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A Third Contribution to the Fossil Small Mammal Fauna of Kohfidisch (Burgenland), Austria

By FRIEDRICH BACHMAYER [1]) and ROBERT W. WILSON [2])

(With 9 textfigures and 3 plates)

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Zusammenfassung

Die Fortsetzung der Bearbeitung der Kleinsäuger von Kohfidisch (Burgenland), Österreich hat *Leptodontomys* (Eomyidae) und *Paraglirulus* (Gliridae) als weitere Elemente der Fauna ergeben. Noch wichtiger ist aber die Erkenntnis vom Auftreten graphiuriner Schläfer, einer Gruppe, die sonst nur südlich der Sahara bekannt ist.

Die Untersuchung der Variabilität mehrerer Arten von Kohfidisch zeigt eine nicht unerwartete morphologische Schwankungsbreite (*Galerix zapfei*, *Anourosorex kormosi*, *Protozapus intermedius*, *Kowalskia fahlbuschi*, *Progonomys woelferi* und *Parapodemus lugdunensis*). Bei *Kowalskia fahlbuschi* aber ist das topotypische Material von Kohfidisch etwas verschieden von anderen dieser Art zugezählten Belegen von Fundorten im Wiener Becken und in Spanien. Es ist weder gewiß, ob diese Unterschiede geographisch oder stratigraphisch bedingt sind oder ob beides zusammenwirkt, noch ist eine besondere nomenklatorische Berücksichtigung dieser Differenzen geklärt.

Probleme der Messung bei fossilen Kleinsäugern werden diskutiert und es wird eine zahlenmäßige Übersicht der untersuchten Exemplare gegeben.

Abstract

Continuing study of small mammal remains from Kohfidisch (Burgenland), Austria, has added *Leptodontomys* (Eomyidae) and *Paraglirulus* (Gliridae) to the fauna. More important, is the recognition of what appears to be graphiurine dormice, a group otherwise known only from south of the Sahara Desert.

Study of variation in several Kohfidisch species (*Galerix zapfei*, *Anourosorex kormosi*, *Protozapus intermedius*, *Kowalskia fahlbuschi*, *Progonomys woelferi*, and *Parapodemus lugdunensis*) shows a not unexpected variation in morphology. In *Kowalskia fahlbuschi*, however, the topotype Kohfidisch sample is somewhat different from other samples referred to that species from localities in the Vienna Basin and Spain. Whether these differences are geographic, temporal, or a combination of the two is not certain, nor is the proper nomenclatural treatment of these differences evident.

A brief discussion of problems of measurement of small fossil mammals, and a „census" of the specimens studied are also given.

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[1]) Division of Geology and Paleontology, Naturhistorisches Museum, A-1014 Wien I., Burgring 7. — Austria.

[2]) Division of Vertebrate Paleontology, Museum of Natural History, University of Kansas, Lawrence, Kansas, 66045. — USA.

Introduction

Work on the small mammal fauna of the fissures at Kohfidisch, the Burgenland, was continued in the springs of 1978 and 1979, and the present contribution has resulted.

Several additions and updating of taxonomic assignments are noted herein, but most of the present paper is concerned with the variation contained in the several previously recorded species known by large numbers of specimens. A census of the total specimens studied in work to date, but not of the total fauna is also included.

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We wish here also to gratefully acknowledge the work of Frl. Christa BACHMAYER, who has done much of the preliminary segregation of the small mammal specimens in recent years.

Census of Kohfidisch Small Mammals

This census is not an accurate projection of the relative abundance of specimens in the Kohfidisch collection. Much material of such abundant species as *Anourosorex kormosi* and *Progonomys woelferi* was not isolated from lots (in vials) of jaws and teeth of various other small mammals, and single teeth were rarely extracted for study. On the other hand, every specimen of rare species, whether jaw or single tooth, was isolated and labelled. Such as it is, counting of individual specimens gave the following results.

Taxonomic Unit	Count
Insectivora	
Erinaceidae	
Galerix cf. *G. socialis*	52
Galerix zapfei	72
Galerix, undifferentiated	130
Lanthanotherium sp.	1
Erinaceus ? sp.	7
Soricidae	
Pentenyia dubia	71
Petenyiella repenningi	90

Anourosorex kormosi	150
Neomyine ? sp.	19
Talpidae	
Desmana pontica ?	24
Cf. *Desmanella crusafonti*	18
Talpa gilothi	6
Talpid sp.	3
Miscellaneous Insectivora	6
Chiroptera	
Megadermidae	
Megaderma vireti	36
Rhinolophidae	
Rhinolophus delphinensis	74
Rhinolophus grivensis	7
Vespertilionidae	
Myotis nr. *M. boyeri*	4
Plecotus (*Paraplecotus*) sp.	1
Cf. *Myotis* sp.	1
Chiroptera, unsorted	59
Lagomorpha	
Ochotonidae	
Prolagus cf. *P. oeningensis*	97
Rodentia	
Sciuridae	
Spermophilinus cf. *S. bredai*	28
Pliopetaurista cf. *P. bressana*	9
Castoridae	
Cf. *Chalicomys jaegeri*	1
Gliridae	
Muscardinus austriacus	47
Cf. *Myomimus dehmi*	24
Cf. *Myomimus multicristatus*	17
Paraglirulus cf. *P. lissiensis*	11
Myomimus ? sp.	2
Graphiurops austriacus	5
Zapodidae	
Protozapus intermedius	26
Eomyidae	
Keramidomys sp.	1
Leptodontomys sp.	1
Eomyid ? sp.	1

Cricetidae	
Kowalskia fahlbuschi	110
Epimeriones cf. *E. austriacus*	3
Promimomys (*Prosomys*) sp.	1
Prospalax petteri	55
Muridae	
Progonomys woelferi	177
Parapodemus lugdunensis	59
Hystricidae	
Hystrix cf. *H. suevica*	18
Total counted:	1524

Genera in actual order of scoring (in high counts may be based largely on single teeth)

Common		
(1) *Galerix*	254	
(2) *Progonomys*	177	
(3) *Anourosorex*	150	
(4) *Kowalskia*	110	
(5) *Prolagus*	97	
(6) *Petenyiella*	90	
(7) *Rhinolophus*	81	
(8) *Petenyia*	71	
(9) *Parapodemus*	59	
(10) *Prospalax*	55	
Fairly Abundant		
(11) *Muscardinus*	47	
(12) *Myomimus*	43	
(13) *Megaderma*	36	
(14) *Spermophilinus*	28	
(15) *Protozapus*	26	
(16) *Desmana*	24	
(17) *Neomyine* ?	19	
(18) Cf. *Desmanella*	18	tied
(19) *Hystrix*	18	tied
(20) *Paraglirulus*	11	
Rare		
(21) *Pliopetaurista*	9	
(22) *Erinaceus* ?	7	
(23) *Talpa*	6	
(24) *Myotis*	4	
(25) *Epimeriones*	3	

and finally one each

Lanthanotherium
Plecotus
Cf. *Myotis*
Cf. *Chalicomys*
Keramidomys
Leptodontomys
Promimomys

Considering the limitations of the census, it did not seem of any use to attempt minimum counts. The main advantage of the census would seem to lie in demonstrating what is common in the collection studied to what is rare.

Accuracy of Measurements and Counts

Making tooth measurements that are useful to other workers has always been a difficult problem to solve in the study of small mammals. It is becoming less so as measuring devices become more sophisticated, but not every one has available at all times such expensive equipment as the Leitz Ortholux microscope with measuring clocks. More often less expensive devices must be used, even calipers of all stages of accuracy. All of these must be calibrated against a standard engraved scale in order to determine the inaccuracies built into the equipment itself, but almost never is any reference to such a calibration made in the literature. A specific example of such error is the rating of the objective. It may be marked as X 1 if fixed, or at a mark indicating the same thing if a zoom, but it can not be exactly this. Errors in the calibration scale itself probably can be safely ignored, but occulars introduce additional error, and are, of course, frequently interchanged, and the kind with travelling cross hairs are certainly not matched with the objectives at the factory. Checking against an engraved scale will make this kind of error of no importance if agreement is reasonable. It is possible, however, with any kind of moving part to have slippage during translation or creep after travel has stopped.

Aside from the above, the operator himself introduces error, and perhaps the principal component. With any measuring device it is rarely possible to repeat the measurement, especially after a lapse of considerable time, and repeat the figures. SIMPSON, ROE & LEWONTIN (1960, p. 6) made an experiment of measuring a tooth with caliper calibrated to 0.1 mm and under a low power binocular microscope on five consecutive days. The results were: 13.0 mm, 13.3, 13.2, 13.1, 13.0, and 12.9. With more accurate equipment and smaller objects the decimal point shifts but the fluctuation remains in the last digit.

There seems to be reason to believe that measuring of teeth in jaws results in slightly smaller length dimensions that with isolated teeth. Refocusing of the microscope during measuring will also introduce variation. Lastly, imprecise orientation of specimens should introduce variation in measuring amounting to several hundredths of a millimeter.

The apparatus used in the measurements of this paper was a Zeiss binocular with Zeiss micrometer occular reading to 0.01 mm. Immediate repeatability without shifting the specimen seemed to be in the 0.01—0.02 range, but greater when the specimen was reoriented at a later time. One-hundredth of a millimeter is a small unit with this apparatus as may be seen by failure to clearly resolve 0.01 lines on an engraved scale. Many small inaccuracies should, however, cancel out in measuring a large number of specimens and averaging.

The Zeiss measuring occular was used with a X 1.0 objective. Measuring against a standard engraved scale showed that a measurement by this device with the X 1.0 objective was 4.6 per cent too small, and the resulting measurement should be multiplied by a correction factor of 1.048. All dimensions cited in the present paper are after correction. Inaccuracies of the instrument itself are further revealed by shifting to other objective powers. These others were measured against the same engraved scale, and corrected for the particular objective power. Results were as follows:

X 0.6	4.5 per cent too small (average of three trials)
X 1.0	4.6 per cent too small (average of six trials)
X 1.6	4.5 per cent too small (average of three trials)
X 2.5	1.6 per cent too small (average of three trials)
X 4.0	2.5 per cent too small (average of three trials).

Some of this fluctuation may be owing to greater ease of measuring the scale at higher magnifications, but deviation from the marked magnifications must be involved as well.

How much these several factors (and some not discussed) affect size comparisons between samples is difficult to estimate. The present measurements with the Zeiss device do give nearly consistently smaller dimensions than our previously published measurements using calipers (1970, 1978). Two examples will demonstrate this.

Protozapus intermedius: Holotype

	M$\underline{1}$, L	M$\underline{1}$, W	M$\underline{2}$, L	M$\underline{2}$, W
1970	1.2	1.0	1.0	0.9
Zeiss	1.12	0.99	0.99	0.95

Kowalskia fahlbuschi: Holotype

	M$\underline{1}$, L	M$\underline{1}$, W	M$\underline{2}$, L	M$\underline{2}$, W	M$\underline{3}$, L	M$\underline{3}$, W
1970	2.3	1.5	1.8	1.5	1.6	1.5
Zeiss	2.21	1.39	1.60	1.31	1.51	1.43

Some of the Kohfidisch specimens were measured by A. VAN DE WEERD of Utrecht University using Leitz equipment as well as by us in Vienna, thus giving the opportunity to compare the combined effect of different workers and different equipment. Means, when a large number of specimens are involved, should cancel out lack of repeatability of measurements by the individual operator, and the first two comparisons are of means only. What remains as differences should be variation between operators and between equipment. The third comparison is of a single specimen of *Parapodemus lugdunensis.*

Progonomys woelferi (v. d. Weerd measurements given second)

	M	N	S	Percent Difference
$M\bar{1}$, L:	1.95	21	0.07	—1
W:	1.21	21	0.05	+2
$M\bar{2}$, L:	1.45	24	0.05	—1
W:	1.28	24	0.04	0
$M\bar{1}$, L:	1.97	27	0.07	
W:	1.19	27	0.05	
$M\bar{2}$, L:	1.46	33	0.06	
W:	1.28	33	0.04	

Parapodemus lugdunensis

	M	N	S	Percent Difference
$M\bar{1}$, L:	1.67	8	0.09	—2
W:	1.02	8	0.05	+2
$M\bar{2}$, L:	1.25	10	0.07	0
W:	1.11	10	0.03	+2
$M\bar{1}$, L:	1.70	8	0.09	
W:	1.00	7	0.05	
$M\bar{2}$, L:	1.25	10	0.05	
W:	1.09	10	0.04	

Parapodemus lugdunensis: $M\underline{1}$—$M\underline{3}$, left

	$M\underline{1}$, L	$M\underline{1}$, W	$M\underline{2}$, L	$M\underline{2}$, W	$M\underline{3}$, L	$M\underline{3}$, W
B & W:	1.98	1.16	1.33	1.15	0.80	0.82
v. d. Weerd:	1.92	1.13	1.32	1.13	0.78	0.80
% diff.:	+3	+3	+1	+2	+2.5	+2

Comparison of means in the two sets of measurements show a fluctuation of two percent too small to two percent too large. We think this is an acceptable difference. Any less would seemingly involve one worker and one instrument making all measurements. The measurements of the individual of *Parapodemus lugdunensis* shows, as would be expected, greater discrepancies. Here our measurements are one percent to three percent larger. The absolute largest error is 0.06 mm, but four of the six measurements are only one to two hundredths apart, a surprisingly close agreement all things considered. To expect much closer agreement is to put reliance in the hundredths column where accuracy is dropping off rapidly. For very small teeth of less than a millimeter in a dimension this is unfortunate because in percent a 0.1 mm may be important.

Counts

Certain variables such as strength of mesolophid are difficult to report with any consistency. Reliance in the present work is placed entirely on visual impression. Van de Weerd (1976, p. 52) reported for his work that results of repeated countings on the same feature appeared to differ up to ten percent. Obviously, different observers reporting on different assemblages will introduce artificial differences difficult to evaluate even with abundant text-figures as a guide. It is all too easy to introduce a false sense of accuracy into our observations and descriptions. Bachmayer & Wilson (1970) have been cited several times for inadequate treatment of some of the common material from Kohfidisch. This present work is an attempt to meet some of these criticisms. Yet it seems to one of us (Wilson) that the only solution is to have one worker study all the material of a given species from all the principal localities, rather than depend on extensive studies of various workers each working largely on his or her own collections. We do believe that there are important distinctions to be made among fossil populations, but that faunal studies, by their very nature, can hardly accomplish the necessary exactness (in this regard see for example the comments of Ramaekers 1975, p. 106—108).

Remarks on Kohfidisch Taxa

Family Erinaceidae

Galerix zapfei Bachmayer & Wilson, 1970

Lower dentition:

Rümke (1976, p. 269), in discussing the relationships of *Galerix atticus*, has indicated the great similarity of the lower molars of *G. zapfei* to this species. At the same time, she stated that the figures in our 1970 paper do not agree with our description, and moreover, that Rabeder's figure of $M\bar{1}$ of the holotype of *G. zapfei* (1973) is, "certainly different from *G. atticus*." In fact, $M\bar{1}$ of the holotype of *G. zapfei* (Bachmayer & Wilson 1970, pl. 5, fig. 7) is reasonably close to Rabeder's figure. It is also much like Rümke's figures 6 and 9, pl. 1, and is less like figures 4 or 8, pertaining to *G. moedlingensis* of Pikermi. Other Kohfidisch specimens of *G. zapfei* seem identical in structure of $M\bar{1}$ and $M\bar{2}$ to those of *G. atticus*.

Rümke has cited as a distinctive feature of *G. atticus* in comparison with *G. zapfei* the two-rooted $P\bar{2}$ of the former versus the single-rooted $P\bar{2}$ of the latter. It should be noted, however, that in *G. atticus*, $P\bar{2}$ is represented only by a single specimen with "roots broken off" [although] "the constriction of the crown enamel shows that the tooth had two roots" (p. 268). In *G. zapfei*, however, $P\bar{2}$ is known only by its single-socketed alveolus. We may not be comparing the same thing. The one clear thing is that the talonid construction of M$\bar{1}$ and M$\bar{2}$ of *G. zapfei* is more like that of *G. atticus* than it is like that of *G. moedlingensis*.

It is curious in view of the large number of *Galerix zapfei* specimens available from Kohfidisch that no jaws are represented in which a single-rooted P$\bar{2}$ is still present. One explanation is that single-rooted teeth fall out of the jaw more frequently than do two-rooted teeth. It also seems likely that not all specimens of *G. zapfei* have single-rooted P$\bar{2}$'s, as the following counts suggest.

P$\bar{2}$ present and double-rooted	Double-rooted socket for P$\bar{2}$	Single socket for P$\bar{2}$	*G. zapfei* lower molars	*G. „socialis“* type lower molars
10	21	37	51	17

These counts give a total of 48 specimens with double-rooted P$\bar{2}$'s or double-rooted sockets, associated with *G. socialis* type lower molars or with molars but lacking P$\bar{2}$ or its alveolus, or vice versa, versus a total of 88 specimens pertaining to *G. zapfei*. As a P$\bar{2}$/M$\bar{1}$—M$\bar{2}$ ratio, *G. zapfei* is represented by 37/51, as opposed to 31/17. Assuming that in fragmented specimens there should be present as many molar dentitions as premolar, and the counts sustain this assumption, there is then a decided overabundance of double-rooted P$\bar{2}$'s and sockets, suggesting that *G. zapfei* must have on occasion double-rooted sockets, in fact in 27 percent of the above sample. Thus, our previous statement of 1970 (p. 545) on the morphologic variations in P$\bar{1}$—P$\bar{2}$ should be modified to read: "(4) *Galerix zapfei*. Kohfidisch. P$\bar{2}$ with single undivided alveolus in majority of cases, but probably some which are double-rooted. P$\bar{3}$: mostly with a small paraconid; heel weak, and, in most cases with high point of heel on lingual side. P$\bar{4}$: heel weak."

Upper dentition:

It does not seem possible to separate the upper dentition of *Galerix zapfei* from the second Kohfidisch species. Certain specimens suggest a separation, but nothing seems consistent. The Kohfidisch uppers collectively are all beyond *G. socialis* in the nearly always divided mesostyle of the molars, and some of these must represent this second species, and some *G. zapfei*. The uppers are intermediate between those of Vösendorf and Eichkogel as Rabeder has reported (1973, p. 440), but the collection spread of the Kohfidisch specimens includes about every feature of specimens from both these localities.

In M$\underline{1}$ there is a rather consistent straightness to the posterior wing of the paracone, and the protoconule lacks in most instances the small posterior arm or fork seen in *G. moedlingensis*. M$\underline{3}$ is variable as might be expected, but in most, if not all, a distinct metacone cusp is present as in *G. moedlingensis*. There seems to be some, but slight, correlation of (a) more open valley between mesostyles, lack of a forked protoconule in M$\underline{1}$—M$\underline{2}$, and less built up metacone on M3̲ on the one hand, and (b) less separation of mesostyles, forked protoconule in M1̲—M2̲, and a more built up metacone on M3̲. It is possible that (a) refers to *G. zapfei* and (b) to the second species, but the separation is poor at best. *G. atticus* may eventually prove to be a synonym of *G. zapfei*.

Galerix cf. *G. moedlingensis*

Galerix exilis, BACHMAYER & WILSON, 1970
Galerix cf. *G. socialis*, BACHMAYER & WILSON, 1978

In regard to the lower dentition it is difficult to see clear differences from those of *G. socialis*, although the upper molars are all more advanced. With almost equal propriety, this species could be referred to as *G.* cf. *voesendorfensis*, but the stratigraphic position favors tentative assignment to *G. moedlingensis*. Evidence at present is not sufficient to justify a new specific name.

Erinaceus ? sp.

Plate 3, Figures 14, 14a

Since the 1978 report, another upper molar has been recovered, but, more importantly, Professor Helmuth ZAPFE has kindly furnished us with a fragment of left lower jaw with P4̄—M2̄, alveolus for P2̄, and partial alveolus of M3̄. This latter specimen is characterized by large size, exceeding in dimensions those of any *Erinaceus*, or related genus, of which we can find a record. Measurements of this new specimen are as follows.

P4̄, L: 4.29 M1̄, L: 6.17 M2̄, L: 5.65 Depth of jaw below M1̄: 8.1
W: 3.03 W: 4.42 W: 3.62

Unfortunately, only one other Kohfidisch specimen is directly comparable, a fragment of lower jaw with M2̄ (L: 4.27; W: 3.29). M2̄ of the ZAPFE specimen is 32 percent longer, but only 9 percent wider. A length variation of 32 percent is distinctly greater than is present in collections of *Erinaceus* cf. *praeglacialis* from Hundsheim (RABEDER 1972) or *Erinaceus samsonowiczi* from Weze (SULIMSKI 1959), in which the variation is 13 and 10 percent respectively. The two M2̲'s from Kohfidisch available for comparison show a size difference of 22 (length) and 15 (width) percent.

Compared to *E. samsonowiczi*, the new specimen is not only larger, but the mental foramen, situated under the posterior root of P4̄, is higher in position, and P4̄ may be relatively larger. Likewise, compared to *E.* cf. *praeglacialis*, P4̄ is larger, M2̄ is longer, and the jaw deeper.

It thus seems that the Kohfidisch jaw warrants separate recognition in the fauna, and perhaps even designation as a new species. We have refrained from so doing in the hope that additional specimens will be found at Kohfidisch and clarify the situation.

Family Soricidae

Anourosorex kormosi Bachmayer & Wilson, 1970

In *Anourosorex squamipes* from the Recent of eastern Asia, M3/3 are present in contrast to the extinct *Amblycoptus oligodon* and *A. topali* from Hungary in which M3/3 have been lost, and M$\underline{2}$ reduced to about the state of M$\underline{3}$ of *Anourosorex*, and M$\overline{2}$ to about the state of M$\overline{3}$ of *Anourosorex* in *A. topali*.

Anourosorex kormosi still retains both third molars. The following is a statement of the amount of reduction seen in the M$\overline{3}$ (see also Bachmayer & Wilson 1978, p. 141) of the Kohfidisch specimens.

M$\overline{3}$ may vary from a two-rooted tooth with the crown bearing a distinctly basined heel through those in which the rear root is tiny to those which have only a single root. As root reduction proceeds the heel is progressively reduced to an extreme condition in which the heel has disappeared and the trigonid hardly more than a selene with excavation toward the lingual margin. The type specimen has a two-rooted M$\overline{3}$, but the heel is small and hardly basined. Of 46 specimens from Kohfidisch in which M$\overline{3}$ is present or its alveoli/alveolus are, 33 at least are two-rooted, and only four are single-rooted or with fused roots. Of 21 specimens with crowns preserved, six have moderately basined heels, 11 have reduced heels (without basin or nearly so), and four have no heel. In nine specimens the ratio of length of M$\overline{3}$ to M$\overline{1}$ can be determined. These ratios range from 0.27 to 0.46 with a mean of 0.40. The ratio for Repenning's illustrated specimen of *A. squamipes* is about one-third (1967, fig. 39).

In a recent paper, Storch (1978, p. 424—425) refers material from Dorn—Dürkheim to "*Anourosorex*" *kormosi*, and comments, „Trotzdem halte ich die Unterschiede für zu zahlreich und den stratigraphischen Abstand für zu groß um das Fossilmaterial ohne Vorbehalt zu *Anourosorex* zu stellen." This reservation is accompanied by a listing of differences between fossil specimens and the Recent *A. squamipes* (see also Bachmayer & Wilson 1970) which are considerable if they prove to be constant. Danger in this regard is seen in the structure of M$\overline{3}$. Storch gives "*A.*" *kormosi* as with "deutlichem kleinem Talonidbecken" and *A. squamipes* as "ohne differenziertes Talonid."

Rzebik-Kowalska established (1975) the genus *Paranourosorex* for fossil specimens from Podlesice, Poland. *Paranourosorex* as described by Rzebik-Kowalska differs from *Anourosorex kormosi* in: (1) larger size, (2) accentuated pigmentation, (3) patterns of P$\underline{4}$, M$\underline{1}$, and M$\overline{1}$, and (4) later geologic age. Rzebik-Kowalska regards the relatively short trigonid of *Paranourosorex* as especially important. Otherwise, M$\underline{1}$ seems to have more of a mesostyle, but the accessory cusp mentioned by her seems also to be present in *A. kormosi* — in some specimens at least (see Bachmayer & Wilson 1970, plate 6, fig. 25 for example). We are not sure that P$\underline{4}$ has any consistent differences. The lower incisor lacks the accessory crenulations of *A. kormosi*. Kowalska thinks that distinctions from *A. kormosi* are sufficient for generic recognition (p. 178).

Another genus in the same general group as *Anourosorex*, *Paranourosorex*, and *Amblycoptus* is *Crusafontina* Gibert (Vallesian of Can Llobateres, Spain). Storch has commented on the similarity of *Crusafontina endemica* to *A. kormosi*, although the similarity in $M\overline{3}$ cited by him is, as indicated above, a somewhat hazardous feature to use. Also Gibert (1975, p. 120) states that his species shows certain similarities to *Anourosorex kormosi*. Generally speaking, *C. endemica* is less advanced than the somewhat younger *A. kormosi*. In the absence of a direct comparison of material, we are not prepared to say whether or not *A. kormosi* is closer to *C. endemica* than to *A. squamipes*, but several distinctions from *C. endemica* seem evident: (1) posterior molars ($M\overline{2}$—$M\overline{3}$) more reduced relative to $M\overline{1}$, (2) $M\underline{1}$ with less posterior emargination, parastyle more prominent, mesostyle less developed, body of tooth less proportionately transversely extended, and (3) $M\underline{2}$ more reduced relative to $M\underline{1}$. These distinctions are in the direction of *A. squamipes*. In more detail, $M\overline{3}$ is represented by ten teeth in *C. endemica*, and are described by Gibert as having entoconid and hypoconid. Reference to the preceding description of $M\overline{3}$ in *A. kormosi* indicates that probably three-fourths of the Kohfidisch specimens are more advanced, several markedly so. If measurements are reliable, and as based on means, the Kohfidisch $M\overline{1}$'s are absolutely larger, $M\overline{2}$'s and $M\overline{3}$'s about the same as those of *C. endemica*. Likewise, $M\underline{1}$ seems absolutely some larger and $M\underline{2}$ nearly the same. Judging from the $M\underline{1}$ figured by Gibert (1975, pl. 2, fig. 6), the first upper molar of *Crusafontina* is much more "normal" than that of *A. kormosi* in which the approach to *A. squamipes* is clearly visible. Measurements do not show change toward anteroposterior elongation, but if attention is directed to the main body of the tooth, especially to the characteristics of the ectoloph, the considerable difference between *Crusafontina* and *A. kormosi* are quite obvious. The paracone and metacone in *Crusafontina*, for example, are subequal rather than as in *A. kormosi* where the paracone is much smaller.

We prefer to retain *kormosi* in *Anourosorex*, or perhaps as Storch has done as „*Anourosorex*" *kormosi*, than to make any other assigment at present.

Family Talpidae

Talpa gilothi Storch, 1978

Talpa ? sp. — Bachmayer & Wilson, 1970.

The humeri described by Bachmayer & Wilson (1970) as *Talpa* ? sp. have been referred to *Talpa gilothi* by Storch (1978, p. 434—436, and especially Table 3).

Family Sciuridae

Spermophilinus cf. *S. bredai*

A number of additional specimens of *Spermophilinus*, including three lower jaws and scattered teeth, both upper and lower, have been added to the Kohfidisch collections. The discussion of relationships given in 1970 still holds however. The great length of M3̄ relative to the more anterior molars cited in 1970 is confirmed. Finally, as stated before, size of M1̄—M2̄ agrees more closely with *S. bredai* than with *S. turolensis.*

Measurements

		R	M
P4̄,	L:	1.59—1.75	1.68
	W:	1.46—1.60	1.52
M1̄,	L:	1.65—1.92	1.80
	W:	2.00—2.14	2.09
M2̄,	L:	1.89—2.14	2.06
	W:	2.34—2.55	2.44
M3̄,	L:	2.54—2.89	2.75
	W:	2.24—2.31	2.27

Family Gliridae

Muscardinus austriacus BACHMAYER & WILSON, 1970

Muscardinus pliocaenicus austriacus. — BACHMAYER & WILSON, 1970.

As a result of fine-screening of Kohfidisch matrix, isolated teeth of the upper dentition of *Muscardinus p. austriacus* are now to be recorded. Association with the lowers of *M. austriacus* seems certain enough because only one species at Kohfidisch has the characteristic flat crowns. A description of the upper molar follows.

M1̲: The tooth crown is supported by four more or less equally developed roots. Seven specimens demonstrate the crown pattern. The anteroloph is a completely separate crest. Protoloph and anterior centroloph are weakly united internally, with the centroloph extending across the tooth crown. A short anterior accessory crest sometimes (3 of 7) lies between them extending from the external side. The metaloph and posteroloph are somewhat more strongly united internally, and a posterior centroloph lies between them which is short in four specimens and long in three. The anterior accessory and the posterior centroloph may be regarded as primitive features in respect to living *Muscardinus*. In more detail, the anterior accessory may be present as a distinct short crest (1), as a style (2), or be completely absent (4). The posterior centroloph is always present, and extends completely across the tooth in one specimen, and nearly so in two more.

M2̲: Only three specimens are available. In two of them the internal root is present as an elongate structure, grooved but not divided except at the tip. Six crests are present reaching a more or less continuous endoloph. All three have an accessory between protoloph and anterior centroloph on the external side, and a corresponding, but weaker, accessory from the endoloph. One of the three teeth has a short posterior accessory extending from the external side between metaloph and posterior centroloph. Finally, in one of the M$\underline{2}$'s, a style is present at the external border between the two centrolophs.

M$\underline{3}$: The third upper molar is three-rooted. Eight teeth in all show the crown pattern. Much variation exists in dimensions of crown and number of crests in this sample. Size variation seems no greater, however, than in *Muscardinus hispanicus* (v. D. WEERD 1976, table 49, p. 149). The number of continuous crests varies from six to eight, with six the more common (5 ? of 8). The crests are generally parallel, but sometimes the posterior ones converge lingually. Seemingly the crest which fails to develop most frequently is the most anterior accessory, lying between anteroloph and protoloph. In those teeth with six continuous crests, the additional missing or incompletely developed crest is most likely the anterior accessory that lies between protoloph and anterior centroloph. One tooth in the sample is essentially five-crested. This tooth is difficult to interpret but probably results from incompleteness of the posterior centroloph.

Measurements

	R	M	N
M$\underline{1}$, L:	1.47—1.71	1.53	7
W:	1.02—1.29	1.29	7
M$\underline{2}$, L:	1.29—1.40	1.35	3
W:	1.26—1.38	1.33	3
M$\underline{3}$, L:	0.96—1.16	1.06	8
W:	1.09—1.32	1.21	8

Discussion: As specimens of the upper dentition from Kohfidisch become available, the seemingly close relationship to *Muscardinus pliocaenicus* of Poland, based originally on a single jaw fragment from Kohfidisch with P$\overline{4}$—M$\overline{1}$, seems to recede. It is perhaps better to view the Kohfidisch form as distinct at a specific level, and be designated as *Muscardinus austriacus*.

Muscardinus austriacus, in comparison with *M. pliocaenicus*, seems to exhibit the following differences: (1) M$\underline{2}$ three-rooted with only tip of internal root divided so far as now known rather than four-rooted; (2) M$\underline{3}$ three-rooted rather than four-rooted; (3) posterior centroloph of M$\underline{1}$ better developed; and (4) M$\underline{2}$ and M$\underline{3}$ seem to have more frequent accessory complications than in the Polish species.

Among other species of *Muscardinus*, the structure of M$\underline{1}$ seems distinctive in comparison with *M. vireti* and *M. hispanicus*, and most like *M. crusafonti* in crown pattern. Indeed, with the small samples available for comparison, it is difficult to cite convincing differences. *M. crusafonti*, however, has lower molars that are all two-rooted. Data in regard to pattern of M$\underline{1}$ and root formation of molar teeth for various species may be summarized in the following two tables.

Pattern of $M\underline{1}$ on some Species of *Muscardinus*
(modified after v. d. Weerd, 1976. Tbl. 50)

	anterior centroloph		posterior centroloph		extra ridge	
	short	long	short	long	present	absent
M. vireti	0	12	0	12	0	12
M. austriacus	0	7	4	3	3 *)	4
M. crusafonti	0	7	5	2	1	6
M. hispanicus	4	16	20	0	8	12

Muscardinus Root System

	$M\underline{1}$	$M\underline{2}$	$M\underline{3}$	$M\overline{1}$	$M\overline{2}$	$M\overline{3}$
M. pliocaenicus	4	4	4	3	4	3—4 3)
M. vireti	4	4—3 4)	4—3 5)	3—4 6)	4	4
M. austriacus	4	3 7)	3	3	4	3
M. crusafonti	3	?	?	2	2	2
M. hispanicus 8)	3	3	3	2	3	3

Increase with time in number of roots on the molars seems rather consistently demonstrated by *Muscardinus* samples from the Vallesian (Can Llobateres), early Turolian (Kohfidisch), late Turolian (Lissieu), and Ruscinian (Podlesice, Weze). Pattern changes are broadly consistent also as a trend toward less complex and variable patterns when *Eomuscardinus* and *Muscardinus* are compared, but seem not altogether consistent within *Muscardinus*. For example, the trend postulated by v. d. Weerd (1976, p. 151) toward longer centrolophs seems not to be continued in *M. pliocaenicus* and *M. avellanarius* (Recent) in respect to the posterior centroloph. In *M. pliocaenicus* the posterior centroloph is absent in two of three available specimens, and in *M. avellanarius* may also be absent. Moreover, root condition suggests that *M. crusafonti* is less rather than more evolved than *M. hispanicus* (see also Hartenberger 1966, tbl. 1, p. 598). However, so fas as *Muscardinus austriacus* is concerned, it seems intermediate in both root formation and crown pattern between the upper Turolian *M. vireti*, and the Vallesian *M. hispanicus*.

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*) Style only.

3) Alveolus indicates 4 roots in one, three roots in another specimen, but posterior root furrowed and bifurcated at tip.

4) Four roots usually, but sometimes internal pair fused.

5) Four roots or better three, by fusion of inner roots.

6) Three roots, sometimes four by division of the anterior root.

7) Inner root broad, grooved and split at tip.

8) On basis of crown pattern of $M\underline{1}$, more primitive than *M. crusafonti*.

Myomimus cf. *M. multicristatus* (DE BRUIJN, 1966)

Specimens assigned to this species (BACHMAYER & WILSON 1978) can be duplicated by material from Eichkogel. It has been suggested (written communication, DE BRUIJN, 1978) that the Eichkogel population belongs to the genus *Vasseuromys* BAUDELOT & DE BONIS, originally described (1966) from the upper Aquitanian of Laugnac, France. The Kohfidisch population exhibits differences from *Vasseuromys rugosus*, as for example in possessing a centrolophid which does not extend to the outer wall of the tooth. *Vasseuromys priscus* from Saint-Gérand-le-Puy (Cluzel Quarry), however, exhibits a centrolophid as in the Kohfidisch specimens (HUGUENEY 1974). Assignment to *Vasseuromys* is certainly more likely than to the Recent *Myomimus*. The name to be applied to the Kohfidisch species awaits completion of work on the Eichkogel glirids now being conducted by DE BRUIJN and HÖCK.

Paraglirulus cf. *P. lissiensis* (HUGUENEY & MEIN, 1965)

Plate 1, Figures 2—5

Our material seems quite in agreement with ENGESSER's diagnosis of *Paraglirulus* (1972, p. 211). The only exceptions are: (1) the principal cusps are not notably higher than the secondary (but not much if any different from ENGESSER's figures), and (2) the centroloph does not end as an independent cusp, but is joined with the anterior crests, but this is probably the case also in *P.* cf. *lissiensis* with which it is close in size.

From *Vasseuromys rugosus*, the Kohfidisch lower molars differ in less continuous external border and shorter centrolophid, but these differences seem not to apply to material referred to *V. priscus* by HUGUENEY 1974. The diagnosis, however, for the genus *Vasseuromys* as given by BAUDELOT & DE BONIS, if taken literally, would seem to exclude *V. priscus*. The teeth from Kohfidisch referred to *Paraglirulus* are smaller than either of the above, or than cf. *M. multicristatus* from Kohfidisch.

Measurements of *Paraglirulus* cf. *P. lissiensis* from Kohfidisch

Tooth		R	M	N
M_1,	L:	0.93—0.94	0.94	2
	W:	1.03—1.05	1.04	2
M_2,	L:	0.92—1.00	0.96	4
	W:	0.92—0.96	0.95	4
M^2,	L:	0.96	0.96	1
	W:	1.00	1.00	1
M^3,	L:	0.85—0.97 *)	0.91	2
	W:	0.82—0.88	0.85	2

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*) The larger of the two M3's may not pertain to this species.

Graphiurops nov. genus

Type Species: *Graphiurops austriacus*, nov. sp.

Generic Diagnosis: Size of cf. *Myomimus dehmi*, BACHMAYER & WILSON, 1978. Protoconid and hypoconid cusps of $M\bar{1}$—$M\bar{2}$ well-separated. Metalophid(?) crest well-developed, other basin structures variable and vestigial. Shape of lower molars as in most glirids, not decisively wider than long as in *Graphiurus*. $M\bar{1}$ two-rooted, $M\bar{2}$ three-rooted.

Graphiurops austriacus nov. sp.
Plate 3, Figures 11—12

Gliridae, indet. BACHMAYER & WILSON, 1978.

Holotype: Fragment of right lower jaw with $M\bar{1}$. Coll. Natural History Museum, Vienna, Div. Geol. Paleont., No. 1980/53/1. Fig. in BACHMAYER & WILSON, pl. 3, fig. 14, 1978.

Referred Specimens: Fragment of left lower jaw with $M\bar{2}$, right $M\bar{1}$?, and right $M\bar{2}$?

Geological Age and Locality: Early Turolian fissure deposits near Kohfidisch, Burgenland.

Diagnosis: Only species known. Diagnosis as given for genus.

Description: The holotype and the additional jaw fragment with $M\bar{2}$ have been described previously (BACHMAYER & WILSON 1978, p. 151—152). An isolated right lower molar, probably $M\bar{1}$, perhaps shows a less complicated tooth pattern than does the holotype. The metalophid (?) crest pursues a more transverse course across the basin of the tooth, and the accessory structure between it and the anterolophid is lacking. The accessory structure adjacent to the hypoconid is also lacking, but one is present adjacent to the entoconid wall of the tooth. The latter may be joined to the metalophid (?) of the holotype, accounting for its more curving course.

The right $M\bar{2}$(?) is damaged in the area of the hypoconid. Its basin pattern is very simple consisting only of the metalophid(?) crest. In this pattern it agrees with $M\bar{2}$ of the jaw fragment except that the small accessory cuspule adjacent to the entoconid in the latter is lacking.

In *Graphiurus* both $M\bar{1}$ and $M\bar{2}$ are decisively wider than long. In the Kohfidisch specimens, $M\bar{1}$ is longer than wide, and $M\bar{2}$ is only slightly longer than wide. Root patterns can not be determined in either of the two isolated teeth.

Measurements of *Graphiurops austriacus*

*) $M\bar{1}$,	L:	1.02	$M\bar{1}$(?),	L:	1.05
	W:	0.90		W:	0.91
$M\bar{2}$,	L:	1.03	$M\bar{2}$(?),	L:	1.01
	W:	1.09		W:	1.04

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*) Holotype.

Comparisons and Relationships: The tooth patterns of the Kohfidisch specimens are unlike any fossil or living glirids hitherto known from Europe. Consequently, we suggested earlier (1978) that they were developed by heavy wear, at the same time admitting that wear in other glirids produced patterns "of a quite different character". Subsequently, we recognized a similarity to patterns of *Graphiurus* as illustrated by STEHLIN & SCHAUB, p. 521, 1950. Also, these authors stressed the point that in *Graphiurus* only the crown borders of the teeth are mechanically active, and the pattern within the tooth basin has only rudimentary relief. This is a fundamental feature of the Kohfidisch specimens except that the metalophid(?) is nearly if not quite so high as the adjacent border of the tooth. From this it seemed rather certain that we were dealing with some kind of graphiurine, and perhaps a species close to some living species of *Graphiurus*. If a graphiurine, it would be a new geographical record because these glirids have not been known previously from any place except Africa south of the Sahara Desert. We now have had opportunity to examine two specimens of *Graphiurus* (*Claviglis*) *murinus* in the Recent collections of the Natural History Museum of Vienna, nos. B825 and B830 from the Congo, and the relationship to *Graphiurus* itself does not seem so close as first thought although closer than to any other member of the Gliridae.

It is not easy to make out the basin pattern of *Graphiurus*, even in those species, for example *G. murinus*, where it is supposed to be most distinct. However, in comparison with the Kohfidisch genus, it is more complicated, but at the same time more subdued. In *Graphiurops* the metalophid(?) is a distinct crest, but other basin structures are essentially absent, and especially to be noted is the absence of the centrolophid and the third principal crest (hypolophid?). Moreover as stated in the description, protoconid-hypoconid separation is pronounced, decidedly more pronounced than in *Graphiurus*, and the shape of the lower molars are much more typically glirid than in the African genus.

The Gliridae seem to have originated in Europe from such a genus as the Eocene *Gliravus*. *Graphiurops* resembles *Gliravus* in having a pronounced metalophid, and in weak and variable structures in the centrolophid position, although in *Graphiurops* these are much less pronounced. On the other hand, in the typical glirids, these structures become strengthened.

STEHLIN & SCHAUB (1951) see similarities in pattern between *Graphiurus* and *Eliomys*, but the separation of *Graphiurus* from typical glirids must have occured early in glirid history even if not as an early Oligocene isolate in Africa. Evidence for this early separation is seen in other structures than the dentition. Important in this regard is the structure of the anterior end of the zygomatic arch. In *Graphiurus* the lower surface of the arch for attachment of the *Masseter lateralis* is narrow and essentially horizontal, whereas in other glirids, the zygomatic plate is more or less tilted upward and is broader. This difference in zygomatic structure led MILLER & GIDLEY (1918) to place *Graphiurus* in a family separate from other glirids, and indeed in the superfamily group

Dipodoidea rather than with the Muroidea. The difference in zygomasseteric structure is not necessarily a major distinction for we have a duplication of these differences within the fossil Cricetidae, but it does suggest early separation of the Graphiurinae from the main part of the Gliridae. Unfortunately, we do not, of course, know what the zygomasseteric structure was like in *Graphiurops*.

Several alternative views as to the relationship of *Graphiurops* to living Graphiurinae seem possible. One is that the former is an early offshoot from the Eocenen glirid stock, just as the Graphiurinae are, with dental modifications along graphiurine lines, but not necessarily with any closer relationship. Second, and this seems more probable, *Graphiurops* is an authentic member of the Graphiurinae. It is possible in this case that the group originated in Europe before migration to Africa occured, arriving on that continent near the beginning of the Oligocene and becoming a relict group there. Third, and this seems the most probable to us, an early primitive branch of the Gliridae became isolated south of the Sahara Desert, there developed into the Graphiurinae, and subsequently an aberrant branch of the stock extended its range back into Europe in Vallesian or early Turolian time.

A single tooth from Eichkogel in the Vienna Basin also shows the pattern of *Graphiurops*. H. de Bruijn & G. Höck are currently describing the Eichkogel glirids, and recognized the peculiar character of this tooth. Independently, de Bruijn (written communication, 1978) has also suggested graphiurine relationships for the Eichkogel specimen to Dr. Höck. It seems now evident that neither malformation nor wear is responsible for producing the *Graphiurops* pattern.

Family Zapodidae

Protozapus intermedius Bachmayer & Wilson, 1970

Textfigure 1; Plate 3, Figure 13

Description: M$\underline{1}$. Nothing need be added to the previous description of M$\underline{1}$ (Bachmayer & Wilson 1970, p. 567). M$\underline{1}$ seems consistently larger than M$\underline{2}$ where the teeth are associated in the same jaw, but of course the sample is small, and the difference may be small.

M$\underline{2}$: The 1970 description is sufficient except to note that M$\underline{1}$—M$\underline{2}$ when divorced from individual jaws do not show the length relations noted above (see text-fig. 1).

M$\underline{3}$: M$\underline{3}$ is known only by one tooth, but that is in a right maxillary with P$\underline{4}$—M$\underline{3}$ complete. The tooth is somewhat circular in outline, but narrows internally. The same five crests are present as in M$\underline{1}$ and M$\underline{2}$, but paracone and metacone are less cuspate. The internal reentrant between protocone and hypocone is absent because the hypocone is reduced or even absent. M$\underline{3}$ is 25 percent shorter in length than M$\underline{2}$, and 12 percent shorter in width. M$\underline{3}$ differs from that figured by Sulimski for *Sminthozapus* (1964, pl. 16, fig. 7) in the strength of the mesoloph which reaches the external border of the tooth. In this it is more like *Eozapus* (STEHLIN & SCHAUB 1951, fig. 231), but the mesoloph and metaloph crests are much more nearly parallel to each other.

M$\bar{1}$: An anteroconid is present in 69 percent (9 of 13) of the M$\bar{1}$'s, and absent in 31 percent (4 of 13). At Eichkogel, the anteroconid is present in all known M$\bar{1}$'s (6). An angulate projection from the mesoconid ("gegensporn" of STEHLIN & SCHAUB (1951)) approaches the protoconid to more or less degree. In about half the available specimens this projection reaches and touches the protoconid; in the remainder the projection fails to touch the protoconid or is lacking. According to STEHLIN & SCHAUB (1951) this angulation is a new feature in *Eozapus*. In two specimens there is a linear extension of the mesoconid (ectolophid) to the protoconid.

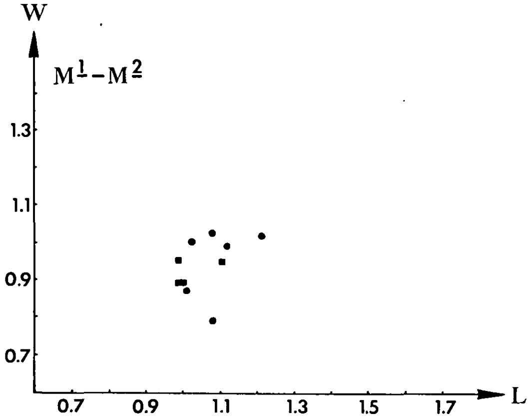

Fig. 1. *Protozapus intermedius*. M$\underline{1}$ = solid circles; M$\underline{2}$ = solid squares

M$\bar{2}$: This tooth is longer than M$\bar{1}$ in two of five specimens, about equal in size in another, and is smaller in two other specimens. The range is from 11 percent longer to 14 percent shorter. The protoconid is cut off from the anteroconid-metaconid in three of the five specimens possessing M$\bar{2}$, and one of those in which it is not is a heavily worn tooth.

M$\bar{3}$: An anteroconid is present in both available specimens. In one, the mesolophid does not reach the metastylid. The other is as described in 1978 (BACHMAYER & WILSON, fig. 15, and p. 153).

Measurements of *Protozapus intermedius* from Kohfidisch

Tooth	R	M	N	S	V
P$\underline{4}$, L:	0.38—0.41	0.39	3	—	—
W:	0.43—0.48	0.46	3	—	—
M$\underline{1}$, L:	1.01—1.21	1.08	7	0.06	5.56
W:	0.79—1.02	0.94	7	0.09	9.57

Tooth	R	M	N	S	V
$M\underline{2}$, L:	0.99—1.10	1.02	5	0.05	4.90
W:	0.84—0.95	0.91	5	0.03	3.30
$M\underline{3}$, L:	0.75	—	1	—	—
W:	0.74	—	1	—	—
$M\overline{1}$, L:	0.96—1.16	1.07	13	0.06	5.61
W:	0.68—0.84	0.76	13	0.05	6.58
$M\overline{2}$, L:	0.99—1.15	1.08	5	0.07	6.48
W:	0.71—0.93	0.83	5	0.06	7.23
$M\overline{3}$, L:	0.90—1.02	0.96	2	—	—
W:	0.74—0.80	0.77	2	—	—

Discussion: Van de Weerd (1976) has stated that *Protozapus* is a synonym of *Eozapus* from the Recent of Szechuen and Kansu provinces, China. We (1978) have not agreed to this synonymy. It is unfortunate that specimens of *Eozapus* seemingly are so rare in collections. In naming the type species of the genus only three skulls, none perfect, were known to Preble (1899). Klingener (1963) had only two (none of the original three), and most authors seem to be relying for details of the dentition on illustrations based on one Preble figure. Thus the parameters of the dentition are far from certain. The dentition of *Protozapus*, however, seems to show distinctions from the available figures of *Eozapus* as follows: (1) shorter $M\underline{2}$, (2) oblique valley frequently separates anteroconid-metaconid from protoconid-mesoconid, (3) weakness of mesolophid in $M\overline{3}$, (4) absence of anteroconid in $M\overline{3}$, and (5) seemingly less reduced $M\underline{3}$. None of these differences may be consistent, but in view of the time and geographic separation may be reason enough to maintain the genus *Protozapus* as separate. Moreover, there seems to have been a small radiation of nearly contemporaneous zapodids with *Eozapus*-like dentitions (*Sminthozapus* Sulimski 1964 and *Pliozapus* Wilson 1936 as well). Of these, *Protozapus* may be closest to *Eozapus*, but largely because it retained a slightly more primitive dental pattern.

Van de Weerd also states (p. 139) that, "the dental features of *Eozapus* and *Sminthozapus* are completely different from those of the genera *Zapus* and *Napaeozapus* in the new world. As a consequence, *Eozapus* is morphologically not intermediate between *Plesiosminthus* and *Zapus* and *Napaeozapus* as has been suggested by Bachmayer & Wilson, 1970." Seemingly, the basis for this remark is our statement (1970, p. 567) that, "both the generic and specific names [i. e., *Protozapus intermedius*] indicate the intermediate position of the fossil remains in zapodid evolution." Our statement was intended to be taken quite broadly and we think van de Weerd took it too literally, especially in view of our concluding statement relating *Protozapus* to "a rather isolated subgroup of zapodines centered in Asia" (Klingener 1966). American authors (Preble, Wilson, Krutzsch, Klingener, Green) have rather consistently placed *Eozapus* or its close relatives in the Zapodinae — not Sicistinae as

STEHLIN & SCHAUB do — and as descendents of one or another species of *Plesiosminthus*. From this point of view, *Protozapus* is more "intermediate" than VAN DE WEERD would have it. However, much more work with more specimens, and more direct comparisons of specimens rather than figures needs to be done before any final conclusions can be made. It may well be that we never will be in a position to do this because there is much more to determining relationships than simply comparing dentitions (see KRUTZSCH 1954, and KLINGENER 1964 as examples).

The most evident consensus that emerges from the work of various authors is that *Eozapus*, *Pliozapus*, *Sminthozapus*, and *Protozapus* are zapodines, not sicistines, and that the four genera are closely related to each other.

It should be noted that DAXNER-HÖCK states (1977, p. 25) that: "der M$\underline{3}$ von *Protozapus* im Obermiozän bereits viel stärker reduziert ist als der M$\underline{3}$ des pliozänen *Sminthozapus* — bzw. des rezenten *Eozapus*." This statement does not agree with conditions in the Kohfidisch specimen which, judging from figure 231 in STEHLIN & SCHAUB (1951) of *Eozapus*, has a less not more reduced third upper molar. The single M$\underline{3}$ from Eichkogel is figured by DAXNER-HÖCK (1977, pl. 4, fig. 10), and comparison with that from Kohfidisch shows clearly that the Eichkogel specimen is not of *Protozapus*. It seems to us to be almost certainly murid, and probably an M$\underline{3}$ of *Parapodemus lugdunensis*.

Family Eomyidae

Leptodontomys species

Plate 1, Figure 1

A second eomyid tooth is now known from Kohfidisch. This is also a right upper M$\underline{1}$ or M$\underline{2}$, but is somewhat larger than the tooth of *Keramidomys* previously reported (1978, p. 147), and, moreover, has a different occlusal pattern, and represents the genus *Leptodontomys*. The pattern agrees well with that of *Leptodontomys bodvanus* of Osztramos Loc. 1, Hungary, illustrated by JANOSSY (1972, pl. III, fig. 4), but the tooth is somewhat larger than in that specimen.

Family Cricetidae

Kowalskia fahlbuschi BACHMAYER & WILSON, 1970

Textfigures 2—3; Plate 1, Figures 6—8; Plate 2, Figures 9—10

A general description of the species, *Kowalskia fahlbuschi*, was given in 1970. The species has since been tentatively identified in the geographically near Eichkogel fauna of Austria (DAXNER-HÖCK 1972), and in more distant localities such as Spain and France. Hence, it is now necessary to investigate more fully than before the variation in the large sample from Kohfidisch. A tooth by tooth discussion follows.

M$\underline{1}$: This tooth is characterized by (1) a weak and delicate labial spur of the anterolophule (see MEIN & FREUDENTHAL 1971b for nomenclature). In

32 percent of the specimens it reaches the outer border, fails to do so in 24 percent, and is essentially absent in 44 percent. In *K.* cf. *fahlbuschi* of Eichkogel these percentages are 61 percent, 23 percent, and 16 percent respectively. In Spanish specimens (v. d. Weerd 1976) referred to *K. fahlbuschi*, the labial part of the anterolophule is constant in its absence. (2) a rather modest development of the mesoloph in which it is long in 38 percent of the specimens, short in 49 percent, and essentially absent in 14 percent. Percentages at Eichkogel are 86 percent, and only 14 percent in which it is short to medium. In the Spanish specimens reported by van de Weerd, the mesoloph is short to absent. (3) anterior closure of the paracone-metacone pit is present in 71 percent of specimens, and 29 percent show poor or no closure. This contrasts with 64 percent and 36 percent respectively at Eichkogel. (4) anterior closure of the metacone-hypocone pit is present in 43 percent of the cases with 57 percent showing poor or no closure. Eichkogel shows 30 percent and 70 percent respectively. (5) pronounced tendency for the inner root to be grooved (with divided tips in at least some specimens) to a completely four-rooted tooth (see Pl. 1, fig. 6—8). It is difficult to determine in many specimens whether or not a divided inner root is present, but if probably divided are included with certainly divided, 46 percent of the teeth are in this category with 54 percent either three-rooted or with grooved inner root. Twenty-seven percent are almost certainly four-rooted. Only 30 percent are simply three-rooted. The Eichkogel specimens are described by Daxner-Höck as, ,,Der M$\underline{1}$ ist dreiwurzelig; er besitzt zwei Außen- und eine Innenwurzel. Allerdings bahnt sich die Teilung der Innenwurzel an, denn an einigen Exemplaren ist sie lingual leicht gefurcht, oder ihre Wurzelspitze ist bereits gespaltet.“ Van de Weerd describes the Spanish specimens as three-rooted. The geologically later, but probably related, "*Cricetus*" *kormosi*, is said to have divided roots 50 percent of the time (Schaub 1930). In comparing various specimens with *K. fahlbuschi* from Kohfidisch, authors have not commented on what seems to be an obvious distinction — character of the roots. The taxonomic significance of this distinction, however, is not at all clear, a point to which we shall return.

M$\underline{2}$: Important variables are the length of the mesoloph and the posterior closure of metacone-hypocone by the posterior metalophule. The mesoloph is long (reaching labial border) in 53 percent of the teeth, and short or almost absent in 47 percent. In Eichkogel specimens these figures are 72 percent and 28 percent respectively. In the Spanish material, the mesoloph is consistently short or absent. The posterior metalophule is rather consistently present (84 percent), absent 16 percent of the time. At Eichkogel this structure is always present. In the Spanish specimens the percentages are 78 and 22 percent respectively.

M$\underline{3}$: Two structures seem important. The lingual half of the anteroloph, and the degree of prominence of the metacone. The lingual half of the anteroloph may be moderately developed (64 percent), or absent with only a faint cingular trace below where the anteroloph should be (36 percent). In the Spanish specimens this part of the anteroloph is present 69 percent of the time. It seems to be consistently present in Eichkogel specimens. Degree of development of the metacone of M3 can be expressed as prominent (36 percent), about on a level with the connecting crests and hence simply part of the posteroloph (29 percent), or intermediate (36 percent). Höck says of the Eichkogel material that the metacone is almost completely reduced. Van de Weerd describes the metacone in the Spanish material as very small.

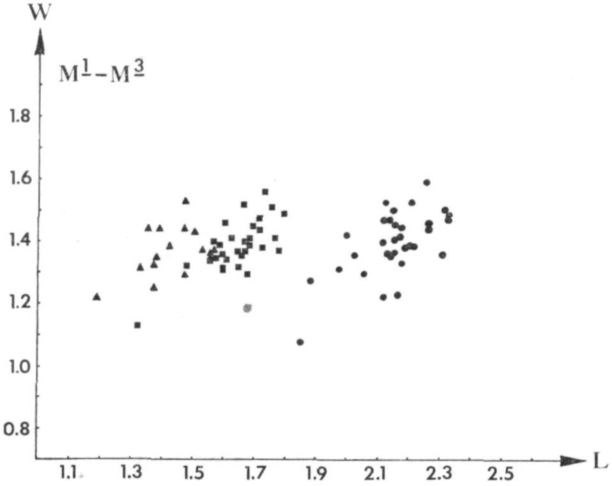

Fig. 2. *Kowalskia fahlbuschi*. M1 = solid circles; M2 = solid squares; M3 = solid triangles

M$\bar{1}$: The anteroconid is double in most specimens, and no three-cusped anteroconids were observed as may be the case in the Eichkogel specimens. The anteroconid connection to the protoconid-metaconid cusps usually is double but may be essentially single. If double, the lingual crest is the stronger in 40 percent of the specimens, weaker in 20 percent, and lingual and labial crests of comparable strength in 40 percent. Eichkogel specimens by comparison have only eight percent of the specimens in which the lingual is stronger. In the Spanish specimens the connection between anteroconid and protoconid-metaconid is usually single, and this is presumably tied to the lesser tendency for subdivision of the anteroconid. The mesolophid of M$\bar{1}$ is a relatively weak crest, but otherwise ranges from extending to the lingual side of the crown (70 percent) to falling short of the lingual side (30 percent). In one tooth it is entirely absent. The Eichkogel specimens seem not to be greatly different. In *K. fahlbuschi* from Spain, 45 percent of the specimens have the mesolophid absent.

M$\bar{2}$: As in the mesolophid of M$\bar{1}$, that of M$\bar{2}$ is not especially robust. It is usually long, however, reaching the lingual margin of the tooth in 81 percent of the specimens. In Spanish *K. fahlbuschi*, the mesolophid of M$\bar{2}$ is absent in

55 percent of the specimens. The mesolophid is present in all(?) specimens from Eichkogel.

M3̄: The mesolophid may be a long independent crest extending to the lingual wall of the tooth (38 percent), or it may be short, touching the metaconid or otherwise weak (62 percent). The Eichkogel *K.* cf. *fahlbuschi* seems to have only 25 percent of the specimens in which there is a mesolophid-metaconid union. The Spanish specimens are too few in number to generalize. The entoconid of M3̄ in the Kohfidisch specimens may be present only as a swelling at the end of a long hypolophid (10 percent), or it may be a large independent cusp, not much smaller than the entoconid on M2̄ with concomitant short hypolophid (60 percent), or be intermediate in morphology (30 percent). Conditions in the Eichkogel specimens seem significantly different. To quote DAXNER-HÖCK (1972, p. 139): „. . . das Entoconid ist zwar andeutungsweise an allen Zähnen als leichte Verdickung am lingualen Ende der Nachjochkante erkennbar, nur an wenigen Stücken ist es gut als selbständiger Höcker ausgeprägt.“ The Spanish specimens may also have more reduced entoconids on M3̄.

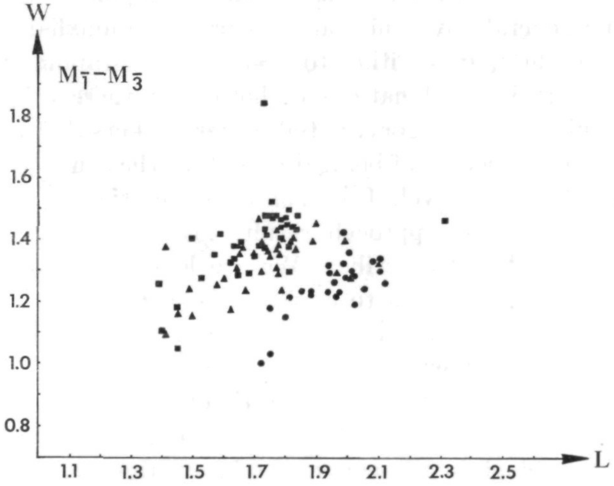

Fig. 3. *Kowalskia fahlbuschi*. M1̄ = solid circles; M2̄ = solid squares; M3̄ = solid triangles

Measurements of *Kowalskia fahlbuschi* from Kohfidisch

Tooth	R	M	N	S	V
M$\underline{1}$, L:	1.88—2.33	2.16	32	0.12	5.56
W:	1.22—1.59	1.39	32	0.10	7.19
M$\underline{2}$, L:	1.32—1.80	1.65	30	0.10	6.06
W:	1.13—1.56	1.39	30	0.08	5.76
M$\underline{3}$, L:	1.19—1.57	1.44	16	0.10	6.94
W:	1.22—1.53	1.37	16	0.08	5.84

Tooth	R	M	N	S	V
$M\bar{1}$, L:	1.72—2.12	1.95	26	0.11	5.64
W:	1.00—1.41	1.24	26	0.09	7.26
$M\bar{2}$, L:	1.39—1.88	1.70	38	0.16	6.47
W:	1.05—1.84	1.39	38	0.13	9.35
$M\bar{3}$, L:	1.41—2.10	1.73	37	0.16	9.25
W:	1.09—1.46	1.32	37	0.09	6.82

Discussion: It is obvious that the population from Kohfidisch differs from those of *Kowalskia* cf. *fahlbuschi* from Eichkogel (see also FRANZEN & STORCH 1975, p. 269), and those of *K. fahlbuschi* from various localities and levels in Spain. It is equally obvious, however, that these differences are not absolute, and that considerable overlap in characters occurs. How to handle the situation nomenclaturally is not clear. Judging from the studies of HOOPER (1952, 1957) on *Peromyscus* and *Reithrodontomys*, as well as others on cricetids, considerable variation may occur within a single species, depending on geographic location. On the other hand, some species are relatively stable in the dentition. A further complication in fossils is stratigraphic variation. Moreover, there has been a general reluctance on the part of mammalian paleontologists to employ subspecific names, either to designate geographic or stratigraphic variation, or uncertain combinations of both. Yet there are advantages to employing the subspecies category. It tells other workers that two populations are different, or are suspected of being different, at the same time emphasizing affinities at the "species" level. The open determination (cf., aff., etc.) is an alternative, but soon this approach results in "synonyms" as more fossil populations are found and described. We are leaving to our colleagues the solution to the present problem to avoid introducing names which may not find acceptance when applied to their local collections. Comments on the more outstanding variations follow.

Such variations as length and strength of (1) mesoloph-mesolophid in M1/1—M2/2, (2) labial part of anterolophule in $M\underline{1}$, and perhaps also (3) lingual half of anteroloph in $M\underline{3}$ seem not to be stratigraphically important, as time relations are currently recognized. Much more likely is it that these variations involving complexity of pattern are owing to environmental distinctions. Both HOOPER & HERSHKOVITZ (1955) have favored the hypothesis that simpler teeth in *Peromyscus* are found in animals inhabiting arid regions, and more complex teeth are developed in more humid regions, for example.

The magnitude of anterocone and anteroconid subdivision is known to be variable from one to another of contemporary species of cricetids. On the other hand, it does have phylogenetic importance in the Cricetinae. For example, stratigraphically older species of *Democricetodon* have single-cusped anterocones in $M\underline{1}$, grooved im more evolved species, and double in presumably derived species of living hamsters such as *Cricetus* and *Cricetulus*. In such a sequence, the Spanish species could be considered primitive.

Kohfidisch specimens have M3/3's in which the metacone and entoconid are prominent, and thus suggesting a more primitive pattern. Whether this can be taken as signifying an older age for Kohfidisch or simply that the Kohfidisch M3/3 is generally primitive among contemporaneous populations can not be established.

Whatever the significance of M3/3, it is in conflict with evidence from root formation in M1. Such stratigraphically younger species of *Kowalskia* as *K. polonica* and *K. intermedia* have four-rooted M1's with only rare exceptions. The oldest *Kowalskia* from Vösendorf is three-rooted, Spanish *K. fahlbuschi* is reported as three-rooted, and the Eichkogel specimens are three-rooted, with only a few teeth with furrowed inner root and divided tip. *Democricetodon* is three-rooted (Mein & Freudenthal 1971a). "*Cricetus* "*kormosi*, younger than the species at Eichkogel and older than *K. intermedia*, has about 50 percent four-rooted M1's. Thus one would suppose that on the basis of root formation Kohfidisch *Kowalskia* was temporally intermediate between Eichkogel and Polgardi. That it is not this simple is seen in the presence of *K. magna* contemporaneous with *K. polonica*. *K. magna* is represented by four M1's. Of these, one specimen has separate inner roots, two are separated by a furrow, and in the fourth, both are united with the metacone root, and only separated through weak furrows. Thus, the Kohfidisch specimens seem more nearly like *K. magna* and "*C.*" *kormosi* in root formation than other species. Jánossy (1972, p. 36) has indicated his scepticism that *K. magna* and *K. fahlbuschi* are taxonomically separable, and the root formation of M1 lends some support to his argument, seemingly based on size. However, it should be emphasized that comparison of the Polish population of *K. magna* with a large sample of *K. fahlbuschi* was made with specimens at hand, and the latter seemed to be smaller. Moreover, there are other distinctions that can be made.

As indicated above, in the original description of *Kowalskia fahlbuschi* (1970), it was stated that the Austrian species was intermediate in size between *K. polonica* and *K. magna* (Fahlbusch, 1969), as based on visual comparison although the published measurements indicated little distinction. De Bruijn, Mein, Montenat, and van de Weerd (1975) suggested also that published measurements were too large. The measurements have all been repeated using a Zeiss micrometer occular. Size comparisons with Eichkogel seem reasonably close, but averaging slightly larger for Kohfidisch. The Spanish specimens from the Teruel-Alfambra region appear to be slightly larger, although those from Tortajada A are essentially the same size. Those from Crevillente 1, 2, 3 are likewise about the same size, but perhaps with slightly more reduced M3/3's. Scattergrams of Kohfidisch size distribution are given in text-figures 2—3.

Epimeriones austriacus Daxner-Höck, 1972

A third specimen of this species is now known from Kohfidisch. This is a right M1 in a fragment of maxillary. It is much more worn than the M1 reported by us in 1978 (pl. 4, fig. 16), but still seems to have faint relict structures inside of the enamel loops. There is no doubt that the new specimen is a right M$\underline{1}$. Comparison with the previously reported M$\underline{1}$ is difficult because of difference in stage of wear, but it seems likely that figure 16 is of a right M$\underline{1}$ as previously stated.

Family Muridae

Progonomys woelferi BACHMAYER & WILSON, 1970

Text figures 4—9

Some comments on variation in tooth morphology of *Progonomys woelferi* are as follows.

M$\underline{1}$: A t_6—t_9 connection is clearly absent in 60 percent of the specimens, and at most, only present in 40 percent. The t_4—t_8 connection is present in all specimens save one, as it is also in M$\underline{2}$. However, it is a lower connection than suggested for *P. cathalai* by VAN DE WEERD (1976, p. 55). The t_4—t_5 and t_5—t_6 connections are strong, but t_{12} can hardly be described as stout or large, as stated for *P. cathalai* by VAN DE WEERD.

M$\overline{1}$: The anteromedian or central cusp is usually absent or present only as a cingular ridge (61 percent of specimens). When present it is almost always minute, and little more than an apex on the cingulum. Most of the characters of this tooth seem highly variable. The two anterior cuspules can be symmetrically developed or not, and the anterolabial one may be larger when the pair is asymmetrically developed. Labial cingular cusps are highly variable, but *P. woelferi* in size of c_1 and frequent presence of more anterior and sizable cusps resembles *P. cathalai* more than *P. hispanicus*.

M$\overline{2}$: Although variable, most teeth are slightly to moderately narrower across the rear half than the anterior half of the tooth. Spurs (see V. D. WEERD, 1976, fig. 9) are rare but present on one M$\overline{2}$ of those examined.

M$\overline{3}$: Breadth of heel of M$\overline{3}$ is not constant in *P. woelferi*.

Measurements of *Progonomys woelferi* from Kohfidisch

Tooth		R	M	N	S	V
M$\underline{1}$,	L:	1.99—2.34	2.16	29	0.11	5.09
	W:	1.28—1.55	1.40	29	0.07	5.00
M$\underline{2}$,	L:	1.35—1.66	1.46	31	0.08	5.48
	W:	1.26—1.50	1.37	31	0.06	4.38
M$\underline{3}$,	L:	0.93—1.17	1.08	14	0.08	7.41
	W:	0.97—1.26	1.08	14	0.08	7.41
M$\overline{1}$,	L:	1.78—2.10	1.93	30	0.15	7.77
	W:	1.11—1.29	1.24	30	0.12	9.68
M$\overline{2}$,	L:	1.36—1.54	1.44	35	0.05	3.47
	W:	1.18—1.36	1.28	35	0.04	3.13
M$\overline{3}$,	L:	1.00—1.21	1.11	23	0.05	4.50
	W:	1.01—1.19	1.06	23	0.08	7.55

Discussion: The problem of measurements has already been discussed. *Progonomys woelferi* is larger than *P. cathalai* (based on visual comparison of Montredon specimens with a sample from Kohfidisch, but size overlap probably exists). Other distinctions lie in (1) the anteroconid complex is not always symmetrically developed, (2) most M$\bar{2}$'s are wider across the anterior half of the tooth than posteriorly rather than equidimensional, (3) t_{12} of M$\underline{1}$ is small rather than large, and (4) stephanodonty may be slightly more advanced. These differences could be viewed as characters of geographic subspecies, but *P. woelferi* is higher stratigraphically than the genotype species, and is associated with fairly abundant remains of *Parapodemus lugdunensis.* For the present, *P. woelferi* may best be left as a full species. *P.* cf. *woelferi* from Crete (DE BRUIJN, SONDAAR & ZACHARIASSE 1971) may have a lesser development of labial accessory cuspules in M$\bar{1}$, and less of a connection between t_6 and t_9, but overall comparison indicates that *P.* cf. *woelferi* is probably identical with *P. woelferi* from Kohfidisch.

Parapodemus lugdunensis SCHAUB, 1938

Textfigures 4—9

Comments on the Kohfidisch specimens are as follows.

M$\underline{1}$: This tooth agrees more or less with VAN DE WEERD's description (1976, p. 77) of the species, but the t_1—t_2 connection is weak, and the transversely compressed nature of t_1 gives it the appearance of having a rather posterior position. The t_1 seems to be pressed in against the lingual wing of t_2 as in *P. lugdunensis* from the Teruel-Alfambra region of Spain. The t_3 has a posterior spur variably, but weakly, present. One of 12 specimens has a tiny t_7. Stephanodonty is developed to a stage clearly over that of *P. woelferi.*

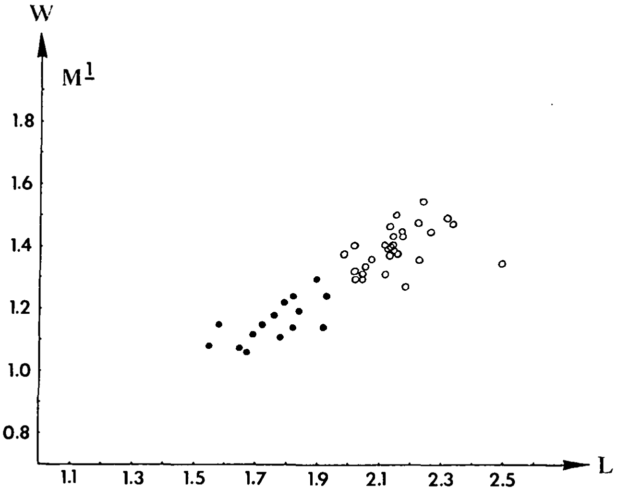

Fig. 4. *Parapodemus lugdunensis.* M$\underline{1}$ = solid circles. *Progonomys woelferi.* M$\underline{1}$ = open circles

M2: The t_3, although small relative to t_1, is distinct. The t_6—t_9 connection is weak (low) although the cusps are close together. M2 is usually longer than wide (one exception). The t_7 is present in one of ten specimens. The inner root of M2 has no appreciable division in 50 percent of the teeth examined. The other half have either a well-marked sulcus (3 of 10), or very nearly divided roots (2 of 10).

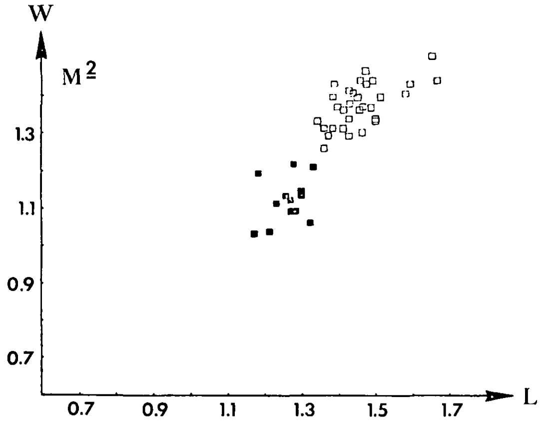

Fig. 5. *Parapodemus lugdunensis.* M2 = solid circles. *Progonomys woelferi.* M2 = open circles

M3: Of the four M3's available, t_3 is present but small relative to t_1 in three, and the fourth is too worn to determine. The t_4 and t_8 are separated by a shallow valley in three of the four teeth. In the fourth, the tooth is sufficiently worn so that all cusps connect.

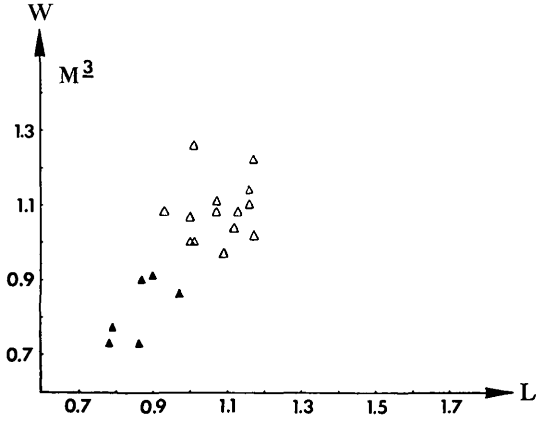

Fig. 6. *Parapodemus lugdunensis.* M3 = solid circles. *Progonomys woelferi.* M3 = open circles

M$\bar{1}$: The anterocentral cusp is absent in 12 percent of the specimens (2 of 17); present but small in 35 percent (6 of 17); and well-developed in 53 percent (9 of 17). The labial cingular cusps are well-developed, especially c_1, but more anterior cusps may also become prominent. Paired anterior cusps may be symmetrical, but perhaps more frequently asymmetrical with the anterolingual cusp farther forward and somewhat more robust. Some of this variation may be owing to wear, or a misidentified small *P. woelferi*. M$\bar{1}$ may be distinguished from that of *P. woelferi* in practically all instances, however, by; (1) smaller size, (2) rather consistent presence of a small anterocentral cusp, and (3) better development of the labial conules.

M$\bar{2}$: These teeth agree well with VAN DE WEERD's description of the Spanish specimens. Some of the Kohfidisch specimens may show a posterior narrowing of the tooth. They may be separated from M$\bar{2}$'s of *P. woelferi* by size and slightly better cingular development.

M$\bar{3}$: The anterolabial cusp is present in the small available sample, but no c_1 cusp. The heel of M$\bar{3}$ is broad.

Although the combination of *Progonomys* and *Parapodemus* is unusual, there is no reason not to refer the present material to *P. lugdunensis*. In general, the associated fauna seems readily assignable to Zone 11 of MEIN (FAHLBUSCH 1976), and the same association with, however, quite different percentages, seems present at Eichkogel (DAXNER-HÖCK 1977). Whether this combination necessarily suggests a very early position in Zone 11 of MEIN, and in the Turolian, is still not certain (BACHMAYER & WILSON 1978, p. 134).

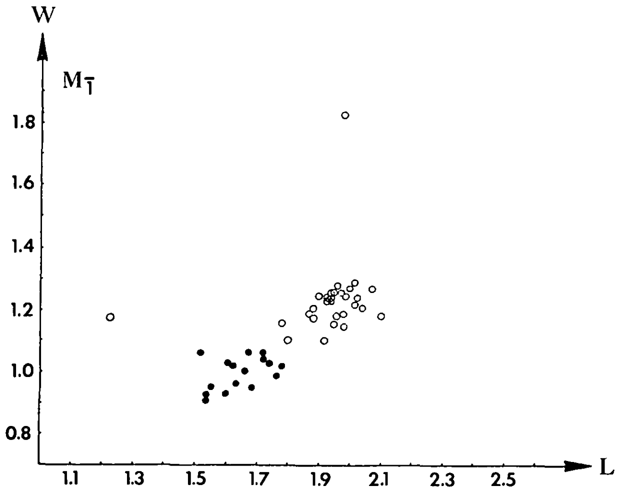

Fig. 7. *Parapodemus lugdunensis*. M$\bar{1}$ = solid circles. *Progonomys woelferi*. M$\bar{1}$ = open circles

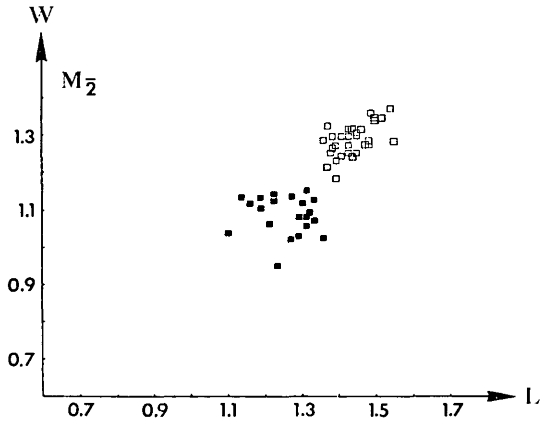

Fig. 8. *Parapodemus lugdunensis.* M$\bar{2}$ = solid circles. *Progonomys woelferi.* M$\bar{2}$ = open circles

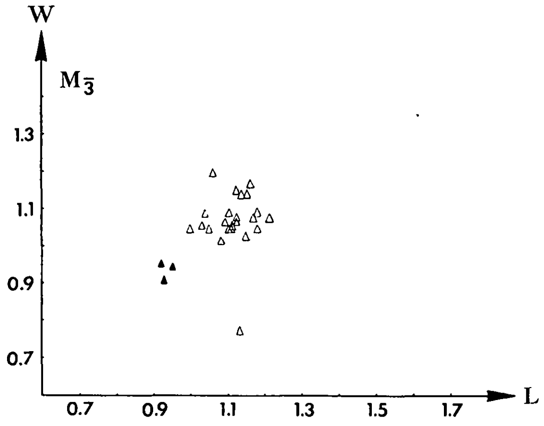

Fig. 9. *Parapodemus lugdunensis.* M$\bar{3}$ = solid circles. *Progonomys woelferi.* M$\bar{3}$ = open circles

Measurements of *Parapodemus lugdunensis* from Kohfidisch

Tooth	R	M	N	S	V
M$\underline{1}$, L:	1.55—1.93	1.76	15	0,12	6.82
W:	1.06—1.29	1.16	15	0.07	6.03
M$\underline{2}$, L:	1.17—1.33	1.26	13	0.05	3.97
W:	1.04—1.22	1.12	13	0.06	5.36
M$\underline{3}$, L:	0.78—0.97	0.86	6	0.07	8.14
W:	0.73—0.91	0.82	6	0.08	9.76
M$\bar{1}$, L:	1.52—1.78	1.65	17	0.09	5.45
W:	0.91—1.06	1.00	17	0.05	5.00

Tooth	R	M	N	S	V
$M\bar{2}$, L:	1.10—1.36	1.26	23	0.07	5.56
W:	1.02—1.15	1.08	23	0.05	4.63
$M\bar{3}$, L:	0.92—0.95	0.93	3	0.02	2.15
W:	0.90—0.95	0.93	3	0.03	3.23

Scattergrams of size distribution for *Progonomys woelferi* and *Parapodemus lugdunensis* (text-figures 4—9) demonstrate the consistently smaller size of teeth in *P. lugdunensis.*

Hystrix cf. *H. suevica* SCHLOSSER, 1884

Four additional teeth have been added to the specimens representing the Kohfidisch *Hystrix.* These are all worn teeth in which the pattern is reduced to isolated lakes surrounded by an enamel ring. They seem to be about the same size as previous specimens.

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Literature

BACHMAYER, F. & R. W. WILSON (1970): Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch fissures of Burgenland, Austria. — Ann. Naturhist. Mus. Wien, 74: 533—587. — Wien.

— (1978): A second contribution to the small mammal fauna of Kohfidisch, Austria. — Ann. Naturhist. Mus. Wien, 81: 129—161. — Wien.

BAUDELOT, S., & L. DE BONIS (1966): Noveaux Glirides (Rodentia) de l'Aquitanien du bassin l'Aquitaine. — C. R. Soc. Geol. France, 1966: 341—343. — Paris.

BRUIJN, H. DE, P. Y. SONDAAR & W. J. ZACHARIASSE (1971): Mammalia and Foraminifera from the Neogene of Kastellios Hill (Crete), a correlation of continental and marine biozones. I. and II. — Konig. Nederl. Akad. Wetenschappen, Proc., (Ser. B) 74/no. 5: 1—22. — Amsterdam.

BRUIJN, H. DE, P. MEIN, C. MONTENAT & A. VAN DE WEERD (1975): Correlations entre les gisements de rongeurs et les formations marines du Miocene Terminal d'Espagne Meridionale I (Provinces d'Alicante et de Murcia). — Kon. Nederl. Akad. Wetenschappen, Proc., (Ser. B), 78/no. 4: 1—32: — Amsterdam.

DAXNER-HÖCK, G. (1972): Cricetinae aus dem Alt-Pliozän vom Eichkogel bei Mödling (Niederösterreich) und von Vösendorf bei Wien. — Paläont. Z., **46** (3/4): 133—150. — Stuttgart.

— (1977): Muridae, Zapodidae und Eomyidae (Rodentia, Mammalia) des Eichkogels bei Mödling (Niederösterreich). — Paläont. Z., **51** (1/2): 19—31. — Stuttgart.

ENGESSER, B. (1972): Die obermiozäne Säugetierfauna von Anvil (Baselland). — Tätigkeitsberichte Naturforsch. Ges. Baselland, **28**: 35—363. — Basel.

FAHLBUSCH, V. (1969): Pliozäne und Pleistozäne Cricetinae (Rodentia, Mammalia) aus Polen. — Acta Zool. Cracoviensia, **14**/ no. 5: 99—137. — Cracow.

— (1976): Report on the International Symposium on mammalian stratigraphy of the European Tertiary. — Newsl. Stratig., 5 (2/3): 160—167. — Berlin, Stuttgart.

FRANZEN, J. L. & G. STORCH (1975): Die unterpliozäne (turolische) Wirbeltierfauna von Dorn-Dürkheim, Rheinhessen (SW-Deutschland). 1. Entdeckung, Geologie, Mammalia: Carnivora, Proboscidea, Rodentia. Grabungsergebnisse 1972—1973. — Senckenbergiana lethaea, **56** (4/5): 233—303. — Frankfurt am Main.

Gibert, J. (1975): New insectivores from the Miocene of Spain. I and II. — Kon. Nederl. Akad. Wetenschappen, Proc. (Ser. B) **78** (2): 108—133. — Amsterdam.

Green, M. (1977): Neogene Zapodidae (Mammalia: Rodentia) from South Dakota. — Journ. Paleont., **51**/no. 5: 996—1015. — Lawrence.

Hartenberger, J.-L. (1966): Les Rongeurs du Vallésien (Miocène supérieur de Can Llaboteres (Sabadell, Espagne): Gliridae & Eomyidae. — Bull. Soc. geol. de France, 8 (7): 596—604. — Paris.

Hershkovitz, P. (1955): South American marsh rats, genus Holochilus, with a summary of sigmodont rodents. — Fieldiana, Zool., **37**: 639—688. — Chicago.

Hooper, E. T. (1952): A systematic review of the harvest mice (Genus *Reithrodontomys*) of Latin America. — Misc. Publ. Mus. Zool., Univ. Michigan, **77**: 1—255. — Ann. Arbor.

— (1957): Dental patterns in mice of the Genus *Peromyscus*. — Misc. Publ. Mus. Zool., Univ. Michigan, **99**: 1—59. — Ann. Arbor.

Hugueney, M. (1974): Gisements de petits mammiferes dans le région de Saint-Gérand-le-Puy (Stratigraphie relative). — Rev. Scientifique du Bourbonnais, Année 1974: 52—68.

Jánossy, D. (1972): Middle Pliocene microvertebrate fauna from the Osztramos Loc. 1. (Northern Hungary). — Ann. Historico-Naturales Mus. Nat. Hungarici, **64**: 27—52. — Budapest.

Klingener, D. (1963): Dental evolution of *Zapus*. — Journ. Mammalogy, **44**/no. 2: 248—260. — Lawrence.

— (1964): The comparative myology of four dipodoid rodents (Genera *Zapus*, *Napaeozapus*, *Sicista*, and *Jaculus*). — Miscl. Publ., Mus. Zool., Univ. Michigan, **124**: 1—100. — Ann. Arbor.

— (1966): Dipodoid rodents from the Valentine Formation of Nebraska. — Occ. Papers Mus. Zool., Univ. Michigan, **644**: 1—9. — Ann Arbor.

Krutzsch, P. H. (1954): North American jumping mice (Genus *Zapus*). — Univ. Kansas Publ., Mus. Nat. Hist., **7**/no. 4: 349—472. — Topeka.

Mein, P. & M. Freudenthal (1971a): Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. — Scripta Geologica, **2**: 1—37. — Leiden.

— (1971b): Les Cricetidae (Mammalia, Rodentia) du Néogène Moyen de Vieux-Collonges. Pt. 1: Le genre *Cricetodon* Lartet, 1851. — Scripta Geologica, **5**: 1—51. — Leiden.

Miller, G. S. Jr. & J. W. Gidley (1918): Synopsis of the supergeneric groups of rodents. — Journ. Washington Acad. Sci., 8/no. 13: 431—448.

Preble, E. A. (1899): Revision of the jumping mice of the Genus *Zapus*. — North Amer. Fauna, **15**: 1—42. — Washington D.C. (U.S. Dept. Agric., Division Biol. Survey).

Rabeder, G. (1972): Die Insectivoren und Chiropteren (Mammalia) aus dem Altpleistozän von Hundsheim (Niederösterreich). — Ann. Naturhist. Mus. Wien, **76**: 375—474. — Wien.

— (1973): *Galerix* and *Lanthanotherium* (Erinaceidae, Insectivora) aus dem Pannon des Wiener Beckens. — N. Jb. Geol. Paläont. Mh., **1973/7**: 429—446. — Stuttgart.

Ramaekers, P. (1975): Using polar coordinates to measure variability in samples of *Phenacolemur*: A method of approach. — In: Szalay: Approaches to primate paleobiology. — Contr. Primat., **5**: 106—135. — Basel (Karger).

Rümke, C. G. (1976): Insectivora from Pikermi and Biodrak (Greece). — Kon. Nederl. Akad. Wetenschappen, Proc., (Ser. B) **79** (4): 256—270. — Amsterdam.

RZEBIK-KOWALSKA, B. (1975): The Pliocene and Pleistocene insectivores (Mammalia) of Poland. II. Soricidae: *Paranourosorex* and *Amblycoptus*. — Acta Zool. Cracoviensia, **20**/no. 6: 167—182. — Cracow.

SCHAUB, S. (1930): Quartäre und jungertertiäre Hamster. — Abh. Schweiz. Paläont. Ges., **49**: 1—49. — Basel.

SIMPSON, G. G., A. ROE & R. C. LEWONTIN (1960): Quantitative Zoology (Revis. Edit.). — Harcourt, Brace, New York.

STEHLIN, H. G. & S. SCHAUB (1951): Die Trigonodontie der simplicidentaten Nager. — Schweiz. Pal. Abh., **67**: 1—385. — Basel.

STORCH, G. (1978): Die turolische Wirbeltierfauna von Dorn-Dürkheim, Rheinhessen (SW-Deutschland). 2. Mammalia: Insectivora. — Senckenbergiana lethaea, **58**: 421—449. — Frankfurt am Main.

SULIMSKI, A. (1959): Pliocene insectivores from Weze. — Acta Palaeont. Polonica, **4**/no. 2: 119—179. — Warsaw.

— (1964): Pliocene Lagomorpha and Rodentia from Weze 1 (Poland). — Acta Palaeont. Polonica, **9**/ no. 2: 149—261. — Warsaw.

WEERD, A. VAN DE (1976): Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra Region, Spain. — Utrecht Micropaleont. Bull. Spec. Publ., **2**: 1—216. — Meppel.

WILSON, R. W. (1936): A Pliocene rodent fauna from Smiths Valley, Nevada. — Carnegie Inst. Wash. Publ., **473**: 15—34. — Washington D.C.

Explanation of the plates

Plate 1

Fig. 1: *Leptodontomys* sp.
Right upper $M\underline{1}$ or $M\underline{2}$.
Occlusal view. 48 ×

Fig. 2: *Paraglirulus* cf. *P. lissiensis* (HUGUENEY & MEIN)
Left $M\underline{1}$?
Occlusal view. 48 ×

Fig. 3: *Paraglirulus* cf. *P. lissiensis* (HUGUENEY & MEIN)
Left $M\underline{2}$?
Occlusal view. 40 ×

Fig. 4: *Paraglirulus* cf. *P. lissiensis* (HUGUENEY & MEIN)
Right $M\bar{2}$.
Occlusal view. 40 ×

Fig. 5: *Paraglirulus* cf. *P. lissiensis* (HUGUENEY & MEIN)
Right $M\bar{3}$.
Occlusal view. 43 ×

Fig. 6: *Kowalskia fahlbuschi* BACHMAYER & WILSON
Right $M\underline{1}$.
Lingual view showing undivided inner root. 18 ×

Fig. 7: *Kowalskia fahlbuschi* BACHMAYER & WILSON
Left $M\underline{1}$.
Lingual view showing channeled inner root, divided at tip. 24 ×

Fig. 8: *Kowalskia fahlbuschi* BACHMAYER & WILSON
Left $M\underline{1}$.
Lingual view showing completely divided inner root. 22 ×

Plate 2

Fig. 9: *Kowalskia fahlbuschi* BACHMAYER & WILSON
Left upper jaw with M$\underline{1}$—M$\underline{3}$. Holotype.
Occlusal view. 20 ×

Fig. 10: *Kowalskia fahlbuschi* BACHMAYER & WILSON
Left lower jaw with M$\bar{1}$—M$\bar{3}$. Fig. 59, BACHMAYER & WILSON, 1970.
Occlusal view. 32 ×

Plate 3

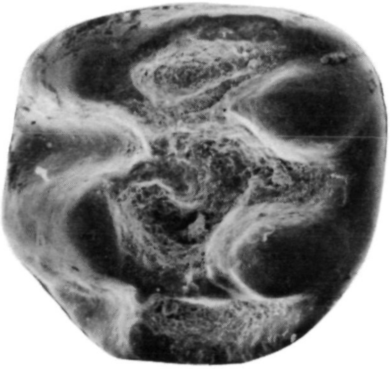
Fig. 11 (line 1): *Graphiurops austriacus*, nov. genus et spec.
Left lower jaw with M$\bar{2}$.
Occlusal view, stereographic pair. 7 ×

Fig. 12 (line 2): *Graphiurops austriacus*, nov. genus et sp.
Right lower M$\bar{1}$ (?).
Occlusal view, stereographic pair. 25 ×

Fig. 13 (line 3): *Protozapus intermedius* BACHMAYER & WILSON
Right upper jaw with P$\underline{4}$—M$\underline{3}$.
Occlusal view, stereographic pair. 20 ×

Fig. 14 (line 4): *Erinaceus* ? sp.
Left lower jaw with P$\bar{4}$—M$\bar{2}$.
External view. 2,85 ×

Fig. 14a (line 5): *Erinaceus* ? sp.
Left lower jaw with P$\bar{4}$—M$\bar{2}$.
Occlusal view. 2,85 ×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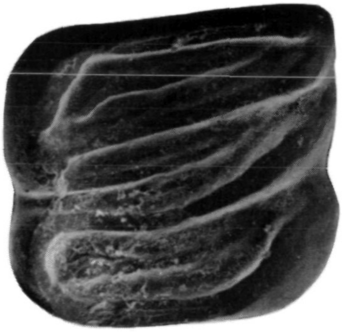
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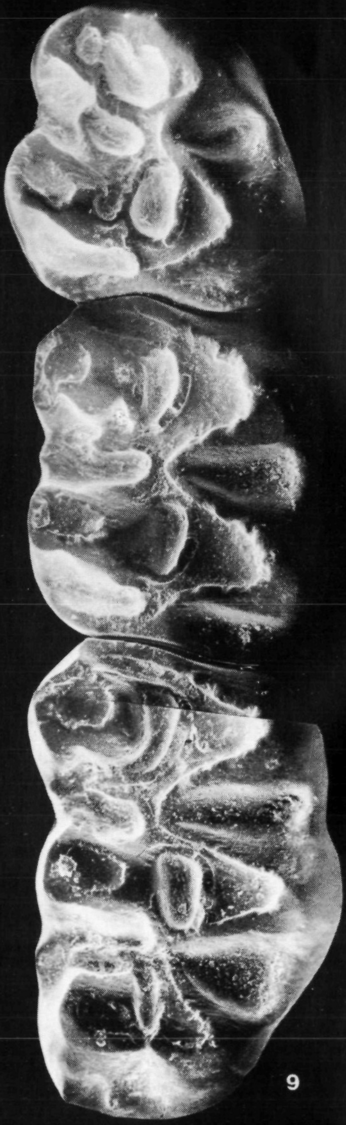

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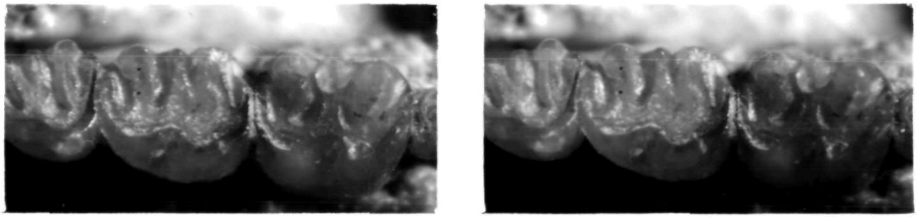
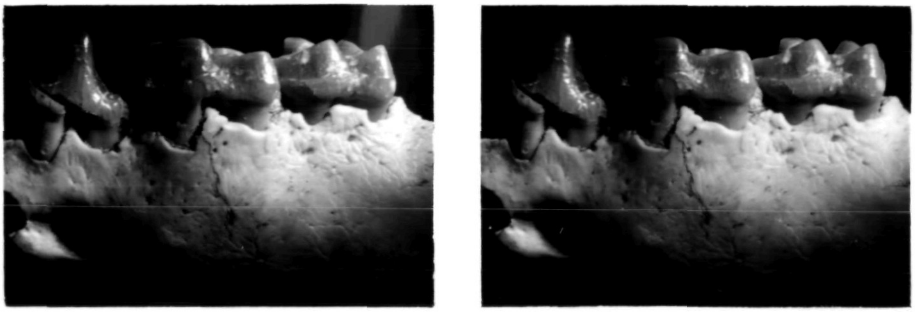
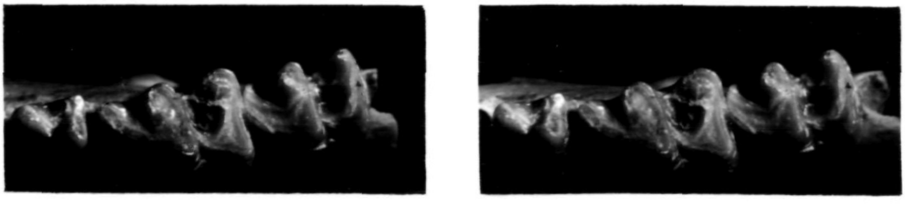
F. BACHMAYER & R. W. WILSON: A third contribution to the Fossil Small Mammal Fauna of Kohfidisch (Burgenland), Austria







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