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EOMYS HELVETICUS N. SP. AND *EOMYS SCHLUNEGGERI* N. SP., TWO NEW SMALL EOMYIDS OF THE CHATTIAN (MP 25/MP 26) SUBALPINE LOWER FRESHWATER MOLASSE OF SWITZERLAND

BURKART ENGESSER[1], DANIEL KÄLIN[2,*]

[1] Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel, Switzerland; e-mail: Burkart.Engesser@bs.ch.
[2] Kronenmattweg 3, CH-3315 Bätterkinden, Switzerland; e-mail: daniel.kaelin@swisstopo.ch.
*corresponding author

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Abstract: Two new small *Eomys* species of the Chattian Lower Freshwater Molasse of Central Switzerland are described. *Eomys helveticus* n. sp. and *Eomys schluneggeri* n. sp. from the localities Rigi 1 and Rigi 2 are characterized by their relatively small dimensions and the metalophid of the lower molars not being connected to the anterolophid. In addition, *E. schluneggeri* n. sp. shows some morphological similarity to the genus *Eomyodon* Engesser, 1987. The two new *Eomys* species have so far never been found in any of the numerous MP 25 and MP 26 localities in Central Europe. In both faunas Eomyidae and Gliridae were extremely frequent, whereas the Theridomyidae, usually the most frequent rodent family in the Late Oligocene, were very rare or absent. We interpret these peculiarities as being linked with the special ecological conditions, namely a relatively wet, forested environment.

Key words: Eomyidae, Rodentia, Mammalia, Swiss Molasse Basin, Palaeoecology

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Introduction

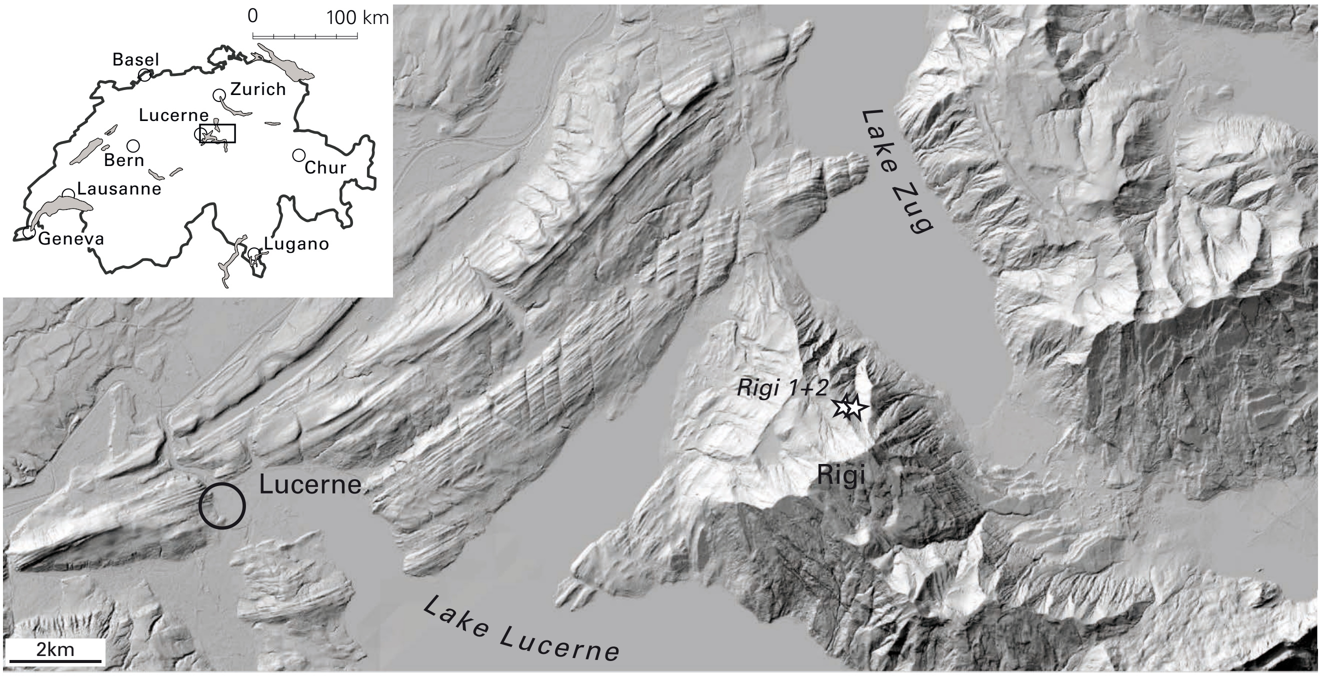
The Swiss Molasse Basin is a classical Foreland Basin and is well known for its detailed bio- and magnetostratigraphic framework established during the past two decades (e.g. Burbank et al. 1992, Schlunegger et al. 1996, Kempf et al. 1997, Strunk and Matter 2002). During the course of these projects many new mammal sites were discovered and large amounts of sediment have been screen-washed. Therefore, the record of fossil mammal groups has been greatly improved. Regarding the biostratigraphically important mammal group, the eomyids, and the time span of the Lower Freshwater Molasse (Rupelian − Aquitanian), all recorded eomyid species from that time have been monographically treated (Engesser 1990). Since then, numerous additional mammal sites have been discovered, but almost no new or additional eomyid species have been recorded.

Rigi is a famous observation mountain in Central Switzerland. Since this mountain consists mainly of Tertiary conglomerates, for a long time it was considered illogical to look for mammals in order to determine the age of these sediments. It was only in 1993 during field work for his thesis, that Dr. Fritz Schlunegger (Berne), discovered two new mammal sites on the northern flank of Mount Rigi (Text-fig. 1). Interestingly, both localities yielded a new eomyid species which are the subject of this paper.

Geological setting

The mammal bearing localities Rigi 1 and Rigi 2 are situated on the northern side of Rigi mountain in Central Switzerland, in a 3,600 m thick section made up of predominately alluvial conglomerates, sand- and siltstones (Text-fig. 1). Mount Rigi is part of a steeply south dipping tectonic slice of the Subalpine Molasse of Central Switzerland. The base of the Rigi section consists of marine sand- and siltstones (Grisigen marls and Horw sandstone, Lower Marine Molasse, UMM), followed by terrestrial sediments from the Rigi alluvial fan (Lower Freshwater Molasse, USM).

The localities Rigi 1 and Rigi 2 are lithostratigraphicaly very close, separated by approx. only 40 m of sediment. Rigi 2 is still accessible, situated directly on the western side of the



Text-fig. 1. Geographical setting. Topographic map (swissALTI^{3D}) showing the position of the Rigi localities (asterisks) in Central Switzerland.

Fischchrattenbach, a small brooklet running down from the steep slope north of Rigi Kulm. In contrast, locality Rigi 1 is not accessible anymore, it is hidden behind a retaining wall along the forest road leading to locality Rigi 2.

Rigi 2 is situated approx. 650 m above the base of the Weggis Formation, and approx. 450 m below the Radiolaritreiche Nagelfluh Member. According to Schlunegger (1995), the magnetostratigraphical age is around 28.5 Ma (Text-fig. 2).

Systematic description

Family Eomyidae Depéret et Douxami, 1902

Genus *Eomys* Schlosser, 1884

***Eomys helveticus* n. sp.**

Text-figs 3, 7a

Holotype. Left M_1 or M_2, inv. no. Rgi 3 (Text-figs 3b, 7a), Basel Museum of Natural History; Dimensions: 0.86 × 0.88 mm.

Derivatio nominis. *helveticus*, because the type locality, the so far only locality in which this species was found, is located in the centre of Switzerland.

Type locality. Rigi 1, coordinates 2679.270/1213.300, 1,020 m a.s.l. (Swiss national grid reference).

Stratum typicum. 2 cm black mudstone.

Age. Late Oligocene, assemblage zone of Bumbach 1 or Mümliswil-Hardberg, MP 25 or MP 26a. Note: In contrast to former papers (Engesser and Mayo 1987, Engesser and Mödden 1997), here we consider Mümliswil-Hardberg as being older than Oensingen.

Referred material. 16 isolated teeth. All specimens are deposited in the Basel Natural History Museum.

Diagnosis. Small species of *Eomys* with short mesoloph and short mesolophid. Anterolophid of lower molars unconnected or connected with the protoconid. Lower molars without labial anterolophid, upper molars without lingual anteroloph. 4th syncline of lower molars very short. M_3 without hypolophid and 4th syncline. Longitudinal crest (entoloph) of upper molars mostly interrupted.

Stratigraphic range. *Eomys helveticus* n. sp. is known so far only from the type locality.

Differential diagnosis.

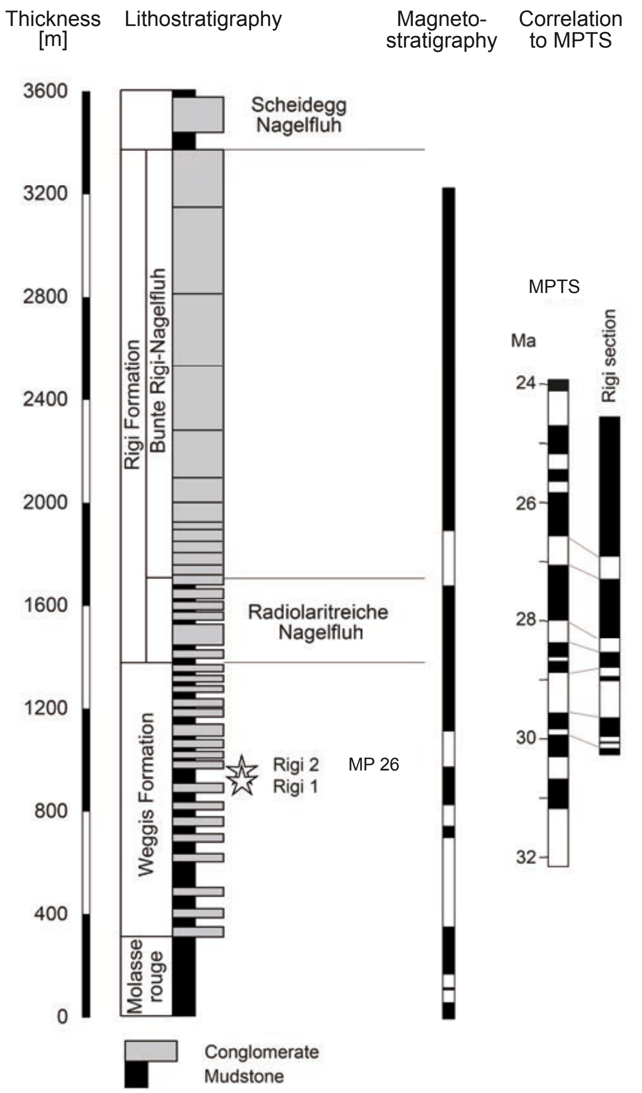
From *Eomys antiquus* (Aymard, 1853) *E. helveticus* n. sp. differs in:

- the absence of a labial anterolophid on the lower molars (present in 100% of M inf. of *E. antiquus* from Montalbán, in 79% from Möhren13 (Maridet et al. 2010));
- the mostly unconnected anterolophid (or only connected to the protoconid) on lower molars;
- the absence of a lingual anterolph on upper molars;
- the frequently interrupted longitudinal crest (entoloph) on M^1 and M^2.

From *Eomys minor* Comte et Vianey-Liaud, 1987 *E. helveticus* n. sp. differs in:

- larger dimensions;
- the presence of a mesolophid on lower molars;
- the longer 4th syncline on M_1 and M_2;
- the unconnected anterolophid of M_1 and M_2 (or only connected to the protoconid).

From all other species of *Eomys* (*E. molassicus* Engesser, 1987, *E. zitteli* Schlosser, 1884, *E. ebnatensis* Engesser, 1987, *E. major* Freudenberg, 1941, *E. quercyi* Comte et



Text-fig. 2. Lithostratigraphy and magnetostratigraphy of the Rigi section with correlation to the MPTS (Magnetostratigraphic Polarity Time Scale) according to Schlunegger (1995). Asterisk = mammal site.

Vianey-Liaud, 1987, *E. huerzeleri* Engesser, 1982, *E. gigas* Comte et Vianey-Liaud, 1987) *E. helveticus* n. sp. differs in:

- smaller dimensions;
- the anterolophid on the lower molars not connected to the metalophid;
- the absence of a labial anterolophid on the lower molars.

D e s c r i p t i o n o f t h e h o l o t y p e. This only slightly worn M_1 or M_2 (Text-fig. 3b) is a little wider than it is long. The anterolophid is not connected with the metalophid nor with the protoconid. The transversal metalophid is slightly backwards directed, connecting with the anterior arm of the protoconid. The mesolophid is short. The posterolophid is very short and therefore the 4^th^ syncline is also very short. The 2^nd^ and 3^rd^ synclines are very long, extending over the middle of the tooth width. The longitudinal crest (entolophid) is uninterrupted.

D e s c r i p t i o n o f t h e d e n t i t i o n. From the P_4 we have only a much worn specimen, showing almost no structure. In comparison with the molars this premolar is relatively large.

From M_1 and M_2 which cannot be distinguished with certainty, four specimens are available. The mesolophid is short. The anterolophid is not connected with the metalophid and with the protoconid only if the tooth is very worn down. The posterolophid is short and consequently the 4th syncline is also short. All lower molars have three roots.

The two M_3 specimens available are similar to M_1 and M_2 except that the posterior part is narrowed and that there is no trace of a hypolophid. The mesolophid is short and the anterolophid is only connected with the protoconid when there is an advanced stage of wear.

There are three specimens of P^4, one of them is very worn, and no details are visible. The two other specimens of P^4 differ greatly in size which is not unusual in eomyids. Both P^4 have no anteroloph. The longitudinal crest (entoloph) is distinctly interrupted in one specimen. The mesoloph is very short or completely absent .

The M^1 and M^2 also cannot be distinguished with certainly. There are five specimens available. Only in two extremely worn specimens is the entoloph not interrupted. The mesoloph in all specimens is short. The first syncline is short, not extending beyond the middle of the tooth width. The anteroloph and posteroloph are shorter than the metaloph and hypoloph and consequently only connected with the protocone and hypocone when in an advanced stage of wear.

An M^3, only present in one specimen, is almost round in occlusal view. It shows a very strong long anteroloph and a very long first syncline. The posterior part of the tooth is very much reduced, showing only the hypocone and a short posterolophid. A trace of the metacone is also discernible. The high paracone stands isolated, not connected with the protoloph in this stage of wear.

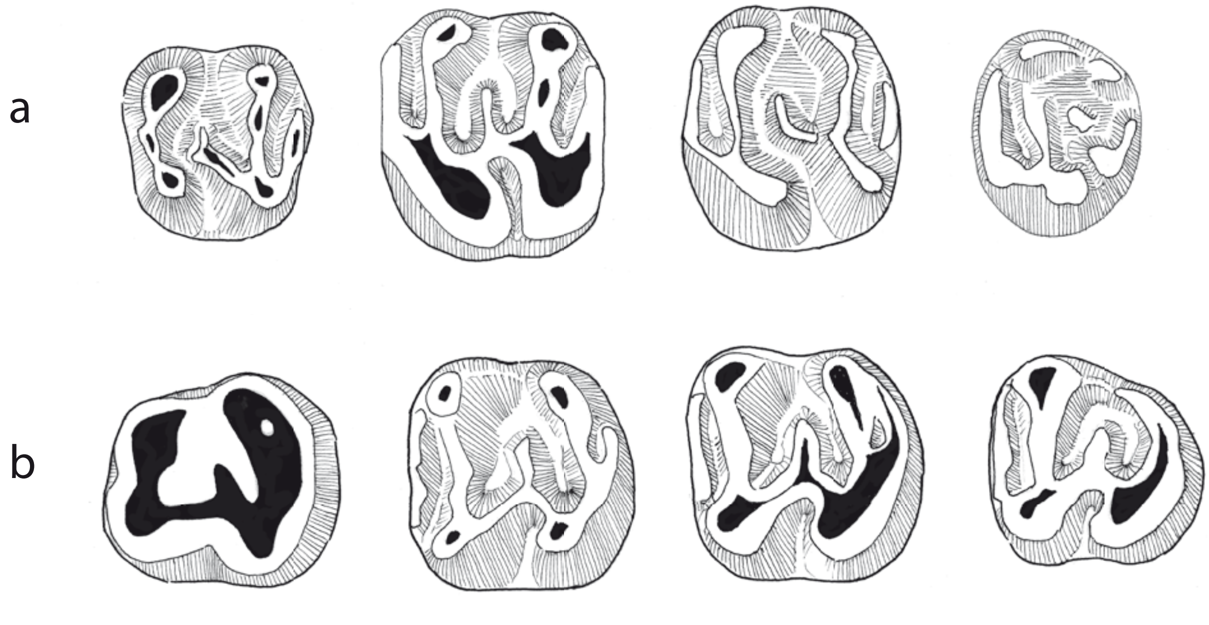
D i s c u s s i o n. *Eomys helveticus* n. sp. was so far only found in the Rigi 1 locality. Since there are a great number of localities of similar age in the Swiss Molasse (Text-fig. 10) and elsewhere in Europe, it is conspicuous that this species was never found so far in another locality. One reason could be that the ecology of Rigi 1, as far we can conclude from the poor material available, was very peculiar. This fauna, which is dominated by glirids and eomyids (see Tab. 1 or Text-fig. 11), and also containing a huge flying squirrel, was probably living in a pure forest biotope. Moreover it is most peculiar in the faunal composition of Rigi 1 that there is a complete absence of Theridomyidae and rarity of Cricetidae, usually the predominant elements of Late Oligocene faunas.

The age of the Rigi 1 fauna is not easily determined, since the characteristic elements for a specific age are lacking. What we know is that Rigi 1 is certainly somewhat older than Rigi 2, because in the geological section it is some 40 meters below Rigi 2. Since we classify the fauna of Rigi 2 with the Molasse mammal zone of Mümliswil-Hardberg (MP 26a, see below) or Oensingen 11 (MP 26b), that of Rigi 1 could be situated in the Bumbach 1 zone (MP 25b) or even an older zone.

Eomys schluneggeri n. sp.

Text-figs 4, 5, 7b

H o l o t y p e. M_1 dext., inv. no. Rgi 20 (Text-figs 4, 7b), Basel Natural History Museum; Dimensions: 1.01 × 0.98 mm.



Text-fig. 3. ***Eomys helveticus*** **n. sp. from Rigi 1. a) P^4 – M^3; P^4 sin.: Rgi 11, M^1 dext. (reversed): Rgi 14, M^2 dext. (reversed): Rgi 12, M^3 dext. (reversed): Rgi 17. b) P_4 – M_3; P_4 sin.: Rgi 2, $M_{1/2}$ sin.: Rgi 3 (holotype), $M_{1/2}$ sin.: Rgi 4, M_3 sin.: Rgi 7. All figures at magnification 35×.**

Derivatio nominis. This new species is dedicated to Prof. Dr. Fritz Schlunegger (Bern), who discovered the mammal localities Rigi 1 and Rigi 2 on a rainy foggy field day.

Type locality. Rigi 2, coordinates 2679.410/1213.240, 1,015 m a.s.l.

Stratum typicum. 20 cm of olive-greenish mud- or siltstone with abundant freshwater gastropods and small coally wood fragments.

Age. Late Oligocene, MP 26, assemblage zone of Mümliswil-Hardberg or Oensingen 11.

Referred material. 67 isolated teeth from Rigi 2. All specimens are deposited in the Basel Natural History Museum.

Diagnosis. Small species of *Eomys* with mid-length mesolophid on lower P and M. Anterolophid of lower molars not connected with the metalophid, but occasionally with the protoconid. M_3 with hypolophid and 4th syncline. Metalophid of lower molars mostly slightly bent posteriorly. 4th syncline of M_1 and M_2 mostly very long, extending beyond the middle of the tooth. Entolophid of lower molars situated labially from the middle of the tooth. Lower P and M frequently with posterior metaconid crest.

Stratigraphic range. *E. schluneggeri* n. sp. is known so far only from the type locality.

Differential diagnosis.

From *Eomys helveticus* n. sp. from Rigi 1 *E. schluneggeri* n. sp. differs in:

- larger dimensions;
- the longer 4th syncline on M_1 and M_2;
- the less frequently and less distinctly interrupted entoloph on M_1 and M_2;
- the presence of a 4th syncline and a hypolophid on the M_3;
- the frequent presence of a posterior metaconid crest on lower P and M.

From *Eomys molassicus* Engesser, 1987 *E. schluneggeri* n. sp. differs in:

- smaller dimensions;
- the mostly unconnected anterolophid (or only connected with the protoconid) on lower molars;
- the longer 4th syncline of M_1 and M_2, often extending beyond the middle of the tooth;
- the mostly shorter mesolophid on P_4, M_1 and M_2;
- the always present 4th syncline on M_3;
- the more frequently present anteroloph on the P^4;
- the mostly shorter mesoloph on P^4, M^1 and M^2;
- the longer 1st syncline on M^1 and M^2.

From *Eomys antiquus* (Aymard, 1853) *E. schluneggeri* n. sp. differs in:

- the anterolophid on lower molars not connected with the metalophid;
- the absence of a labial anterolophid on lower molars;
- the longer 4th syncline on M_1 and M_2;
- the presence of a hypolophid and therefore of a 4th syncline on the M_3;
- the longer mesolophid on lower molars;
- the more labially situated entolophid of M_1 and M_2;
- the longer mesolophid on P_4, M_1 and M_2.

From *Eomys minor* Comte et Vianey-Liaud, 1987 *E. schluneggeri* n. sp. differs in:

- the larger dimensions, especially the greater width of M_1 and M_2;
- the longer mesolophid on M_1 and M_2;
- the more developed 4th syncline on M_1 and M_2;
- the anterolophid not connected with the metalophid;
- the M_3 with three roots.

From all other species of *Eomys* (*E. zitteli* Schlosser, 1884, *E. ebnatensis* Engesser, 1987, *E. major* Freudenberg, 1941, *E. huerzeleri* Engesser, 1982, *E. quercyi* Comte et Vianey-Liaud, 1987, *E. gigas* Comte et Vianey-Liaud, 1987) *E. schluneggeri* n. sp. differs in:

- the smaller dimensions;
- the anterolophid on lower molars not connected with the metalophid;
- the longer 4th syncline posterolophid respectively on M_1 and M_2;
- the presence of a hypolophid and therefore a 4th syncline on its M_3.

From *Eomys* n. sp. 2 from Bumbach 1 (Engesser 1990) *E. schluneggeri* n. sp. differs in:

- the unconnected anterolophid on lower molars;
- the longer 4th syncline on M_2;
- the presence of a hypolophid and therefore of a 4th syncline on the M_3;
- the shorter mesoloph on M^1 and M^2.

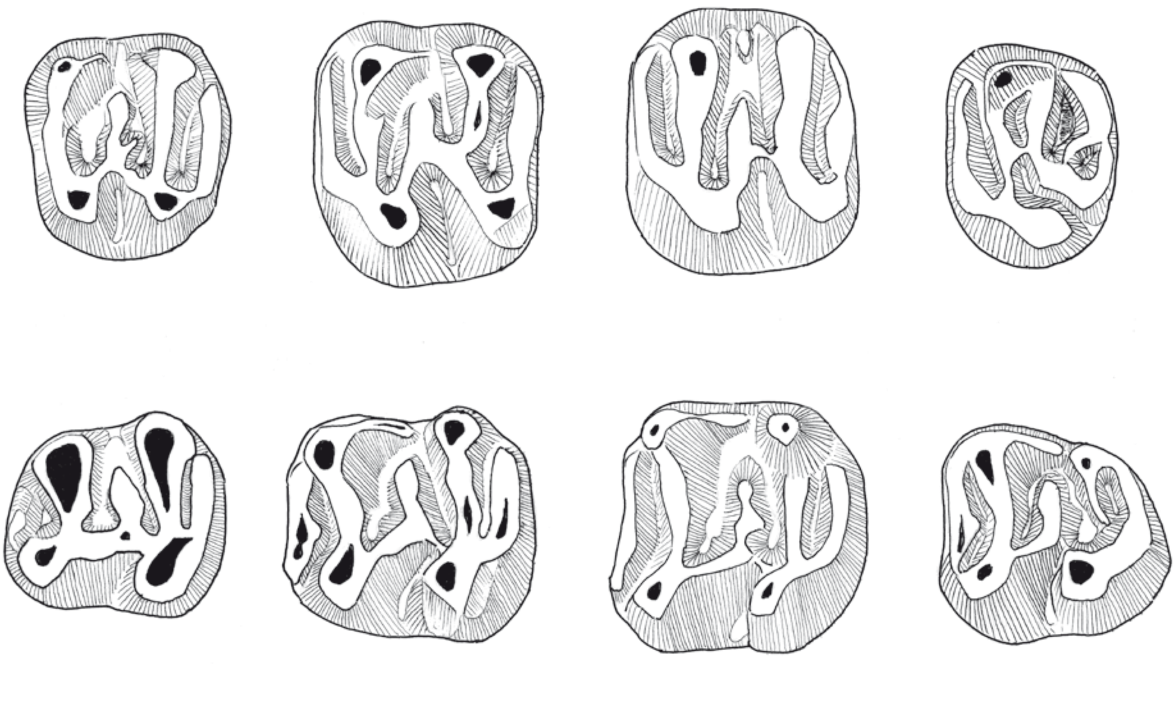
From *Eomys* n. sp. 1 from Lovagny (Engesser 1990) *E. schluneggeri* n. sp. differs in:

- the somewhat larger dimensions on average;
- the not connected anterolophid on lower molars;
- the distinctly longer 4th syncline on M_1 and M_2;
- the absence of the beginnings of a lingual anteroloph on M^1 and M^2;

Text-fig. 4. *Eomys schluneggeri* n. sp. from Rigi 2. m_1 dext. (reversed): Rgi 20, holotype. Magnification 35×.

- the presence of a posterior metaconid crest on P_4, M_1, M_2 and M_3.

D i s c u s s i o n . *Eomys schluneggeri* n. sp. has many characters in common with smaller species of the genus *Eomyodon* Engesser, 1987 (*E. volkeri* Engesser, 1987, *E. mayoi* Engesser, 1990): the unconnected anterolophid on the lower molars, the well developed 4th syncline on the lower P and M, the presence of a hypolophid and therefore a 4th syncline on the M_3, the transversal or slightly backward directed metalophid on the lower molars, and the posterior metaconid crest on the lower P and M. Consequently the question arises as to whether it would have been justified to place the species *schluneggeri* n. sp. in the genus *Eomyodon*. This possibility conflicts with the fact that most of the aforementioned characters (transversal



Text-fig. 5. *Eomys schluneggeri* n. sp. from Rigi 2. a) P^4 – M^3; P^4 sin.: Rgi 31, $M^{1/2}$ sin.: DKRgi1, $M^{1/2}$ dext. (reversed): DKRgi2, M^3 dext. (reversed): DKRgi3. b) P_4 – M_3 sin.; P_4 sin.: DKRgi4, M_1 sin.: DKRgi5, M_2 sin. Rgi 23, M_3 sin.: DKRgi6. All figures at magnification 35×.

metalophid, unconnected anterolophid) are considered as primitive and are therefore less meaningful for phylogenetic considerations. In addition the cheek teeth of *Eomyodon* (with exception of *E. volkeri*) are more lophodont and more hypsodont (Text-fig. 7). The cheek teeth of *Eomyodon* are more planely worn, whereas in *Eomys schlueneggeri* n. sp. the lingual cusps of the lower and the labial cusps of the upper cheek teeth are hardly worn even in an advanced stage of wear. Finally the lower cheek teeth of *Eomyodon* are mostly characterized by a long mesolophid, extending to the lingual tooth border, whereas in *Eomys schlueneggeri* n. sp. this crest is always short or mid-length.

The placing of *Eomys schlueneggeri* n. sp. in the genus *Eomyodon* gives rise to the question as to whether *Eomys helveticus* n. sp. from Rigi 1, which has some characters in common with *E. schlueneggeri* n. sp., should also be integrated within this genus. This is not really possible, because *E. helveticus* n. sp. has a typical *Eomys* dentition.

In this connection another question also arises, if *E. schlueneggeri* n. sp. could possibly be derived from *E. helveticus* n. sp. This can not be excluded since in some characters, in which the two species are different, *E. helveticus* n. sp. is more primitive: smaller size, shorter 4th syncline on M_1 and M_2, a small P^4 compared with M^1 and M^2, eventually also the lack of a hypolophid on M_3. Whether *E. schlueneggeri* n. sp. really derives from *E. helveticus* n. sp., of course, cannot be stated with certainty, but overall there are no characters clearly conflicting with such a derivation (Engesser 1975).

Very conspicuous within the *Eomys schlueneggeri* n. sp. material from Rigi 2 is the fact that among the 67 isolated teeth there are indeed 22 premolars (9 P_4 and 13 P^4) present, but not a single milk tooth. This lack is so far astonishing, as within the very rich *Eomys molassicus* material, which we collected in 1995 in Oensingen 11, 29 milk teeth (10 D_4 and 19 D^4) compared with 34 premolars (15 P_4 and 19 P^4) were discovered. In the *E. molassicus* material collected in Boningen 1 in 1994, the numerical relationship between premolars and milk teeth is even more surprising: here 53 milk teeth (26 D_4 and 27 D^4) compared with 19 premolars (11 P_4 and 8 P^4) were found.

In fossil deposits milk teeth are in general rarer than permanent teeth. This is for two reasons: milk teeth are functional for a shorter time than permanent teeth, and they are preserved less well because their enamel is thinner and often attacked by resorption processes.

We are convinced that *E. schlueneggeri* n. sp. had a D_4 and a D^4 as in all known eomyids. The fact that not a single specimen, not even a fragment, was found seems to be the result of chance.

Eomys molassicus **Engesser, 1987**
Text-figs 6, 7c

Holotype. Right mandible fragment with I, P_4–M_3, inv. no. U.M. 2926, Basel Natural History Museum.

Type locality. Oensingen, coordinates 2620.960/1238.180, 525 m a.s.l.

Referred material. 42 isolated teeth from Rigi 2. All specimens are deposited in the Basel Natural History Museum.

Description. In morphology and dimensions *E. molassicus* from Rigi 2 closely matches the form from Oensingen[1], the type locality of this species. However, in the frequency of certain characters some differences between the two forms can be observed, which should not be overestimated in view of the rather limited amount of material from Rigi 2.

P_4. The P_4 of *E. molassicus* from Rigi 2 is relatively large in comparison with the M_1. All 5 specimens partly show a distinct anterolophid. In 2 specimens the mesolphid is very long reaching the lingual crown rim. In 3 specimens the mesolophid is mid-length. In 13 from 15 P_4 from Oensingen 11 the mesolphid is very long. Only in 2 specimens it is short.

M_1. In 2 from 6 M_1 the mesolphid reaches the lingual tooth rim (very long). In 4 specimens it is mid-length. In *E. molassicus* from Oensingen the number of specimens with a very long mesolophid is somewhat greater: out of 32 specimens 16 show a very long mesolophid, 15 a mid-length mesolohid and 1 a short mesolophid.

M_2. In 2 from 3 M_2 from Rigi 2 the mesolophid is mid-length, in 1 specimen it is very long. In 13 M_2 from Oensingen the mesolophid is mid-length, in 9 very long.

M_3. 3 out of 5 M_3 from Rigi 2 show a very long mesolphid, in 2 it is mid-length. Of the 23 M_3 from Oensingen, 14 have a very long, and 9 a mid-length mesolophid.

P^4. From the 6 P^4 of *E. molassicus* from Rigi 2 none exhibits an anterolph. Among the 19 P^4 from Oensingen, 3 have a very small anteroloph. From the 6 P^4 from Rigi 2, 4 have a very long mesoloph, in 2 it is short. From 19 P^4 from Oensingen, 8 have a short mesoloph, 7 a mid-length one and in only 4 it is very long.

M^1. Among the 8 M^1 from Rigi 2, 6 have a very long and 2 a mid-length mesoloph. Among 23 M^1 from Oensingen there are 20 which have a very long mesoloph and 3 with mid-length. Out of the 23 M^1 from Oensingen, 6 show the beginnings of a lingual anteroloph. Among the 8 M^1 from Rigi 2 this character cannot be observed in any specimen.

M^2. All 4 M^2 from Rigi 2 show a very long mesoloph. In *E. molassicus* from Oensingen, 19 have a very long, 2 a mid-length and 2 a short mesoloph.

M^3. 3 M^3 from Rigi 2 show a very long mesoloph, 1 specimen a short one. The M^3 of *E. molassicus* from Oensingen have a very variable morphology. From 22 M^3, 12 have a very long mesoloph, 4 a mid-length one, 4 a short one and in 2 it is absent.

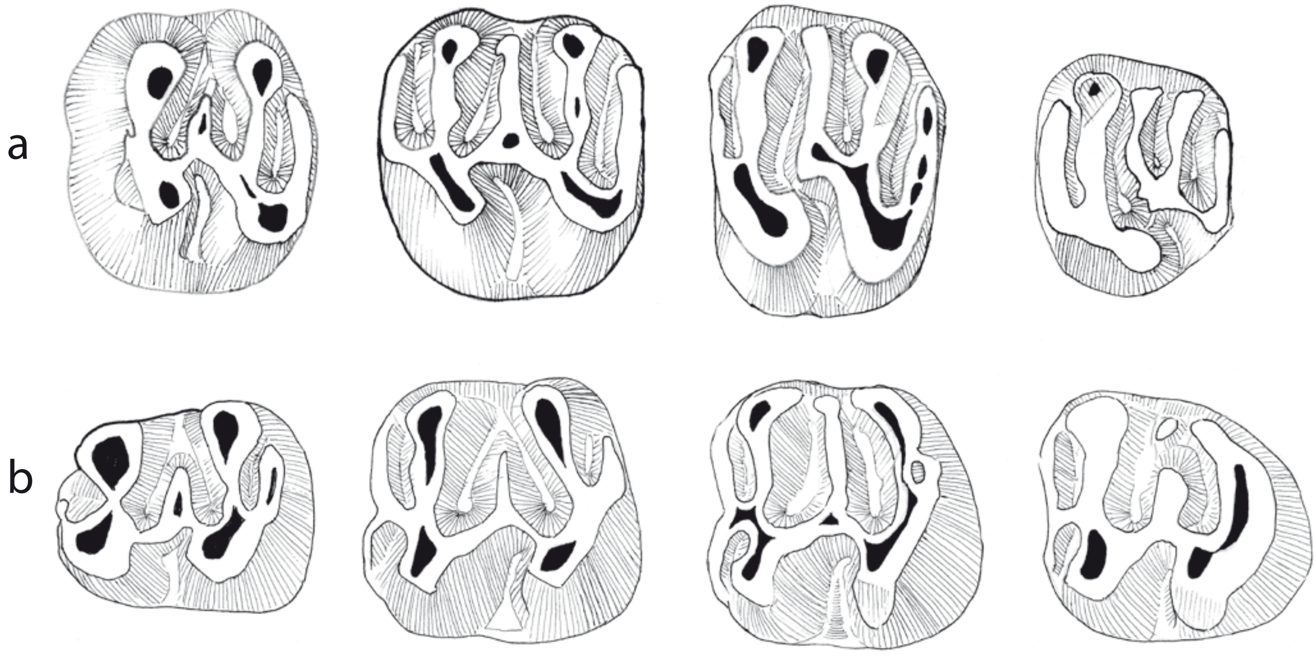
The biostratigraphic age of the Rigi 2 fauna

The localities Rigi 1 (57 teeth) and Rigi 2 (308 teeth) yielded a total of 365 isolated teeth (including identifiable fragments). The faunal lists are:

Faunal list of Rigi 1

Erinaceidae cf. *Tetracus*
Talpidae indet.

1 The type material of *E. molassicus* Engesser, 1987 originates from the old collection from Oensingen. Here, the new material from Oensingen 11, excavated in 1995, is included in the compared material.



Text-fig. 6. ***Eomys molassicus*** **ENGESSER, 1987 from Rigi 2. a) $P^4 – M^3$; P^4 dext. (reversed): DKRgi7, M^1 sin.: Rgi 45, M^2 sin.: DKRgi8, M^3 dext. (reversed): DKRgi9. b) $P_4 – M_3$; P_4 sin.: DKRgi9, M_1 sin.: DKRgi10, M_2 sin.: DKRgi11, M_3 sin.: DKRgi12. All figures at magnification 35×.**

Sciuridae n. gen. n. sp.
Eomys helveticus n. sp
Microdyromys praemurinus (FREUDENBERG, 1941)
Bransatoglis fugax (HUGUENEY, 1967)
Oligodyromys cf. *planus* BAHLO, 1975
Pseudocricetodon sp.

Faunal list of Rigi 2

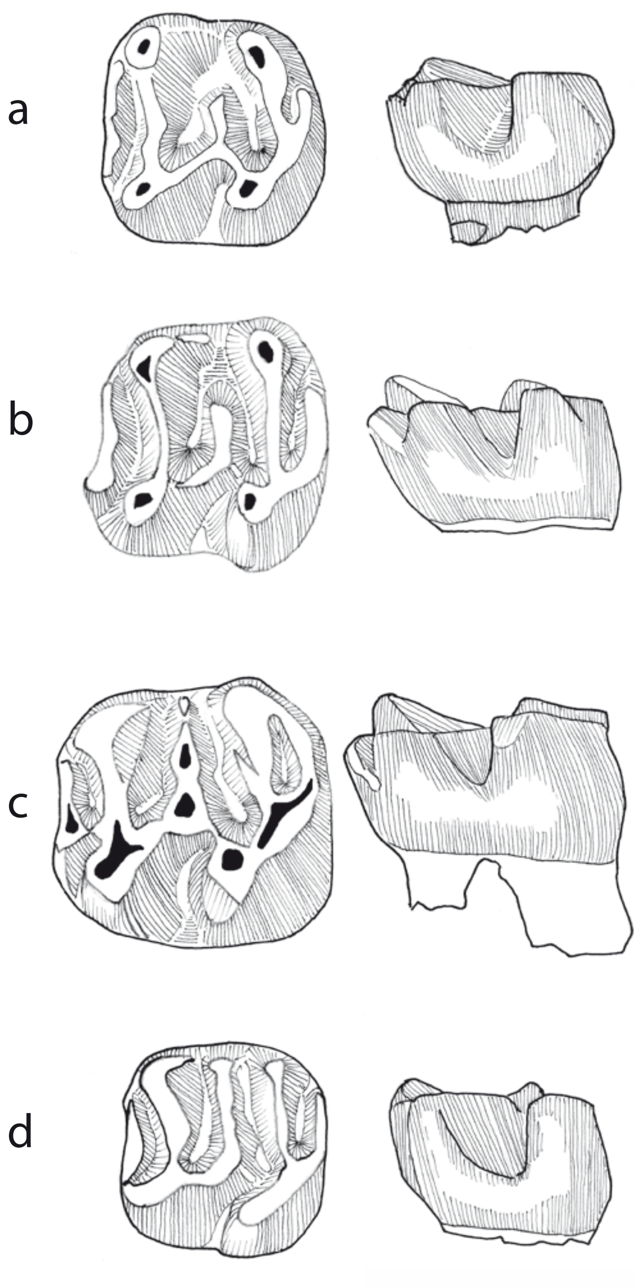
Didelphidae indet.
Erinaceidae cf. *Tetracus*
Heterosoricidae indet.
Soricidae indet.
Chiroptera indet.
Sciuridae n. gen. n. sp.
Plesiospermophilus aff. *ernii* STEHLIN et SCHAUB, 1951
Eomys molassicus ENGESSER, 1987
Eomys schluneggeri n. sp.
Gliravus n. sp. (same species as in Bumbach 1)
Microdyromys praemurinus (FREUDENBERG, 1941)
Bransatoglis fugax (HUGUENEY, 1967)
*Plesiosminthu*s sp.
Pseudocricetodon cf. *thaleri* (HUGUENEY, 1969)
Pseudocricetodon cf. *philippi* HUGUENEY, 1971
Allocricetodon aff. *incertus* (SCHLOSSER, 1884)
"*Eucricetodon*" *murinus* (SCHLOSSER, 1884)
Eucricetodon huerzeleri VIANEY-LIAUD, 1972
Paracricetodon cf. *cadurcensis* (SCHLOSSER, 1884)
Protechimys major SCHLOSSER, 1884
Carnivora indet.
Artiodactyla indet. 1
Artiodactyla indet. 2

There are quite a number of arguments for a correlation of the Rigi 2 fauna with the Paleogene Mammal Unit MP 26. The taxa *Eucricetodon huerzeleri*, *Allocricetodon incertus*, *Eomys molassicus* and *Plesiosminthus*, all documented in Rigi 2, have never been found in layers older than MP 26a (Molasse Mammal Zone of Mümliswil-Hardberg; Text-figs 9, 10). Consequently we get a maximum age for Rigi 2. On the other hand we found *Paracricetodon* and *Protechimys* in Rigi 2, two genera never discovered in layers younger than MP 26. Thus we get a minimum age.

Even though the Rigi 2 locality yielded 308 isolated teeth (including identifiable fragments), there are no conclusive arguments as to whether Rigi 2 should be classified within the Molasse Zone of Mümliswil-Hardberg (MP 26a) or that of Oensingen (MP 26b). This may be due to the extraordinary ecological conditions of Rigi 2 which resulted in the absence of taxa normaly considered reliable for biostratigraphy .

Some reflections on the ecological conditions of Rigi 1 and 2

Regarding the composition of the faunas of Rigi 1 and 2, it quickly became conspicuous that the Theridomyidae, the most frequent small mammal group in most Late Oligocene localities, are very rare (Rigi 2) or absent (Rigi 1). In contrast the Eomyidae and Gliridae are very frequent in both localities. The Eomyidae are generally considered as forest or tree dwellers. In one *Eomys* species (*E. quercyi*) it could be proved that the animals were gliders (Storch et al. 1996). This way of life prerequisites the presence of tall trees. The Gliridae genera *Bransatoglis* HUGUENEY, 1967



Text-fig. 7. Comparison of lower molars of different Eomyidae in occlusal (left) and labial (right) view. a) ***Eomys helveticus*** **n. sp. from Rigi 1, $M_{1/2}$ sin.: Rgi 3, holotype. b)** ***Eomys schlunegg-geri*** **n. sp. from Rigi 2, M_1 dext. (reversed): Rgi 20, holotype. c)** ***Eomys molassicus*** **Engesser, 1987 from Rigi 2, M_1 sin.: DKR-gi13. d)** ***Eomyodon mayoi*** **Engesser, 1990 from Krummenau/Thur, M_1 dext. (reversed): Tpl A16. All figures at magnification 35×.**

and *Microdyromys* de Bruijn, 1965 [1966] are generally considered as forest dwellers and to a large extend tree dwellers (Mayr 1979).

Conversely the Theridomyidae of the Late Oligocene with their high crowned teeth, are generally considered as inhabitants of open, relatively dry environments (Vianey-Liaud 1979).

In the localities Rigi 1 and 2 extraordinary ecological conditions must have prevailed during the Oligocene. This also becomes evident from the fact that the two new *Eomys* species and a yet undescribed gigantic squirrel have not been found in any of the numerous MP 25 and 26 localities in central Europe.

Very revealing is a comparison of the faunal composition of the two Rigi faunas with that of the localities Mümliswil-Hardberg and Oensingen which are about the same age (Text-fig. 10). An extreme contrast appears when comparing the Rigi 2 fauna with that of Mümliswil-Hardberg: the latter being dominated by Theridomyidae (58.5%) and Cricetidae (25.3%), whereas in Rigi 2 the Eomyidae (37.7%), Cricetidae (27.9%) and Gliridae (16.25) prevail (Tab. 1). Theridomyidae on the other hand are very rare in Rigi 2.

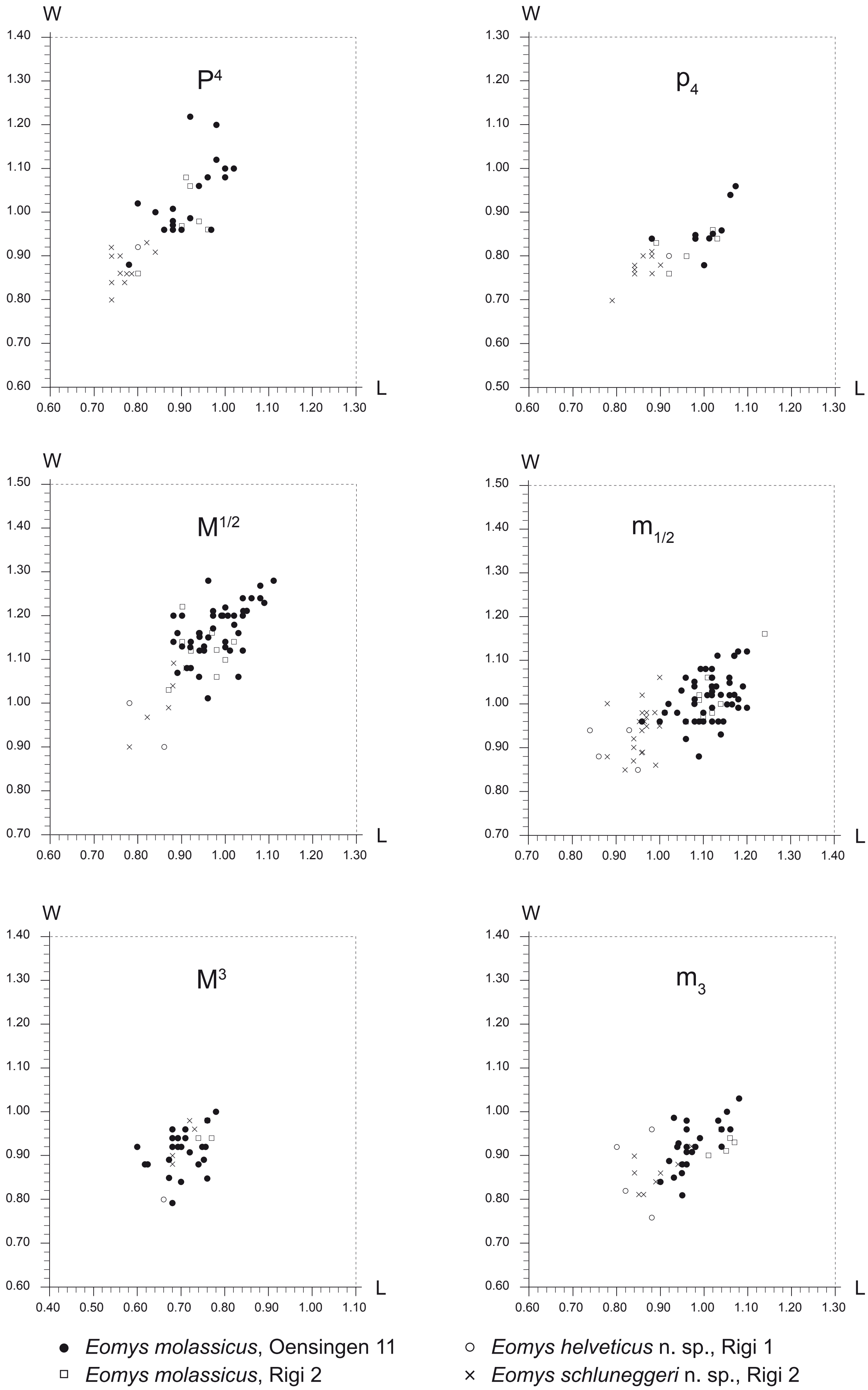
There is little known about the ecological preferences of the Oligocene Cricetidae, but it seems clear, that the Oligocene members of this family occupied very different ecological niches. The Cricetidae show great diversity in many localities of the Late Oligocene: 10 species in Oensingen 11, 8 species in Mümliswil-Hardberg (Engesser and Mödden 1997), and it is most improbable that all these species had the same ecological demands.

An even larger contrast exists between the faunas of Mümliswil-Hardberg and Rigi 1. With only 57 identifiable teeth from Rigi 1, any comparison with this fauna must be limited. However, it stands out that the Gliridae (33.3%) prevail, followed by the Eomyidae (31.65) and Insectivora (22.8%). Cricetidae are represented by only 7% of the identifiable teeth and Theridomyidae are absent. It appears as if in Rigi 1 we were dealing with an extreme forest fauna in which dwellers of open, rather dry landscapes are completely absent. Also the insectivores – with the exception of the spiny hedgehogs (Erinaceinae) lacking in Rigi 1 – are considered as dwellers of rather humid biotopes. In Rigi 1 they are more frequent than in the other compared faunas (Text-fig. 11 and Tab. 1).

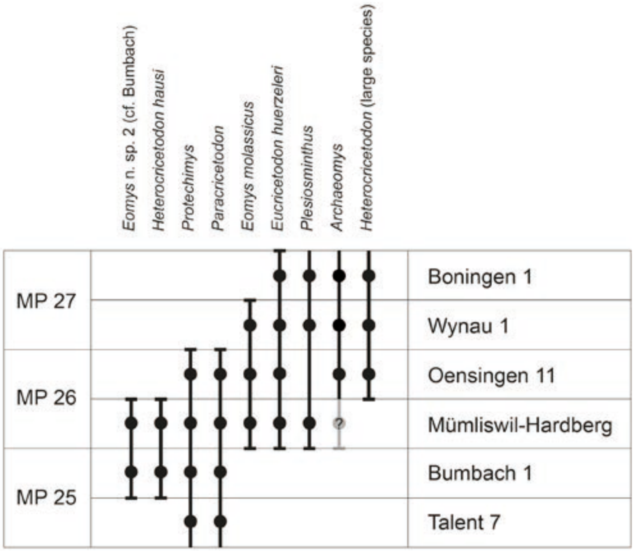
In comparison with most other Late Oligocene faunas Mümliswil-Hardberg stands out due to the rarity of forest dwelling forms and the higher frequency of the Theridomyidae (in particular *Issiodoromys* Croizet in

Table 1. Relative frequency of mammal groups in the mammal sites Rigi 1and Rigi 2 compared with the mammal sites Mümliswil-Hardberg and Oensingen 11.

Taxa	Rigi 1	Rigi 2	Mümliswil	Oensingen 11
Didelphidae	–	2.6%	0.5%	2.0%
Insectivora	22.8%	6.1%	7.7%	9.5%
Chiroptera	–	1.0%	0.5%	0.3%
Gliridae	33.3%	16.2%	2.5%	6.5%
Sciuridae	5.3%	0.7%	–	0.1%
Aplodontidae	–	2.9%	–	–
Eomyidae	31.6%	37.7%	2.1%	27.0%
Dipodidae	–	0.7%	1.0%	–
Cricetidae	7.0%	27.9%	25.3%	33.0%
Theridomyidae	–	2.3%	58.5%	20.5%
Artiodactyla	–	1.9%	3.7%	0.6%



Text-fig. 8. Scatter diagrams (length and width) of *Eomys* measurements from Rigi 1 and 2 in comparison with those of *Eomys molassicus* Engesser, 1987 from Oensingen 11.



Text-fig. 9. The stratigraphic range of significant rodent taxa in the Mammal Zones MP 25, 26 and 27.

Blainville, 1840) normally considered as dwellers of open landscapes or steppes (Vianey-Liaud 1976, 1979).

Considering the frequency of the compared taxa, Oensingen is intermediate between the two Rigi faunas and Mümliswil-Hardberg and corresponds with the majority of Late Oligocene faunas.

In the localities Rigi 1 and 2 similar ecological conditions seem to have prevailed: a relatively humid, forested landscape. However, a comparison of the two faunas shows that the inhabitants of open, rather dry landscapes

Epoch	Stage	MP unit	Swiss reference localities	Faunas of the same age
Oligocene	Chattian	MP 27	Boningen 1	Boningen 9, Losenegg 1 + 2, La Vaudèze, Talent 4
			Wynau 1	*Balsthal-Holzflue*, Bavois grès sup., Mümliswil-Näsihöfi, Bellières, Wynau 2, Bois de Tey 5 & 7, Wolfwil
		MP 26	Oensingen 11*	Talent 1, 8, 11, 16, Schwendibach, *? Einsiedeln-Chrüzweid*
			Mümliswil-Hardberg*	*Rigi 2*, Cuennet
		MP 25	Bumbach 1	Réchauvent-Cristallin, Talent 2, 13
	Rupelian		Talent 7	
		MP 24	Grenchen 1	*Wengibach*, *Stirzelwälder*; *Dürrenberg, Court 1*, *La Beuchille, Poillat*

Text-fig. 10. Biozonation of the Lower part of the Lower Freshwater Molasse of Switzerland and Savoy on the basis of fossil mammals (mainly after Engesser and Mödden 1997). Localities not as yet known or considered by Engesser and Mödden (1997) are in italics. Asterisk: the Mümliswil reference fauna is considered here to be older than the Oensingen reference fauna.

(Theridomyidae) are lacking in Rigi 1 and the ubiquists (Cricetidae) are very rare (Text-fig. 11). On the other hand the insectivores, Gliridae and Eomyidae, considered as inhabitants of forested, rather humid areas, are very frequent.

Another sign, in our opinion, of unusual ecological conditions is also the presence of Aplodontidae in Rigi 2. These rodents with unknown ecological preferences are extremely rare in localities of the Late Oligocene.

Acknowledgments

This paper is dedicated to our colleague Prof. Dr. Oldřich Fejfar. We are indebted to many people for their help. Prof. Dr. Fritz Schlunegger provided us with information on the mammal sites. U. Leuthold, M. Weick and F. Wiedenmayer assisted in the field work. Dr. C. Beer generously gave support for the laboratory work. To all these people we would like to express our sincere thanks. Many thanks to Marguerite Hugueney and Thomas Mörs for their constructive reviews of the manuscript.

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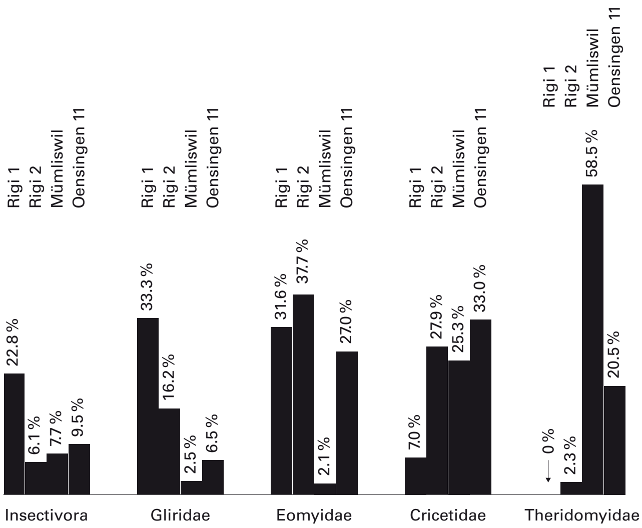

Text-fig. 11. Relative frequency of mammal groups in the mammal sites Rigi 1 and Rigi 2 compared with the mammal sites Mümliswil-Hardberg and Oensingen 11.

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Appendix 1. Measurements of *Eomys helveticus* n. sp. from Rigi 1 (in mm). L = length, W = width, ø = mean, n = number of specimens.

	P^4L	P^4W	$M^{1/2}L$	$M^{1/2}W$	M^3L	M^3W		P_4L	P_4W	$M_{1/2}L$	$M_{1/2}W$	M_3L	M_3W
	0.80	0.92	0.78	1.00	0.66	0.80		0.92	0.80	0.86	0.88	0.82	0.82
	0.72	0.76	0.86	0.9						0.88	0.88	0.88	0.76
	0.95	0.85	0.84	0.94						1.00	0.92		
			0.88	0.96						0.93	0.94		
			0.80	0.92									
ø	0.82	0.84	0.83	0.94	0.66	0.80		0.92	0.80	0.92	0.91	0.85	0.79
n	3		5		1			1		4		2	

Appendix 2. Measurements of *Eomys schluneggeri* n. sp. from Rigi 2 (in mm). L = length, W = width, ø = mean, n = number of specimens.

	P^4L	P^4W	$M^{1/2}$L	$M^{1/2}$W	M^3L	M^3W		P_4L	P_4W	$M_{1/2}$L	$M_{1/2}$W	M_3L	M_3W
	0.74	0.84	0.88	1.04	0.72	0.98		0.88	0.80	1.01	0.98	0.89	0.84
	0.76	0.90	0.87	0.99	0.68	0.90		0.88	0.81	0.99	0.86	0.94	0.88
	0.78	0.86	0.91	1.08	0.73	0.96		0.90	0.78	0.94	0.92	0.84	0.90
	0.78	0.86	0.82	0.97	0.68	0.88		0.79	0.70	0.94	0.90	0.90	0.86
	0.74	0.80	0.88	1.09				0.86	0.80	0.94	0.87	0.85	0.81
	0.76	0.86	0.78	0.9				0.84	0.76	0.96	0.89	0.86	0.81
	0.77	0.84						0.84	0.77	0.92	0.85	0.97	0.92
	0.74	0.92						0.88	0.76	0.96	0.89	0.84	0.86
	0.82	0.93						0.84	0.78	0.96	0.98		
	0.74	0.90								0.97	0.95		
	0.84	0.91								0.97	0.97		
										0.96	1.02		
										0.96	0.96		
										1.00	0.95		
										0.88	0.88		
										0.96	0.96		
										0.88	1.00		
										0.96	0.96		
										0.97	0.98		
										1.00	0.97		
										1.00	1.06		
										0.96	0.94		
										0.99	0.98		
ø	0.77	0.87	0.86	1.01	0.70	0.93		0.86	0.77	0.97	0.92	0.89	0.87
n	11		6		4			9		23		8	

Appendix 3. Measurements of *Eomys molassicus* from Rigi 2 (in mm). L = length, W = width, ø = mean, n = number of specimens.

	P^4L	P^4W	$M^{1/2}$L	$M^{1/2}$W	M^3L	M^3W		P_4L	P_4W	$M_{1/2}$L	$M_{1/2}$W	M_3L	M_3W
	0.94	0.98	1.00	1.10	0.74	0.94		1.03	0.84	1.14	1.00	1.06	0.94
	0.90	0.97	0.98	1.06	0.76	0.98		1.02	0.86	1.10	0.96	1.04	0.96
	0.92	1.06	0.87	1.03	0.77	0.94		0.92	0.76	1.24	1.16	1.07	0.93
	0.96	0.96	1.02	1.14				0.96	0.80	1.10	0.97	1.05	0.91
	0.80	0.86	0.90	1.14				0.89	0.83	1.09	1.01	1.01	0.90
	0.91	1.08	0.92	1.08						1.06	0.96		
			0.97	1.16						1.12	0.98		
			0.98	1.12						1.12	1.04		
			0.90	1.22						1.11	1.06		
			0.92	1.12						1.09	1.02		
ø	0.91	0.99	0.95	1.12	0.76	0.94		0.96	0.82	1.12	1.02	1.05	0.93
n	6		10		3			5		10		5	