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**Artikel:** New Eomyidae, Dipodidae, and Cricetidae (Rodentia, Mammalia) of the Lower Freshwater Molasse of Switzerland and Savoy

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on the eomyids of the Swiss Molasse. In this latter publication, which will soon be completed, extensive comparisons and discussions of the relationships will be given. The new species of *Heterocricetodon* and that of *Plesiosminthus* are treated more extensively, because these two genera are small groups to which I will not refer again in the near future.

I am indebted to many persons for their help. The geologists Dr. M. Weidmann, Lausanne, Dr. H. A. Haus, Überlingen, and Dr. A. Breitschmid, Bern, helped me in the field and provided me with lithostratigraphical sections. Prof. Dr. V. Fahlbusch, Munich, Dr. M. Hugueney, Lyon, and U. Oberli, St. Gallen, lent me fossil material. P. Hornisberger, Bern, D. Kälin, Balsthal, and H. Winistörfer, Balsthal, provided me with material from localities that they had discovered. Prof. Dr. V. Fahlbusch, Dr. Joh. Hürzeler, N. A. Mayo, and Dr. M. Weidmann discussed problems with me, and provided me with much information and numerous suggestions. Our preparators, D. Oppliger and M. Weick, helped me in the field, washed sediments and made casts. H. Gredig, H. Pouget, P. Schwarz, my wife Wies, and J. Zimmermann did the picking of the washed sediments. Dr. and Mrs. T. Harrison went over the manuscript which was typed by H. Pouget. To all these people I wuld like to express my thanks.

## 2. Systematic description

### Family ***Eomyidae*** DEPÉRET & DOUXAMI 1902

### Genus *Eomys* SCHLOSSER 1884

### *Eomys molassicus* n. sp.

Fig. 2b–c, 3b, 4b, 5d, 6a, 7–8

*Diagnosis.* – Small species of *Eomys* with brachyodont, short, and wide lower molars which show a well-developed anterior cingulum (labial and lingual branch) and a medium to long mesolophid. $P_4$ also with long mesolophid. $M_1$ and $M_2$ both with 4th labial syncline, but more reduced in $M_2$ than in $M_1$. $M^1$ and $M^2$ mostly with long mesoloph and well-developed 1st labial syncline. Lower incisor relatively large, almost as large as in *Eomys zitteli.*

*Derivatio nominis.* – molassicus, because this species is so far known only from the Molasse basin.

*Type.* – Right mandible fragment with I, $P_4$–$M_3$, U.M. 2926, Basel, Museum of Natural History. Dimensions: $P_4$: 0,94 × 0,92 mm, $M_1$: 0,98 × 1,00 mm, $M_2$: 1,02 × 2,08 mm, $M_3$: 0,86 × 0,98 mm. Incisor (cross-section): 0,66 × 1,12 mm, height of the mandible below $P_4$: about 3,25 mm; (fig. 2c, 5d).

*Referred material from Oensingen.* – Right mandible fragment with $M_1$–$M_2$, right maxillary fragment with $P^4$–$M^1$, 7 isolated teeth.

*Type locality.* – Freshwater limestone of Oensingen–Ravellen (Canton of Solothurn, Switzerland), coordinates of the "Schweizer Landeskarte" 1:25 000: 620 850/238 100 (see MAYO 1980, p. 1098 and ENGESSER & MAYO 1987).

*Age:* Middle Oligocene, assemblage zone of Oensingen (ENGESSER & MAYO 1987).

*Stratigraphic range.* – Assemblage zones of Oensingen and Mümliswil–Hardberg.

Other localities with *Eomys molassicus:*

Schwendibach (near Steffisburg, Canton of Bern)
Mümliswil–Hardberg } (*E.* cf. *molassicus*)
Cuennet (Canton of Vaud) } (*E.* cf. *molassicus*)

*Differential diagnosis.* –

From *Eomys antiquus* (AYMARD 1853), *E. molassicus* differs in:

- its larger dimensions,
- the more strongly developed anterior cingulum on the lower molars,
- the longer mesolophids on the lower molars,
- the less reduced 4th lingual syncline on $M_2$,
- the higher ramus horizontalis of the mandible.

*Remark.* – *Eomys antiquus* is only poorly known. The species is documented only by the type mandible (with I, $M_1$ and $M_2$) an another mandibular fragment with $M_1$.

From *Eomys zitelli* SCHLOSSER 1884, *E. molassicus* differs in:

- the smaller dimensions of its molars,
- the smaller lower incisor (despite the similar height of the mandible),
- the longer mesolophid on the lower P and M,
- the longer mesoloph on the upper P and M,
- the more transversely aligned metalophid on the lower P and M,
- the more brachyodont lower P and M,
- the more developed 1st labial syncline on $M^1$ and $M^2$.

From *Eomys major* FREUDENBERG 1941 and *Eomys huerzeleri* ENGESSER 1982, *E. molassicus* differs in:

- its considerably smaller dimensions,
- the longer mesolophid on lower P and M,
- the longer mesolophs on upper P and M.

Differential diagnosis with *Eomys ebnatensis* n. sp. see p. 952

From *Eomys minor* COMTE & VIANEY-LIAUD 1987 (no specimen seen), *E. molassicus* differs in:

- its larger dimensions,
- its less elongated $M_1$ and $M_2$,
- the presence of a mesolophid on $M_1$ and $M_2$,
- the less reduced 4th lingual syncline of $M_1$ and $M_2$.

From *Eomys quercyi* COMTE & VIANEY-LIAUD 1987 (no specimen seen), *E. molassicus* differs in:

- its considerably smaller dimensions,
- the longer mesolophid on lower P and M,
- its more transversely metalophid on the lower molars,
- the longer mesoloph on upper P and M,
- its less reduced $M^3$.

From *Eomys gigas* COMTE & VIANEY-LIAUD 1987 (no specimen seen) *E. molassicus* differs in:

— its much smaller dimensions,
— the longer mesoloph on upper P and M.
— the less reduced $M^3$.

*Description of the type* (Fig. 2c). – Of the type mandible only the incisor, $P_4$–$M_3$ and the anterior part of the ramus horizontalis are preserved. In front of the anterior root of $P_4$ a foramen mentale can be recognized.

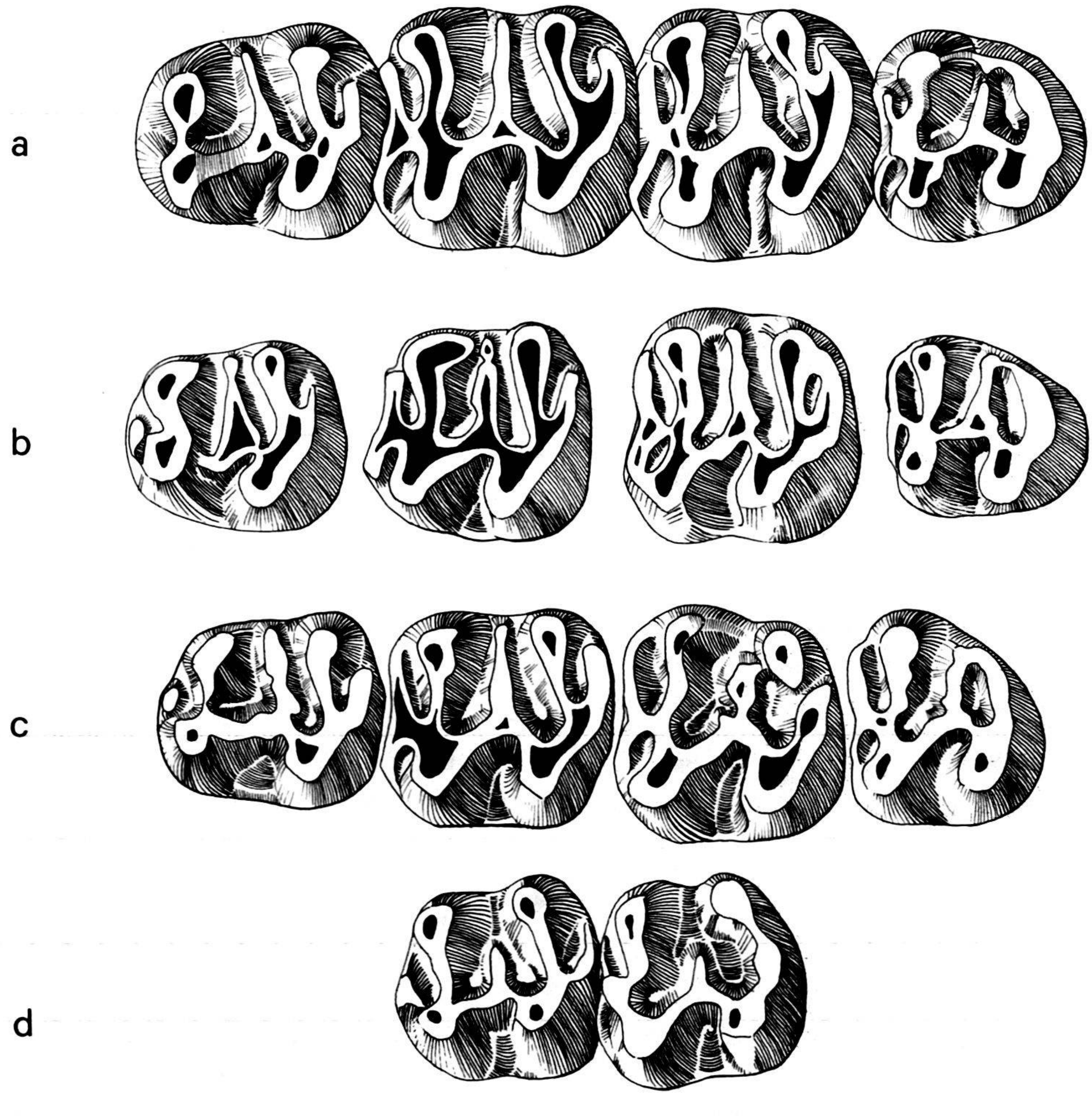


Fig. 2 a) *Eomys ebnatensis* n. sp. from Ebnat-Kappel, right mandible (inverse) with $P_4$–$M_3$, type, EKO-1, collection Urs Oberli, St. Gallen.

b) *Eomys molassicus* n. sp. from Schwendibach, $P_4$–$M_3$, left $P_4$: Scb 1, left $M_1$: Scb 2, right $M_2$ (inverse): Scb 3, left $M_3$: Scb 4, Naturhistorisches Museum Basel.

c) *Eomys molassicus* n. sp. from Oensingen, right mandible (inverse) with $P_4$–$M_3$, type, U.M. 2926, Naturhistorisches Museum Basel.

d) *Eomys antiquus* (AYMARD) from Ronzon (carrière d'Exbrayat), left mandible with $M_1$–$M_2$, type, LP R6, Muséum nat. d'Histoire naturelle Paris. all figures 25×.

The exterior side of the incisor shows a longitudinal enamel ridge typical of most eomyid incisors (Fig. 6a).

The $P_4$ shows a relatively low crown, though it is only a little worn. Its very long mesolophid reaches the lingual edge of the tooth. The longitudinal crest is situated labially of the midline. A small anteroconid is developed. A strong posterior cingulum borders the rather shallow 4th lingual syncline.

The $M_1$ is almost as long as wide and very brachyodont. It also shows a long mesolophid reaching the lingual edge of the tooth. The labial branch of the anterior cingulum is relatively short. The metalophid is transversal, ending in the anterior arm of the protoconid. The longitudinal crest is situated labially of the midline too. The short 4th lingual syncline does not even reach the middle of the tooth.

The $M_2$ is wider than long, very brachyodont and shows a moderately long mesolophid. The anterior cingulum is better developed than in $M_1$. The 4th lingual syncline is very much reduced, but still perceptible. The 3rd, and even more so, the 2nd lingual syncline, extends labially beyond the middle of the tooth. The metalophid is transversely aligned and ends in the anterior arm of the protoconid.

The $M_3$ is very wide and short. Its mesolophid is connected with the entoconid. The latter is not developed as a cusp, but is merged in the posterior cingulum. The metalophid is transversely aligned, but bends anteriorly and joins the anterior arm of the protoconid.

*Description of the dentition.* – No other specimens are known of $P_4$ and $M_3$ besides those in the type jaw.

Two additional $M_1$s correspond well with the $M_1$ of the type. In both specimens the anterior cingulum is slightly longer. The metalophid is transversely aligned in both

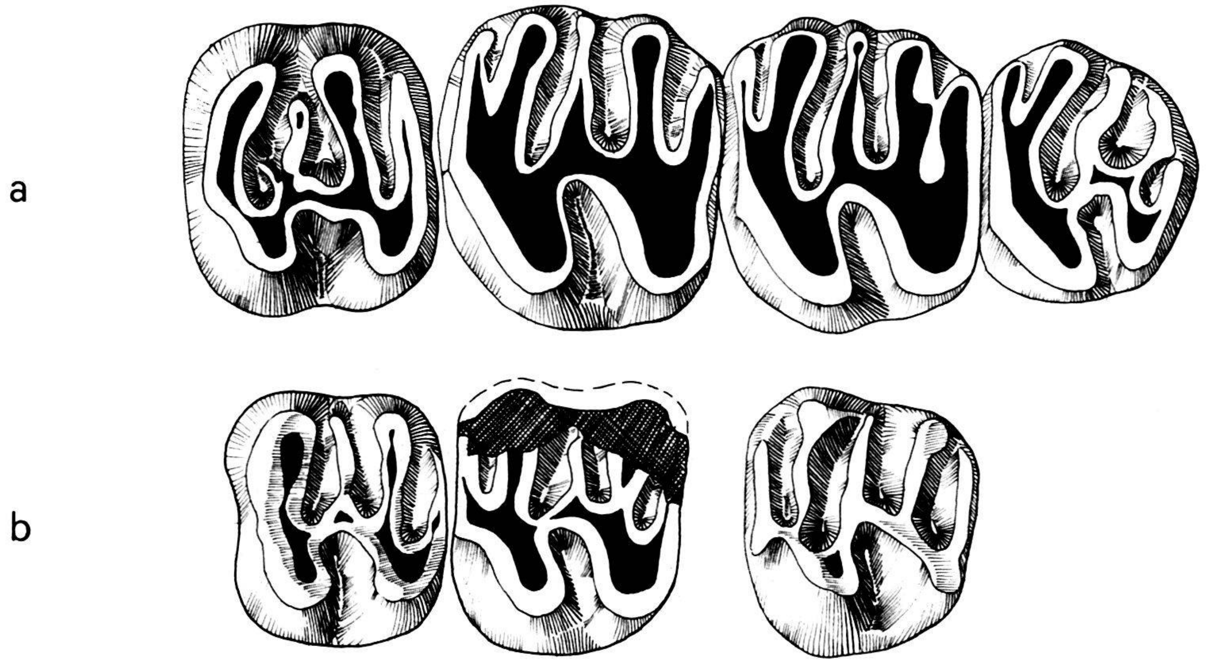


Fig. 3 a) *Eomys ebnatensis* n. sp. from Ebnat-Kappel, left maxillary with $P^4$–$M^3$, EKO-23, collection Urs Oberli, St. Gallen.

b) *Eomys molassicus* n. sp. from Oensingen, right maxillary fragment (inverse) with $P^4$–$M^1$, U.M. 2181, left $M^2$: U.M. 480, Naturhistorisches Museum Basel. all figures 25 ×.

specimens, but in one of them it joins directly with the protoconid. In the same specimen the mesolophid is shorter than in the $M_1$ of the type. All three specimens show a great conformity in the long 2nd and 3rd syncline which goes beyond the midline of the crown, and in the development of the 4th syncline.

Two other $M_2$s besides the type are present. These two molars correspond in size and morphology very well with the $M_2$ of the type, except that in one specimen the mesolophid reaches the lingual edge of the tooth.

The $P^4$ is documented only by one specimen. This tooth is relatively large and shows a very long mesoloph reaching almost the labial edge of the tooth. The 4th labial syncline is longer than the 2nd and the 3rd.

The only known $M^1$ is damaged on its labial side. It is from the same maxillary as the $P^4$ described above. Its 1st labial syncline is well developed. The mesolophid is moderately long.

The only $M^2$ is a little worn, and shows a very long mesoloph and a very long 1st labial syncline extending beyond the middle of the tooth. The 2nd and the 4th syncline also extend far lingually. The paracone shows a posterior crest.

From Oensingen no $M^3$ of *E. molassicus* is known, but in the locality of Schwendibach two specimens were found. These teeth are little reduced and have a well developed 1st labial syncline and a long mesoloph.

Dimensions (of the type see page 946)
$P^4$: 0,96 × 1,10 mm
$M^2$: 0,92 × 1,06 mm
$M_1$: 1,10 × 1,04 mm
1,08 × 1,04 mm
$M_2$: 1,00 × 1,08 mm
1,04 × 0,96 mm

*Discussion.* – See under *Eomys ebnatensis.*

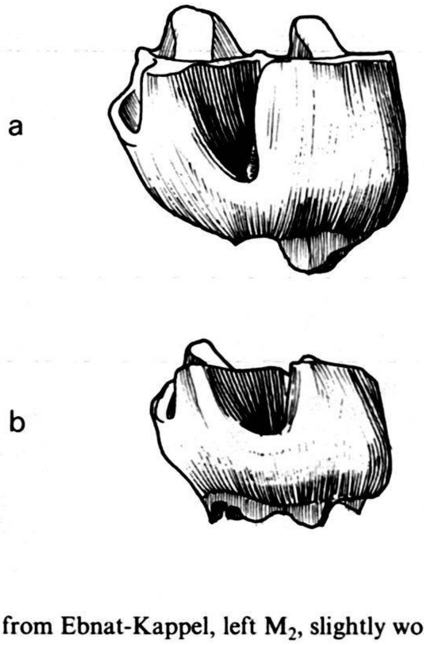


Fig. 4 a) *Eomys ebnatensis* n. sp. from Ebnat-Kappel, left $M_2$, slightly worn, view from labial, EKO-40, collection Urs Oberli, St. Gallen.

b) *Eomys molassicus* n. sp. from Oensingen, left $M_2$, not worn, view from labial, U.M. 7166, Naturhistorisches Museum Basel.

both figures 25×.

### *Eomys ebnatensis* n. sp.

Fig. 2a, 3a, 4a, 5a–b, 6b, 7–8

partim 1979 *Eomys zitteli* Schlosser – Frei, p. 141–142.
1982 *Eomys zitteli* Schlosser – Engesser & Hugueney, p. 64–67.
1985 *Eomys* aff. *zitteli* Schlosser – Engesser, Mayo & Weidmann, p. 21–22, 27–28.
1985 *Eomys* aff. *zitteli* Schlosser – Mojon et al., p. 640–643, 646.

*Diagnosis.* – Medium-sized species of *Eomys*, somewhat larger than *E. zitteli* with relatively hypsodont cheek teeth. $M_1$ and $M_2$ with long or moderately long mesolophid, mostly transversely aligned metalophid, and well developed 4th lingual syncline. Mesoloph of $P^4$ short to moderately long, of $M^1$ very variable, and of $M^2$ mostly long. Mandible with strong ramus horizontalis and a high condyle.

*Derivatio nominis.* – After Ebnat-Kappel the type locality.

*Type.* – Right mandible fragment with I, $P_4$–$M_3$, EKO 1, collection of Urs Oberli, St. Gallen, (Fig. 2a, 5a).

*Dimensions.* – $P_4$: 1,08 × 1,02 mm, $M_1$: 1,24 × 1,16 mm, $M_2$: 1,10 × 1,18 mm, $M_3$: 0,98 × 1,00 mm, $P_4$–$M_3$: 4,34 mm, I (width × height): 0,64 × 1,08 mm, height of mandible below $P_4$: 3,42 mm.

*Referred material from Ebnat-Kappel.* – 4 skull fragments with complete dentition; 6 maxillary fragments; 4 mandibles with complete dentition; 5 mandible fragments; 61 isolated teeth.

*Type locality.* – Grey marls about 11,5 m above the base of the section in the quarry "Schmitt", 1,5 km NE of Ebnat-Kappel in Toggenburg (Canton of St. Gallen, Switzerland). Coordinates of the "Schweizerische Landeskarte" 1:25000: 728870/236475 (see Frei 1979).

*Age.* – Upper Oligocene, assemblage zone of Fornant 6 (see Engesser & Mayo 1987).

*Stratigraphic range.* – Assemblage zones of Wynau 1 through Fornant 6. From the zone of Rickenbach a similar form is known, but as only a few isolated teeth of it were recovered, it is listed as *E.* cf.*ebnatensis*.

Other localities with *E. ebnatensis*

Fornant 6 and 7 (Engesser & Hugueney 1982)
Boudry-La-Fabrique (Mojon et al. 1985)
Bois de Tey 7 (Engesser, Mayo & Weidmann 1984)
Wolfwil
Wynau 1 (Engesser & Mayo 1987)
Boningen
Gösgen-Kanal (Engesser 1982)

With *E.* aff. *ebnatensis*

Ebnat-Kappel (*Eomys* 1; Frey 1979)

With *E.* cf. *ebnatensis*

La Cornalle (Engesser, Mayo & Weidmann 1984)
Findreuse 18 (Engesser & Hugueney 1982)
Rances (Hugueney & Kissling 1972)
Rickenbach (Engesser & Mayo 1987)

*Differential diagnosis.* –

*E. ebnatensis* differs from *E. zitteli* SCHLOSSER in:

- its larger dimensions,
- its more hypsodont cheek teeth,
- the longer mesolophid of lower P and M,
- the better developed 4th lingual syncline of $P_4$ and $M_1$,
- the more transversely aligned metalophid on $P_4$, $M_1$ and $M_2$,
- the higher ramus horizontalis of the mandible,
- the higher position of the condyle on the mandible.

*E. ebnatensis* differs from *E. molassicus* n. sp. in:

- its large size,
- its more hypsodont cheek teeth,
- its shorter 2nd and 3rd lingual syncline on $M_1$ and $M_2$,
- its relatively longer $M_1$.

*E. ebnatensis* differs from *E. antiquus* (AYMARD) in:

- its distinctly larger size,
- its more hypsodont cheek teeth,
- the better developed anterior cingulum on $M_1$ and $M_2$,
- the longer mesolophid on the lower molars,
- the more developed 4th lingual syncline on $M_2$,
- its relatively longer $M_1$,
- its shorter 2nd and 3rd lingual syncline on $M_1$ and $M_2$,
- the higher ramus horizontalis of the mandible.

*E. ebnatensis* differs from *E. major* FREUDENBERG in:

- its smaller size,
- the longer mesolophid of lower P and M,
- the more transversely aligned metalophid on $M_1$ and $M_2$,
- the less reduced $M^3$, having mostly a sinus,
- never developing a 1st labial syncline on $P^4$.

*E. ebnatensis* differs from *E. huerzeleri* in:

- its smaller size,
- the longer mesolophid of $P_4$ and $M_1$,

Fig. 5. Comparison of *Eomys*-mandibles in labial view.

a) *Eomys ebnatensis* n. sp. from Ebnat-Kappel, right mandible (inverse), type, EKO-1, collection Urs Oberli, St. Gallen.

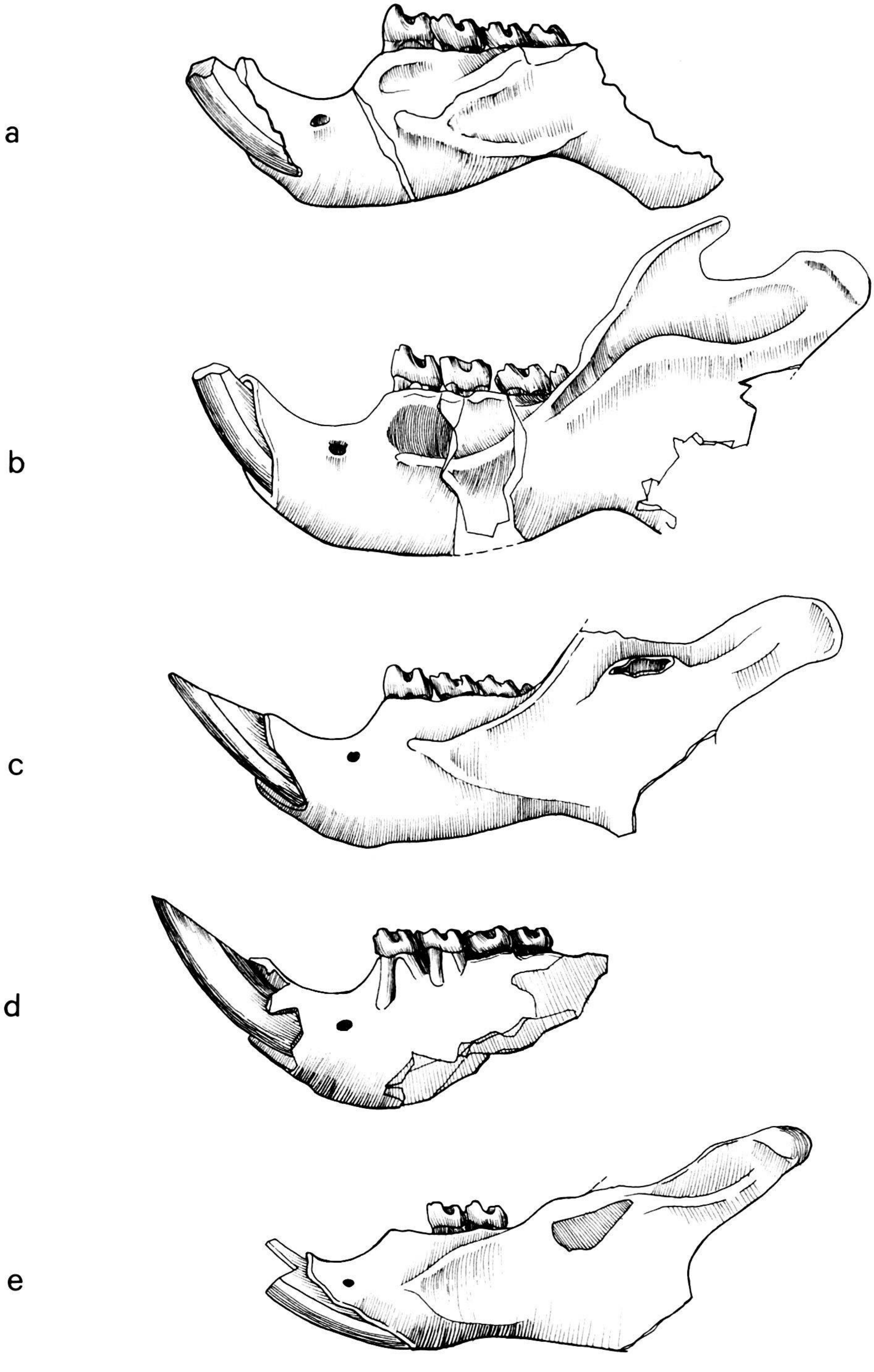
b) *Eomys ebnatensis* n. sp. from Ebnat-Kappel, right mandible (inverse), EKO-19, collection Urs Oberli, St. Gallen.

c) *Eomys zitteli* SCHLOSSER from Quercy, right mandible (inverse) neotype, Q.T. 928, Naturhistorisches Museum Basel.

d) *Eomys molassicus* n. sp. from Oensingen right mandible (inverse), type, U.M. 2926, Naturhistorisches Museum Basel.

e) *Eomys antiquus* (AYMARD) from Ronzon, left mandible, type, LP R6, Muséum nat. d'Histoire naturelle Paris.

all figures 6×.


a
b
c
d
e

— its more elongated $M_1$,
— the longer mesoloph of $P^4$, $M^1$ and $M^2$.

*E. ebnatensis* differs from *E. minor* COMTE & VIANEY-LIAUD (no specimen seen) in:

— its larger size,
— its well developed mesolophid on $M_1$ and $M_2$,
— the more developed 4th lingual syncline of $M_1$ and $M_2$,
— the longer anterior cingulum of $M_1$ and $M_2$.

*E. ebnatensis* differs from *E. quercyi* COMTE & VIANEY-LIAUD (no specimen seen) in:

— its well developed mesolophid on $M_1$ and $M_2$,
— the better developed 4th lingual syncline on $P_4$, $M_1$ and $M_2$,
— its less reduced $M^3$,
— the more transversely aligned metalophid on $M_1$ and $M_2$.

*E. ebnatensis* differs from *E. gigas* COMTE & VIANEY-LIAUD (no specimen seen) in:

— its smaller size,
— its longer mesoloph on the upper molars,
— its less reduced $M^3$.

*Description of the type* (Fig. 2a, 5a). – The type is a right mandibular fragment with I, $P_4$–$M_3$. The teeth are moderately worn. The tip of the incisor is broken.

The $P_4$ shows a long mesolophid which reaches the lingual edge of the tooth, and a well developed 4th lingual syncline. An anteroconid is not present.

The $M_1$ is somewhat longer than wide. Its mesolophid is long and reaches the lingual edge. The metalophid is transversely aligned, but a little curved and ends in the anterior arm of the protoconid. The 2nd lingual syncline is somewhat shorter than the 3rd. Both extend beyond the middle of the tooth. The 4th lingual syncline is well-developed.

The $M_2$ is wider than long. Its mesolophid is moderately long. As in the $M_1$, the metalophid ends in the anterior arm of the protoconid. The 2nd and the 3rd lingual synclines are about equal in length and extend a little beyond the middle of the tooth. The 4th lingual syncline is less well-developed than in $M_1$.

The $M_3$ is relatively small. Its mesolophid is moderately large. The entoconid is incorporated into the posterior cingulum. The sinusid is more posteriorly directed than in $M_1$ and $M_2$.

The mandible is very robust. Its ramus horizontalis reaches its maximum height below the $P_4$. The ramus ascendens is broken away. Of the processus angularis only the lower edge is preserved. The masseteric fossa is distinctly perceptible. The foramen mentale is situated in front of the $P_4$, somewhat below the deepest point of the upper edge of the mandible. The groove for the insertion of the temporalis muscle is visible below the $P_4$.

The lower incisor is about the size of that of *E. zitteli* and shows a distinct longitudinal enamel ridge on its outside.

*Description of the dentition.* – Most $P_4$s have a long or moderately long mesolophid and a well-developed 4th lingual syncline. In contrast to that of the type, most $P_4$s show a more or less well-developed anteroconid.

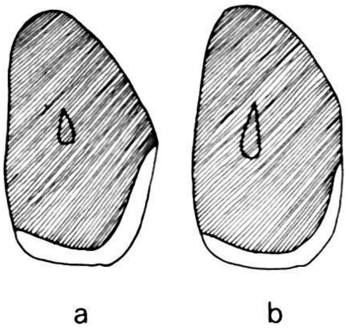


Fig. 6. Cross-section of the lower incisor.
a) *Eomys molassicus* n. sp. from Oensingen, U.M. 2926 (type) Naturhistorisches Museum Basel.
b) *Eomys ebnatensis* n. sp. from Ebnat-Kappel, EKO-19, collection Urs Oberli, St. Gallen. both figures 25×.

With the exception of one specimen, which is as long as wide, the $M_1$ is longer than wide. Its mesolophid is mostly long, more rarely moderately long. The 4th lingual syncline is generally well-developed. In most $M_1$s the metalophid extends transversely to the protoconid.

The $M_2$ is often wider than long. It usually has a moderately long mesolophid, or occasionally a long one. As in the $M_1$, no specimen with a short mesolophid was found. The 4th lingual syncline of $M_2$ almost always is weakly developed. The metalophid is less often transversely aligned than in $M_1$.

The $M_3$ is distinctly smaller than $M_1$ and $M_2$. Its mesolophid is usually fused with the posterior cingulum. A swelling in this latter ridge, which can be interpreted as an entoconid, is only rarely present.

The $P^4$ is relatively large. The 1st labial syncline is lacking. The mesoloph is usually short.

The $M^1$ usually has a weakly developed 1st labial syncline. The mesoloph is very variable. About equal percentages of teeth show a short, a moderately long or a long mesoloph. The 1st labial syncline, generally reaches the middle of the tooth. In most specimens the 1st labial syncline is a little longer than the 3rd one. The $M^1$ is more hypsodont than the $M^2$.

The $M^2$ has a less well-developed 1st labial syncline than on $M^1$, and usually a long, never a short mesoloph. The 2nd labial syncline extends beyond the middle of the tooth, and is always longer than the 3rd one.

Compared with the $M^3$ of other species of *Eomys*, that of *E. ebnatensis* is little reduced. In almost all the specimens a sinus is present. The 1st labial syncline is even more reduced than in $M^2$. The mesoloph is generally long or occasionally moderately long.

### *Discussion*

Having the evolution of all European eomyids in view, a number of features of *Eomys molassicus* can be classified as primitive: Its small size, its brachyodont premolars and molars, the transversely aligned metalophid and the labially situated longitudinal crest of the lower molars, and the long 2nd labial syncline of the upper molars. *E. molassicus* shares most of these characters with *E. antiquus*, which is one of the oldest eomyids in Europe. In other features, *E. molassicus* differs from the latter species, especially in the

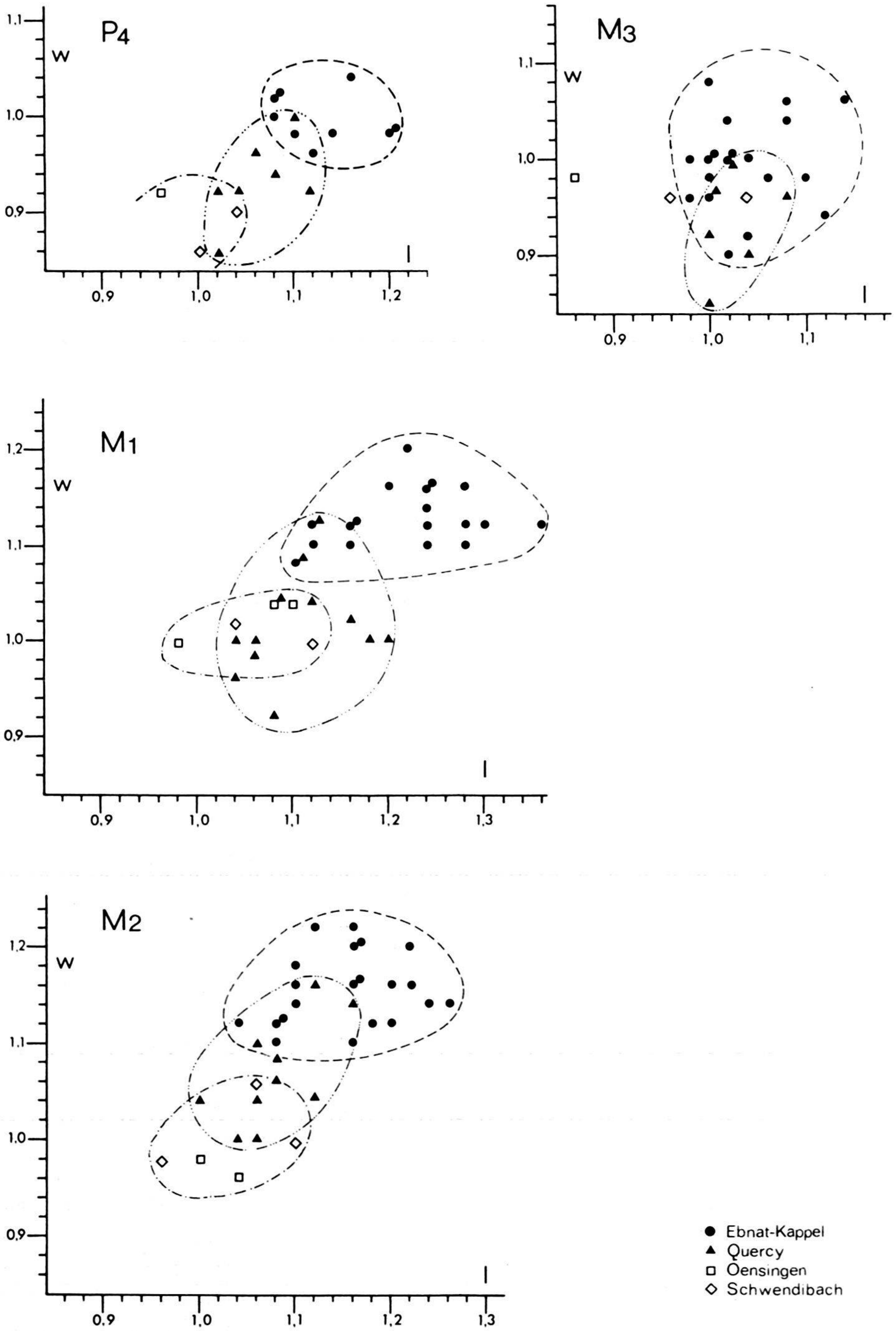


Fig. 7. Scatter diagrams of length (l) and width (w) in $P_4$, $M_1$ $M_2$ and $M_3$ of various *Eomys*-species: Ebnat-Kappel = *E. ebnatensis;* Quercy = *E. zitteli;* Oensingen = *E. molassicus;* Schwendibach = *E. molassicus.*

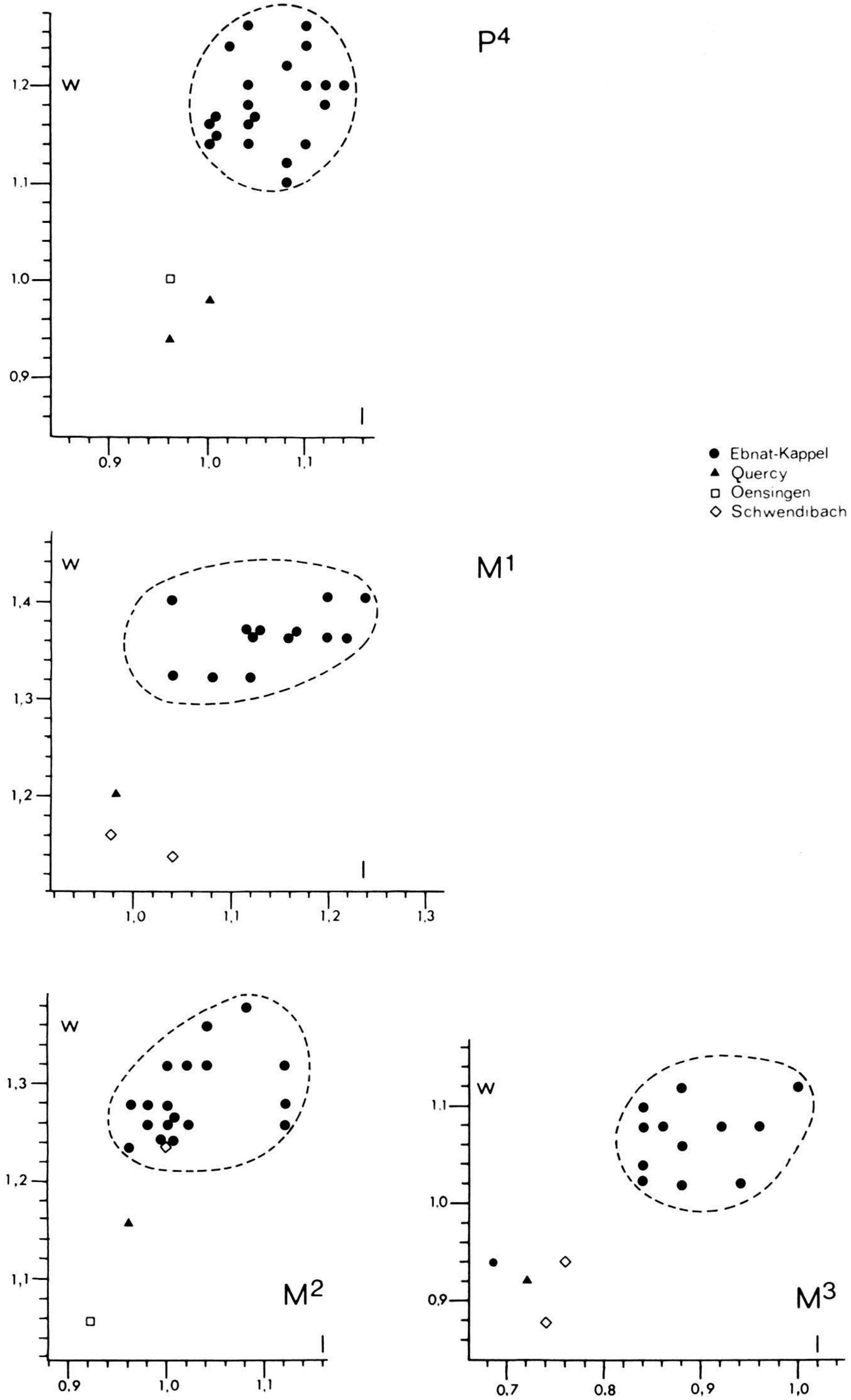


Fig. 8. Scatter diagrams of length (l) and width (w) in $P^4$, $M^1$, $M^2$ and $M^3$ of various *Eomys*-species (see Fig. 7).

better developed anterior cingula, the mesolophids, and the 4th lingual syncline on $M_1$ and $M_2$. With these characters *E. molassicus* fits very well with later species of *Eomys* of the Molasse[1]). Species with a very short mesolophid, as in *E. minor* from Belgarric or *E. quercyi* from Pech du Fraysse (COMTE & VIANEY-LIAUD 1987), are not known from the Molasse.

*E. ebnatensis* is very similar to *E. molassicus*. Both species show long mesolophs in the upper molars, and long mesolophids and transversely aligned metalophids in the lower molars. The most obvious difference between the two species is the crown height of the teeth (Fig. 4): *E. molassicus* has very brachyodont teeth, while those of *E. ebnatensis* are distinctly more hypsodont. In this character the latter species is clearly more advanced. It is easy to infer that *E. ebnatensis* was descended from *E. molassicus*.

*Eomys ebnatensis* has a quite large stratigraphical range. The species occurs in 5 assemblage zones (Wynau 1 – Fornant 6), or even in 6 if *E.* cf. *ebnatensis* from the zone of Rickenbach is included. During this time the species does not undergo any appreciable evolutionary development. In the zone of Wynau 1, for example, the tooth pattern is not more primitive than in that of Fornant 6. Also no increase in size or crown height can be observed. Nevertheless, it is important to keep in mind that, except for Ebnat-Kappel, all other localities have yielded only isolated teeth of *E. ebnatensis*. Whether there is a change in the mandible, we do not yet know.

## Genus *Rhodanomys* DEPÉRET & DOUXAMI 1902

### *Rhodanomys hugueneyae* n. sp.

Fig. 9–14

1969 ?partim *Rhodanomys* sp. B – HUGUENEY, p. 89–90.
1979 *Rhodanomys* sp. – VIANEY-LIAUD, p. 229.
1982 *Rhodanomys transiens* HUGUENEY – ENGESSER & HUGUENEY, p. 62–64.
1984 *Rhodanomys* cf. *transiens* HUGUENEY – ENGESSER, MAYO & WEIDMANN, p. 22.
1984 *Rhodanomys transiens* HUGUENEY – ENGESSER, MAYO & WEIDMANN, p. 31.

*Diagnosis.* – So far the largest species of *Rhodanomys* with primitive *Eomys*-like tooth pattern: $M^1$ mostly with well developed 1st labial syncline and continuous longitudinal crest. $M^2$ mostly with rudimentary 1st labial syncline and continuous or only slightly interrupted longitudinal crest. Mesoloph of $P^4$ moderately long or long. Mesolophid of $M_1$ and $M_2$ medium length to long. 4th lingual syncline of $M_1$ and $M_2$ frequently perceptible.

*Derivatio nominis.* – Named in honor of Dr. Marguerite Hugueney, Lyon, for her important studies on *Rhodanomys*.

*Type.* – Left $M_2$, NMB U.M. 3515, dimensions: 1,28 × 1,14, (Fig. 9b).

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[1]) In a very recent paper COMTE & VIANEY-LIAUD (1987, p. 953) declared that the relationship between the different populations of *Eomys* in the Oligocene seem relatively clear. With this statement, these authors have overestimated the state of our present knowledge and the completeness of our fossil record. It is not possible to fully discuss this problem here. However I would like to state that in my opinion *Eomys* is a very complex and highly ramified group. That the relationships within this genus appear relatively clear is due to the fact that there are no striking changes in the evolution of *Eomys*, and that the different populations are difficult to distinguish. I will deal further with this problem in my monograph on the eomyids of the Swiss Molasse.

*Type locality.* – Road cutting of Rombach, commune of Küttigen, Canton of Aargau (Switzerland), co-ordinates 645975/250650 of the "Schweizerische Landeskarte" 1:25000, sheet 1089 Aarau.

*Age.* – Upper Oligocene, assemblage zone of Küttigen (see ENGESSER & MAYO 1987).

*Stratigraphic range: Rh. hugueneyae* is limited to the assemblage zone of Küttigen. It was also found in some small faunas intermediate in age between the zones of Rickenbach and Küttigen (La Cornalle, Rance, Brochene Fluh 19/20, Basel-St. Jakob) mostly associated with *Eomys huerzeleri* and/or *Issiodoromys*. In the assemblage zone of Brochene Fluh 53 we find a more advanced form: *Rh.* aff. *hugueneyae*.

Other localities with *Rh. hugueneyae:*

Le Gérignoz (ENGESSER, MAYO & WEIDMANN 1984)
La Cornalle (ENGESSER, MAYO & WEIDMANN 1984)
Basel-St. Jakob (ENGESSER & MAYO 1987)
Choulex (Canton of Geneva)
Rances (HUGUENEY & KISSLING 1982; KISSLING 1974)
Brochene Fluh 19/20 (ENGESSER & MAYO 1987)
Talent 18, 19c (ENGESSER, HÜRZELER & MAYO 1986)
Appenzell–Kaubach 3
?Coderet "couche 1" ( = *Rhodanomys* sp. B.)
Hochheim–Flörsheim (SCHAUB 1925)

Localities with *Rh.* aff. *hugueneyae:*

Brochene Fluh 53 (ENGESSER & MAYO 1987)
Findreuse 8 (ENGESSER & HUGUENEY 1982)

*Differential diagnosis:*

*Rh. hugueneyae* differs from *Rh. transiens* HUGUENEY in:

- its larger dimensions,
- the more frequently occurring and more strongly developed 1st labial syncline on $M^1$ and $M^2$,
- its longer mesolophid on $M_1$ and $M_2$,
- its longer mesoloph on $P^4$,
- the less frequent and less distinct interruption of the longitudinal crest of $M^1$ and $M^2$,
- the more frequently developed 4th lingual syncline of $M_2$ and $P_4$.

*Rh. hugueneyae* differs from *Rh. schlosseri* DEPÉRET & DOUXAMI in:

- its distinctly larger dimensions,
- the 1st labial syncline of $M^1$ which is always present and usually well-developed,
- the more developed 1st labial syncline of $M^2$,
- the more continuous longitudinal crest of $M^1$,
- the rarer and less distinct interruption of the longitudinal crest of $M^2$,
- the more frequent occurrence of the 4th lingual syncline on $M_1$ and $M_2$,
- the general presence of the mesoloph on $P^4$,
- having a moderately long mesolophid on $M_1$ and $M_2$ which is never lacking.

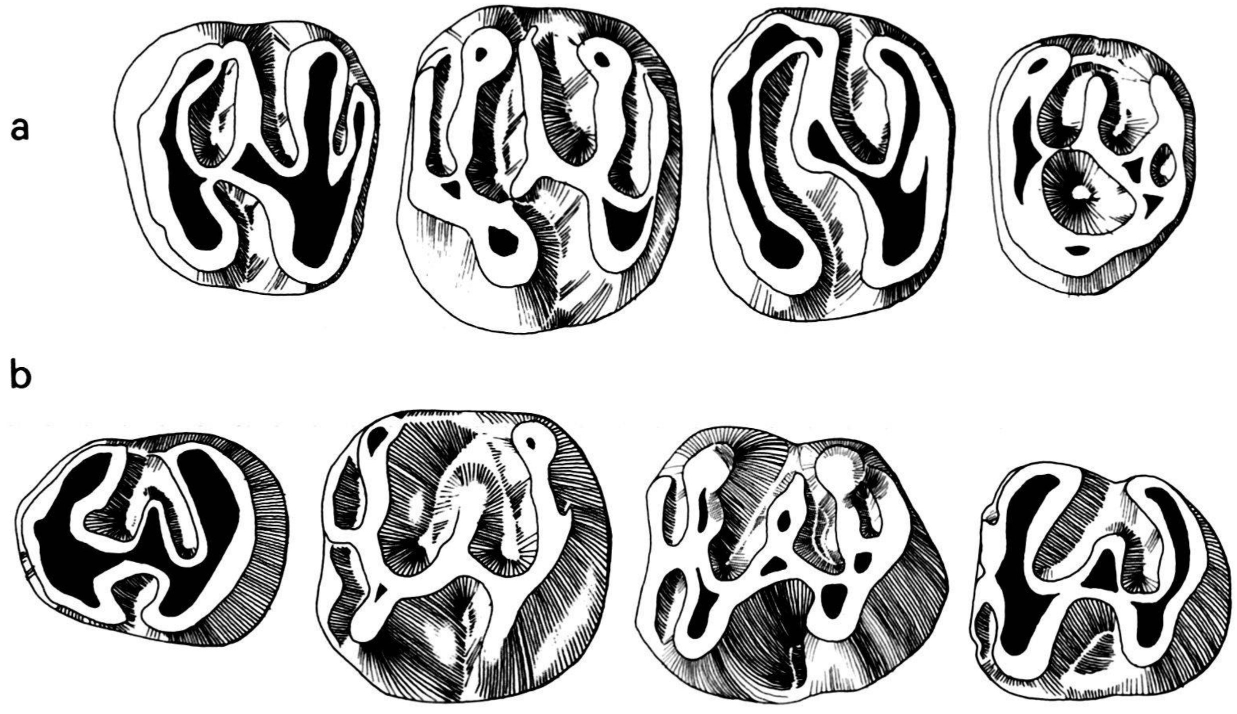


Fig. 9. *Rhodanomys hugueneyae* n. sp. from Küttigen.
a) $P^4$–$M^3$; left $P^4$: U.M. 3498, left $M^1$: H.R. 463, right $M^2$ (inverse): U.M. 3493, right $M^3$ (inverse): U.M. 3518.
b) $P_4$–$M_3$; left $P_4$: H.R. 832, left $M_1$: H.R. 783, left $M_2$, type: U.M. 3515, left $M_3$: U.M. 3509, Naturhistorisches Museum Basel. all figures 25×.

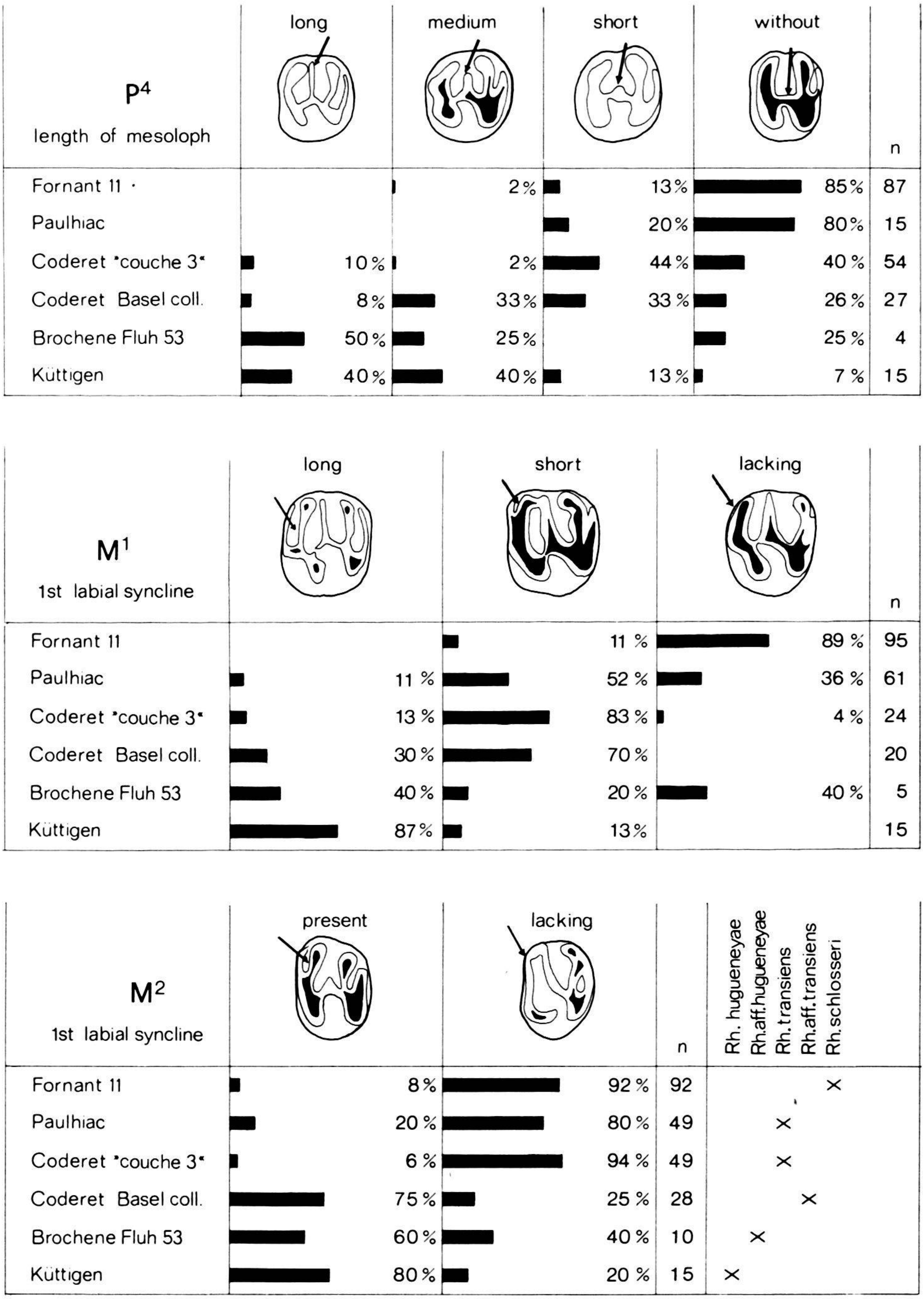
*Rh. hugueneyae* differs from *Rh. oscensis* ALVAREZ SIERRA 1986 in:

— its distinctly larger dimensions,
— its uninterrupted longitudinal crest on $P^4$ and $M^1$,
— the more frequent and better developed 1st labial syncline of $M^1$ and $M^2$,
— the less reduced $M^3$,
— the more frequently developed 4th lingual syncline on $P_4$,
— never lacking the mesolophid on $M_1$ and $M_2$,
— the better developed 4th syncline of $M_1$ and $M_2$.

*Description of the type* (Fig. 9b). – This moderately worn left $M_2$ is quite hypsodont. The lingual cusps are higher and more voluminous than the labial ones. The protoconid is elongated. The metalophid is connected with the anterior arm of the protoconid and the anterior cingulum. The labial part of this ridge is longer than the lingual one. The mesolophid fills almost the whole space between the metalophid and the hypolophid. It is long, but does not reach the lingual edge of the tooth. The hypolophid ends in the posterior arm of the hypoconid. A distinct 4th lingual syncline and a short posterior cingulum are developed.

## *Discussion*

*Rhodanomys* is probably the best documented rodent in the range of the Oligocene/Miocene boundary. It is known from most faunas in this range, and from many localities

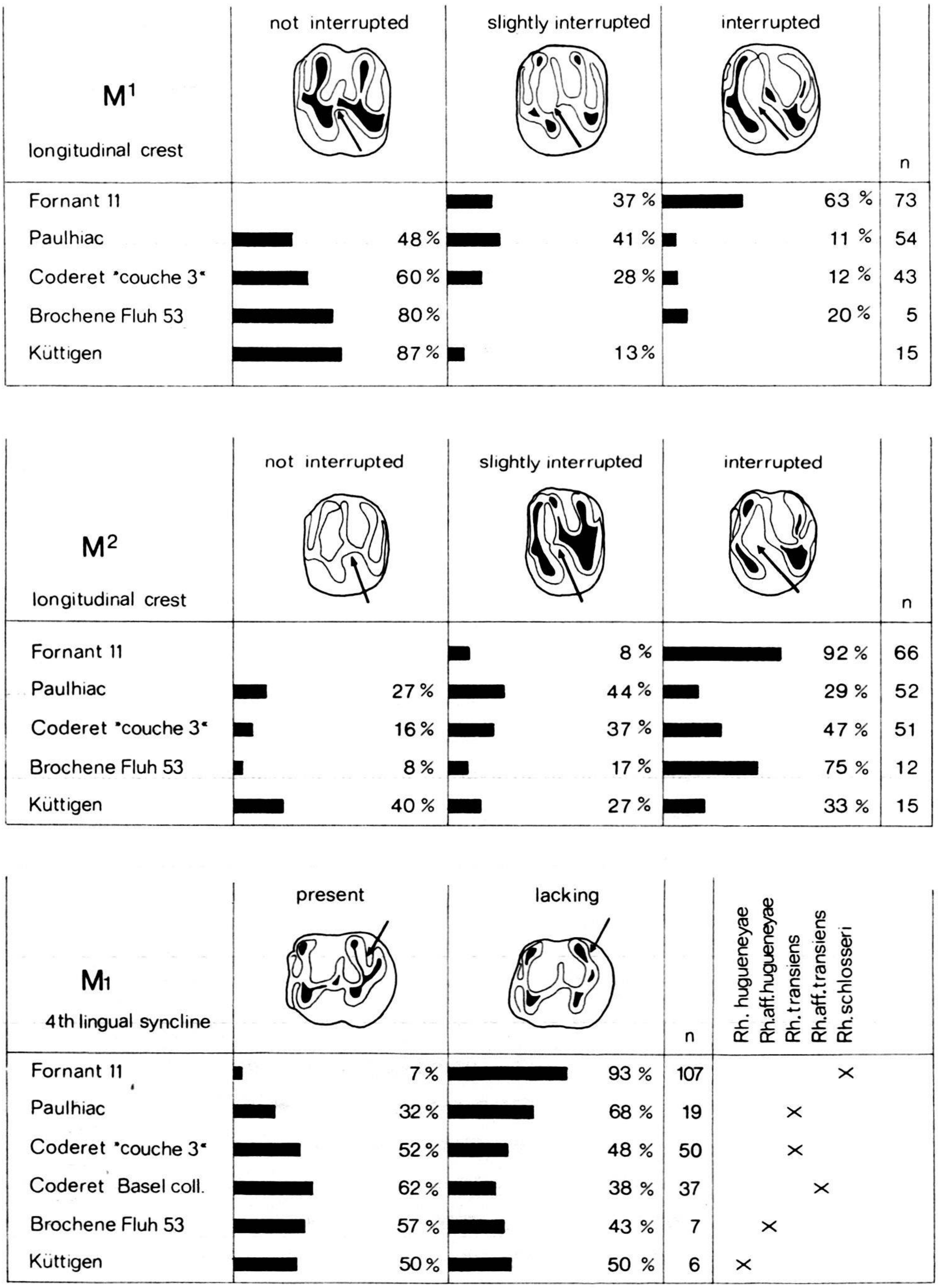


| $P^4$ length of mesoloph | long | medium | short | without | n |
|---|---|---|---|---|---|
| Fornant 11 |  | 2% | 13% | 85% | 87 |
| Paulhiac |  |  | 20% | 80% | 15 |
| Coderet "couche 3" | 10% | 2% | 44% | 40% | 54 |
| Coderet Basel coll. | 8% | 33% | 33% | 26% | 27 |
| Brochene Fluh 53 | 50% | 25% |  | 25% | 4 |
| Küttigen | 40% | 40% | 13% | 7% | 15 |

| $M^1$ 1st labial syncline | long | short | lacking | n |
|---|---|---|---|---|
| Fornant 11 |  | 11 % | 89 % | 95 |
| Paulhiac | 11 % | 52 % | 36 % | 61 |
| Coderet "couche 3" | 13 % | 83 % | 4 % | 24 |
| Coderet Basel coll. | 30 % | 70 % |  | 20 |
| Brochene Fluh 53 | 40 % | 20 % | 40 % | 5 |
| Küttigen | 87 % | 13 % |  | 15 |

| $M^2$ 1st labial syncline | present | lacking | n | Rh. hugueneyae | Rh.aff.hugueneyae | Rh.transiens | Rh.aff.transiens | Rh.schlosseri |
|---|---|---|---|---|---|---|---|---|
| Fornant 11 | 8 % | 92 % | 92 |  |  |  |  | × |
| Paulhiac | 20 % | 80 % | 49 |  |  | × |  |  |
| Coderet "couche 3" | 6 % | 94 % | 49 |  |  | × |  |  |
| Coderet Basel coll. | 75 % | 25 % | 28 |  |  |  | × |  |
| Brochene Fluh 53 | 60 % | 40 % | 10 |  | × |  |  |  |
| Küttigen | 80 % | 20 % | 15 | × |  |  |  |  |

Fig. 10. Quantitative character analysis of various species of *Rhodanomys*.



| M$^1$ longitudinal crest | not interrupted | slightly interrupted | interrupted | n |
|---|---|---|---|---|
| Fornant 11 | | 37 % | 63 % | 73 |
| Paulhiac | 48 % | 41 % | 11 % | 54 |
| Coderet "couche 3" | 60 % | 28 % | 12 % | 43 |
| Brochene Fluh 53 | 80 % | | 20 % | 5 |
| Küttigen | 87 % | 13 % | | 15 |

| M$^2$ longitudinal crest | not interrupted | slightly interrupted | interrupted | n |
|---|---|---|---|---|
| Fornant 11 | | 8 % | 92 % | 66 |
| Paulhiac | 27 % | 44 % | 29 % | 52 |
| Coderet "couche 3" | 16 % | 37 % | 47 % | 51 |
| Brochene Fluh 53 | 8 % | 17 % | 75 % | 12 |
| Küttigen | 40 % | 27 % | 33 % | 15 |

| M$_1$ 4th lingual syncline | present | lacking | n | Rh. hugueneyae | Rh.aff.hugueneyae | Rh.transiens | Rh.aff.transiens | Rh.schlosseri |
|---|---|---|---|---|---|---|---|---|
| Fornant 11 | 7 % | 93 % | 107 | | | | | × |
| Paulhiac | 32 % | 68 % | 19 | | | × | | |
| Coderet "couche 3" | 52 % | 48 % | 50 | | | × | | |
| Coderet Basel coll. | 62 % | 38 % | 37 | | | | × | |
| Brochene Fluh 53 | 57 % | 43 % | 7 | | × | | | |
| Küttigen | 50 % | 50 % | 6 | × | | | | |

Fig. 11. Quantitative character analysis of various species of *Rhodanomys*.

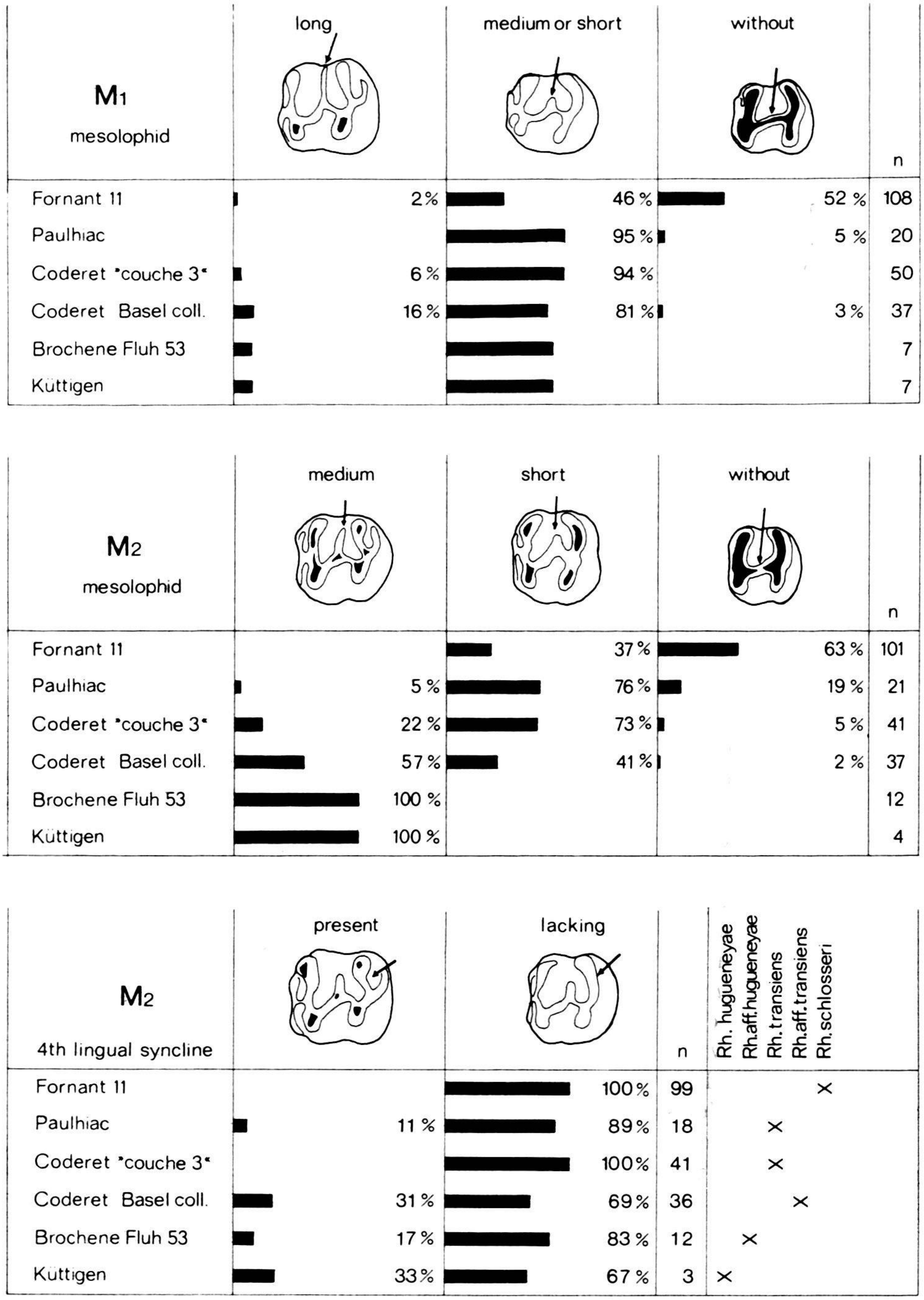


Fig. 12. Quantitative character analysis of various species of *Rhodanomys*.

a rich collection of *Rhodanomys* is available. Therefore we have a clear appreciation of the succession of the several forms, and *Rhodanomys* is very useful for biostratigraphy. In the range of the Neogene mammal zones MN 0 through NM 2a, we can observe the development of the *Rhodanomys* tooth pattern, starting with *Rh. hugueneyae* n. sp. through *Rh. transiens* to *Rh. schlosseri,* and even *Ritteneria.* Consequently, we have quite a precise idea of what is primitive in this genus and what is advanced.

Large size, an *Eomys*-like tooth pattern, with 4 synclines in upper and lower molars, long mesolophs in upper premolars and molars, long mesolophids in lower premolars and molars, and a continuous longitudinal crest in lower molars, are certainly primitive characters.

Based on these criteria *Rhodanomys hugueneyae* is without doubt the most primitive species of the genus. In some cases it might even be difficult to distinguish isolated teeth from those of *Eomys.* In all the features mentioned in the differential diagnosis, *Rh. hugueneyae* is more primitive than *Rh. transiens.* Of course none of these differences is absolute. As is shown in Fig. 10–12 the proportional frequency of characters within the "populations" makes up the differences. With one exception, all the characters mentioned above occur in both species. The exception is the 4th lingual syncline of $M_2$, which occurs only in *Rh. hugueneyae.* Among 41 $M_2$ of *Rh. transiens* from Coderet "couche 3" I could not find any specimen with this syncline.

In 1969, M. Hugueney separated some *Rhodanomys* jaws and teeth, outstanding in size, from *Rh. transiens,* and listed them as *Rhodanomys* sp. B. She (op. cit. p. 90) did not mention any morphological difference compared with *Rh. transiens,* but noted that the $M_1$ was especially large. In its dimensions *Rhodanomys* sp. B comes very well within the range of *Rh. hugueneyae.* I have not seen any material from "couche 1", where most of the material of this rare species comes from. The few isolated teeth I have seen from "couche 3" seem more advanced than those of *Rh. hugueneyae.*

The Figures 10–12 show that *Rh. transiens* from Coderet "couche 3" [the material on which the thesis of M. HUGUENEY (1969) is based] is not identical with the *Rhodanomys* material of the Basel collection. In many respects the latter species is more primitive: The 4th lingual syncline of $P_4$, $M_1$ and $M_2$ is more developed, the mesolophid of $M_1$ and $M_2$ is longer, the mesoloph of $P^4$ is longer and the 1st labial syncline of $M^2$ is better developed. As stated elsewhere (MOJON et al. 1985; ENGESSER & MAYO 1987), the fauna from Coderet of the Basel collection is distinctly older than that of "couche 3".

In the assemblage zone of Brochene Fluh 53 we find a *Rhodanomys* which is quite similar to *Rh. hugueneyae* but more advanced: The 1st labial syncline of $M_1$ and $M_2$ is more reduced, the longitudinal crest of $M^2$ is more often interrupted, and the 4th lingual syncline of $M_2$ shows further reduction. This form which I specify as *Rh.* aff. *hugueneyae* is also known from Findreuse 8 (ENGESSER & HUGUENEY 1982).

In the western Molasse, *Rh. transiens* apparently does not occur in the Oligocene. This species, which is somewhat smaller and more advanced than *Rh. hugueneyae,* has so far been found only in the zone of Boudry 2 (Lowermost Miocene). The best material of *Rh. transiens* has been found in Les Pierrettes near St-Sulpice, a new locality discovered by Marc Weidmann. *Rh. transiens* also occurs in the lower Miocene of Paulhiac. As shown in Figures 10–12 the *Rhodanomys* from Coderet "couche 3" and Paulhiac are very similar. In some features the form from Paulhiac is a little more advanced, while in others the Coderet form is more advanced. Also they are almost identical in size.

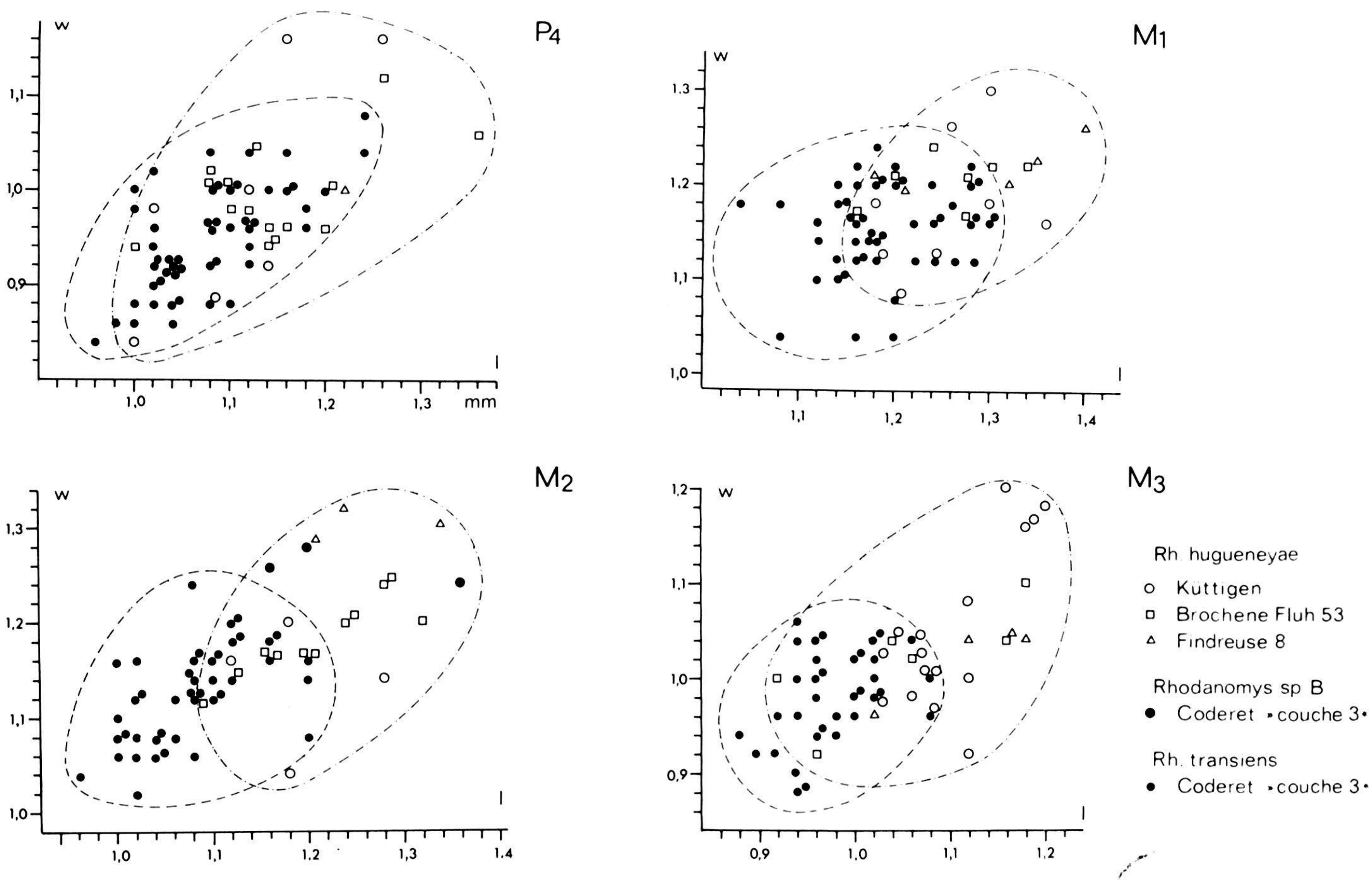


Fig. 13. Scatter diagrams of length (l) and width (w) in $P_4$, $M_1$, $M_2$ and $M_3$ of various *Rhodanomys* «populations»: Küttigen = *Rh. hugueneyae*; Findreuse 8 = *Rh.* aff. *hugueneyae*; Brochene Fluh 53 = *Rh.* aff. *hugueneyae*; Coderet «couche 3» = *Rh. transienes* and *Rh.* sp. B.

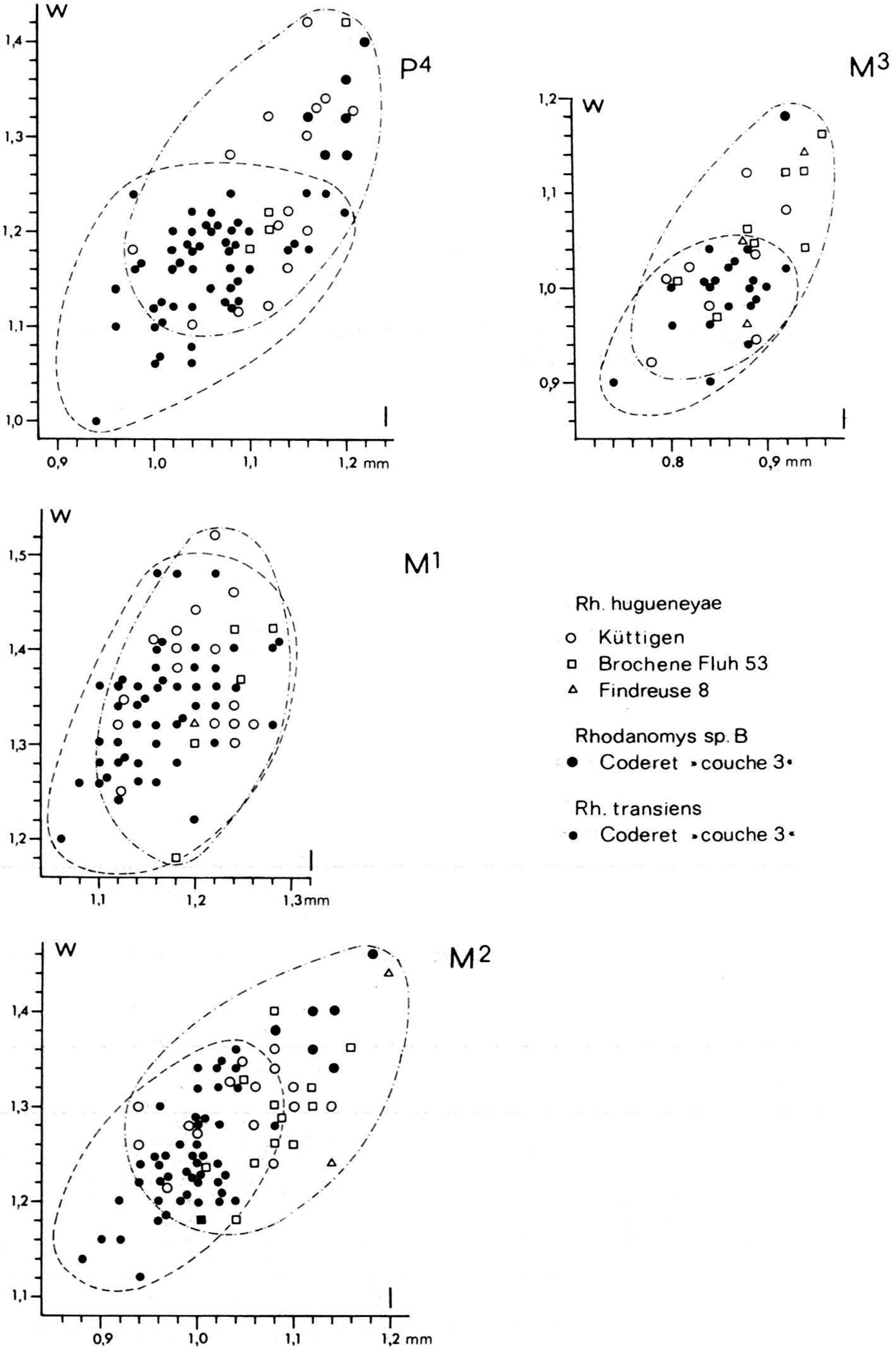


Fig. 14. Scatter diagrams of length (l) and width (w) in $P^4$, $M^1$, $M^2$ and $M^3$ of various *Rhodanomys* «populations» (see Fig. 13)

As a consequence of the fact that *Rh.* aff. *hugueneyae*, a primitive *Rhodanomys*, is found in the Uppermost Oligocene of the Molasse and that *Rh. transiens* occurs only in the Lowermost Miocene, the question arises as to the position of the Coderet "couche 3" in the zonation of the Molasse. If we suppose that *Rh. transiens* succeeds *Rh. hugueneyae* – the consequent simplification of the tooth pattern and the decrease in size point to this[2]) – we have to calibrate Coderet "couche 3" between the assemblage zones of Brochene Fluh 53 and Boudry 2. The only difficulty with this calibration is the occurrence of *Issiodoromys* and *Archaeomys* in Coderet "couche 3". In the Molasse, *Issiodoromys* has already disappeared within the Rickenbach zone, *Archaeomys* within the Küttigen zone. These differences might be due to ecological differences or to regional differences in the faunal composition between the two basins.

*Rhodanomys schlosseri* has an even more simplified tooth pattern than *Rh. transiens* (see Fig. 10–12), and is distinctly smaller. This species seems to be limited to the zone of Fornant 11. Within this zone, the record of the genus *Rhodanomys* is coming to an end. However, the process of simplification of the tooth pattern and size decrease continues with *Ritteneria* in which the marginal synclines and the longitudinal crests become very reduced. The genus *Ritteneria* is known only from the assemblage zone of La Chaux.

## Genus *Eomyodon* n. gen.

*Diagnosis.* – Small to medium sized eomyids with an *Eomys*-like tooth pattern, and a tendency to develop lophodont cheek teeth. Molars of primitive species very brachyodont, of the advanced ones, moderately hypsodont. Longitudinal crest of upper and lower molars often interrupted, more in advanced forms than in primitive ones. Hypolophid of $P_4$, $M_1$, and $M_2$ joining the posterior cingulum respectively the posterior arm of hypoconid as in *Eomys*. Anterior cingulum of lower molars connected far labially, with the protoconid, or not connected at all; in primitive forms connected with the anterior arm of protoconid as in *Eomys*. Mesoloph of upper premolars and molars, and mesolophid of the lowers, mostly long. Metalophid of lower molars often backwardly directed. $P^4$ mostly lacking a 1st labial syncline or very poorly developed. $M_3$ quite often with hypolophid. Lower incisor with longitudinal enamel ridge on the outside.

*Derivatio nominis.* – *Eomyodon* = greek "*Eomys* toothed", because of the similarity of the tooth pattern with that of *Eomys*. Originally I was proposing to name this genus "*Eomyoides*", but Volker Fahlbusch found that this name was too difficult to pronounce. At a concert in Munich in January 1986, during the 5th symphony of Schubert, Volker passed to me his concert programme on which he had written the name "*Eomyodon*".

*Type species.* – *Eomyodon volkeri* n. sp.

*Other species included in this genus.* – *Eomyodon pusillus* (FAHLBUSCH 1969) ( = *Pseudotheridomys pusillus*) and two undescribed species of the lower Aquitanien.

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[2]) In their recent paper COMTE & VIANEY-LIAUD (1987) derive *Rh. transiens* from *Eomys quercyi*. This is not possible in my opinion because – as shown in Figure 12 – the lower molars of *Rhodanomys* undergo a reduction of the mesolophid. Based on the description and the figure presented by COMTE & VIANEY-LIAUD (1987), *E. quercyi* has a much shorter mesolophid than does *Rh. transiens*. Consequently, *E. quercyi* has to be considered as more advanced than *Rh. transiens* in this feature. In addition, the $M^1$ and $M^2$ of *Rh. transiens* usually show a long mesoloph, whereas those of *E. quercyi* (see Fig. 4 in COMTE & VIANEY-LIAUD) seem to have a moderately long one. In my opinion *Rh. transiens* is more likely to have been derived from *Rh. hugueneyae* than from *E. quercyi*.

*Stratigraphical range of the genus.* – Upper Oligocene to Lower Miocene, assemblage zones of Fornant 6 to Fornant 11.

*Differential diagnosis.* –

From *Pseudotheridomys* SCHLOSSER 1926, *Eomyodon* differs in:

- its hypolophid of lower P and M, which is directed backward and ends in the posterior cingulum or the posterior arm of hypoconid, but never meets the anterior arm of hypoconid as in *Pseudotheridomys,*
- its much shorter 1st labial syncline on the upper molars,
- its lack of a well developed 1st labial syncline on P$^4$,
- the labial connection of the anterior cingulum with the protoconid on the lower molars,
- the lack of the secondary ridge between metalophid and mesolophid on the lower molars, which is typical of *Pseudotheridomys,*
- the commonly backwardly directed metalophid of lower molars.

From *Eomys* SCHLOSSER 1884, *Eomyodon* differs in:

- its more lophodont cheek teeth,

Fig. 15 a) *Eomyodon volkeri* n. gen., n. sp. from Chavanne, D$^4$, P$^4$–M$^3$; right D$^4$ (inverse): Sav. 408, left P$^4$: Sav. 400, left M$^1$: Sav. 401, left M$^2$: Sav. 402, left M$^3$: Sav. 403.

b) *Eomyodon volkeri* n. gen., n. sp. from Chavanne, D$_4$, P$_4$–M$_3$; left D$_4$: Sav. 409, left P$_4$: Sav. 404, left M$_1$, type: Sav. 405, right M$_2$ (inverse); Sav. 406, right M$_3$: Sav. 407.

c) *Eomyodon volkeri* n. gen., n. sp. from Fornant 6, P$_4$–M$_3$; right P$_4$ (inverse): Sav. 410, left M$_1$: Sav. 67, right M$_2$ (inverse); Sav. 412, left M$_3$: Sav. 413. – All specimens of the Naturhistorisches Museum Basel.

all figures 25×.

- the more frequently interrupted longitudinal crest of the lower and upper molars,
- its tendency to replace the junction of the anterior cingulum and the anterior arm of protoconid by a more labially placed connection,
- the better developed 1st labial syncline of the upper molars,
- the more frequently backwardly directed metalophid of the lower molars,
- the more frequent presence of a hypolophid on $M_3$.

### *Eomyodon volkeri* n. gen., n. sp.

Fig. 15–18

partim 1968 *Pseudotheridomys* aff. *parvulus* (SCHLOSSER) – FAHLBUSCH, p. 224–232.
partim 1969 *Pseudotheridomys pusillus* n. sp. – FAHLBUSCH p. 673–679.
partim 1970 *Pseudotheridomys pusillus* FAHLBUSCH – FAHLBUSCH p. 1–133.
partim 1977 *Pseudotheridomys parvulus* SCHLOSSER – AGUILAR, p. 88–89.
1981 *Pseudotheridomys schaubi* LAVOCAT, morphotype *Eomys* – BRUNET et al., p. 334, 346–348.
1982 *Pseudotheridomys* aff. *pusillus* FAHLBUSCH – ENGESSER & HUGUENEY, p. 67–69.
1985 *"Pseudotheridomys" pusillus* FAHLBUSCH – MOJON et al., p. 640–644.
partim 1986 *Eomys pusillus* (FAHLBUSCH) – ALVAREZ SIERRA, p. 161.

*Derivatio nominis.* – Honoring Prof. Dr. Volker Fahlbusch, the eminent expert in eomyids.

*Type.* – Left $M_1$, Sav. 405, Naturhistorisches Museum Basel

*Dimensions.* – 0,93 × 0,82 mm.

*Type locality.* – Chavanne near Frangy, Savoy.

*Referred material from the type locality.* – 18 isolated teeth.

*Age.* – Upper Oligocene, assemblage zone of Fornant 6 (see ENGESSER & MAYO 1987).

*Stratigraphic range.* – Assemblage zone of Fornant 6 until Brochene Fluh 53.

*Other localities with E. volkeri:*

Fornant 6 (ENGESSER & MAYO 1987)
Boudry-La-Fabrique (Mojon et al. 1985)
Ruisseau du Bey (JORDI 1955)
Appenzell-Kaubach 3
Brochene Fluh 19/20 and 53 (ENGESSER & MAYO 1987)
Gaimersheim (FAHLBUSCH 1969, 1970)
?Weissenburg 6 (FAHLBUSCH 1968)
?Nouvelle Faculté de Médecine (AGUILAR 1977).

*Differential diagnosis.* –
From *Eomyodon pusillus* (FAHLBUSCH), *E. volkeri* differs in:

- the smaller size of its cheek teeth,
- its much smaller lower incisor (fig. 16),
- the longer mesolophid on its lower P and M,
- the larger 4th lingual syncline of its lower P and M.

*Description of the type.* – This slightly worn left $M_1$ is longer than wide. Its anterior cingulum is not connected with the protoconid. The metalophid is transversely aligned and joins the anterior arm of the protoconid. The mesolophid is very long and ends in a mesostylid. The longitudinal crest is aligned along the longitudinal axis of the tooth. It is

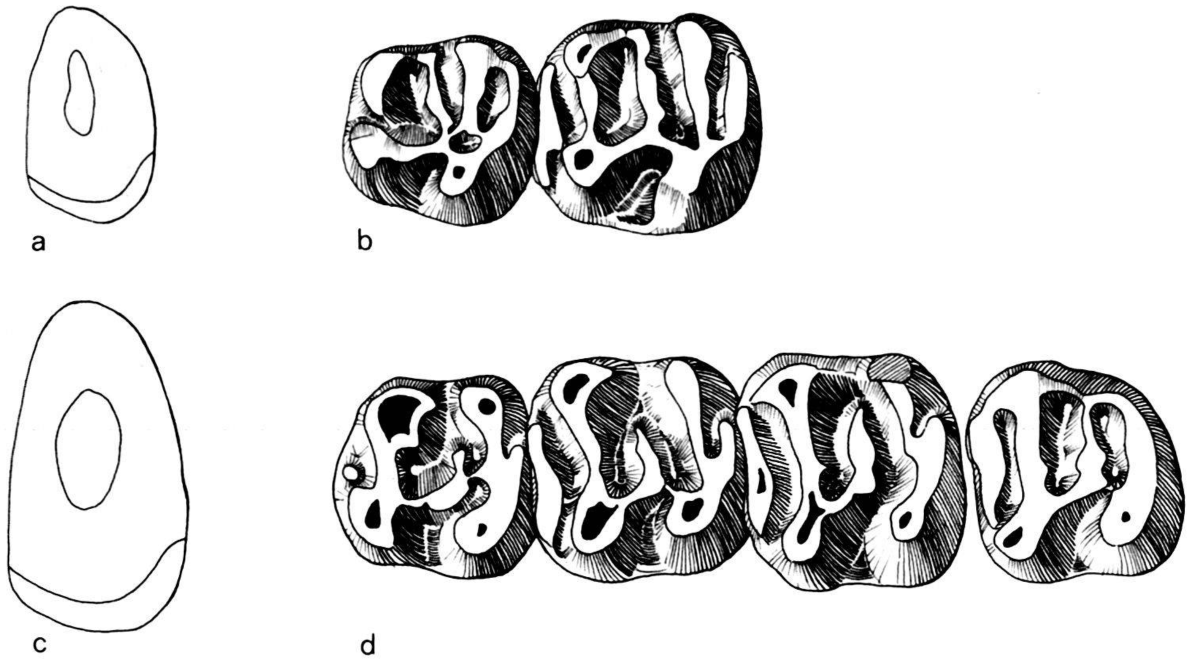

Fig. 16 a) *Eomyodon volkeri* n. gen., n. sp. from Gaimersheim, right lower incisor (inverse, cross-section) of the mandible fragment 1952 II 2236.

b) same mandible as under a), right $P_4$–$M_1$ (inverse).

c) *Eomyodon pusillus* (Fahlbusch) from Gaimersheim right lower incisor (inverse, cross-section): 1952 II 2204.

d) *Eomyodon pusillus* (Fahlbusch) from Gaimersheim, right mandible (inverse) with $P_4$–$M_3$, type: 1952 II 2198. – All specimens of the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.
all figures 25×.

interrupted behind the moderately developed mesoconid. The hypolophid is backward directed and joins the posterior arm of hypoconid. The 4th lingual syncline is very spacious.

*Description of the dentition* (based on the material from Chavanne, Fornant 6, and Boudry-La-Fabrique). – The $P_4$ generally does not have an anteroconid. The mesolophid is usually long, and the longitudinal crest is only rarely interrupted. The 4th lingual syncline is very well developed.

The other $M_1$s correspond well with the type specimen, except that the longitudinal crest is not always interrupted, and that the anterior cingulum is sometimes connected with the anterior arm of the protoconid. Some specimens show a medium to long mesolophid.

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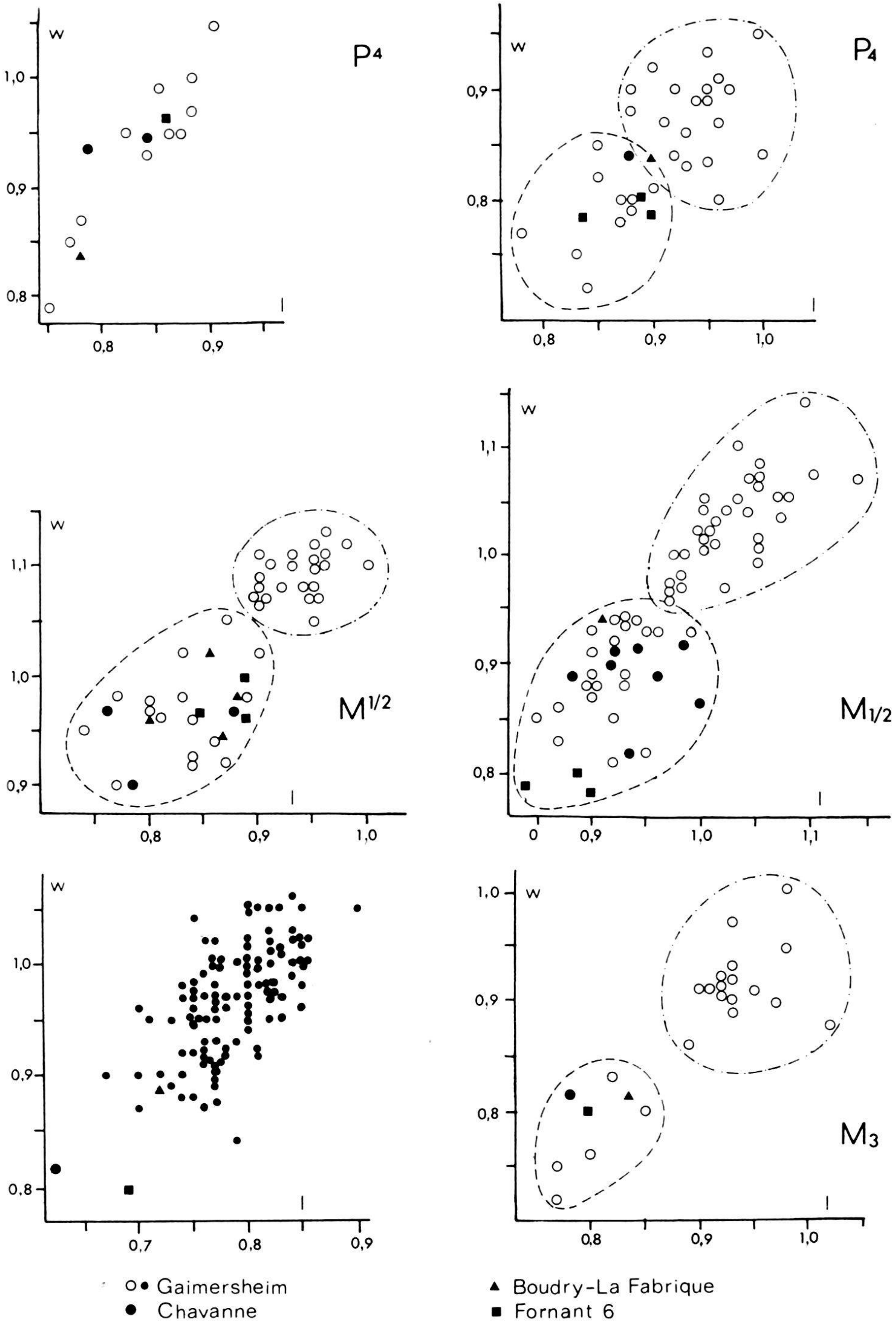
Fig. 17. Scatter diagrams of length (l) and width (w) of upper and lower premolars and molars of *Eomyodon volkeri* and *E. pusillus*.

Gaimersheim *E. volkeri* and *E. pusillus*
Chavanne
Fornant 6 } *E. volkeri*
Boudry-La-Fabrique

Measurements of the specimens from Gaimersheim after Fahlbusch (1970).
in $M^3$: Eomyodon and Eomys from Gaimersheim are not distinguishable.


P4
w
1,0
0,9
0,8
l
0,8
0,9
P4
w
0,9
0,8
l
0,8
0,9
1,0
M1/2
w
1,1
1,0
0,9
l
0,8
0,9
1,0
M1/2
w
1,1
1,0
0,9
0,8
l
0
0,9
1,0
1,1
w
1,0
0,9
0,8
l
0,7
0,8
0,9
M3
w
1,0
0,9
0,8
l
0,8
0,9
1,0
○● Gaimersheim
● Chavanne
▲ Boudry-La Fabrique
■ Fornant 6

In the $M_2$ the longitudinal crest is less often interrupted than in $M_1$, and the mesolophid is often moderately long.

The $M_3$ is relatively large. Its anterior cingulum is mostly connected with the anterior arm of the protoconid. The mesolophid is very long and the longitudinal crest is uninterrupted. Some specimens show a well-developed hypolophid (see Fig. 15c).

The $P^4$ is almost as large as the $M^1$. It has mostly a continuous longitudinal crest and a long mesoloph.

The $M^1$ and $M^2$ have a well-developed 1st labial syncline. Their paracone often has a posterior ridge. The mesoloph is very variable. It can be short, moderately long or long. The longitudinal crest is more often interrupted in $M^1$ than it is in $M^2$.

The $M^3$ mostly shows 5 anticlines and a sinus.

### *Discussion*

Fahlbusch was the first author to notice the peculiarity of the eomyids described here as *Eomyodon.* He also pointed out the morphological similarity with *Pseudotheridomys* and with *Eomys,* and he saw in his *P. pusillus* a primitive *Pseudotheridomys.* For this reason he considered it unnecessary to create a new genus (1970, p. 83).

The co-occurrence of *Eomyodon* and *Pseudotheridomys schaubi* in most localities prevented for a long time the recognition of the two eomyids as separated taxa. Thus FAHLBUSCH (1970), in his description of the eomyids from Weissenburg 6, emphasized the great variability of *"Pseudotheridomys* aff. *parvulus".* Similarly, AGUILAR (1977), in his publication of the fauna from Nouvelle Faculté de Médecine, mentioned teeth of *Eomys* type and others of *Pseudotheridomys* type among his material of *Pseudotheridomys parvulus.* Also BRUNET et al. (1981), in their description of the fauna of Cournon-Les-Souméroux, pointed to the great variability of *Pseudotheridomys schaubi,* from which they were able to distinguish two morphotypes: Morphotype *Eomys* and morphotype *Pseudotheridomys.* With the exception of Weissenburg 6 I have not seen any original material from these localities. Nevertheless I have been convinced for a long time (see MOJON et al. 1985) that in all three faunas two eomyids of about the same size occur together: *Pseudotheridomys schaubi* and *Eomyodon volkeri.* More recently ALVAREZ-SIERRA (1986, p. 158) has also suggested that the two morphotypes of *Pseudotheridomys schaubi* from Cournon-Les-Souméroux represent two different taxa, namely *P. schaubi* and a small species of *Eomys.*

In the Swiss Molasse *Eomyodon* and *Pseudotheridomys* are found together in most localities, but there are several localities in which only *Eomyodon* occurs (e.g. Fornant 6 and Chavanne). It is also very intriguing that the two genera emerge at about the same time, in the assemblage zone of Fornant 6[3]). In addition, it is interesting to note that a still undescribed species of *Eomyodon* co-exists with a possible new species of *Pseudotheridomys* in the lower Aquitanien. However, *Eomyodon* disappears after the zone of Fornant 11, while *Pseudotheridomys* persists until the Neogene mammal zone MN3.

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[3]) M. HUGUENEY (1980) mentions *Pseudotheridomys pusillus* from St-Henri. I have not seen any material from this locality, which corresponds in age with our assemblage zone of Wynau 1. In the Swiss Molasse in the Wynau zone, a small eomyid is recorded which a have identified as *Eomys molassicus.* This form is probably identical with that from St-Henri.

The fact that *Pseudotheridomys* and *Eomyodon* occur separately at different sites proves that the two taxa cannot be merely morphotypes of a single species. Moreover, in samples which contain both genera, isolated teeth can easily been attributed to one or the other taxon (see differential diagnosis of the genera). Teeth with an intermediate morphology, as mentioned by BRUNET et al. (1981), I have never come across.

Some authors (FAHLBUSCH 1970, BRUNET et al. 1981, COMTE & VIANEY-LIAUD 1987) considered *Eomyodon pusillus* as an ancestor of *Pseudotheridomys parvulus* respectively *P. schaubi*. In my opinion, taking into account the new materials of the western Molasse, it can be demonstrated that we are dealing with two independent lines (see Fig. 18). The fact that *Eomyodon* and *Pseudotheridomys* emerged at the same time also points in this direction. It is true of course that *Eomyodon* has a more primitive tooth pattern, from which the more complicated one of *Pseudotheridomys* theoretically could have been developed, but the primitive characters of *Eomyodon* are those of *Eomys*. It is very easy to consider that both genera developed from primitive *Eomys* forms. In the case of *Eomyodon* and *Pseudotheridomys* we are apparently dealing with parallel evolution, in the course of which several morphological conformities were developed: lophodont cheek teeth, interruption of the longitudinal crest in upper and lower premolars and molars, development of a 1st labial syncline in $P^4$ (but in *Eomyodon* only in the youngest forms). While crown height stays about the same in *Pseudotheridomys* during the course of its evolution, it is possible to observe a distinct increase of crown height over time in *Eomyodon*.

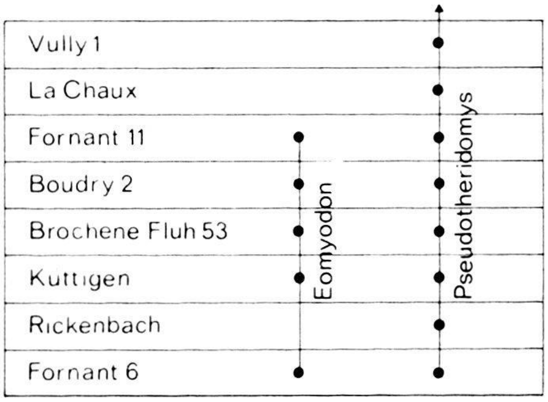

Fig. 18. The stratigraphical range of *Eomyodon* and *Pseudotheridomys*.

## Family ***Dipodidae*** WATERHOUSE 1842
## Genus *Plesiosminthus* VIRET 1926

### *Plesiosminthus winistoerferi* n.sp.

Fig. 19–26

*Diagnosis.* – Very large species of *Plesiosminthus* with very long and strong posterior arm of protoconid on $M_2$ and $M_3$, double protoloph on $M^2$ and $M^3$, and little reduced $M^3_3$. $M_1$ always with secondary ridge between metalophid and mesolophid. Entoloph of $M^2$

situated far lingually, ectolophid of $M_2$ and $M_3$ far labially. Connection between protoconid and anterior cingulum of $M_2$ and $M_3$ sometimes interrupted. $M_2$ equally as wide as $M_1$ but somewhat longer. Upper molars with 3 roots. Upper incisor with longitudinal groove (dental terminology after WANG 1985).

*Derivatio nominis:* Honoring Mr. Herbert Winistörfer from Balsthal who found the type locality together with Mr. Daniel Kälin. These two students also collected most of the reference material of this new species.

*Type:* left $M_2$, Br. F. 1, Naturhistorisches Museum Basel, dimensions: 1,34 × 1,04 mm.

*Referred material:* 32 isolated teeth.

*Type locality:* Section of Brochene Fluh near Waldenburg (Baselland, Switzerland), level 53 (numeration after BAUMBERGER 1927): conglomeratic layer of about 10 cm with Unios.

*Age:* Uppermost Oligocene, assemblage zone of Brochene Fluh 53 (see ENGESSER & MAYO 1987).

*Stratigraphic range: P. winistoerferi* seems to be limited to the assemblage zone of Brochene Fluh 53. It has not yet been found in older or younger assemblage zones.

Other localities with *P. winistoerferi:*

Findreuse 11 (ENGESSER & HUGUENEY 1982)
Findreuse 14.

*Differential diagnosis. –*

From *Plesiosminthus promyarion* SCHAUB 1930, *P. winistoerferi* differs in:

- its considerably larger dimensions,
- its well-developed posterior arm of protoconid of $M_2$ and $M_3$, which in $M_2$ is mostly in ontact with the mesolophid (respectively the mesostylid),
- having $M^2_2$ distinctly larger than $M^3_3$,
- its better developed protoloph II on $M^2$ and $M^3$,
- its more labially situated ectolophid on $M_2$ and $M_3$,
- its more lingually situated entoloph on $M^2$,
- its more anteriorly inclined hypolophid on $M_1$ and $M_2$,
- its secondary ridge between metalophid and mesolophid on $M_1$,
- the occasional interruption of the connection between the anterior cingulum and the protoconid on $M_2$ and $M_3$.

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Fig. 19 a) *Plesiosminthus winistoerferi* n. sp. from Findreuse 11, fragment of a right $M_2$ (inverse): Sav. 414.

b) *Plesiosminthus winistoerferi* n. sp. from Brochene Fluh 53, $M_1$–$M_3$; left $M_1$: K.B.F. 1, left $M_2$, type: Br. F. 1, right $M_3$ (inverse): K.B.F. 2.

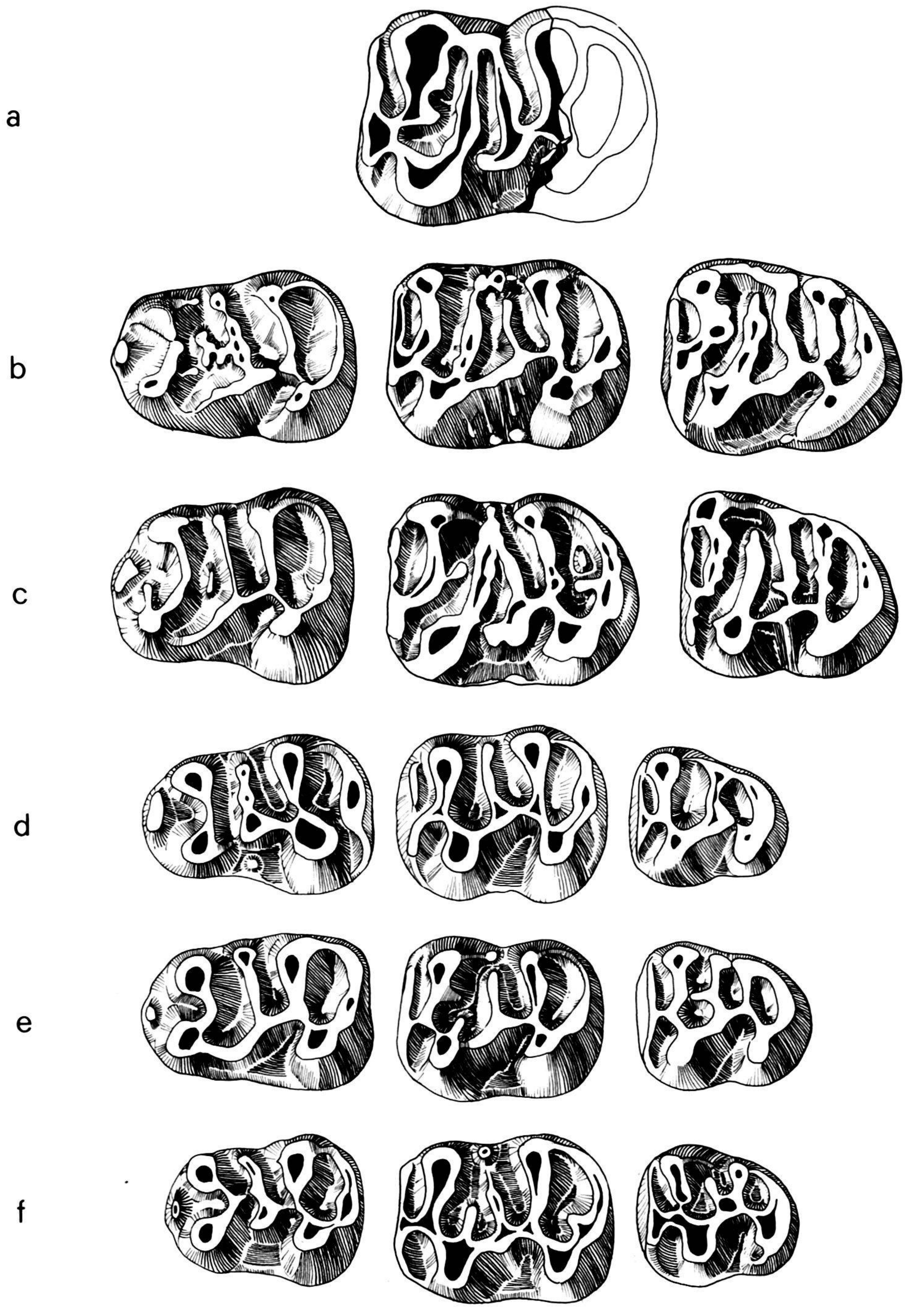
c) *Plesiosminthus winistoerferi* n. sp. from Brochene Fluh 53, $M_1$–$M_3$; right $M_1$ (inverse): K.B.F. 3, right $M_2$ (inverse): K.B.F. 4, left $M_3$: K.B.F. 5.

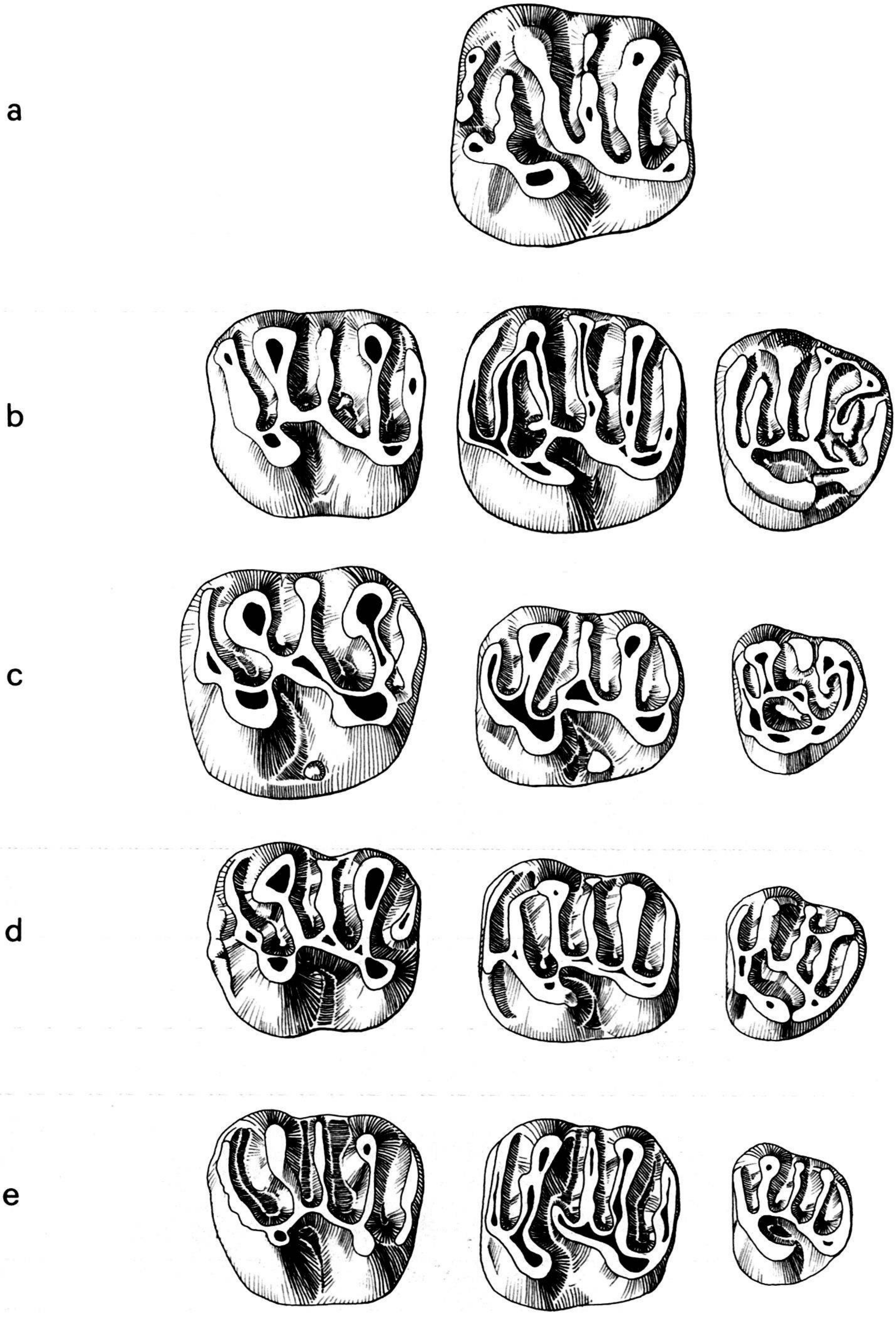
d) *Plesiosminthus schaubi* VIRET from Coderet (Basel collection), $M_1$–$M_3$; left $M_1$: Cod. 2852, left $M_2$: Cod. 2853, left $M_3$: Cod. 2854.

e) *Plesiosminthus myarion* SCHAUB from Fornant 11, $M_1$–$M_3$; left $M_1$: Sav. 416, left $M_2$: Sav. 417, right $M_3$ (inverse): Sav. 418.

f) *Plesiosminthus promyarion* SCHAUB from Ruisseau du Bey, $M_1$–$M_3$; left $M_1$: R.B. 50, left $M_2$: R.B. 51, right $M_3$ (inverse): MGL 42287. – Specimens with K.B.F.-numbers: collection D. Kälin, Balsthal, those with MGL-numbers: Musée géologique Lausanne, all the other specimens: Naturhistorisches Museum Basel.

all figures 25×.


a
b
c
d
e
f


a
b
c
d
e

From *Plesiosminthus schaubi* VIRET 1926, *P. winistoerferi* differs in:

- its larger dimensions,
- its well-developed posterior arm of protoconid on $M_2$ and $M_3$, a ridge never observed in *P. schaubi*,
- its much larger $M_3^3$ (with 5 lingual anticlines instead of 3 in *P. schaubi*),
- its double protoloph on $M^2$ and $M^3$,
- its less developed mesoconid on the lower molars,
- its less bunodont structure of the molars,
- the occasional interruption of the connection between the anterior cingulum and the protoconid on $M_2$ and $M_3$.

From *Plesiosminthus myarion* SCHAUB 1930, *P. winistoerferi* differs in:

- its considerably larger dimensions,
- its posterior arm of protoconid on $M_2$ and $M_3$ better developed than the mesolophid, and mostly connected with the mesolophid,
- its better developed protoloph II on $M^3$,
- its more lingually situated endoloph on $M^2$,
- its secondary ridge between metalophid and mesolophid on $M_1$,
- the occasional interruption of the connection between the anterior cingulum and the protoconid on $M_2$ and $M_3$.

*Description of the type* (Fig. 19b). – The rather low-crowned $M_2$ shows four not very voluminous main cusps connected by strong ridges. The lingual part of the anterior cingulum is well-developed, whereas the labial part is very short. The metalophid joins the anteroconid. The posterior arm of the protoconid is very strong, and connected with the mesostylid. A distinct mesoconid cannot be observed. The mesolophid, which is much weaker than the posterior arm of protoconid, joins the mesostylid. The entoconid is situated close to the mesostylid, with the consequence that the hypolophid is inclined anteriorly. On the posterior cingulum a hypoconulid can be observed. The sinusid is strongly oblique and narrow.

*Description of the dentition.* – $M_1$ (Fig. 19b, c) shows in all specimens a small anteroconid which is not connected with the protoconid or metaconid. These latter two cusps are connected by a curved metalophid II. The mesolophid in all specimens is long and ends in a mesostylid. Between metaconid and mesolophid there is a secondary ridge in all specimens. The ectolophid ends at the base of the protoconid without reaching it. There is

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Fig. 20 a) *Plesiosminthus winistoerferi* n. sp. from Findreuse 14, right $M^2$ (inverse): Sav. 415.

b) *Plesiosminthus winistoerferi* n. sp. from Brochene Fluh 53, $M^1$–$M^3$; right $M^1$ (inverse): K.B.F. 6, left $M^2$: K.B.F. 7, right $M^3$ (inverse): K.B.F. 8.

c) *Plesiosminthus schaubi* VIRET from Coderet (Basel collection), $M^1$–$M^3$; left $M^1$: Cod. 2855, left $M^2$: Cod. 2856, left $M^3$: Cod. 2857.

d) *Plesiosminthus myarion* SCHAUB from Fornant 11, $M^1$–$M^3$; left $M^1$: Sav. 419, left $M^2$: Sav. 420, right $M^3$ (inverse): Sav. 421.

e) *Plesiosminthus promyarion* SCHAUB from Ruisseau du Bey, $M^1$–$M^3$; left $M^1$: R.B. 52, left $M^2$: R.B. 53, right $M^3$ (inverse): MGL 42290. – Specimens with K.B.F.-numbers: collection D. Kälin, Balsthal, those with MGL-numbers: Musée géologique Lausanne, all the other specimens: Naturhistorisches Museum Basel.

all figures 25×.

no distinct mesoconid. The hypolophid is inclined anteriorly. The last syncline is very wide. Three of the four $M_1$s show a little hypoconulid, of which two have a short anterior spur.

$M_2$ (Fig. 19b, c): In contrast to the type (and the two other specimens), one $M_2$ shows a posterior arm of the protoconid which is not connected with the mesolophid (respectively the mesostylid). The connection between the protoconid and the anterior cingulum in all specimens is not very strong. In one specimen, this connection is clearly interrupted, and the metalophid is curved anteriorly. Such an interruption could not be observed in any other species of *Plesiosminthus*. Two of four specimens show a hypoconulid, one with a short anterior spur.

The $M_3$ (Fig. 19b, c) is very large and shows the same pattern as the $M_2$. A strong posterior arm of protoconid is always present, but it does not reach the mesolophid in all specimens. In one specimen it reaches the base of the metaconid, as is often the case in the $M_2$ of *P. myarion*. As in $M_2$, the protoconid is not always connected with the anterior cingulum. The mesolophid is long in all specimens. In some $M_3$s a distinct ectomesolophid is developed. The ectolophid is situated far lingually.

The $M^1$ (Fig. 20b) is almost of the same size as $M^2$. The anterior cingulum is very close to the protolophid. The protocone is not always connected with the entoloph. The mesoloph is long in all specimens. The metaloph ends at the entoloph in front of the hypocone.

The $M^2$ (Fig. 20b) always shows a double protoloph: protoloph I and II. In most specimens the protocone is not connected with the entoloph. All specimens, with one exception, do not show a lingual anterior cingulum. The entoloph is situated in the lingual half of the tooth. In only one specimen the roots are preserved: There are 3 of them.

The $M^3$ (Fig. 20b) is little reduced. All structural elements of the $M^2$ are also present in this tooth. Like the $M^2$, the $M^3$ always shows a double protoloph. In most specimens the entoloph is connected with the protoloph I, but in some this connection is interrupted.

The $P^4$ of *P. winistoerferi* is not yet known, but since all other species of *Plesiosminthus* have this tiny tooth it is quite certain that *P. winistoerferi* also has it.

The upper incisor (Fig. 24a) is very high and relatively narrow (0,68 × 1,52 mm in cross-section) and shows the typical longitudinal groove.

### *Plesiosminthus winistoerferi* from Findreuse 11 and 14

Fig. 19a and 20a,

The level 11 of the Findreuse section in Savoy has yielded a fragment of $M_2$ which shows the typical features of *P. winistoerferi* conprising a very strong posterior arm of protoconid connected with the mesolophid on the lingual side, and a far labially situated ectolophid. The tooth is distinctly wider than the four known $M_2$s from Brochene Fluh 53.

Also a very large $M^2$ (1,28 × 1,28 mm) was found in level 14 of the Findreuse section. It shows a double protoloph. The protocone is not connected with the endoloph. The protoloph I does not reach the paracone, and the anterocone and the labial anterior cingulum are disconnected.

Morphologically both molars fit very well with *P. winistoerferi* from Brochene Fluh 53. It is true that both teeth are somewhat larger than the equivalent molars from

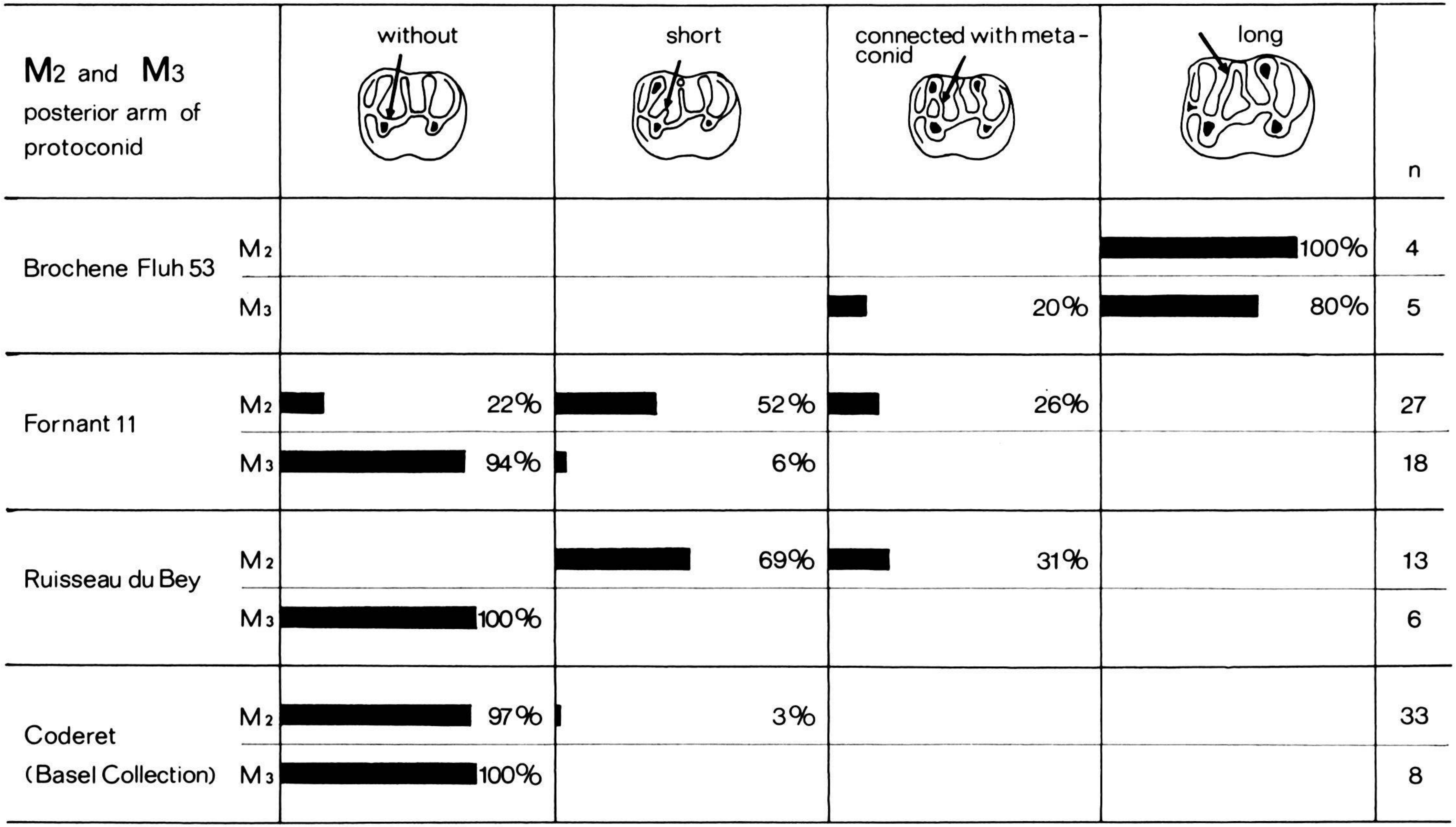
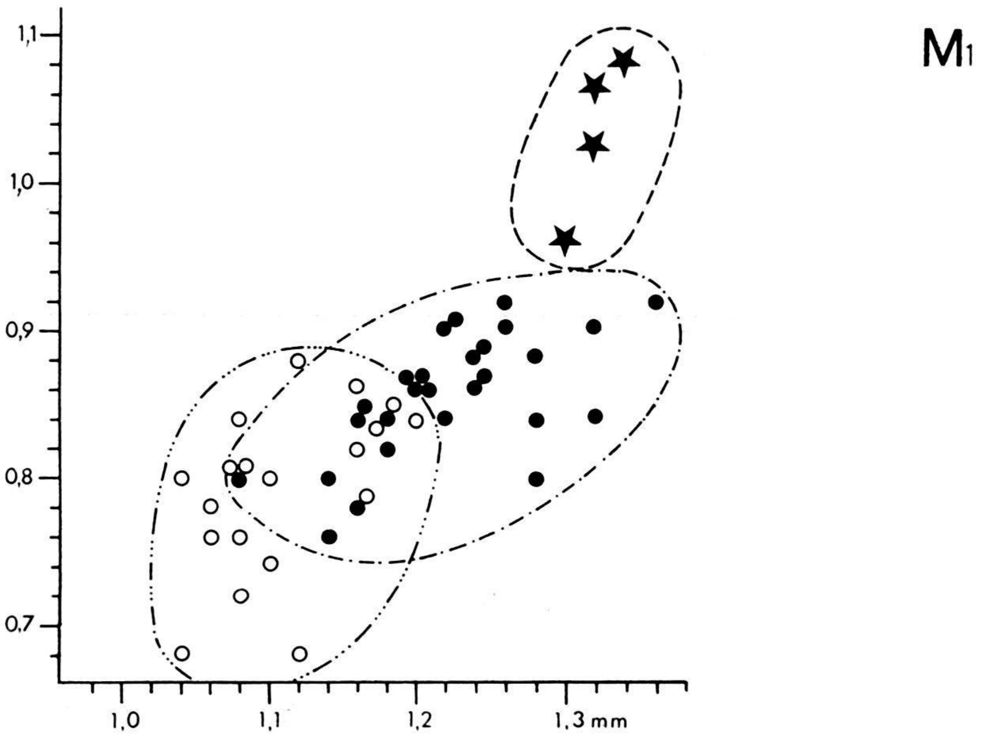
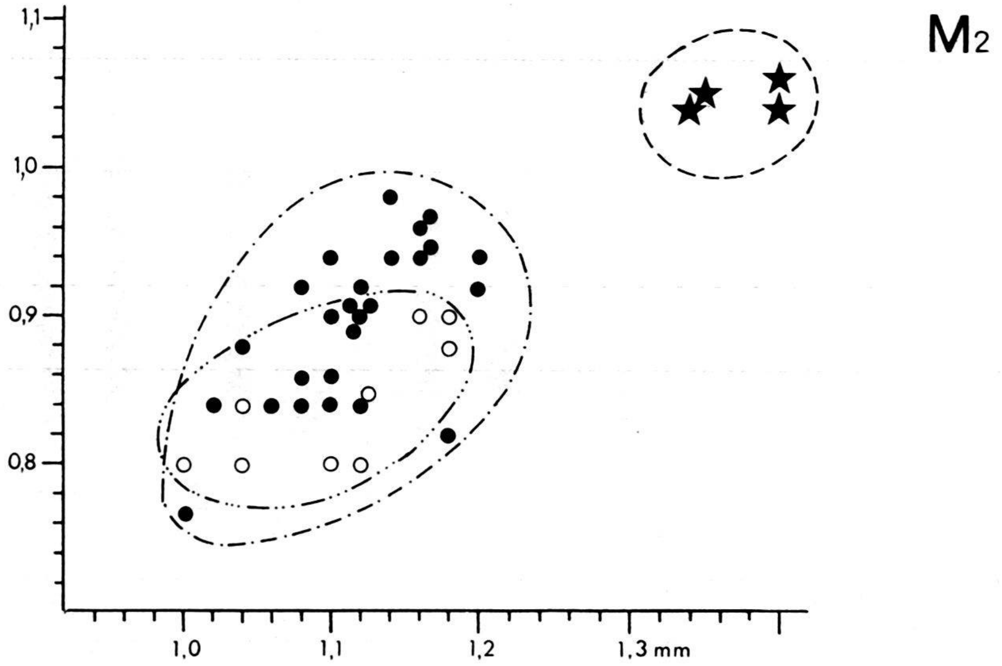


Fig. 21. Quantitative character analysis of the posterior arm of the protoconid on $M_2$ and $M_3$ of *Plesiosminthus*. – Brochene Fluh 53: *P. winistoerferi*. – Fornant 11: *P. myarion*. – Ruisseau du Bey: *P. promyarion*. – Coderet: *P. schaubi*.


M1
1,1
1,0
0,9
0,8
0,7
1,0
1,1
1,2
1,3 mm


M2
1,1
1,0
0,9
0,8
1,0
1,1
1,2
1,3 mm

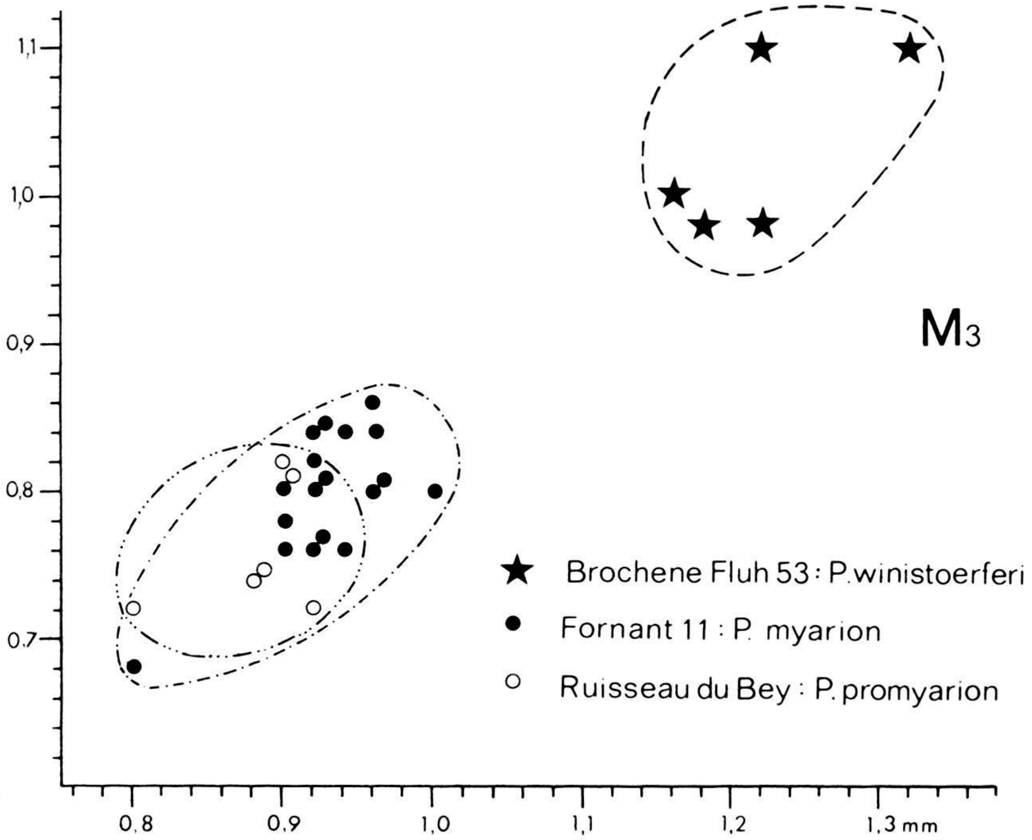


Fig. 22. Scatter diagrams of length (l) and width (w) in $M_1$, $M_2$ and $M_3$ of three *Plesiosminthus* species of the western Molasse.

Brochene Fluh 53. However the sample from the latter locality is not large enough to give a clear impression of the size variability of *P. winistoerferi*, and I therefore tentatively classify the two molars from Savoy with this latter species.

### *Discussion*

Of all of the species of *Plesiosminthus*[4]), *P. myarion* SCHAUB 1930 is morphologically closest to *P. winistoerferi*. In most $M_2$s this early Miocene species also shows a posterior arm of the protoconid, although in most specimens (52%) this ridge is very short. In 26% of the $M_2$s it is connected with the metaconid (see Fig. 21), but I could not find any $M_2$ of *P. myarion* in which the posterior arm of protoconid is connected with the mesolophid, as is always the case in the $M_2$ of *P. winistoerferi*. The $M_3$ of the latter species always has a long posterior arm of the protoconid, but in the $M_3$ of *P. myarion* only 6% have such a ridge. As in *P. winistoerferi* the $M^2$ of *P. myarion* also has a double protoloph. The $M^3$ of *P. myarion* shows this feature too, but to a lesser extent. (Only in 28% of the $M^3$s does protoloph I and II reach the paracone). In 43% of the teeth these two lophs are very short, and in 29% only one protoloph is developed. In the $M^3_3$ these two species also show similarities in that they are little reduced, but those of *P. winistoerferi* are less reduced than in *P. myarion*.

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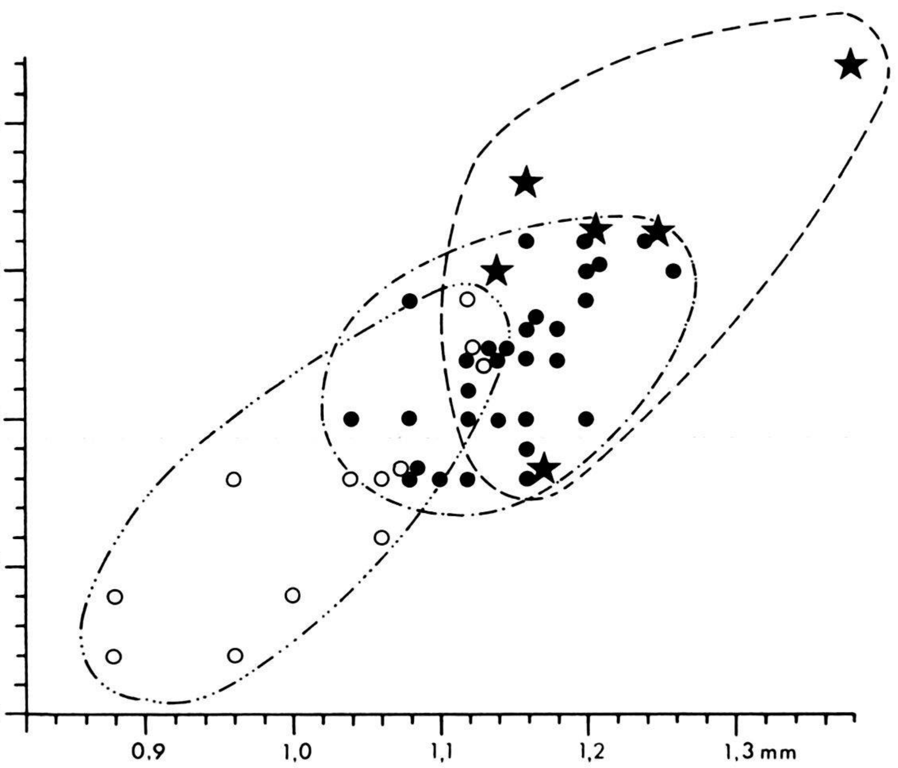
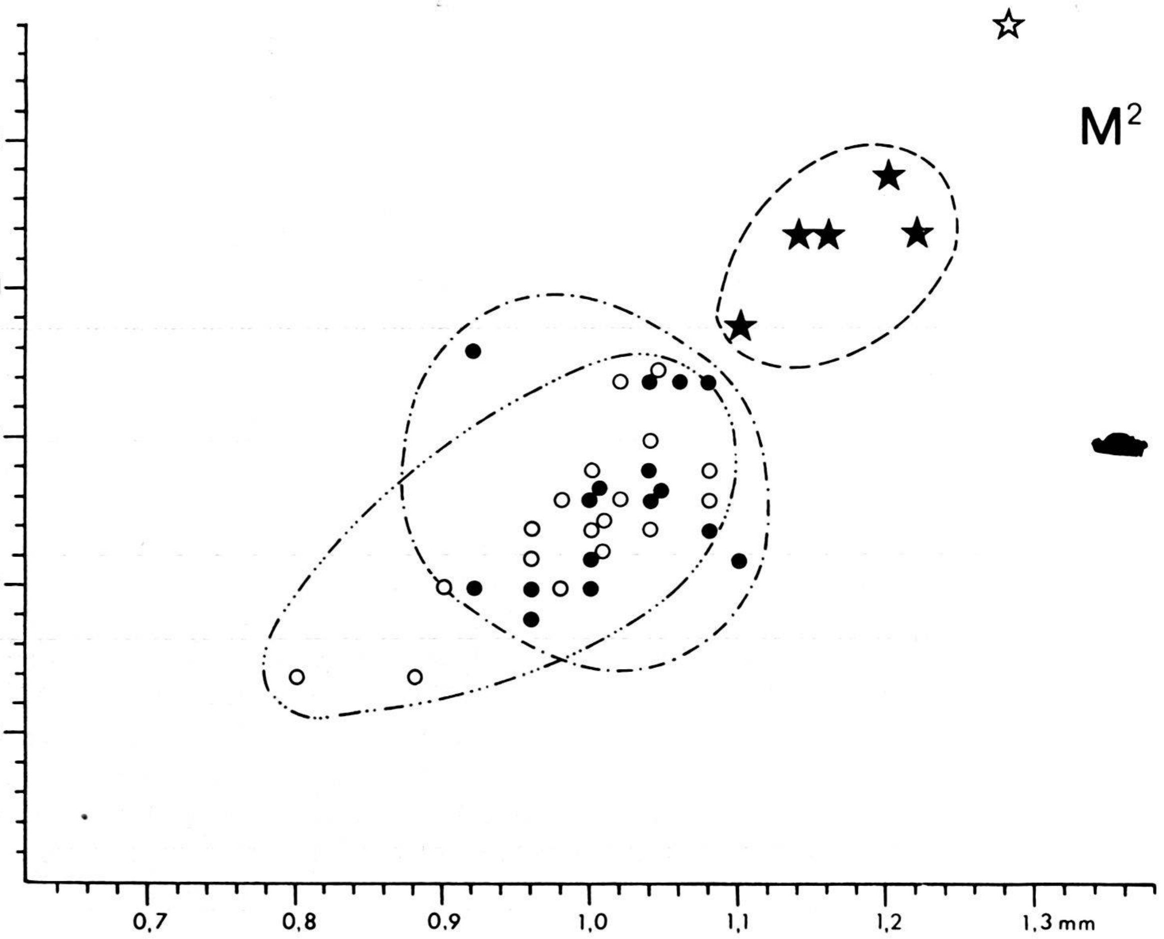
[4]) As discussed elsewhere (see ENGESSER 1979), I consider *Schaubeumys* WOOD 1935 and *Parasminthus* BOHLIN 1946 as genera distinct from *Plesiosminthus*.


$M^1$
1,2
1,1
1,0
0,9
0,8
0,9
1,0
1,1
1,2
1,3 mm


$M^2$
1,2
1,1
1,0
0,9
0,8
0,7
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0,9
1,0
1,1
1,2
1,3 mm

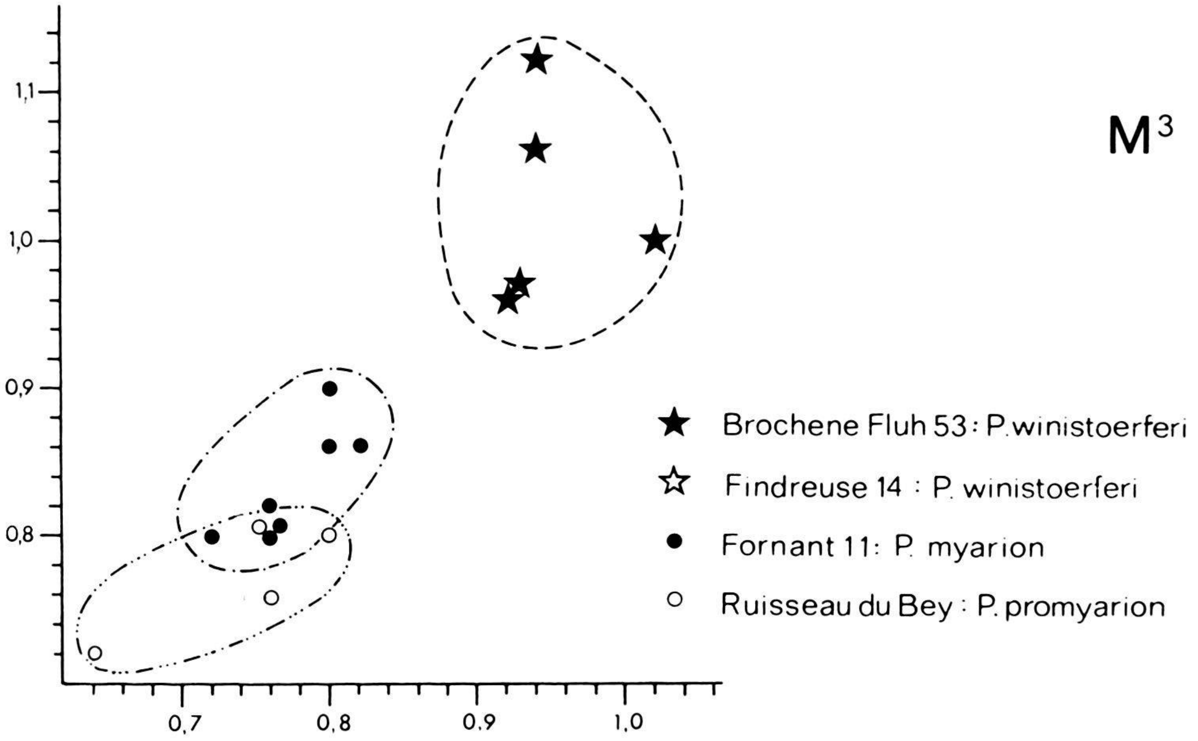

Fig. 23. Scatter diagrams of length (l) and width (w) in $M^1$, $M^2$ and $M^3$ of three *Plesiosminthus* species of the western Molasse.

Of the features compared above, at least two can be classified as primitive: the strong posterior arm of the protoconid of $M_2$ and $M_3$, and the slightly reduced $M^3_3$. The Early Oligocene genera *Allosminthus* WANG 1985, *Sinosminthus* WANG 1985, and *Heosminthus* WANG 1985 already show these characters very distinctly. In the case of the posterior arm of the protoconid HUGUENEY & VIANEY-LIAUD (1980) also came to the conclusion, on the basis of comparisons of populations of *P. promyarion* from Pech Desse and Pech du Fraysse, that the strong development of this ridge is a primitive feature. Since

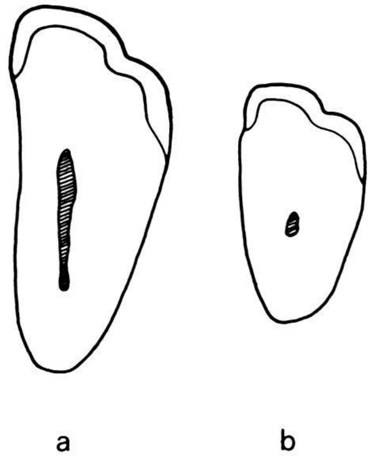

Fig. 24 a) *Plesiosminthus winistoerferi* n. sp. from Brochene Fluh 53, cross-section of the upper incisor: K.B.F. 9, collection D. Kälin, Balsthal.

b) *Plesiosminthus promyarion* SCHAUB from Ruisseau du Bey, cross-section of the upper incisor: MGL 44343, Musée Géologique Lausanne. both figures 25×.

*P. winistoerferi* shows these characters to a greater extent than *P. myarion* it can be considered as more primitive. Is it then possible, that *P. winistoerferi* is the ancestor of *P. promyrion?* Against such a derivation is the larger size of *P. winistoerferi,* because the general tendency in dipodids, as in most rodents, is towards the direction of size increase. In addition, all authors (Schaub 1930, Hugueney & Vianey-Liaud 1980) are in agreement, that *P. myarion* developed from *P. promyarion.* As will be shown, in connection with *P. promyarion, P. winistoerferi* does not fit at all in this scheme of evolution. Therefore, it seems probable, that *P. myarion* is not closely related with *P. winistoerferi,* and that the similarities of the two species can be considered as shared primitive features.

*P. myarion* is morphologically very close to *P. promyarion* (Schaub 1930), and in general it is considered as having been derived from this latter species. *P. promyarion* is actually more primitive in several features: the teeth are somewhat smaller, the $M\frac{1}{1}$ are almost of the same size as the $M\frac{2}{2}$ (see Fig. 25), and a posterior arm of the protoconid on $M_2$ is always developed, whereas in *P. myarion* 22% of the $M_2$s show no trace of this ridge (see Fig. 21). Concerning the posterior arm of the protoconid, *P. winistoerferi* is more primitive than *P. promyarion.* Also the less reduced $M\frac{3}{3}$ of *P. winistoerferi* as shown above, have to be considered as more primitive. Therefore it does not seem possible to derive *P. winistoerferi* from *P. promyarion.*

*P. schaubi* Viret 1926 is without doubt the most advanced species of *Plesiosminthus* so far known. This species not only shows a very reduced $M\frac{3}{3}$ and a relatively large $M\frac{1}{1}$, but in $M_2$ and $M_3$ the posterior arm of the protoconid is completely lacking. Accordingly, *P. winistoerferi* seems to have no close relationship with any other species of *Plesiosminthus.* Apparently this species represents a separate evolutionary line that immigrated into the Molasse basin during the Uppermost Oligocene (see Fig. 26). It is very conspicuous that *P. winistoerferi* is known only in the assemblage zone of Brochene Fluh 53, and that it was not found outside the Molasse basin.

## *Plesiosminthus* in the Molasse of Switzerland and Savoy

*Plesiosminthus* appears for the first time in the zone of Mümliswil–Hardberg. The genus is documented over a range of 11 mammal zones. Only in the zone of Aarwangen are no *Plesiosminthus* known. But the lack is certainly due to the scarcity of small mammals from this zone. In the range of these 11 zones, 4 species of *Plesiosminthus* are known. It is noticeable that these species replace each other, and that there is no overlapping at all. Especially peculiar is the fact that in the zones of Küttigen and Brochene Fluh 53 no representative of the *P. promyarion/myarion* group has been found so far. Hugueney & Vianey-Liaud (1980) propose the following explantation for this absence: The group may have been displaced in fringe areas by the more advanced and larger species, *P. schaubi.* Only after the disappearance of *P. schaubi* could the *P. promyarion/myarion* group regain its territory. This explanation sounds quite reasonable. However, the situation becomes more complicated by the appearance of *P. winistoerferi.* For example, did *P. winistoerferi* in its turn displace *P. schaubi* in the Molasse basin? This would certainly explain the short stratigraphical range of the latter species. But if this is the case, which species was responsible for the disappearance of the large species, *P. winistoerferi?*

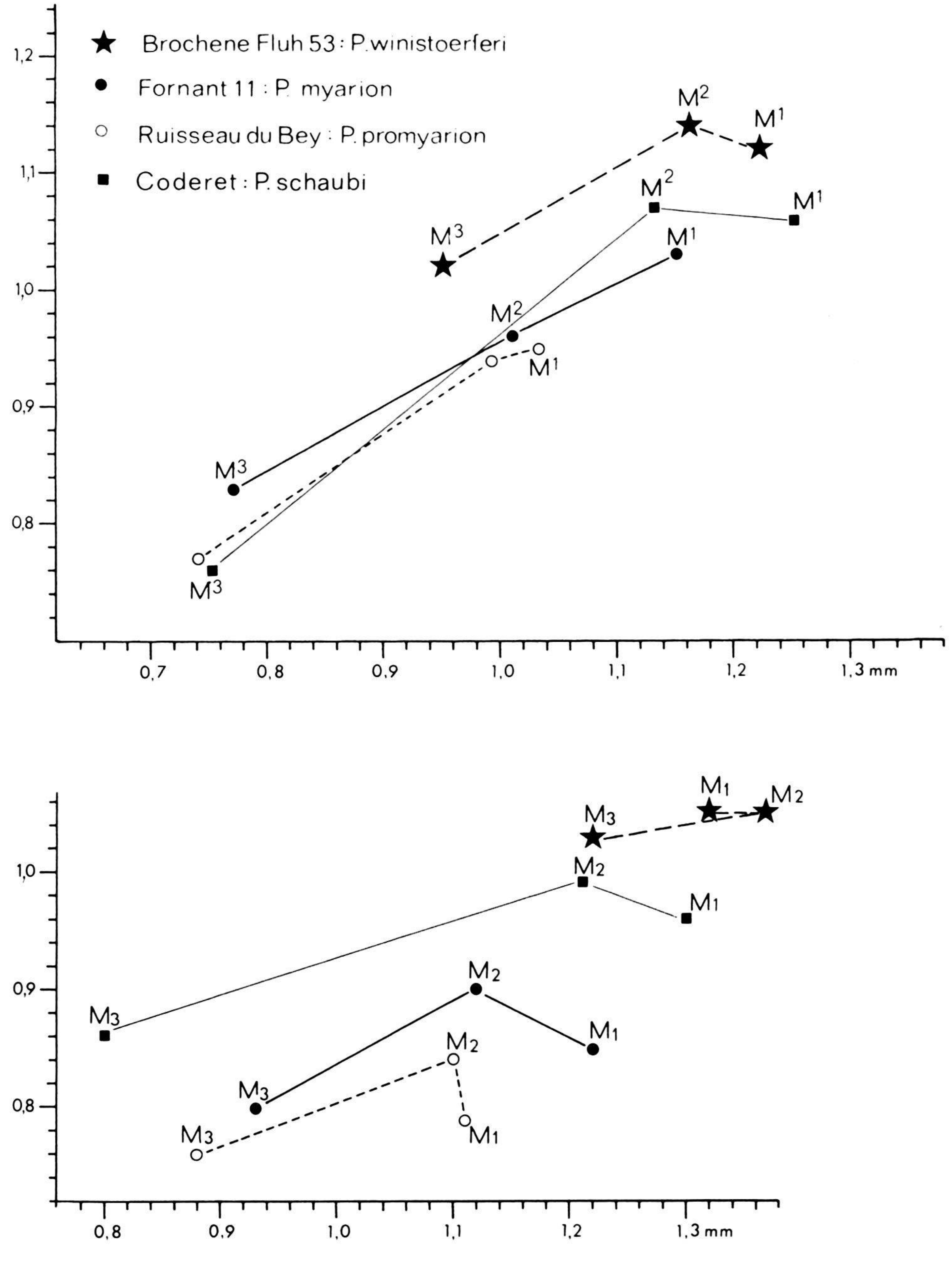

Fig. 25. Mean values of the molars of four species of *Plesiosminthus*.

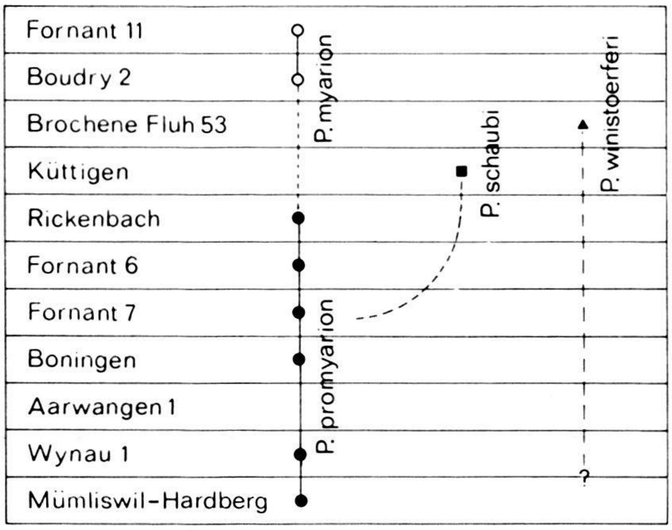

Fig. 26. The stratigraphical range of the various species of *Plesiosminthus*.

## List of the mammal faunas with *Plesiosminthus* in the Molasse of Switzerland and Savoy

*P. promyarion* SCHAUB 1930
- Mümliswil–Hardberg (ENGESSER & MAYO 1987)
- Wynau 1 (ENGESSER & MAYO 1987)
- Wolfwil (STEHLIN & SCHAUB 1951)
- Boningen (ENGESSER & MAYO 1987)
- Ruisseau du Bey (JORDI 1955)
- Le Coudray 2 (ENGESSER, HÜRZELER & MAYO 1986)
- Fornant 6 (ENGESSER & HUGUENEY 1982; ENGESSER & MAYO 1987)
- Fornant 7 (ENGESSER & HUGUENEY 1982; ENGESSER & MAYO 1987)
- Findreuse 16 (ENGESSER & HUGUENEY 1982)
- Route de Serrasson (Savoy)
- La Chaude Fontaine (ENGESSER & MAYO 1987)
- Boudry-La-Fabrique (MOJON et al. 1985)
- Rickenbach (SCHAUB 1925, 1930; ENGESSER & MAYO 1987)
- Rances (HUGUENEY & KISSLING 1972)
- Brochene Fluh 4/5 (BAUMBERGER 1927)

*P. schaubi* VIRET 1926
- Le Gérignoz (ENGESSER, MAYO & WEIDMANN 1984)
- Küttigen (ENGESSER & MAYO 1987)

*P. winistoerferi* n. sp.
- Brochene Fluh 53 (ENGESSER & MAYO 1987)
- Findreuse 11 (ENGESSER & HUGUENEY 1982)
- Findreuse 14

*P. myarion* SCHAUB 1930
- Les Pierrettes
- Fornant 11 (ENGESSER & MAYO 1987)

Findreuse 3, 4 (ENGESSER & HUGUENEY 1982)
Findreuse 22
Messen (ENGESSER 1976)
Seligraben (BLAU 1969)
Boudry Viaduc VI (MOJON et al. 1985)
Bois Genoud (MUMENTHALER, PETERS & WEIDMANN 1981)

## Family ***Cricetidae*** ROCHEBRUNE 1883

## Subfamily ***Pseudocricetodontinae*** new subfam.

## Genus *Heterocricetodon* SCHAUB 1925

### *Heterocricetodon hausi* nov. sp.

Fig. 27–28

*Diagnosis.* – Smallest known species of *Heterocricetodon* with small $M^3$, and relatively short posterior arm of the protoconid and mesolophid in $M_1$ and $M_2$. $M^3$ with a double protoloph. In $M^2$ protoloph I more strongly developed than protoloph II. $M^2$ always with lingual anterior cingulum. $M^3$ with lingual anterior cingulum poorly developed or absent and no posteriorly elongated protocone.

*Derivatio nominis.* – Honoring Dr. H. A. Haus (Überlingen, Germany) for his geological work in the area of Bumbach, the type locality.

*Type.* – Left $M^2$, Bum. 5, Naturhistorisches Museum Basel, dimensions: 1,82 × 1,68 mm, Fig. 27c.

*Referred material.* – 25 isolated teeth and 14 fragments.

*Type locality.* – Bumbach 1 near Schangnau (Kanton Bern, Switzerland, see HAUS 1937).

*Age.* – Middle Oligocene, assemblage zone of Bumbach 1 (see ENGESSER & MAYO 1987).

*Stratigraphic range.* – Assemblage zone of Bumbach to that of Mümliswil-Hardberg (see ENGESSER & MAYO 1987).

Other localities with *H. hausi:*

(Réchauvent-Cristallin, assemblage zone of Bumbach (see ENGESSER, HÜRZELER & MAYO 1986)
Mümliswil-Hardberg (ENGESSER & MAYO 1987).

*Differential diagnosis.* –

From *Heterocricetodon stehlini* SCHAUB 1925[5]) *H. hausi* differs in:

- its smaller dimensions,
- its less enlarged $M^3$,
- its lingual anterior cingulum on $M^2$,
- its more developed protoloph I (compared with protoloph II) on $M^2$,
- its double protoloph on $M^3$,

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[5]) About *H. stehlini* and *H. schlosseri*, see p. 991–992.

— its shorter posterior arm of the protoconid on $M_2$,
— its anticlines on $M_2$ and $M_3$ which are perpendicular to the longitudinal axis.

From *Heterocricetodon schlosseri* SCHAUB 1925[6]), *H. hausi* differs in:

— its smaller dimensions,
— its less enlarged $M\frac{3}{3}$,
— its better developed lingual anterior cingulum on $M^2$,
— its stronger protoloph I on the $M^2$.

From *Heterocricetodon helbingi* STEHLIN & SCHAUB 1951, *H. hausi* differs in:

— its distinctly smaller dimensions,
— its much less enlarged $M\frac{3}{3}$,
— its more developed protoloph I on $M^2$ mostly reaching the paracone,
— the less developed lingual anterior cingulum on $M^3$.

*Description of the type* (Fig. 27c). – Paracone and metacone rise far above the other cusps and crests of this $M^2$. The entoloph is as high as the protocone and hypocone. The protoloph I is connected with the anterior arm of the protocone, and is higher and stronger than the protoloph II. This latter ridge ends at the base of the paracone. The labial anterior cingulum is very long but the lingual part is not as well developed, and does not reach the lingual edge of the tooth. The mesoloph is not so high as the entoloph and is not connected with the pronounced mesostyle. The metaloph is parallel to the posterior cingulum, and ends in the entoloph somewhat behind the mesoloph.

*Description of the dentition* (Fig. 27). – The $M_1$ is a long and narrow tooth. It has a pointed anteroconid which is connected with the protoconid. In the only complete specimen the metaloph is directed backwards and fuses with the anterior arm of the protoconid. The posterior arm of the protoconid of this specimen is very short. The paracone shows a distinct posterior crest. In one specimen the mesolophid is of medium length, while in another it is divided into three little crests. The ectomesolophid is very variable: in one $M_1$ it is very distinct and long, in the two other specimens there is no ectomesolophid at all. Only one specimen shows a posterior arm of the hypoconid.

The $M_2$ is less variable than the $M_1$. The labial anterior cingulum is mostly shorter than the lingual one. The posterior arm of the protoconid is of medium length and always stronger than the short mesolophid. The metaconid also has a posterior crest.

Only three fragments of the $M_3$ were found, and in all of them, only the anterior half is preserved. The posterior arm of the protoconid is very long, and apparently there is no mesolophid.

The $M^1$ is very variable. Some specimens show two anterocones, others only one. The labial anterocone is sometimes connected with the anterior arm of protocone. In other specimens this arm is very short and ends freely. The protoloph is always curved backwards, and the mesoloph is always long.

The $M^2$ is much less variable than the $M^1$. In general these teeth correspond very well with the type specimen. All specimens show a lingual anterior cingulum, but in some it is more developed than that of the type, in others less so. Of the 11 $M^2$s, only one has an

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[6]) About *H. stehlini* and *H. schlosseri*, see p. 991–992.

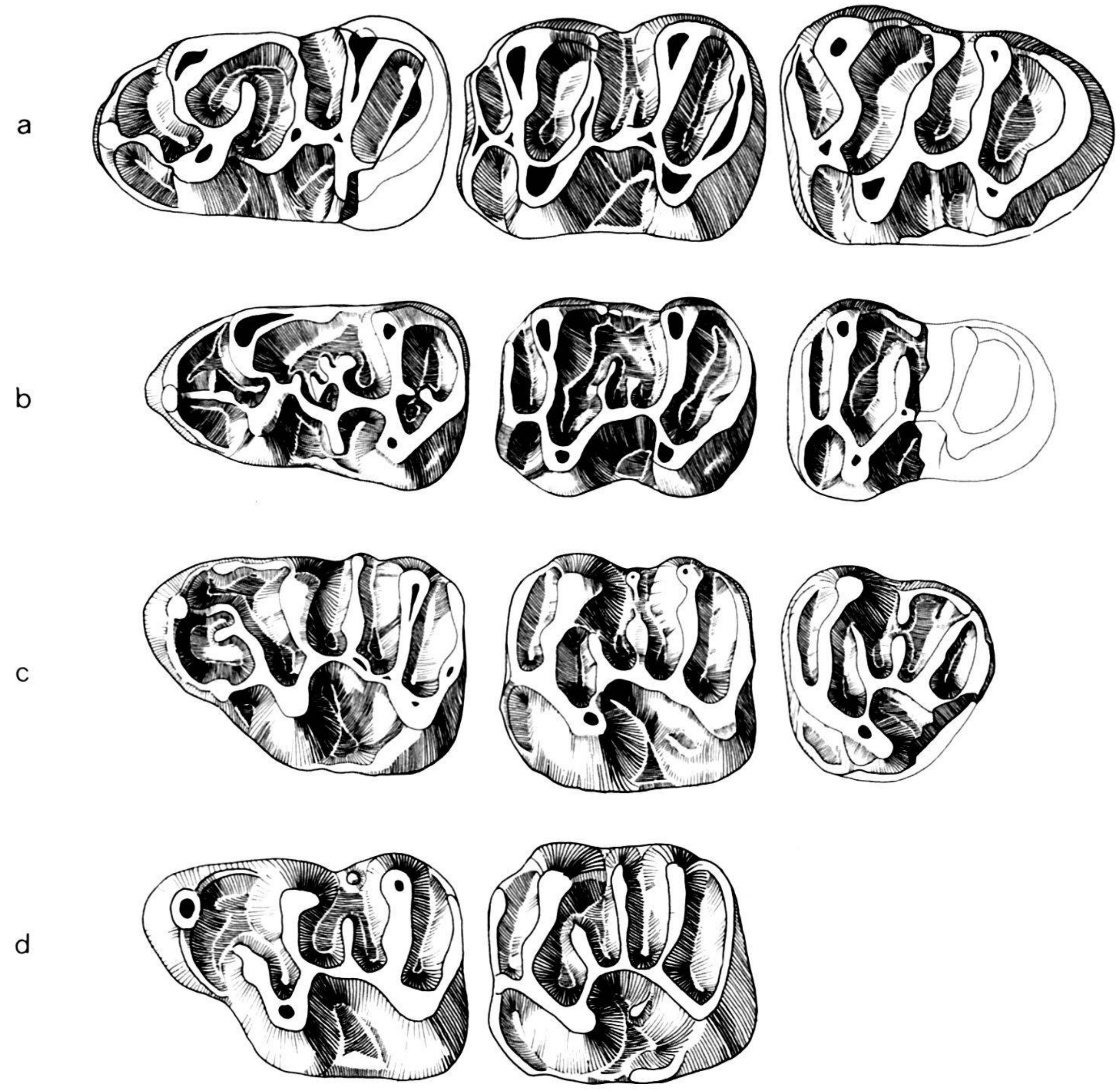

Fig. 27 a) *Heterocricetodon stehlini* Schaub from Route de Serrasson ($M_1$) and Fornant 7 ($M_2$ and $M_3$), left $M_1$: Sav. 422, right $M_2$ (inverse): Sav. 423, right $M_3$ (inverse): Sav. 424.

b) *Hetericricetodon hausi* n. sp. from Bumbach 1, $M_1$–$M_3$; right $M_1$ (inverse): Bum. 1, left $M_2$: Bum. 2, fragment of left $M_3$: Bum. 3.

c) *Heterocricetodon hausi* n. sp. from Bumbach 1, $M^1$–$M^3$; left $M^1$: Bum. 4, left $M^2$, type: Bum. 5, right $M^3$ (inverse): Bum. 6.

d) *Heterocricetodon hausi* n. sp. from Bumbach 1, $M^1$–$M^2$; left $M^1$: Bum. 7, left $M^2$: Bum. 8. – all specimens of the Naturhistorisches Museum Basel. all figures 15×.

interrupted protoloph I. In all other specimens this ridge reaches the paracone, and is higher and longer than the protoloph II. Some specimens show a distinct posterior crest of the paracone. The length of the mesoloph varies from short to long.

The $M^3$ is very small compared with other species of *Heterocricetodon*. The lingual anterior cingulum is little developed or is completely lacking. As in $M^2$, there is always a double protoloph, and the anterior arm is always higher and longer than the posterior one. The mesoloph is mostly long, and the metacone is incorporated in the metaloph.

Dimensions of *Heterocricetodon hausi* from Bumbach 1 in millimeters

| | length<br>minimum | mean | maximum | width<br>minimum | mean | maximum | n |
|---|---|---|---|---|---|---|---|
| $M^1$ | 2,28 | 2,34 | 2,42 | 1,52 | 1,60 | 1,66 | 6 |
| $M^2$ | 1,68 | 1,77 | 1,88 | 1,60 | 1,66 | 1,72 | 9 |
| $M^3$ | 1,48 | 1,51 | 1,56 | 1,44 | 1,50 | 1,60 | 5 |
| $M_1$ | | 2,30 | | | 1,36 | | 1 |
| $M_2$ | 1,84 | 1,89 | 1,96 | 1,44 | 1,50 | 1,60 | 4 |

### *Discussion*

*Heterocricetodon hausi* is so far the oldest species of the genus. It also shows a number of characters which can be interpreted as primitive:

- small $M^3_3$,
- a lingual anterior cingulum of $M^2$,
- protoloph I on $M^2$ more developed than protoloph II,
- short posterior arm of the protoconid on $M_2$,
- anticlines on $M_2$ and $M_3$ perpendicular to the longitudinal axis.

In many respects *H. hausi* is very similar to *Pseudocricetodon*. When we found the first specimens of this species from Bumbach, I had my doubts whether it was a new species of *Heterocricetodon* or of *Pseudocricetodon*. When more material came to light it became clear that the new species had to be considered as a primitive *Heterocricetodon*. The cusps of the teeth are little voluminous and ridge like; the labial cusps of the lower molars are situated very close to the labial edge of the teeth, the mesoloph of the upper molars is always long; the $M_1$ is very much elongated; the posterior arm of the protocone on $M^2$ shows a tendency to become connected with the paracone, and the lingual anterior cingulum of the same tooth seems to become reduced. All these characters are typical for *Heterocricetodon*.

Schaub (1925, p. 62) already recognized the similarity between *Heterocricetodon schlosseri* and *Pseudocricetodon incertus*. Since *H. hausi* also shows characters of *Pseudocricetodon* (large, often two-cusped prelobe, and long anterior arm of the protocone on $M^1$, well-developed posterior arm of the protoconid on $M_2$, double mesolophid and posterior crest of the paraconid on $M_1$), it seems to be a form intermediate between *Pseudocricetodon* and *Heterocricetodon*. Therefore I think the two genera are closely related and I could easily consider the possibility that *Heterocricetodon* originated from *Pseudocricetodon*. It is true that the $M^3_3$ of some species of *Pseudocricetodon* are very little, and it is hard to imagine how the large $M^3_3$ of *Heterocricetodon* could develop from such tiny teeth. However, it seems evident that in *Heterocricetodon* there is a tendency towards enlargement of $M^3_3$. Even if it is not possible at this stage to determine the exact species of *Pseudocricetodon* from which *Heterocricetodon* developed, it seems very probable that the two genera are closely related, and I therefore propose to include the two genera in a new subfamily, the Pseudocricetodontinae.

Diagnosis of the subfamily *Pseudocricetodontinae*

Small to large Oligocene and lower Miocene cricetids with rather lophodont molars. $M^1$ with large prelobe, straight or even concave labial edge, and often long anterior arm of protocone. $M^2$ with double protoloph. $M_1$ mostly with posterior crest of the paraconid and often double mesoloph. $M_1$ and $M_2$ mostly without the posterior arm of the hypoconid.

*Type genus.* – *Pseudocricetodon* THALER 1969

*Remark.* – M. HUGUENEY (1980) was the first author to classify the species *incertus* within the genus *Pseudocricetodon*, although THALER (1969) had already suggested this possibility. She wrote (p. 60) "L'évolution des caractères crâniens décrits chez *P. incertus* (HARTENBERGER 1967) et chez *P. montalbanensis* (VIANEY-LIAUD 1974) ne semble pas en contradiction avec ce point de vue". It is true, as far as the infraorbital foramen is concerned, that the skulls of the two species are very similar. But in the anterior palatine foramen there is a difference: In *P. montalbanensis* it is quite short, and does not reach backwards to the anterior edge of the $M^1$ (see VIANEY-LIAUD 1974, Fig. 18c). In *P. incertus*, on the other hand, the foramen is much longer, and reaches further backwards than the prelobe of the $M^1$ (see HARTENBERGER 1967, p. 1b). As no skulls of other species of *Pseudocricetodon* are known, it is difficult to estimate the importance of this difference. It seems possible that *Pseudocricetodon*, in the sense of HUGUENEY (1980), is not a homogeneous genus. With the material presently available it is not possible to resolve this problem. In any case, *Heterocricetodon* seems to be close to *P. incertus* in this character: In the type specimen of *H. stehlini*, a fragment of a left maxilla, the posterior edge of the anterior palatine foramen is preserved. It reaches backwards to the prelobe of $M^1$, almost as far as in *P. incertus*.

### *Heterocricetodon* in the western Molasse

*Heterocricetodon* is a very rare cricetid. *H. hausi*, the oldest species so far known, was found only in the zones of Bumbach anf Mümliswil–Hardberg. Besides Bumbach it has been found in two other localities. In Réchauvent-Cristallin (near Yverdon, Canton of Vaud), a new locality slightly younger than that of Bumbach, a fragment of a $M^2$ was found, and in Mümliswil–Hardberg a $M^3$ has been recovered.

When SCHAUB (1925) described *H. schlosseri* he had only three mandibles of this species from the Quercy, while *H. stehlini* was known only from a maxilla with $M^1$–$M^3$. In each case the age of the species was unknown.

FREUDENBERG (1941) considered *H. stehlini* as a synonym of *H. schlosseri*. This was followed with some reservation by M. HUGUENEY (1980). On the basis of new material from the Molasse, I came to the conclusion that both species are justified. *H. stehlini* is somewhat smaller than *H. schlosseri*. The posterior arm of the protoconid on the $M_2$ of *H. stehlini* is long, whereas in the $M_2$ of *H. schlosseri* it is short. The anticlines of $M_2$ and $M_3$ in *H. stehlini* are oblique (Fig. 27). In the corresponding teeth of *H. schlosseri* these crests are perpendicular to the longitudinal axis of the molars. The $M^3$ of *H. schlosseri* shows a well developed protoloph I, and the protoloph II is interrupted. In contrast,the $M^3$ of *H. stehlini* has a strong protoloph II and the protoloph I, if present at all, is interrupted. In the only known $M_1$ of *H. stehlini* the metalophid is fused with the anterior arm of protoconid, and the posterior arm of this cusp is directed backwards (Fig. 27), as de-

| Assemblage zones | H. hausi | H. schlosseri | H. helbingi | H. stehlini |
|---|---|---|---|---|
| Fornant 7 | | | Rte. de Serrasson | Rte de Serrasson<br>Fornant 7 |
| Boningen | | | Boningen | |
| Aarwangen 1 | | | | |
| Wynau 1 | | Bavois grès inf.<br>Wynau 1<br>Talent 16 | Wynau 1, Wolfwil<br>Eclagnens<br>Talent 16<br>Mümliswil-Näsihöfli | |
| Mümliswil-Hardberg | Mümliswil-Hardberg | | | |
| Oensingen | | Schwendibach | | |
| Bumbach 1 | Réchauvent<br>Bumbach 1 | | | |

Fig. 28. The stratigraphical range of various *Heterocricetodon* species in the western Molasse.

scribed for *H. gaimesheimensis* by FREUDENBERG (1941). On the $M_1$ of *H. schlosseri* by contrast the posterior arm of protoconid fuses with the metalophid.

In most of these features *H. stehlini* is more advanced than *H. schlosseri*. In addition *H. stehlini* was actually found in younger layers (in the assemblage zone of Fornant 7), whereas *H. schlosseri* is known in the zones of Oensingen and Wynau 1 (Fig. 28).

*H. helbingi* which covers quite a large stratigraphical range (from the zone of Wynau until that of Fornant 7) shows a combination of primitive and advanced features. On the one hand, the enlarged $M^3_3$, the long posterior arm of the protoconid on $M_2$, and a protoloph II which is always well developed on $M^2$ can be classified as advanced characters. The lingual anterior cingulum on $M^2$ and $M^3$, on the other hand, are primitive features.

The most extensive material of *Heterocricetodon* known is that from Gaimersheim, and described by FREUDENBERG (1941) as *H. gaimersheimensis*. However Volker Fahlbusch has informed me that of the 22 lower and 6 upper jaws of the species originally described only 5 jaw fragments survived the Second World War. Among them is the type, with the number 1939 XI 4 (not indicated in FREUDENBERG 1941)[7]. From the measurements given in Freudenberg, the material from Gaimersheim exhibits a large range of variability in molar length (23,2% for $M_2$, 27,2% for $M_3$). In addition, this material seems morphologically heterogeneous. The type mandible (op. cit. Pl. 12, Fig. 3) shows features of *H. stehlini:* long posterior arm of the protoconid on $M_2$, backwardly directed posterior arm of te protoconid in $M_1$, oblique anticlines in $M_2$ and $M_3$. Also the dimensions of the type are very close to those of *H. stehlini*. In contrast, the upper jaw fragments illustrated

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[7] I am indebted to Prof. Dr. V. Fahlbusch for providing me with additional information about *H. gaimersheimensis* not mentioned in FREUDENBERG (1941).

by Freudenberg in Figures 5 and 6 (Plate 12) show distinct lingual anterior cingula on $M^2$ and $M^3$. I conclude from this that the material from Gaimersheim described by Freudenberg includes two species: *H. stehlini* and *H. helbingi*. Without having seen any of the material from Gaimersheim, I infer that *H. gaimersheimensis* represents a synonym of *H. stehlini* because the type of the former species is very similar to the lower dentition of the latter. Further studies of the Gaimersheim material (which now includes a complete skull with mandible recovered from more recent excavations) will undoubtedly shed some light upon this problem.

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