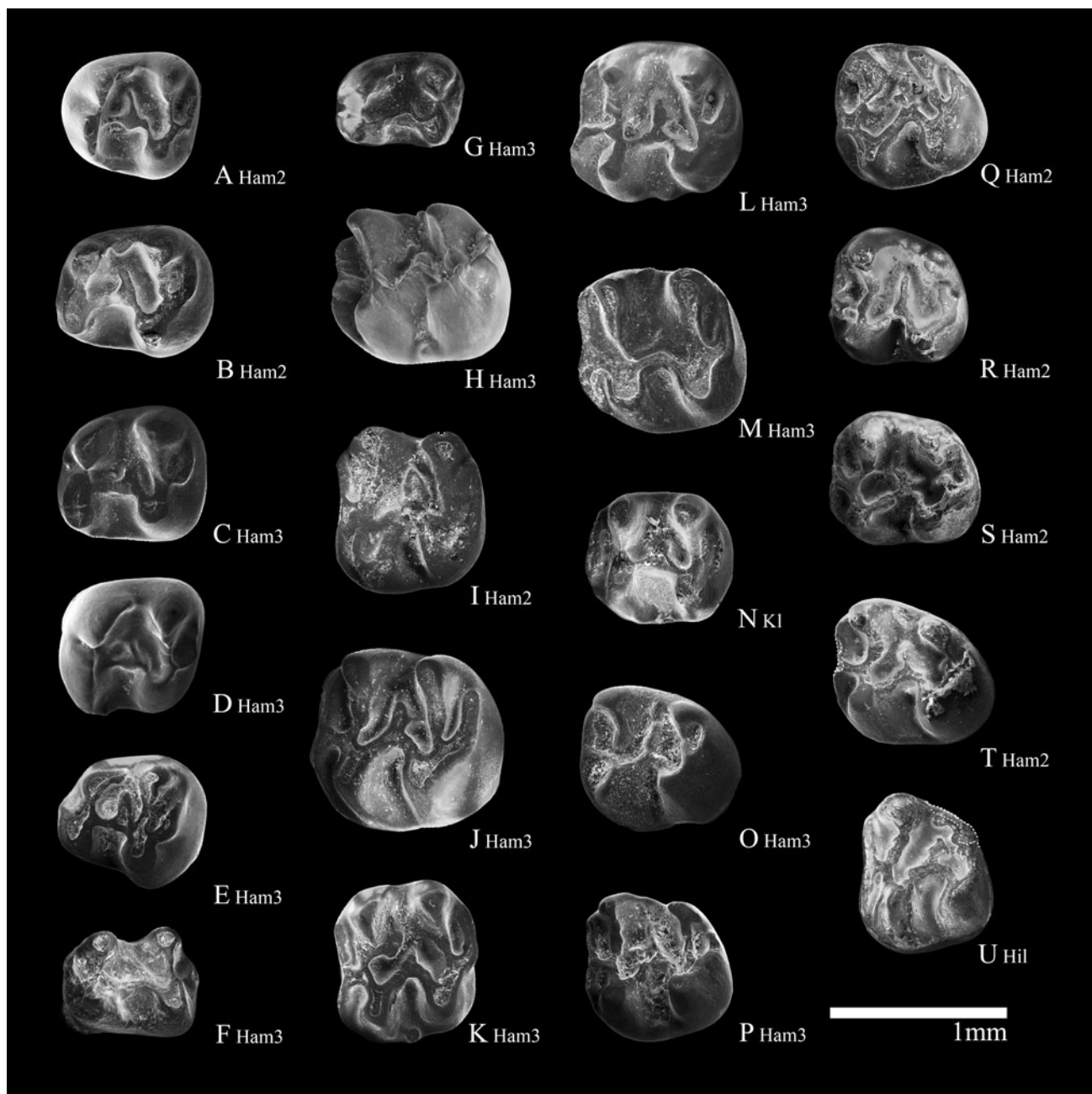


Fig. 2 Lower dentition of *Eomyops catalaunicus* (Hartenberger, 1966) from Hammerschmiede (*Ham*) and Hillenloh (*Hil*), and *E. oppligeri* Engesser, 1990 from Kleineisenbach (*Kl*). **a–e** p4,

f and g d4, **h–n** m1,2; **o–u** m3. Reversed teeth: **b, d, h, l, n, q, r, t** and **u**. *Ham*2 BSPG 1980 XXVII 1–7, *Ham*3 BSPG 1980 XXVIII 316–327, *Hil* BSP 1979 XVIII 88, *Kl* BSPG 1972 XVI 1764)

Qiu 1994). Based on isolated teeth, the generic assignment of specimens is very difficult, and the dental characters emphasized by Engesser (1979) do not provide solid evidence to separate the two genera (Qiu 1994). Furthermore, the differences observed in the incisor enamel surface are obvious, and de Bruijn et al. (2012) do not accept the separation of the genera based on this characteristic.

Because neither mandible nor assignable incisors were found in either of the studied localities, assignment of the

specimens to *Eomyops* remains tentative, and it seems equally well possible that they belong to *Leptodontomys*, but also *Plesieomys*, *Heteroeomys* and *Pentabuneomys* of which the morphology is also similar.

Apart from the type species, the following species are traditionally recognized as *Eomyops* (all European): *E. bodvanus* (Janossy, 1972), *E. oppligeri* Engesser, 1990, *E. hebeiseni* Kälin, 1997, *E. noelinae* Ruiz-Sánchez, Calatayud and Freudenthal, 2009. On the other hand, North

American species are usually assigned to the genus *Leptodontomys*. Following the proposal of Korth (1994) based on the synonymies of Korth and Bailey (1992), besides *L. oregonensis* Shotwell (1956, type species) and *L. quartzii* Shotwell (1967), *L. russeli* Storer 1970, 1975 and *L. stirtoni* Lindsay 1972 belong to this genus and extend the stratigraphic range of *Leptodontomys* into the Oligocene.

Several Asian species are intermediate (Qiu 1994): *Leptodontomys gansus* Zheng and Li, 1982, *L. lii* Qiu, 1996, *L. pusillus* Qiu, 2006. While Qiu (1994) does not recognize the *Leptodontomys/Eomyops* separation for the Asian species based on dental morphology as stated by Engesser (1979), he nevertheless agrees in that important differences are found in the lower jaw and incisor morphology. Based on the in-between morphology of the mandible of *L. gansus* he assigns the Chinese specimens to *Leptodontomys*.

Qiu (2006) also introduces the new monospecific eomyid genera *Plesieomys* and *Heteroeomys* for fossils from the Late Miocene of the Yunnan Province in China. *Plesieomys* differs from both *Eomyops* and *Leptodontomys* “in the larger dimension (except *E. hebeiseni*); having an enlarged end of the mesoloph on upper molars; and a much less distinct lingual anteroloph of M1 and m2”. With regard to size, however, *P. mirabilis* does not differ from various *Eomyops* records from the upper Miocene of Austria (Daxner-Höck and Höck 2009, see Fig. 3). The enlargement of the mesoloph is a weak argument for a discrimination of the Chinese form from *Eomyops*, as *E. noelinae* also shows a division/enlargement at the end of the crest (Ruiz-Sánchez et al. 2009). This feature is also recognizable in our material (see below in “*E. catalaunicus*”). Similarly, the reduction of the lingual anteroloph is variable in the European *Eomyops* species. *Heteroeomys* is also defined based on dental characteristics that are subject to variability, and thus do not provide a sound basis to the definition of a separate genus.

Pentabuneomys is a monospecific genus established based on eomyid teeth from vieux-Collonges; the genus is a rare element of the faunas from the North Alpine Foreland Basin (Engesser 1990). It differs from *Eomyops* in dental characters only.

It is beyond the scope of this paper to draw conclusions on the generic assignment of all these species. In the following we follow the traditional taxonomy, although we agree with de Bruijn et al. (2012) in that the Eurasian eomyids are presently oversplit.

Species: *Eomyops oppligeri* Engesser, 1990 (Figs. 1r, 2n)

1973 *Leptodontomys* sp. [Giggenhausen]. Fahlbusch: Plate 9, Figs. 11–15.

1975 *Leptodontomys* aff. *catalaunicus* (Hartenberger, 1967). Fahlbusch: p. 75, Figs. 4a–f.

1990 *Eomyops oppligeri*. Engesser, p. 122.

1997 *Eomyops* sp. [Giggenhausen]. Kälin, Fig. 2

2007 *Eomyops oppligeri* Engesser, 1990. Prieto (unpublished): p. 53, Fig. 20A.

Diagnosis: Engesser 1990.

Type locality: Anwil, Switzerland, Middle Miocene.

Material and measurements:

Kleineisenbach: 2 isolated teeth (BSPG 1972 XVI 1764 and 1765): 1 M1/2 (0.75 × 0.82); 1 m1/2 (0.80 × 0.82)

Giggenhausen: see Fahlbusch 1975.

Description:

For the material from Giggenhausen, we refer to Fahlbusch 1975.

Kleineisenbach:

m1/2: The tooth has an isolated anterolophid; the metalophid is transverse, connecting both metaconid and protoconid on their lingual and labial walls; the short mesolophid is directed backwards; the posterolophid is isolated on the posterior part of the molars; three roots.

M1/2: The anteroloph is isolated from the protoloph; the mesoloph is strongly inclined in forward direction, reaching the base of the curved protoloph somewhere near its centre.

Species: *Eomyops catalaunicus* (Hartenberger, 1966) (Figs. 1, 2)

1975 *Leptodontomys catalaunicus* (Hartenberger, 1967). Fahlbusch: pp. 69–73, Figs. 2 and 3.

1997 *Eomyops* sp. [Hammerschmiede]. Kälin, Fig. 2

2007 *Eomyops* aff. *catalaunicus*. Prieto (unpublished), pp. 53–54.

Diagnosis: Hartenberger 1966

Type locality: Can Llobateres (Spain, Vallès Penedès, early Vallesian, Late Miocene).

Material:

Hammerschmiede 1: Specimens published by Fahlbusch (1975) and additional material, all together 99 isolated teeth: 11 D4, 7 P4, 28 M1/2, 5 M3, 5 d4, 11 p4, 24 m1/2, 8 m3.

Hammerschmiede 2: 13 isolated teeth: 1 P4, 5 M1/2, 2 p4, 1 m1/2, 4 m3 (BSPG 1980 XXVII 1–13).

Hammerschmiede 3: 33 isolated teeth: 1 D4, 4 P4, 11 M1/2, 2 d4, 6 p4, 5 m1/2, 3 m3 and 1 undeterminable tooth (BSPG 1980 XXVIII 316–348).

Hillenloh: 5 isolated teeth: 2 D4, 1 M1/2, 1 m3, 1 tooth fragment (BSP 1979 XVIII 88–92).

Measurements: see Table 1 and Fig. 3.

Table 1 Sample statistics of *Eomyops catalaunicus* (Hartenberger, 1966) molars from Hammerschmiede and Hillenloh

	D4						M1/2						M3															
	Length			Width			Length			Width			Length			Width												
	n	Min	Mean	Max	Min	Mean	Max	n	min	Mean	Max	Min	Mean	Max	n	Min	Mean	Max										
Ham1	11	0.70	0.76	0.82	0.77	0.83	0.90	7	0.79	0.82	0.85	0.82	0.88	0.92	25	0.77	0.86	0.94	1.07	4	0.70	0.73	0.79	0.80	0.85	0.88		
Ham2								1		0.83			0.92		5	0.80	0.84	0.90	0.94				0.95					
Ham3	1	0.79		0.83		0.83	0.80	3	0.78	0.80	0.83	0.80	0.87	0.91	10	0.85	0.89	0.95	0.98				0.98			1.04		
Hil	2	0.75	0.88	0.88		0.90																						
	d4						m1/2						m3															
	Length			Width			Length			Width			Length			Width												
	n	Min	Mean	Max	Min	Mean	Max	n	Min	Mean	Max	Min	Mean	Max	n	Min	Mean	Max										
Ham1	5	0.79	0.84	0.88	0.57	0.63	0.68	11	0.76	0.83	0.89	0.70	0.75	0.81	22	0.82	0.92	1.00	0.89	0.95	1.00	0.81	0.84	0.89	0.80	0.83	0.86	
Ham2								2	0.80		0.87	0.75		0.78	1		0.85						0.82	0.86	0.90	0.78	0.82	0.86
Ham3	2	0.83		0.83	0.53		0.65	4	0.83	0.89	0.96	0.78	0.82	0.85	5	0.90	0.98	1.01	0.85	0.96	1.11	0.84	0.89	0.89	0.83	0.88		
Hil																												0.89

Fig. 3 Scatter diagram of the *Eomyops* molars from Germany, and comparison with the tooth length of selected Eurasian samples. The data from Nebelbergweg (*Eomyops* aff. *catalaunicus* and *E.* aff. *oppligeri*) come from Kálin and Engesser (2001); the Felsőtárkány sections (*E. oppligeri*) from Hír (2003, 2006) and Hír and Kókay (2009, 2010); Mátrazólós (*E. oppligeri*) from Gál et al. (2000) and Hír and Kókay (2004); Tauț (*E. oppligeri*) from Hír et al. (2011); Rudabánya (*E. catalaunicus*) from Daxner-Höck (2005); Giggenhausen (*E. oppligeri*) and Can Llobateres (*E. catalaunicus*) from Fahlbusch (1975); Anwil (*E. oppligeri*) from Engesser (1972); Austrian records (*Eomyops catalaunicus*) from Daxner-Höck and Höck (2009); Tunggur (*Leptodontomys lii*) from Qiu (1996); Lufeng and Yuanmou (*Plesieomys mirabilis*, *Heteroeomys yunnannensis*, *L. pusillus*) from Qiu (2006); Morteral-20A (*Eomyops noeliae*) from Ruiz-Sánchez et al. (2009); Osztramos 1 (*E. bodvanus*) from Jánossy (1972); Chatzloch (*E. hebeiseni*) from Kálin (1997); Borský Sv. Jur (*Eomyops catalaunicus*) from Joniak (2005); *Pentabuneomys rhodanicus*, compiled data from France, Germany and Switzerland (Huguency and Mein 1968; Fahlbusch 1970; Engesser 1990)

Description:

Part of the Ham1 material is described in Fahlbusch (1975), and thus we restrict our description to the variability in the molars from Ham1–3 and Hil.

D4: (Ham1: 11 teeth; Ham3: 1; Hil: 2).

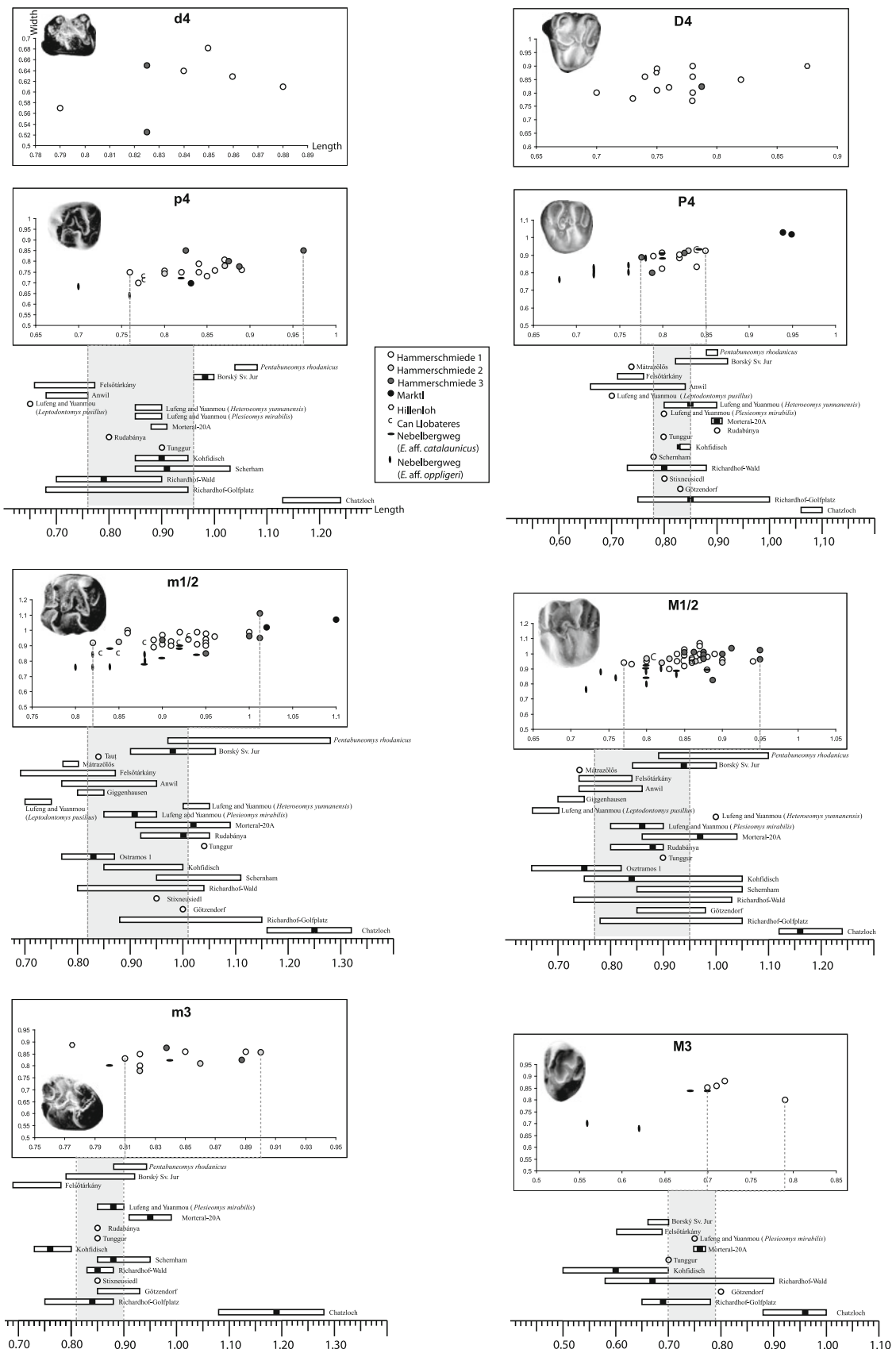
The most variable morphological feature is the protoloph, which may either be present and connecting to the anteroloph (Ham1: 7 premolars, Ham3: 1, Hil: 2; Fig. 1d–f), or missing (Ham1: 4; see Fahlbusch 1975, Fig. 3a); the mesoloph is usually absent in Ham1 (7, Hil: 1; Fig. 1F), but may also be present (Ham1: 4, Ham3: 1, Hil: 1; Fig. 1d, E); if present, it is directed forwards; a cingulum always closes the central syncline labially.

P4: (Ham1: 7 teeth; Ham2: 1; Ham3: 3)

The anteroloph may be present and interrupted (Ham1: 2 molars, Ham2: 1, Ham3: 1; e.g.), reduced to vague enamel thickenings positioned on the front of the tooth (Ham1: 4, Ham3: 1; see Fahlbusch 1975, Fig. 3d) or missing (Ham1: 1); the mesoloph is curved but transverse (Ham1: 1, Ham2: 1; see Fahlbusch 1975, Fig. 3e), simply transverse (Ham1: 3, Ham3: 1; Fig. 2b), directed forwards (Ham1: 2), bifurcate (Ham3: 2; Fig. 1c); the central labial syncline is open (Ham1: 5, Ham3: 1; Fig. 1b) or closed by a style or cingulum (Ham1: 2, Ham2: 1, Ham3: 2; Fig. 1c).

M1/2: (Ham1: 24 teeth; Ham2: 4; Ham3: 11)

The anteroloph is rarely isolated from the protoloph (Ham1: 3 teeth, Ham2: 1, Ham3: 1; e.g. Fig. 1q); several teeth tend to the development of a double anteroloph–protoloph connection (Ham1: 1), or clearly display this double connection (Ham1: 1; see Fahlbusch 1975, Fig. 3i); the mesoloph is most often directed forwards (Ham1: 10, Ham3: 5; e.g. Fig. 1t); depending on the wear of the molars the mesoloph may be bifurcate (Ham1: 4, Ham2: 2, Ham3: 2; e.g. Fig. 1u) or labially enlarged (Ham1: 5, Ham3: 2); one molar from Ham1 has a transversal mesoloph with a clear enlargement that tends to reach the protoloph; the



crest may also be transversal (Ham1: 4, Ham2: 2; Ham3: 1; see Fahlbusch 1975, Fig. 3j); one M1/2 from Ham1 and one from Ham3 have a double mesoloph (Fig. 1n); the central labial syncline is usually closed by a cingulum or style, but it may also be open (Ham1: 5); the latter is especially well recognizable in Ham3 (7; e.g. Fig. 1t).

M3: (Ham1: 5 teeth)

The anteroloph is isolated in only one specimen (see Fahlbusch 1975, Fig. 3m); the mesoloph is most often interrupted (4 M3), but may also be complete; one specimen has a short crest developed backwards, posteriorly of the protocone (Fahlbusch 1975, Fig. 3m).

d4: (Ham1: 5 teeth, Ham3: 2)

The overall morphology of the milk teeth is not very variable in Ham1; the anterolophid may be isolated in the front of the d4, or well developed and connected to the protoconid; the two specimens from Ham3 differ from Ham 1 in the presence of a narrow, medium-sized and forwardly directed mesolophid; this structure may also be present in Ham1, but is extremely reduced (Fahlbusch 1975, Fig. 2b). The anterolophid is missing in one d4 from the layer Ham 3 (Fig. 2g).

p4: (Ham1: 10 teeth; Ham2: 2; Ham3: 4)

The majority of teeth do not have anterolophids (Ham1: 6; Ham2: 2, Ham3: 2), but a thickening of the enamel on the anterior part of the p4 may be present (Ham1: 3, Ham3: 1); the crest is rarely well developed (Ham1: 1, Ham 3: 2; Fig. 2e); the mesolophid may be extremely short (Ham1: 2; see Fahlbusch 1975, Fig. 2e), but is often short and directed forwards (Ham1: 5; see Fahlbusch 1975, Fig. 2d) or transverse (Ham3: 2; Fig. 2c), medium-sized and transverse (Ham1: 3) or directed forwards (Ham2: 2, Ham3: 1; Fig. 2a, b, e); the mesolophid is complete on one tooth from Ham3; the longitudinal crest is usually interrupted, but a low and narrow connection may be present at the base of the protoconid, or the crest is continuous (Fig. 2e); a stylid might close the main labial syncline (Fig. 2b).

m1/2: (Ham1: 21 teeth; Ham2: 1; Ham3: 5)

The anterolophid is rarely isolated (one molar from Ham1); the lingual anterolophid is missing in one specimen from Ham1, usually variable in development, either shorter than the labial anterolophid or about the same length; the mesolophid is most often directed forwardly in Ham1 (13, against 3 transverse), it is transverse in the single tooth from Ham2 (Fig. 2i, senil tooth) and in 4 molars from Ham3 (e.g. Fig. 2l); it is rarely almost absent (Ham1 1; Ham3: 1; e.g. see Fahlbusch 1975, Fig. 2j, and herein Fig. 2m); the main lingual syncline is most often open (Ham1: 18; Ham3: 2; e.g. Fig. 1j), but may also be closed by a cingulid or stylid (e.g. Fig. 2i); a stylid may be present in the labial syncline (Ham1: 7, Ham3: 3 teeth; Fig. 2m).

m3: (Ham1: 7 teeth, Ham2: 4, Ham3: 3, Hil: 1)

The mesolophid is either medium-sized (transverse or directed forwards, Ham1: 5; Ham2: 3; e.g. Fig. 2t), or somewhat longer (Ham2: 1, Ham3: 1; e.g. Fig. 2o), isolated (Ham1: 1; see Fahlbusch 1975, Fig. 2l), bifurcate (Ham1: 1, Ham3: 2; e.g. Fig. 2p), or tends to be double (see Fahlbusch 1975, Fig. 2l and herein Fig. 2q); the entoconid may be isolated, the hypolophid being present but interrupted (Ham1: 1; Ham2: 1; see Fahlbusch 1975, Fig. 2m), or the hypolophid is completely missing, and a crest connects the longitudinal crest to the posterolophid (Ham1: 1; see Fahlbusch 1975, Fig. 2n); in one m3 from Ham 2 the posterolophid is missing (Fig. 2r); the hypolophid is single and complete in 3 molars from Ham1, 1 from Ham2, 3 from Ham3 (e.g. Fig. 2o); it may also be double, the two branches connecting to the posterolophid and longitudinal crest (Ham1: 1; see Fahlbusch 1975, Fig. 2l); the anterior connection may be interrupted (Ham1: 1, Ham2: 1; Fig. 2r); a stylid may be present in the lingual syncline (Ham1: 2).

The single m3 from Hil (Fig. 2u) is labialo-posteriorly slightly damaged; it differs from the corresponding teeth from Ham especially in being relatively shorter; the crests are somewhat stronger, and the lingual syncline transversally longer; the broad mesolophid is directed backwards; the posterolophid is missing, and the entoconid connects to the stylid that closes the labial syncline.

Discussion

The co-occurrence of two *Eomyops* species has been reported from the locality Nebelbergweg (Kälin and Engesser 2001). In this locality, *E. aff. catalaunicus* and *E. aff. oppligeri* differ from each other principally in the relative size of their premolars and M3. In Hammerschmiede, we see no evidence of a taxonomical mixture of the *Eomyops* tooth sample. The late Miocene *Eomyops* record from Austria shows that the intraspecific variability is large for this genus (Daxner-Höck and Höck 2009, and Figs. 1–3). Daxner-Höck and Höck (2009) recognized also in their *E. catalaunicus* samples several morphological features that otherwise are commonly attributed to *E. oppligeri*. As a result, the presence of two species in Nebelbergweg is questionable, or, inversely, the homogeneity of the Austrian sample might be not correct. The size differences between the two species from Nebelbergweg are quite weak. Thus, I presently tend to consider all before-cited samples as homogeneous and referable to *E. catalaunicus*. Following this assumption, we recognize the problem that the German teeth are generally distinctly larger than the teeth from Nebelbergweg. Indeed, the size variability in *E. catalaunicus* is large (Fig. 3). Considering this fact, it is proposed that both Hammerschmiede and Nebelbergweg contain only *E. catalaunicus* fossils. The size differences

may be due to differences in the environmental context, and may be indicative of a high morphological plasticity in *Eomyops catalaunicus*.

The originality of the m3 from Hillenloh is considered as not sufficient not to assign the whole tooth sample to *Eomyops catalaunicus*.

Species: *Eomyops* sp.

1973 *Leptodontomys* sp. [Marktl]. Fahlbusch: Plate 9, pp. 16–19.

1975 *Leptodontomys* n. sp. 1. Fahlbusch: p. 75, Figs. 4g–j.

1997 *Eomyops* sp. [Marktl]. Kälin: Fig. 2

Occurrence: Marktl

Material, measurements and description: see Fahlbusch (1975): 6 isolated teeth (BSPG 1952 X 66, 75, 129–132).

Discussion

Fahlbusch (1975) considered the species from Marktl to be new because of its larger size, but refrained from naming it. Although clearly larger than most of the specimens assigned to *Eomyops/Leptodontomys*, the teeth belong to the variation domain of the Austrian samples referred to *E. catalaunicus* by Daxner-Höck and Höck (2009, and Fig. 3), and are smaller than *E. hebeiseni*. Morphologically the teeth look somewhat more robust. As noticed by Fahlbusch, the lack of sufficient material does not allow confident conclusion. Interesting is the find of a large-sized *Eomyops*—listed as new—species in Bełchatów A by Garapich (2002), a locality biostratigraphically close to Hammerschmiede because of the presence of *Collimys* (see biostratigraphic comments in Prieto and Rummel 2009, reviewed by Prieto et al. 2010, 2011).

Discussion

At least two *Eomyops* species are recorded in the *Jüngere Serie* of the German part of the NAFB. The third form, only found at the locality Marktl, is retained in open nomenclature because of the lack of sufficient material.

E. oppligeri occurs in the two stratigraphically and geographically close localities Kleineisenbach and Gigggenhausen. The faunas from these localities are taxonomically very similar to that from Anwil (Engesser 1972; Prieto 2007), which is the type locality of the species *E. oppligeri*. Apart from the localities addressed in this paper, *E. cf. oppligeri* is listed in Bolliger and Rummel (1994) from the German fissure filling Petersbuch 10. In western Europe the species occurs in La Grive (France), and perhaps also in Arroyo del Val and Manchones (Spain, Kälin

1997). The central/eastern European record is more extensive, and *E. oppligeri* has been recorded for Bełchatów A (Poland, Garapich 2002) and Vračevići (Serbia, Marković and Milivojević 2010), but neither detailed illustrations nor descriptions are available at present for this material. Kälin (1997) mentions the presence of the species in Devínska Nová Ves (Neudorf, Slovak Republic). *E. catalaunicus* has been described from Borský Sv. Jur and Pezinok (Slovakia, Joniak 2005). In Hungary and Romania, *E. oppligeri* is known from Mátrazölös (Gál et al. 2000; Hír and Kókay 2004), from the Felsőtárkány sections (Hír 2003; Hír and Kókay 2009, 2010) and from Tauț (Hír et al. 2011). The specimens are generally small (Fig. 3), but belong to the variation domain of the Austrian *E. catalaunicus* teeth described by Daxner-Höck and Höck (2009). This renders the specific assignment of these samples difficult. Concerning Mátrazölös, the form of the posterolophid, the direction of the mesolophid, and the isolation of the anterolophid in the m1/2 (Gál et al. 2000, Figs. 20 and 21) confirm the original assignment to *E. oppligeri*. For the other Hungarian and Romanian tooth samples, taxonomic uncertainties occur because of the lack of sufficient material.

We refer to the work of Daxner-Höck and Höck (2009) to characterize the intraspecific variation of *E. catalaunicus*, as the type sample (Can Llobateres, Spain, Hartenberger 1966) is much reduced. In western Europe the species has been recorded from diverse French localities, including Priay II (Welcomme et al. 1991), Soblay (Guérin and Mein 1971), Montredon (Aguilar 1982), Lissieu (*E. aff. catalaunicus*, Hugueney and Mein 1968), and Ambrieu 1 + 2 (Farjanel and Mein 1984). The species has also been recorded for the Mediterranean (Maramena, Greece, de Bruijn 1995). In central and eastern Europe, *E. catalaunicus* is listed as occurring in Petersbuch 14 (Germany, Bolliger and Rummel 1994) and Rudabánya (Hungary, Daxner-Höck 2005). A few questionable samples have been reported from Poland (Podlesice, Fahlbusch 1978) and the Czech Republic (Suchomasty, Fejfar 1989). The co-occurrence of two *Eomyops* species at Nebelbergweg (Switzerland, Kälin and Engesser 2001) has been discussed above.

The evolution of *Eomyops* at the transition Middle to Late Miocene in central Europe remains largely unresolved. *E. oppligeri* is well established in the NAFB in localities correlated to MN 8 (Anwil, Gigggenhausen, Kleineisenbach). An absolute dating for these localities is not possible at present, but age estimates at 13–13.5 Ma are quite conceivable. In Hungary the species is known in the late Badenian (Mátrazölös), and thus close in time to the NAFB localities.

While most of the *E. catalaunicus* samples are probably Late Miocene in age, earlier occurrences of the species at

the end of the Middle Miocene cannot be ruled out, as the original dating of Hammerschmiede, assigned to the Late Miocene, has recently been challenged (see discussion in Prieto et al. 2010, 2011), and might be older than traditionally believed. Unfortunately the time gap between the localities containing *E. oppligeri* and *E. catalaunicus* is too large to precisely understand the relations between the species, and thus to propose a more in-depth phylogenetic scenario. In addition, the large *Eomyops* sp. from Markt, because of the in-between biostratigraphic position of the locality, renders the interpretation of these fossils even more problematic.

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