

Vertebrates from the Early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria):

6. Rodentia 1 (Mammalia)

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(With 2 text-figures and 6 plates)

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Abstract

The assemblages from Oberdorf contain material of two species of ground squirrels, one species of giant tree squirrel and three species of flying squirrels. One of the latter, *Hylopetes hoeckarum*, is new and constitutes the oldest record of the genus.

The dormice are represented by ten different species which is an unusually large number for a locality in bedded sediments. One new genus and species, *Seorsumuscardinus alpinus*, and one new subspecies, *Glis minor complicatus*, are described.

The assemblage is interpreted as indicating a marsh-forest environment. The age of the fauna from the levels 3 and 4 is considered to be Late Early Miocene (MN4).

Key words: Early Miocene, Ground-, tree- and flying squirrels, dormice, South Alpine molasse.

Zusammenfassung

Die Faunen von Oberdorf umfassen zwei Arten von Erdhörnchen, eine große Baumhörnchenart und drei Arten von Flughörnchen. Aus den letztgenannten stellt *Hylopetes hoeckarum* eine neue Art und gleichzeitig den ältesten Beleg der Gattung dar.

Schlafmäuse sind durch zehn verschiedene Arten vertreten, eine ungewöhnlich hohe Zahl für eine Lokalität mit geschichteten Sedimenten. Es wurden eine neue Gattung und Art *Seorsumuscardinus alpinus*, und eine neue Unterart, *Glis minor complicatus*, beschrieben.

Die Fauna deutet auf ein Sumpfwald-Habitat hin. Das Alter der Fauna aus den beiden Fundschichten O3 und O4 dürfte dem späten Unter-Miozän (MN4) entsprechen.

Introduction

The vertebrate bearing beds Oberdorf 3 and 4 exposed in the upper part of the section limiting the east quarry of the lignite mine of Oberdorf to the north were discovered during a prospecting trip by Dr. G. HÖCK-DAXNER, Ulli HÖCK, Dimitri FOUSSEKIS and

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the author in the summer of 1989. The fossiliferous beds (lignitic clays containing bones as well as wood, seeds and gastropods) are interpreted as paleosols. These paleosols occur at the top of two subsequent sedimentary cycles showing fining upwards. Magneto-stratigraphic and cyclostratigraphic research of sections of similar age in other continental basins suggests that such cycles are often related to the ± 100 kyr eccentricity cycle of the Earth's orbit (KRIJGSMAN et al. 1994). Whether or not this is the case in Oberdorf will probably be impossible to ascertain because the cyclically developed part of the section is thin. The great similarity of the rodent associations from the levels Oberdorf 3 and 4 suggests that the amount of time represented in the ± 10 metres of sediment that separates these two beds is limited. The samples from the two levels will therefore be treated taxonomically as if they represent one association. However, the provenance of each fossil is indicated in the catalogue.

The geographical position of Oberdorf south of the Alpine range makes the fauna of particular interest because most of the information on faunas of similar age (upper part of the Lower Miocene = MN4) is available from north of the Alps and south of the Pyrenees.

The material from Oberdorf described below will be kept in the collections of the "Naturhistorisches Museum Wien". The measurements, given in 0.1mm units, have been taken with a Leitz Ortholux microscope with mechanical stage and measuring clocks. The teeth shown on the plates are $\pm \times 20$ and figured as if they are from the left side. If the original is from the right side its number is underlined on the plates.

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Taxonomy

Sciuroidea GILL, 1872

I recognize the Sciuridae and Petauristidae as separate families within Sciuroidea because fossil evidence suggests that these two groups do not share the same ancestry (de BRUIJN & ÜNAY 1989).

Sciuridae GRAY, 1821

The Sciuridae are represented in the collection from Oberdorf by two genera and two species of ground squirrel and one species of tree squirrel.

Palaeosciurus POMEL, 1853

The genus *Palaeosciurus* as understood here is restricted to Europe and Western Asia and contains four species: *P. goti* VIANEY-LIAUD, 1974, *P. feignouxi* POMEL, 1853, *P. fissurae* DEHM, 1950, and *P. sutteri* ZIEGLER & FAHLBUSCH, 1986. Of these four species the skull is known of the two geologically older species *P. goti* and *P. feignouxi*. These skulls show ground squirrel characteristics and so does the mandible of *P. fissurae*. The cheek teeth have the morphology of a generalized sciurid. The dentition of the geologically youngest *P. sutteri* shows more resemblance to those of the tree squirrel *Sciurus* in having better developed entoconids and mesostylids in the lower first and second molars and isolated mesostyles in the upper first and second molars. This observation led ZIEGLER & FAHLBUSCH (1986) to the conclusion that *Palaeosciurus* may well be the ancestor of *Sciurus*. This attractive hypothesis for the origin of the tree squirrels in Europe seems to be contradicted by the long hiatus in the record between the last occurrence of *P. sutteri* in MN6 (Ebershausen, S. Germany) and the first appearance of the unquestionable tree squirrel *Sciurus wartae* in MN14 (Podlesice, Poland; Taşova, Turkey). I therefore prefer to regard *Palaeosciurus* as a ground squirrel until its tree squirrel affinities will be better documented.

***Palaeosciurus sutteri* ZIEGLER & FAHLBUSCH, 1986**
(Plate 1, Figs 1–8)

Locality: Oberdorf 3 and 4.

Material: 21 teeth; O3: Coll. NHMW 1997z0194/0001/1–21.
27 teeth; O4: Coll. NHMW 1997z0194/0002/1–27.

Measurements:

	Length			N	Width		
	min.	max.	mean		mean	min.	max.
D4	18.3	20.4	19.3	4	20.4	19.1	21.5
P4	16.8	18.2	17.6	4	20.1	18.5	21.5
M1-2	19.9	22.2	20.9	13	24.9	23.0	26.5
M3	21.2	26.3	24.3	7/8	23.9	22.1	25.7
d4	18.5	18.7	18.6	3	16.2	15.1	17.4
p4	18.0	22.8	20.3	3	17.2	15.6	18.8
m1	20.2	22.2	21.5	5	22.5	21.0	23.3
m2	22.4	24.5	23.2	4/3	24.5	23.0	26.0
m3	25.8	27.8	26.8	3/2	23.1	22.8	23.3

Remarks: The material of *P. sutteri* from Oberdorf is somewhat larger than the type material, but otherwise very similar. The metalophid of the lower m1 and m2 seems to be more often complete and the mesostyle of the upper M1 and M2 more often connected to the paracone. In other respects our specimens fit the description given by ZIEGLER & FAHLBUSCH (1986).

Spermophilinus de BRUIJN & MEIN, 1968

Representatives of the genus *Spermophilinus* are common in many European and Western Asiatic faunas of Late Early Miocene to Early Pliocene age. Four species are currently recognized: *S. besanus* CUENCA, 1988; *S. bredai* (von MEYER, 1848); *S. turo-lensis* de BRUIJN & MEIN, 1968; and *S. giganteus* de BRUIJN et al. 1970. The slanting postero-internal corner of the m1 and m2 and the converging protoloph and metaloph of the M1 and M2 in *Spermophilinus* are unmistakable ground squirrel characteristics. The dental morphology is very similar in all the four species, so species identification is largely based on size (de BRUIJN 1995). The M3 and m3 are on average less expanded and the P4 and p4 are more molariform in the geologically oldest species *besanus*, but assemblages from single localities show considerable variation. *Spermophilinus besanus* arrives as an immigrant in Europe. Its first appearance in MN4 seems to be either simultaneous or somewhat later than the arrival of the first "Miocene" cricetine *Democricetodon*. This genus is known from considerably older faunas in Central Anatolia and therefore considered of Asian origin. Unfortunately the Anatolian Early Miocene record of the Sciuridae is very poor. Even the very large collections of small mammals from the Early Miocene of Anatolia made by E. ÜNAY, G SARAÇ and the author during the last decade contain only few teeth of the *Spermophilinus* type next to a somewhat larger species of *Palaeosciurus*. Although the evidence is not yet convincing my working hypothesis is that *S. besanus* and *Democricetodon franconicus* are both of Asiatic origin and represent the same migration wave.

Spermophilinus besanus CUENCA, 1988

(Plate 2, Figs 1–10)

Type locality: Vargas 1A.

Locality: Oberdorf 3 and 4.

Material: 21 teeth; O3: Coll. NHMW 1997z0195/0001/1–21.
78 teeth; O4: Coll. NHMW 1997z0195/0002/1–78.

Measurements:

	Length		mean	N	Width		
	min.	max.			mean	min.	max.
D4	14.2	17.0	15.4	5	15.8	14.0	17.7
P4	12.8	14.9	14.1	6	17.0	15.5	18.0
M1–2	15.1	17.1	16.0	24	20.1	18.3	21.7
M3	18.1	20.7	19.4	18	18.7	17.4	20.0
d4	11.9	12.6	12.3	2	11.0	10.1	11.9
p4	12.9	15.0	14.1	6	12.9	11.6	13.8
m1	14.9	16.8	15.8	13	17.1	16.2	18.1
m2	16.1	19.3	17.7	12/13	18.7	17.4	19.5
m3	19.7	22.5	21.2	9/10	17.5	16.8	18.2

Remarks: The species *S. besanus* (= *besana* in CUENCA, 1988) was defined on the basis of a few teeth from Vargas 1A and Olmo Redondo 5. Fortunately CUENCA (op. cit.) included the rich material from Vieux Collonges, long since known as *S. cf. bredai*, so

her species is well represented in collections. The material from Vieux Collonges described by ZIEGLER & FAHLBUSCH (1986) and the *Spermophilinus* assemblages from Erkertshofen 1, Rembach and Puttenhausen assigned to *S. aff. bredai* by these authors were all referred to *S. besanus* by me in 1995. Judging by the measurements given by CUENCA the specimens from Vargas 1A are smaller than the average for any of the associations referred to *S. besanus* including the one from Oberdorf. This difference may be due to sampling bias or be the effect of differences in measuring techniques. The morphological characteristics of *besanus* teeth given by CUENCA (op. cit.) appear to show considerable variation in larger series and are therefore not diagnostic. It is true, however, that the anteroloph of the upper M1, M2 ends lingually more separate from the protocone than in geologically younger species. The metalophid of the m1 and m2 reported as "residual" by CUENCA is short but complete in all the specimens from Oberdorf.

Ratufa GRAY, 1867

Early Miocene fossils of the south Asiatic giant tree squirrel *Ratufa* have to my knowledge become known exclusively from the Europe. DEHM (1950) was the first to tentatively include his species *obtusidens* from Wintershof-West into *Ratufa* on the basis of dental similarity. The low-crowned large cheek teeth of *obtusidens* with their low, but robust, cusps and lophs and shallow basins are indeed very similar to the situation in *R. bicolor*, the only extant species that I have seen. The well developed entoconids of the lower molars, the short diastema of the holotype mandible as well as the height of the jaw are all very similar to the situation in *Ratufa* and seem to leave no doubt that *R. obtusidens* is a tree squirrel. I therefore do not agree with ALDANA CARRASCO (1992) who transfers the species *obtusidens* to the genus *Palaeosciurus*. This conclusion is of special interest because the tree squirrels of the *Sciurus* group appear in Europe as late as the Early Ruscinian (MN14) and seem to have evolved independently. Allocation of the species *obtusidens* to the giant squirrels therefore implies that the adaption of the squirrels to arboreal life occurred at least twice, so the tree squirrel division is polyphyletic.

Ratufa n.sp.

(Plate 2, Fig. 11)

L o c a l i t y: Oberdorf 4.

M a t e r i a l and **m e a s u r e m e n t s:** 1 M1–2 (34.4 x 41.2); Coll. NHMW 1997z0196/0002/1+2.

R e m a r k s: The M1–2 from Oberdorf assigned to *Ratufa* is about thirty percent larger than the specimens from Wintershof-West and the M1–2 from Ulm-Westtengarten assigned to *R. obtusidens* by WERNER (1994), but otherwise quite similar. The low relief of the occlusal surface in combination with the voluminous cusps and lophs and the low, but long, anteroloph that ends lingually separate from the protocone and labially separate from the paracone without forming a parastyle, suggest giant squirrel affinities.

The two M1–2 from the Oligocene of Kocayarma tentatively assigned to *Miopetaurista* by de BRUIJN & ÜNAY (1989) are similar in size to the specimen from Oberdorf. However, the relief of these teeth is much higher although they are more worn than the

specimen from Oberdorf. The anteroloph of the M1–2 from Kocayarma does not reach as far lingually as in the specimen from Oberdorf and ends labially in a parastyle.

Petauristidae MILLER, 1912

The Petauristidae are represented in the collection from Oberdorf by three genera and three species.

Miopetaurista KRETZOI, 1962

The genus *Miopetaurista* as understood here is restricted to Europe. That is to say that I tentatively exclude *Sciuropterus jamesi* LINDSAY, 1972 and *Parapetaurista tenrugosa*, QUI & LIU, 1986 from *Miopetaurista*. This is not done because the few remains of these American and Chinese taxa are very different from *Miopetaurista*, but rather because the available evidence seems insufficient to refer them to this genus with certainty.

Seven species of *Miopetaurista* are currently recognized: *M. dehmi* de BRUIJN et al, 1980 (geologically oldest species), *M. lappi* (MEIN, 1958), *M. gaillardi* (MEIN, 1970), *M. neogrivensis* (MEIN, 1970), *M. gibberosa* (HOFMANN, 1893), *M. crusafonti* (MEIN, 1970), and *M. thaleri* (MEIN, 1970). This last species is the largest and geologically youngest representative. The stratigraphic range of the genus is from MN3 to MN14. Species identification in *Miopetaurista* is impeded by the small number of specimens available per locality. The intraspecific variation in size and morphology is therefore not known for any of the seven species listed above. The type material of the species *M. diescalidus* DAAMS, 1977, which is intermediate in size between *M. dehmi* and *M. lappi*, is so poorly preserved that it has been considered insufficiently characteristic (de BRUIJN et al, 1980) to define the species. The result is that specimens from Forsthart, Rembach, Puttenhausen and Langenmoosen that are intermediate in size between the types of *M. dehmi* and *M. lappi* have been published as *Miopetaurista* cf. *dehmi* (ZIEGLER & FAHLBUSCH, 1986). The material from Oberdorf is in size closer to the type material of *dehmi* from Wintershof-West than to that of *lappi* from Vieux Collonges and will therefore be referred to *M. dehmi*.

***Miopetaurista dehmi* de BRUIJN et al., 1980** (Plate 3, Figs 1–5)

Type locality: Wintershof-West.

Locality: Oberdorf 3 and 4.

Material and measurements:

1 P4(22.9 x 23.7), 1 M1–2 (27.4 x 31.0), 1 M3 (30.6 x 29.7), 1 m1 (26.5 x 27.5), 2 m2 (29.5 – 31.0 x 31.3 – 31.7).

6 teeth; O3: Coll. NHMW 1997z0197/0001/1–6.

3 teeth; O4: Coll. NHMW 1997z0197/0002/1–3.

R e m a r k s: The anteroloph of the D4 forms a low and narrow connection between the parastyle and the protocone. This connection is absent in the specimen from Wintershof-West. One of the D4 has a double metaconule, but in the other the metaconule is almost absent. Both milk molars show a thin ridge between the middle of the metaloph and the lingual part of the posteroloph. This peculiar connection is not present in the D4 of this species from other localities, but occurs in the holotype of *M. neogrivensis*. The P4 has the low and narrow posteroloph characteristic for *Miopetaurista*. The metaloph has a double metaconule just as the specimen from Wintershof-West. There is a low ridge-shaped metastyle and a short extra ridge in the postero-lingual corner of the occlusal surface (between the metaloph and the posteroloph). The M1–2 with its laterally compressed protocone, well marked spur between the protoloph and metaloph and weak mesostyle is very similar to the M1–2 of *M. dehmi* and *M. lappi*. The specimen from Oberdorf does not have the double metaconule as the one from Wintershof-West. In this respect this specimen is very similar to the ones from Forsthart and Rembach. The M3 from Oberdorf is somewhat larger than the one from Wintershof-West, but very similar otherwise. The m1 has a rather weak entoconid and the mesostylid is almost absent. The metalophid is short and incomplete and the labial end of the anterolophid is separated from the protoconid by a narrow valley. The two m2 show considerable difference in the development of the mesostylid. The entoconid is separated from the mesostylid by a deep valley in both specimens. One m2 is peculiar in having a long anterior arm of the hypoconid that is directed lingually instead of connecting to the mesoconid.

Blackia MEIN, 1970

In the more than thirty years that have elapsed since BLACK (1966) described two lower molars from Gigggenhausen of the small sciurid that is now known as *Blackia*, specimens of this genus have become known from many Neogene sites from all over Europe. In spite of the great increase of information on the dentition of *Blackia* its phylogenetic relationships to other genera of flying squirrels have remained obscure. Five species of *Blackia* have been formally named: *B. miocaenica* MEIN, 1970 (genotype), *B. woelfersheimensis* MEIN, 1970, *B. parvula* BAUDELLOT, 1972, *B. polonica* BLACK & KOWALSKI, 1974 and *B. ulmensis* WERNER, 1994. Considering that all students of the group have stressed the remarkable stability of the dental features through time this number of species is certainly too high. I follow ENGESSER (1972) in synonymizing *B. parvula* with *B. miocaenica* and agree with DAXNER-HÖCK (1975) that the type material of *woelfersheimensis* is insufficiently known to define a separate species. This leaves us with three species: *B. ulmensis* (the geologically oldest (MN2) and largest), *B. miocaenica* (M. Miocene (MN4–MN10) and intermediate in size) and *B. polonica* (the geologically youngest (MN14) and smallest). Distinction of these three species is mainly based on size. Since differences between the measuring techniques used by different authors may strongly influence the data it seems unwise to plot the measurements from the literature in one diagram (WERNER 1994) and reach a conclusion on that basis. Distinction of species on size alone remains hazardous because of possible clinal geographic variation (KOCH 1986) within a single species. I therefore think that all the available material of *Blackia* will have to be re-studied in order to be able to judge the validity of the existing species.

***Blackia miocaenica* MEIN, 1970**

(Plate 4, Figs 1–10)

Type locality: La Grive L7.

Locality: Oberdorf 3 and 4.

Material: 1 tooth; O3: Coll. NHMW 1997z0198/0001/1.
36 teeth; O4: Coll. NHMW 1997z0198/0002/1–36.

Measurements:

	Length		mean	N	Width		
	min.	max.			mean	min.	max.
D4	10.7	11.6	11.2	2	10.4	10.0	10.8
P4	11.9	12.5	12.2	2/3	13.0	12.8	13.2
M1–2	12.2	14.7	13.4	5	16.1	15.1	18.1
M3	14.5	15.9	15.0	7	15.2	14.8	16.1
d4	10.7	12.6	11.9	3	10.0	9.2	10.4
p4	11.6	12.6	12.2	4	11.2	9.9	11.8
m1	12.8	14.2	13.6	4	13.2	12.0	13.8
m2	14.9	15.6	15.2	4	15.2	14.2	15.9
m3	17.8	19.6	18.7	2	14.3	14.0	14.6

Remarks: The specimens from Oberdorf are within the size range given for *B. miocaenica* from La Grive, Sansan and Anwil. That is to say that they are on average ± 0.2 mm larger than the measurements of *B. polonica* given by BLACK & KOWALSKI (1974) and on average ± 0.2 mm smaller than the values of *B. ulmensis* given by WERNER (1994). The poor quality of the figures in BLACK & KOWALSKI does not allow the evaluation of details of the dental morphology of *B. polonica*. The excellent S.E.M. photographs in WERNER (1994) suggest that the parastyle of the upper molars and the metalophid of the lower molars are somewhat better developed in the material from Ulm than in that from Oberdorf. The differences in dental morphology between the species *polonica*, *miocaenica* and *ulmensis* are, however, so subtle that distinction of these species may well prove to be an artifact. The conclusion is therefore that the dental morphology of the representatives of the genus *Blackia* has essentially not changed between MN2 and MN15, which is an order of magnitude of twenty million years. The ancientness of the group is also suggested by the specimens from the Oligocene of Kocayarma (Turkey) provisionally assigned to *Blackia* by de BRUIJN & ÜNAY (1989).

Hylopetes THOMAS, 1908

The assignment of ten sciurid cheek teeth from the lower Miocene of Oberdorf to the extant genus *Hylopetes* from southeast Asia needs explaining. This the more so because the record from Oberdorf is the geologically oldest of the genus. Next in line is one upper molar from the upper Miocene of Anwil (ENGESSER 1972). Assignment of isolated fossil teeth to the genus *Hylopetes* (sensu BOUWENS & de BRUIJN 1986) is based on the characteristic hummocky surface of the enamel of unworn cheek teeth, the shape of

these teeth, the presence of a parastyle in P4–M2 and of a rather well-developed entoconid in the p4–m3. The first record in Europe of teeth showing these characteristics is now from the lower Miocene, and the phylogenetic affinities of the species seem uncertain. All I can say is that I feel unable to separate the fossil teeth assigned to various species of *Hylopetes* from Europe from the extant ones from southeast Asia on the generic level. This therefore leaves no other choice than to include the fossils in *Hylopetes*.

***Hylopetes hoeckarum* n.sp.**

(Plate 4, Figs 11–14)

Derivatio nominis: The species is named after the four ladies HÖCK acknowledging their contribution to the collecting at Oberdorf.

Type locality: Oberdorf 3.

Holotype: M1/2 sin.; Coll. NHMW 1997z0199/0001/1.

Type level: Early Miocene (MN4).

Other localities with *H. hoeckarum*: Oberdorf 4.

Diagnosis: Enamel of unworn cheek teeth hummocky. Protoloph and metaloph of the M1–2 weak and devoid of conules. Mesostyl of the M1–2 and mesostylid and mesoconid of the m1–2 small.

Differential diagnosis: *H. hoeckarum* is larger than *H. macedoniensis* BOUWENS & de BRUIJN, 1986 and has a weaker protoloph and metaloph in the M1–2.

Material: 5 teeth; O3: Coll. NHMW 1997z0199/0001/1–5.
4 teeth; O4: Coll. NHMW 1997z0199/0002/1–4.

Measurements:

	Length		mean	N	Width		
	min.	max.			mean	min.	max.
M1–2	17.7	19.4	18.4	5/6	20.9	18.4	23.9
M3	-	-	21.2	1	20.2	-	-
m1	-	-	18.6	1	19.5	-	-
m2	-	-	19.5	1	21.2	-	-

Remarks: Among the extant and fossil *Hylopetes* the species from Oberdorf is closest to *H. macedoniensis* from Maramena. The protoloph and metaloph of the M1–2 are thin complete crests without conules. The small mesostyle may be connected to the paracone or not. The extra ridge between the protoloph and metaloph that is characteristic for the M1–2 of many species of *Hylopetes* is absent in the specimens from Oberdorf. In the M1–2 of *H. macedoniensis* this ridge is either weak ($\pm 50\%$) or absent ($\pm 50\%$). The shape and structure of the M3, m1 and m2 from *H. hoeckarum* and *H. macedoniensis* are very similar. *H. hoeckarum* from Oberdorf is the oldest record of *Hylopetes*. However, two teeth (fig. 106 a and b) figured by WERNER (1994) and assigned to *Heteroxerus lavocati* are reminiscent of *Hylopetes*. These specimens from Eggingen-Erdbeerhecke (MP 30) are of special interest because they could push the first record of the genus even further down.

Gliridae THOMAS, 1897

Pending the decision of the International Commission on Zoological Nomenclature in the dispute about the correct family name for the dormice (WAHLERT et al. 1993, DAAMS & de BRUIJN 1995). I continue to use Gliridae THOMAS, 1897 instead of Myoxidae GRAY, 1821 trusting that this will contribute to the stability of nomenclature. The subdivision of the Gliridae follows the classification of DAAMS & de BRUIJN 1995. The Gliridae are represented in the collection from Oberdorf by seven (sub) genera (one new) and ten species (one new). This unusually high diversity for an Early Miocene assemblage from bedded sediments suggests that the fossiliferous beds Oberdorf 3 and Oberdorf 4 contain a mixture of species from different biotopes.

Glis BRISSON, 1762

Until the discovery of teeth with the characteristic dental pattern of *Glis* in the Early Miocene faunas of Oschiri, Sardinia and Weissenburg 6, Germany (de BRUIJN & RÜMKE 1974; MAYR 1979) the genus was considered to be a relatively young branch of the Gilirinae. This erroneous concept is understandable because the Plio–Pleistocene species *G. sackdillingensis*, *G. minor* and *G. suessenbornensis* are all very similar to extant *Glis glis*. After *Glis apertus* MAYR, 1979 from the Early Miocene had been recognized as a true representative of *Glis* a number of Oligo–Miocene species were assigned to the genus: *Glis truyolsi* DAAMS, 1979 (MN2), *G. vallesiensis* AGUSTI, 1981 (MN9), *G. galitopouli* van der MEULEN & de BRUIJN, 1982 (MN4), *G. guerbuezi* ÜNAY, 1989 (MP23–26) and *G. transversus* ÜNAY, 1994. I follow WERNER (1994) in transferring *G. truyolsi* to the genus *Myoglis* (see below). The remaining Oligo–Miocene species show that the group is phylogenetically complex, but that all species can be derived from upper molars with a dental pattern consisting of the four main ridges, a long anterior centroloph, a shorter posterior centroloph, one extra ridge in the anterior valley or between the proto-loph and the anterior centroloph and one in the posterior valley. The pattern of the lower molar is obviously derived from a tooth with the four main ridges, a long centrolophid with an extra ridge on either side and one extra ridge in the anterior and in the posterior valley. That is a pattern with a ridge at nine possible locations for the upper as well as for the lower teeth.

The characteristic *Glis* features were evidently acquired at different times (and places?) in different groups of species within the genus because *Glis galitopouli* (MN4) is in many respects more primitive than *G. apertus* (MN1) and the material from Oberdorf (MN4) described below. This parallel evolution in different branches of the same genus makes its representatives unsuitable for biostratigraphy until the complex phylogenetic history of the different lineages will be reconstructed.

Derived features that characterize *Glis* are:

Upper dentition

1. Thick main ridges that in unworn specimens have a symmetrical cross section with rounded apex.
2. Rather large rounded P4.

3. A protoloph and metaloph that do not connect lingually.
4. A protoloph that is labially neither connected to the anteroloph nor the anterior centroloph.
5. A long anterior centroloph that is of the same height and thickness as the protoloph and metaloph.
6. A posterior centroloph that is either short, and much lower and thinner than the protoloph and the metaloph, or is absent.

Lower dentition

1. Thick main ridges that in unworn specimens have a symmetrical cross section with rounded apex.
2. A m3 that is about as long as the m1 and m2
3. A metalophid that is not connected to the anterolophid.
4. A centrolophid that does not reach the lingual edge of the occlusal surface and is not connected to the metaconid.
5. A mesolophid that is not connected to the entoconid.
6. A posterior extra ridge that is confluent with the posterolophid lingually.

Glis minor complicatus n.ssp.

(Plate 5, Figs 1–6)

Derivatio nominis: *complicatus* because the dental pattern of the P4 and M1–2 from Oberdorf is on average more complex than in the type material of *G. minor*.

Type locality: Oberdorf 4.

Holotype: M2, sin.; Coll. NHMW 1997z0200/0002/1.

Type level: Early Miocene (MN4).

Other localities with *G. minor complicatus*: Oberdorf 3.

Diagnosis: The teeth of *G. minor complicatus* are about the same size as those of *G. minor minor*. The posterior centroloph is present in all M1–2 and most P4.

Differential diagnosis: *G. minor complicatus* differs from *G. minor minor* in having the anterior as well as the posterior centroloph in three of the four P4 and in all thirteen M1–2. In *G. minor minor* the posterior centroloph has been reported as always absent in P4, M1 and M2 (KOWALSKI 1963), but in two out of the four M1–2 from Podlesice available to me for comparison a weak posterior centroloph is present.

The teeth of *G. minor complicatus* are larger than those of *G. apertus*. The anterior centroloph of the M1–2 of this last species is confluent with the protoloph, in the M1–2 of *minor complicatus* this is the case in one out of eleven specimens. Moreover there is an extra ridge between the protoloph and anterior centroloph in eleven of the fifteen M1–2 from Oberdorf in which this feature can be studied. This extra ridge is absent in the six specimens from Weissenburg. The mesolophid ends free lingually in the m1, m2 and in one of the two m3. In *G. apertus* the mesolophid is confluent with the posterolophid.

M a t e r i a l: 2 teeth; O3: Coll. NHMW 1997z0200/0001/1–2.
21 teeth; O4: Coll. NHMW 1997z0200/0002/1–21.

M e a s u r e m e n t s:

	Length			N	Width		
	min.	max.	mean		mean	min.	max.
P4	11.1	11.7	11.3	3	13.5	13.1	14.0
M1	14.1	15.4	15.0	7	16.1	15.0	16.8
M 2	14.7	15.3	15.0	5/4	17.0	16.0	17.5
M3	-	-	-	-	-	-	-
p4	-	-	15.0	1/0	-	-	-
m1	15.0	15.7	15.4	2	15.4	15.3	15.5
m2	-	-	16.2	1	16.6	-	-
m3	15.6	17.1	16.4	2	15.0	14.8	15.2

R e m a r k s: In the four two-rooted P4 the protoloph and the metaloph are not connected lingually. The anterior centroloph is always present, but the posterior centroloph is developed in three specimens only. Two P4 have a very weak extra ridge in the anterior valley and a much stronger one in the posterior valley. The other two specimens have no extra ridges.

The M1–2 have the lingual ends of the protoloph and metaloph separated. The two centrolophs are present and there is one extra ridge in the anterior as well as in the posterior valley. The individual variation is essentially restricted to the extra ridge between the protoloph and the anterior centroloph. This ridge is present in eleven and absent in four M1–2.

The only p4 is damaged. It shows the four main ridges, a lingually as well as labially isolated centrolophid and one extra ridge in the anterior as well as the posterior valley. This tooth is remarkably molariform.

The m1 have the characteristic pattern of modern *Glis* with the four main ridges ending free labially and with a well-marked notch between the lingual ends of the mesolophid and the posterior extra ridge. The centrolophid has a central position and reaches neither the lingual nor the labial edge of the occlusal surface. The posterior extra ridge is long and lingually confluent with the posterolophid.

The dental patterns of the m2 and one of the two m3 are essentially the same as in m1. The second m3 has a more archaic pattern because the mesolophid is lingually confluent with the posterolophid and the posterior extra ridge ends free lingually.

C o n c l u s i o n s: The similarity of *G. minor complicatus*, extant *Glis glis* and the Pliocene *G. minor minor* shows the remarkable stability of the dental pattern in this genus over a period of some fourteen millions of years. The material from Oberdorf occupies an intermediate position between *G. apertus* and *G. minor* in many respects, but is closer to *minor*. This is particularly indicated by the fusion of the lingual root and the postero-labial root of the P4, for glirids unusual. This peculiar feature that is characteristic for the *G. minor minor* specimens from the type locality Podlesice is also present in the P4 from Oberdorf.

Muscardinus KAUP, 1829, *Heteromyoxus* DEHM, 1938,
Myoglis BAUDELLOT, 1965, and *Glirudinus* de BRUIJN, 1966.

The reconstruction of the phylogenetic relationships of the various genera of the Glirinae proposed by DAAMS & de BRUIJN (1994) shows that *Glis* (containing species in which teeth have thick main ridges that are not everywhere equally wide) and *Glirudinus* (containing species in which teeth have ridges that remain equally wide all over) appear more or less simultaneously. These two groups indeed seem to have been separate since the middle Oligocene. The diagram (op.cit. fig.3) also shows that *Muscardinus* is probably derived from *Glirudinus* and that *Myoglis* and *Heteromyoxus* are very closely related. These conclusions are strongly supported by dental evidence.

The species *truyolsi* DAAMS, 1976, assigned to *Glis* by DAAMS (1976) and transferred to *Myoglis* by WERNER (1994) does not seem to fit in either genus. Its dental characteristics –fine ridges without inflated ends and extra ridges that are similarly developed as the main ridges– make it structurally intermediate between *Glirudinus* and *Myoglis*. I tentatively follow WERNER (1994) and include it in *Myoglis*.

The flat-crowned Glirinae teeth from Oberdorf described below as *Seorsumuscardinus alpinus* n.g. n.sp. present a similar problem because they show similarities to *Muscardinus* as well as to *Myoglis*, but cannot be assigned to either genus. I prefer to restrict the genus name *Muscardinus* to species that have longitudinally "stretched" M1 and extra ridges that are as well developed as the main ridges, and the name *Myoglis* for species with square M1 and extra ridges that are much weaker than the main ridges.

***Seorsumuscardinus* n.gen.**

Derivatio nominis: *Seorsum* means in Latin to be different from.

Type species: *Seorsumuscardinus alpinus* n.sp.

Diagnosis: Medium sized Glirinae with flat occlusal surface of the cheek teeth. Premolars small and rounded with four transverse crests. Extra ridges not subordinate to main ridges. Proto-loph and metaloph of the upper cheek teeth not strongly converging towards the protocone. Main ridges of the m1, m2, M1 and M2 essentially neither connected on the lingual nor on the labial margin of the occlusal surface.

Differential diagnosis: *Seorsumuscardinus* differs from *Muscardinus* in having square-not longitudinally "stretched" – M1, in having longer M3 and m3 relative to the M2 and m2 and in having stronger ridges. *Seorsumuscardinus* differs from *Myoglis* and *Heteromyoxus* in having extra ridges that are not subordinate to the main ridges and in having the ridges rather more at right angles to the longitudinal axis of the teeth.

***Seorsumuscardinus alpinus* n. sp.**

(Plate 5, Figs 7–14)

Derivatio nominis: *alpinus* adjective of Alps because this species is known from the molasse North and South of the Alps.

Type locality: Oberdorf 4.

Holotype: M1 sin.; Coll. NHMW 1997z0201/0002/1.

Type level: Early Miocene (MN4).

Other localities with *Seorsumuscardinus alpinus*: Oberdorf 3 and Tägernastrasse-Jona (Switzerland), Karydia 2 (Greece).

Diagnosis: *S. alpinus* has four ridges in the P4, five in the M1, six in the M2 and seven in the M3.

Material: 6 teeth; O3: Coll. NHMW 1997z0201/0001/1–6.
17 teeth; O4: Coll. NHMW 1997z0201/0002/1–17.

Measurements:

	Length			N	Width		
	min.	max.	mean		mean	min.	max.
D4	-	-	-	-	-	-	-
P4	9.3	10.1	9.7	2	10.9	10.6	11.2
M1	12.0	12.9	12.4	5	13.7	13.1	14.3
M2	12.1	12.4	12.2	4	13.7	13.3	14.5
M3	-	-	10.3	1	11.9	-	-
d4	-	-	-	-	-	-	-
p4	-	-	8.0	1	6.5	-	-
m1	12.5	12.7	12.6	3	12.9	12.6	13.1
m2	-	-	-	-	-	-	-
m3	11.5	12.8	12.3	3	11.6	10.6	12.7

Remarks: The P4 has two roots, the M1–2 have three roots that are centrally placed. The p4 has one root, the lower molars have sometimes two, sometimes three roots.

The occlusal surface of the P4 has an oval shape and four sub-parallel ridges that are neither connected on the lingual nor on the labial side. Since these teeth have lost the original tricuspid pattern completely the homologisation of the four ridges is not obvious. Comparison of the patterns of P4 and M1 leads me to the interpretation that the four crests are the anteroloph, the protoloph, the metaloph and the posteroloph. Supposing that this is correct the reduction of the P4 in *Seorsumuscardinus* and *Muscardinus* develops along very different paths. In *M. sansaniensis* the P4 usually has five ridges (= the four main ridges plus the anterior centroloph) and the protoloph and metaloph remain lingually connected and form a U. In some specimens the anteroloph is missing. This is the case in *M. thaleri* also. In *M. hispanicus* the P4 usually have three ridges (= a short centroloph and the lingually connected protoloph and metaloph). The posteroloph in these teeth is always absent, but remnants of the anterior centroloph occur occasionally. The pattern of the P4 of *M. pliocaenicus* and of extant *M. avellanaruis* consists of two ridges forming a U. There seems no doubt that these two ridges represent the protoloph and the metaloph although this implies that the P4 of *M. pliocaenicus* figured by KOWALSKI (1963) seems to be a specimen from the left side sitting in a jaw fragment from the right side. In *Seorsumuscardinus alpinus* the anteroloph and the posteroloph of the P4 are not reduced and long. The specimen figured by BOLLIGER (1992) on figure 63 as P4 of Gliride indet 2 from Tägernastrasse shows conclusively that the four ridges of the P4 of *Seorsumuscardinus* are the four main ridges.

The protoloph, the anterior centroloph and the metaloph of the M1 slightly converge lingually. In three out of five specimens the anterior centroloph connects lingually to the protoloph. The protoloph and the metaloph are weakly connected on the lingual border

of the occlusal surface in two out of the five M1. With the exception of the metaloph and the posteroloph of two M1 the labial ends of the ridges are separated by valleys.

The dental pattern of the M2 differs from that of the M1 in having the five long ridges more parallel and at right angles to the longitudinal axis of the teeth. A short posterior centroloph that is equally well developed as the other ridges is present in all four M2.

The anteroloph, protoloph, posterior centroloph and metaloph of the M3 are slightly convergent towards the lingual border. The anterior centroloph is very long reaching the lingual border of the occlusal surface. The M3 has a short extra ridge between the protoloph and the anterior centroloph.

The only p4 of *S. alpinus* available from Oberdorf is not well preserved. It shows four ridges. The anterior and the posterior pair of these are lingually as well as labially connected. Figure 63 in BOLLIGER (1992) shows that the p4 of Gliride indet. 2 from Tägernastrasse that I assign to the species *alpinus* has essentially the same pattern. In this specimen that is less worn than the one from Oberdorf the ridges end free labially. These teeth are not very different from the p4 of *M. hispanicus* from the Early Vallesian of Pedregueras 2c, but the anterior portion of the p4 is, relative to the posterior portion much wider and longer in *Seorsumuscardinus* than in any *Muscardinus*.

The pattern of the m1 consists essentially of four complete transverse ridges that are separated by three valleys. The second ridge (= metalophid) bulges somewhat forward near the median axis of the occlusal surface. There is a short extra ridge in the valley between the anterolophid and the metalophid and a much longer extra ridge in the valley between the mesolophid and the posterolophid. Both extra ridges have a lingual position as in all Glirinae.

The m2 is not known from Oberdorf, but a specimen from Tägernastrasse has been figured by BOLLIGER (1992). This specimen identified as a left second lower molar of Gliride indet. 2 (op.cit. fig. 63) seems to be a right m2 of *S. alpinus*. Its pattern perfectly matches that of the m1 from Oberdorf with the exception that the short anterior extra ridge is missing.

The pattern of the m3 is similar to that of the m1, but the ridges are somewhat oblique. The anterior as well as the posterior extra ridge are short in all four specimens. The anterolophid/metalophid and the mesolophid/posterolophid are connected on the lingual border in all four specimens and on the labial border in three specimens.

C o n c l u s i o n s: *Seorsumuscardinus alpinus* has teeth with a perfectly flat occlusal surface, centrally situated roots, enamel that continues on the lower side of the crown and extra ridges that are situated labially in the upper teeth and lingually in the lower teeth. All these features characterize it as a member of the Glirinae proper. The style of architecture of its teeth clearly shows that it is related to *Muscardinus*.

The occurrences of *Seorsumuscardinus alpinus* in Oberdorf and Tägernastrasse are supposedly slightly older than the first record of *Muscardinus*. Yet it has more derived dental characteristics, i.e. the separation of the protoloph and the metaloph of the M1 at the protocone. Its teeth are also larger and the ridges are stronger, so it does not seem to be a candidate for the ancestry of *Muscardinus*. The generic separation of *Muscardinus* and *Seorsumuscardinus* seems justified because the first upper molars of the latter are wider than they are long and do not show the slightest trace of the longitudinal "stretching" that characterizes all species of *Muscardinus*.

Glirudinus de BRUIJN, 1966

The number of species assigned to the genus *Glirudinus* has grown to nine in recent years and with the exception of WERNER (1994), who suggested that *G. glirulus* (DEHM, 1935) and *G. eggingensis* WERNER, 1994, might be better placed in a separate genus, there has been general consensus on the generic assignment of these nine species. Species identification, however, has remained difficult because the material from the type locality of the species *G. gracilis* (DEHM, 1950) and *G. modestus* (DEHM, 1950), Wintershof-West, shows so much variation in size and dental pattern that not all specimens can be identified to species (MAYR 1979, WU, 1993). WU (op.cit.) reached the conclusion that there is a third species – *G. minutus* WU, 1993 represented in that locality. This unfortunate problem cannot be solved at this moment.

In an effort to get a better overview I group the known species into two categories: The species with relatively simple dental patterns and the ones with very complex patterns. In the first category are: *G. engesseri* ÜNAY, 1994, *G. eggingensis*, *G. euroydon* van der MEULEN & de BRUIJN, 1982, *G. glirulus* (DEHM, 1935), *G. haramiensis* ÜNAY, 1994, and *G. modestus*. It is remarkable that within this group the species from Greece and Turkey show a much stronger tendency to form a complete endolph in the M1–M2 than the species from central and southwest Europe do. Otherwise, the differences between the six species in this category are restricted to minor differences in pattern of the upper molars.

The second category, containing species with very complex dental pattern, has only three species: *G. gracilis* (genotype), *G. minutus* WU, 1993 and *G. undosus* MAYR, 1979. All these are so far known from central and southwest Europe only. Differences between the three species in this category are primary restricted to differences in the size of their molars.

Glirudinus minutus WU, 1993

(Plate 5, Figs 15–19)

Type locality: Petersbuch 2.

Locality: Oberdorf 3 and 4.

Material: 8 teeth; O3: Coll. NHMW 1997z0202/0001/1–8.

13 teeth; O4: Coll. NHMW 1997z0202/0002/1–13.

Measurements:

	Length		mean	N	Width		
	min.	max.			mean	min.	max.
M1	8.7	9.5	9.2	4	10.7	10.2	11.0
M2	9.4	9.8	9.6	2	11.7	10.9	12.4
M3	-	-	-	0/1	10.3	-	-
p4	-	-	6.2	1	6.0	-	-
m1	8.8	9.6	9.2	5/3	8.9	8.6	9.2
m2	9.3	10.3	9.8	3	9.3	9.0	9.5
m3	8.0	9.1	8.6	4	8.2	7.7	8.5

Remarks: The size range of the teeth from Oberdorf falls within the range of the material from the type locality of *G. minutus*, although these seem to be relatively somewhat wider. The dental pattern of the teeth from Oberdorf is not consistently different

from that of *G. minutus*, *G. gracilis* and *G. undosus*, species that have been described in detail by DEHM (1950), MAYR (1979) and WU (1993). Peculiar is that the ridges outside the trigone of the M1–2 are poorly developed in our material and that the pattern of the m3 is more similar to that of *G. gracilis* and *G. undosus* than to that of *G. minutus*.

C o n c l u s i o n s: This short review of the various species of *Glirudinus* suggests that this genus had an extremely large geographical range during the Late Oligocene–Middle Miocene. The phylogenetic history of the group seems complex and the lineages that have been proposed seem to be artifacts because there are no consistent evolutionary trends in size and in the dental pattern of the teeth.

Dryomyinae de BRUIJN, 1967

The (sub) genera *Glirulus* THOMAS, 1906 and *Paraglrulus* ENGESSER, 1972.

The content of the (sub) genera *Glirulus* and *Paraglrulus* suggested by DAXNER-HÖCK and de BRUIJN (1981), and formally defined in van der MEULEN & de BRUIJN (1982), has been widely followed by later workers. Finds made during the last fifteen years have shown the surprising stability of the dental pattern within the *Glirulus* group as well as in the *Paraglrulus* group throughout their stratigraphic and geographic ranges. The dental similarity of *Glirulus* and *Paraglrulus* is striking, so it seems reasonable to suppose that they share the same ancestry (see below).

Identification of the seven formally named species of *Glirulus* on the basis of dental pattern is difficult because the individual variation within assemblages from single localities is great relative to the evolutionary change observed during the more than twenty millions of years that the genus is known. This is surprising because MEIN & ROMAGGI (1991) have shown that adaptations in other respects than dentition may differ considerably in *Glirulus*.

The overlap in size and in dental pattern of the type material of some fossil species is so great that it does not define discrete entities even if the material available is good as in the case of *G. lissiensis* HUGUENEY & MEIN, 1995 and *G. conjunctus* (MAYR, 1979). The recognition of a species based on only one or a few teeth as is the case for *G. gemmula* KRETZOI, 1962 is therefore impossible.

The evolutionary trend from *G. diremptus* to *G. conjunctus* observed by MAYR (1979) in successive populations from southern Germany may well be an artifact because *conjunctus* morphotypes occur as early as MN3 in Turkey. Possibly there are two groups of *Glirulus* species:

- 1) Those with m1 and m2 that usually have two extra ridges between the anterolophid and metalophid (*japonicus*, *pusillus*, *lissiensis*, *conjunctus* and *ekremi*).
- 2) Those with usually only one extra ridge between the anterolophid and metalophid of the m1 and m2 (*minor* and *diremptus*). A detailed statistical analysis of all the European material is required to establish whether or not this sub-division is realistic and in order to decide on synonymies.

The material from Oberdorf usually shows two extra ridges in the anterior valley of the lower molars that have a centrolophid of medium length. The anteroloph of the upper

molars is always connected to the endoloph and the anterior centroloph of the M1 and M2 is usually connected to the endoloph. Our material thus clearly resembles *G. lissiensis*.

Glirulus THOMAS, 1906

Glirulus (Glirulus) lissiensis HUGUENEY & MEIN, 1965

(Plate 6, Figs 1–7)

L o c a l i t y: Oberdorf 3 and 4.

M a t e r i a l: 18 teeth; O3: Coll. NHMW 1997z0203/0001/1–18.

44 teeth; O4: Coll. NHMW 1997z0203/0002/1–44.

M e a s u r e m e n t s:

	Length			N	Width		
	min.	max.	mean		mean	min.	max.
D4	-	-	-	-	-	-	-
P4	5.7	7.0	6.5	7	7.7	6.7	8.4
M 1-2	8.0	9.4	8.6	17	9.7	9.2	10.6
M3	6.9	8.3	7.7	9	8.9	8.1	10.0
d4	-	-	-	-	-	-	-
p4	7.0	7.4	7.2	2	6.1	5.9	6.2
m1	8.9	10.7	9.4	10	8.8	8.2	9.6
m2	9.1	10.4	9.7	12	9.6	8.8	10.3
m3	8.2	9.8	9.1	5	8.4	7.8	9.0

R e m a r k s: The upper premolars are rather small for a species of *Glirulus* and it cannot be excluded that the smallest specimen (no. 3217) is a milk tooth. The anterior centroloph is long, but does not reach the endoloph. The posterior centroloph is absent. The number of extra ridges shows individual variation between two and four. The ones between the anteroloph and the protoloph and between the metaloph and the posteroloph are invariably present.

The endoloph of the M1–2 is always complete. The anterior centroloph is long and connected to the endoloph in thirteen out of seventeen specimens. Labially the anterior centroloph is continuous with the anteroloph. The posterior centroloph is variable in length and never reaches the endoloph. This ridge has the habitus of an extra ridge. Three extra ridges are invariably present.

The dental pattern of the M3 is not as constant as in the M1–2. In some specimens the anterior centroloph is longer than the posterior centroloph, in others the situation is the reverse and in one M3 one of the centrolophs is absent. In many M3 the labial connections between the ridges are interrupted. Eight out of nine M3 have three extra ridges. One of these is situated in the anterior valley and one in the posterior valley. The position of the third extra ridge is variable.

The lower premolars are rather small also. Their centrolophids are long and there is an extra ridge in the anterior as well as in the posterior valley. One p4 shows a short extra ridge between the centrolophid and the mesolophid also.

The endolophid of the m1 shows a notch behind the centrolophid, but in the m2 this ridge is usually complete. The centrolophid is long in all m1 and m2, but never reaches

the labial border of the occlusal surface. Nine out of ten m1 and eight out of twelve m2 have two extra ridges in the valley between the anterolophid and the metalophid. All m1 and m2 have three further extra ridges: one on either side of the centrolophid and one in the posterior valley. One m2 deviates from this pattern by having three extra ridges in the posterior valley.

The dental pattern of the third molar is, as in the upper dentition, more variable than in the m1 and m2. The centrolophid is always long, but the double extra ridge in the anterior valley is present in two out of five specimens only. Peculiar is specimen no. 3281 because it also has a double extra ridge in the posterior valley. Extra ridges on either side of the centrolophid are present in two out of five m3.

C o n c l u s i o n s: The *Glirulus* (*Glirulus*) from Oberdorf clearly belongs in the same group as the species *japonicus*, *pusillus*, *lissiensis*, *conjunctus* and *ekremi*. The dental pattern within this group shows a surprising stability through time. Even *G. ekremi* from the lower Miocene of Anatolia differs from extant *G. japonicus* in small details only.

***Glirulus* (*Paraglrulus*) sp.**
(Plate 5, Figs 8 and 9)

L o c a l i t y: Oberdorf 3 and 4.

M a t e r i a l a n d m e a s u r e m e n t s:

Two P4 (7.4–7.6x8.7–8.8) and two M1–2 (8.9–10.5x10.1–10.2)

1 teeth; O3: Coll. NHMW 1997z0204/0001/1.

3 teeth; O4: Coll. NHMW 1997z0204/0002/1–3.

R e m a r k s: The upper premolars are quite molariform. In one specimen the anterior centroloph is long and connected to the protoloph. The posterior centroloph is well developed. In the other P4 there is one long centroloph that is constricted just before reaching the endoloph, while the other centroloph is developed as a short extra ridge. Both teeth show three extra ridges: One between the anteroloph and the protoloph, one between the protoloph and the long centroloph and one between the metaloph and the posteroloph.

The two upper molars have an almost square occlusal surface. The endoloph is complete and the anterior centroloph is long and firmly connected to the endoloph. Labially the anterior centroloph ends in a small cusp and there is a well-marked notch between this cusp and the paracone. The posterior centroloph is long, but does not reach the endoloph. Both M1–2 have three long extra ridges. In one there are some short and low incipient ridges also.

C o n c l u s i o n s: The *Glirulus* (*Paraglrulus*) molars from Oberdorf are somewhat longer than the ones assigned to *Glirulus* (*Glirulus*) *lissiensis*. Their dental pattern with labially free ending anterior centroloph is identical to that of the specimens of the genotype *Paraglrulus werenfelsi* from Anwil (Switzerland), but they are much smaller. It thus seems that the size of *Paraglrulus* teeth increases through time. This is in sharp contrast to the situation in *Glirulus* which species all are essentially the same size.

In this context it is of interest that we have transferred the rather large species *Paraglrulus agelakisi* van der MEULEN & de BRUIJN, 1982 to the genus *Bransatoglis*.

Myomiminae DAAMS, 1981

***Peridyromys murinus* (POMEL, 1853)**

(Plate 6, Fig. 11)

L o c a l i t y: Oberdorf 4.

M a t e r i a l a n d m e a s u r e m e n t s:

1D4(6.0x6.8), 1P4 (7.0x8.0), 2/1 M1–2 (10.1–10.2x10.7); Coll. NHMW 1997z0205/0001/1–4.

R e m a r k s: The few teeth of *P. murinus* from Oberdorf fit in size as well as in dental pattern within the variation of the sample of this species from Montaigu le Blin available to me for comparison. For a detailed description of this species, which is a common constituent of many Early Miocene rodent assemblages from South Western Europe, see de BRUIJN (1967).

Microdyromys de BRUIJN, 1966***Microdyromys* cf. *legidensis* DAAMS, 1981**

(Plate 6, Fig 12)

L o c a l i t y: Oberdorf 4.

M a t e r i a l a n d m e a s u r e m e n t s:

1m2 (8.8x8.3); Coll. NHMW 1997z0206/0002/1.

R e m a r k s: The m2 tentatively assigned to *M. legidensis* has the basal dental pattern for glirids consisting of the four main ridges, a long centrolophid and an extra ridge in the anterior as well as in the posterior valley. This pattern also occurs in *Microdyromys praemurinus* (FREUDENBERG, 1941), *M. koenigswaldi* de BRUIJN, 1966, *M. monspeliensis* AGUILAR, 1977, and *Peridyromys obtusangulus* (von MEYER, 1859) and *P. aquatilis* (de BRUIJN & MOLZER, 1974). The identification of this single m2 is therefore primarily based on its size. Since this tooth is in all respects indistinguishable from the type material of *M. legidensis* from Villafeliche II A it is tentatively assigned it to this species.

***Microdyromys* cf. *hildebrandti* WERNER, 1994**

(Plate 6, Fig 10)

L o c a l i t y: Oberdorf 3.

M a t e r i a l a n d m e a s u r e m e n t s:

1 M1–2 (6.7x7.5); Coll. NHMW 1997z0207/0001/1.

R e m a r k s: This very small M1–2 with its typical *Microdyromys* dental pattern is just within the lower part of the size range of the smallest species of the genus *M. hildebrandti*. Its dental pattern is peculiar in showing a short posteroloph that meets the metaloph and does not reach to the labial border of the occlusal surface. It is not known if this pattern, for *Microdyromys* aberrant, occurs in the rich type material from Ulm-Westtangente, but the irregular course of the metaloph in most of the specimens from that locality figured by WERNER (1994) suggests that the specimen from Oberdorf fits within the morphological variation of the species *hildebrandti*.

Bransatoglininae DAAMS & de BRUIJN, 1995***Bransatoglis* HUGUENEY, 1967**

The representatives of the genus *Bransatoglis* combine a remarkable stability (late Eocene to late Miocene) of some characteristic dental features with a wide intraspecific variation in the degree of organization of the ridges. In almost any larger association specimens with neat straight parallel ridges and specimens with a disorderly pattern occur. The earliest representative *B. bahloi* BOSMA & de BRUIJN, 1982 from the Late Eocene of the Isle of Wight has a simple pattern, *B. concavidens* HUGUENEY, 1967 from the Late Oligocene of France and *B. complicatus* ÜNAY, 1994 from the Early Miocene of Anatolia have the more complex dental pattern. In the first and second upper molars of the Eocene–Oligocene representatives there is a clear evolutionary change from a V-shaped arrangement of the protoloph and metaloph to a U-shaped arrangement. This change is accompanied by the development of a continuous endoloph, the lengthening of the centrolophs and extra ridges and the increase of the number of extra ridges. These trends seem to reach an optimum in the Late Oligocene species *B. concavidens* and the Early Miocene *B. complicatus* and *B. agelakisi*. All other Miocene species of *Bransatoglis* have essentially the same dental pattern. Since the number of specimens per locality is usually small and the variation in dental pattern within single associations invariably large, species identification is primarily based on size. The list of formally defined "Miocene" species contains *B. cadeoti* BULOT, 1978, *B. concavidens* HUGUENEY, 1967, *B. spectabilis* (DEHM, 1950) *B. astaracensis* (BAUDELLOT, 1970), *B. infralactorensis* (BAUDELLOT & COLLIER, 1982), *B. fugax* (HUGUENEY, 1967), *B. complicatus* ÜNAY, 1994 and *B. agelakisi* (van der MEULEN & de BRUIJN, 1982). In this list the species are arranged according to size, *B. cadeoti* being the largest and *B. agelakisi* the smallest species. The size differences between *B. complicatus* and *B. agelakisi* and between *B. fugax* and *B. infralactorensis* as given in the literature are small and may not warrant their distinction. However, comparison of measurements taken in different ways does not allow a conclusion. Direct comparison of material of *agelakisi* and *complicatus* leaves no doubt about their identity. This the more so because the anteroloph and the posteroloph of the M1–2 are confluent with the centrolophs in *agelakisi* and separated by a notch in *complicatus*. Unfortunately, I have no material of *fugax* and *infralactorensis* available.

The status of the species *B. rimosus* and *B. parvus* from the Early Oligocene of Olalla 4 described in an unpublished thesis by PELAEZ-CAMPOMANES (Universidad Complutense, Madrid, 1993) has become doubtful since FREUDENTHAL (1996) described material from the same locality under the name *B. parvus*. A decision on this matter is outside the scope of this paper, but the obvious lack of communication between colleagues working in the same area is an offense to science.

***Bransatoglis fugax* HUGUENEY, 1967**

(Plate 6, Figs 13–20)

L o c a l i t y: Oberdorf 3 and 4.

M a t e r i a l: 6 teeth; O3: Coll. NHMW 1997z0208/0001/1–6.
20 teeth; O4: Coll. NHMW 1997z0208/0002/1–20.

Measurements:

	Length			N	Width		
	min.	max.	mean		mean	min.	max.
D4	8.1	9.5	8.8	2	9.4	8.8	10.0
P4	-	-	-	-	-	-	-
M1	12.0	15.0	13.3	4	13.9	12.9	15.0
M2	12.2	14.3	13.6	4	14.3	13.7	15.0
M3	9.9	12.4	10.8	3	13.6	12.0	14.7
d4	8.3	9.1	8.7	2	8.2	7.5	8.8
p4	9.8	10.7	10.4	3	9.4	9.0	10.0
m1	13.0	13.9	13.6	5	12.9	12.1	14.0
m2	12.0	13.8	12.9	2/1	12.0	-	-
m3	-	-	13.3	1	11.7	-	-

Remarks: The two small D4 are sub-triangular and have short anterolophs and posterolophs. One of these specimens has only one labially isolated centroloph; in the other the anterior and posterior centroloph are partially fused. This last D4 has a short low extra ridge between the posterior centroloph and the metaloph.

The endoloph of three of the four M1 is complete. In one specimen the anterloph is separated from the protocone by a notch. The long anterior centroloph reaches the endoloph in one specimen, in another it is constricted just before reaching the endoloph and in the two remaining M1 it ends before reaching the endoloph. Labially the anterior centroloph is separated from the paracone in three, but connected to the paracone in one specimen. The number of extra ridges varies between one and three per tooth. The ridges may be straight and parallel or irregular.

The dental pattern of the M2 is similar to that of the M1, but the occlusal surface is more rectangular and relatively wider. The endoloph is complete and the anterior centroloph is connected to the endoloph in one specimen only.

The pattern of the ridges within the trigon is disorderly in all three M3. The protoloph is long and straight the metaloph connects postero-labially with the posteroloph in the characteristic *Bransatoglis* way. The number of extra ridges outside the trigon varies between zero and two.

The two small d4 have an oval shape and an irregular dental pattern. In one specimen the basic glirid pattern is completely lost. Its main feature is a continuous ridge along the edge of the occlusal surface. The short ridges inside this ring are difficult to homologize.

The modal pattern of the m1 has the four main ridges, a long rather thin centrolophid and one extra ridge in the posterior as well as in the anterior valley. All the five m1 show minor deviations from this pattern. Short longitudinal connections between ridges are common and unusual confluences or interruptions of the transverse ridges occur in almost all specimens. One m2 has two extra ridges in the anterior as well as in the posterior valley.

The two m2 and one m3 in our collection have the same basic structure as the m1, but lack the irregular variations.

***Bransatoglis* cf. *astaracensis* (BAUDELLOT, 1970)**
(Plate 6, Fig. 21)

Locality: Oberdorf 4.

Material and measurements:

1 m2 (15.3x14.6); Coll. NHMW 1997z0209/0002/1.

Remarks: This second lower molar has a concave occlusal surface. The centrolophid is long and there is an extra ridge in the anterior as well as in the posterior valley as in most species of *Bransatoglis*. This specimen is too large to include it in the previous species and about the same size as the smallest specimens of *B. astaracensis* from Sansan and Anwil (see ENGESSER 1972: diagram 29b). This tooth is therefore tentatively identified as *B. cf. astaracensis*.

Conclusion: The majority of the *Bransatoglis* material from Oberdorf is of about the same size as the type material of *B. fugax* and *B. infralactorensis*. These species are both based on small collections that show a large overlap in size as well as in dental pattern, so it cannot be excluded that the name *infralactorensis* BAUDELLOT & COLLIER, 1982 is a junior synonym of *fugax* HUGUENEY, 1969. The two characteristics that are used by BAUDELLOT & COLLIER to distinguish *B. infralactorensis* from *B. fugax* (absence of the extra ridge in the posterior valley of the M1–2 and fusion of the lingual end of the proto-loph to the endoloph) are both within the range of variation of the material from Oberdorf. I prefer to use the name *fugax* because it has priority in case *fugax* and *infralactorensis* are synonyms. The dimensions of the teeth from Oberdorf seem to be slightly higher than in the type material of *B. fugax*.

The m2 from Oberdorf tentatively identified as *B. cf. astaracensis* seems to be too large to be within the variation of *B. fugax*.

Family	Genera and species	N
Sciuridae	<i>Palaeosciurus sutteri</i>	22
	<i>Spermophilinus besanus</i>	50
	<i>Ratufa</i> n. sp.	1
Petauristidae	<i>Miopetaurista dehmi</i>	4
	<i>Blackia miocaenica</i>	13
	<i>Hylopetes hoeckarum</i>	8
Gliridae	<i>Glis minor complicatus</i>	15
	<i>Seorsumuscardinus alpinus</i>	12
	<i>Glirudinus minutus</i>	14
	<i>Glirulus (Glirulus) lissiensis</i>	39
	<i>Glirulus (Paraglrulus) sp.</i>	2
	<i>Peridyromys murinus</i>	2
	<i>Microdyromys cf. legidensis</i>	1
	<i>Microdyromys cf. hildebrandti</i>	1
	<i>Bransatoglis fugax</i>	15
<i>Bransatoglis cf. astaracensis</i>	1	

Fig. 1: List of the genera and species of the squirrels and dormice from Oberdorf. N is the number of M1–2 plus m1–2 per taxon.

Dentition types (after van der MEULEN & de BRUIJN 1982)	Genera and Species	Number of ridges counted on the M1–2 and the m1–2									
		4	5	6	7	8	9	10	11	12	N
Flat molar group	<i>Glirudinus minutus</i>						6	2	3	3	14
	<i>Seorsumuscardinus alpinus</i>	4	8								12
Complicated intermediate molar group	<i>Glirulus (Glirulus) lissiensis</i>						25	11	2		38
	<i>Glirulus (Paraglrulus) sp.</i>						1		1		2
	<i>Microdyromys cf. hildebrandti</i>	1	1								1
	<i>Microdyromys cf. legidensis</i>				1						1
Symmetrical molar group	<i>Glis minor complicatus</i>				3	2	10				15
	<i>Bransatoglis fugax</i>				6	5	3				14
	<i>Bransatoglis cf. astaracensis</i>				1						1
Asymmetrical molar group	<i>Peridyromys murinus</i>	1	1								2
Number of specimens per category		0	5	10	11	7	45	13	6	3	100

Fig. 2: The genera and species of dormice from Oberdorf listed according to type of dentition. N-horizontal is number of M1–2 plus m1–2 with a particular number of ridges. N-vertical is number of M1–2 plus m1–2 per taxon. The total number of ridges counted in hundred specimens = 855, so the Ridge Index is 8.55.

Biostratigraphy and Paleocology

Representatives of the families Sciuridae, Petauristidae and Gliridae are in general poor biostratigraphic markers because of the longevity of their species. The very diverse sciuroid and gliroid assemblage from Oberdorf containing only a few species that are restricted to one or two mammal units is no exception to the rule. Among the sixteen species recognized (fig. 1) the ground squirrels *Palaeosciurus sutteri* (MN4) and *Spermophilinus besanus* (MN4) are probably the best biostratigraphic markers. The dormice *Glirudinus minutus* (MN3–4) and *Peridyromys murinus* (MN2–4) do not contradict the assignment of late Early Miocene age (MN4) to the Oberdorf fauna.

The paleoecological interpretation of an Early Miocene fauna is difficult, because most of the genera and all of the species represented have become extinct. However, the presence of three species of flying squirrel suggests that a mixed (sub)tropical forest with tall trees was present. A species of *Glis* that is not very different from the arboreal fat dormouse *Glis glis* is consistent with this interpretation.

Van der MEULEN & de BRUIJN (1982) recognized six ecological groups in the Gliridae and suggested that species with seven or more ridges on the cheek teeth are vegetarian. This leads me to define a ridge index for the dormouse assemblage that is based on the assumption that not only presence or absence of a particular species is indicative of biotope, but also the relative abundance of species with many or few ridges on their cheek teeth. The index is obtained by counting the number of ridges on all the M1–2 + m1–2 of the assemblage and by adding the numbers of specimens in each category. This shows that the modal pattern in Oberdorf has nine ridges (fig. 2). If all the ridges of all the specimens are added and divided by number of specimens the ridge index of 8.55 is obtained.

Following van der MEULEN & de BRUIJN (1982) this indicates that a diverse vegetarian diet must have been available. With the exception of the two teeth of *Peridyromys murinus* in the collection the dormice from Oberdorf belong to the "Flat Molar Group", the "Complicated Intermediate Molar Group" and the "Symmetrical Molar Group" of van der MEULEN & de BRUIJN (op cit). These groups are supposedly indicative of a forested biotope with undergrowth. Although this forest may have been standing in water during part of the year in a similar way as the present-day Pantanal Wetlands of Brazil, the absence of beavers in Oberdorf suggests that permanent open water surfaces were absent. This reconstruction of the paleoenvironment is in accordance with the botanical and sedimentological information available to me.

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Plate 1

Palaeosciurus sutteri from Oberdorf

- Fig. 1: P4 (NHMW 1997z0194/0002/1);
figs 2 and 3: M1–2 (NHMW 1997z0194/0002/2 and (NHMW 1997z0194/0001/1);
fig. 4: M3 (NHMW 1997z0194/0002/3);
fig. 5: p4 (NHMW 1997z0194/0002/4);
fig. 6: m1 (NHMW 1997z0194/0002/5);
fig. 7: m2 (NHMW 1997z0194/0002/6);
fig. 8: m3 (NHMW 1997z0194/0002/7).

Fig. 3 from Oberdorf 3.

Figs. 1, 2, 4, 5, 6, 7 and 9 from Oberdorf 4.

Plate 2

Spermophilinus besanus from Oberdorf

- Fig. 1: D4 (NHMW 1997z0195/0002/1);
figs 2 and 3: M1–2 (NHMW 1997z0195/0002/2 and NHMW 1997z0195/0001/1);
figs 4 and 5: M3 (NHMW 1997z0195/0002/3 and 4);
fig. 6: d4 (NHMW 1997z0195/0002/5);
fig. 7: p4 (NHMW 1997z0195/0002/6);
fig. 8: m1 (NHMW 1997z0195/0002/7);
fig. 9: m2 (NHMW 1997z0195/0001/2);
fig. 10: m3 (NHMW 1997z0195/0002/8).

Figs. 3 and 9 from Oberdorf 3.

Figs. 1, 2, 4, 5, 6, 7, 8 and 10 from Oberdorf 4.

Plate 3

Miopetaurista dehmi from Oberdorf

Fig. 1: D4 (labial side damaged; NHMW 1997z0197/0001/1);

fig. 2: P4 (NHMW 1997z0197/0001/2);

fig. 3: M1–2 (NHMW 1997z0197/0002/1);

fig. 4: M3 (NHMW 1997z0197/0001/3);

fig. 5: m2 (NHMW 1997z0197/0001/4).

Figs. 1, 2, 4, and 5 from Oberdorf 3.

Fig. 3 from Oberdorf 4.

Plate 4

Blackia miocaenica from Oberdorf

- Fig. 1: D4 (NHMW 1997z0198/0002/1);
fig. 2: P4 (NHMW 1997z0198/0002/2);
figs 3 and 4: M1–2 (NHMW 1997z0198/0002/3 and 4);
fig. 5: M3 (NHMW 1997z0198/0002/5);
fig. 6: d4 (NHMW 1997z0198/0002/6);
fig. 7: p4 (NHMW 1997z0198/0002/7);
fig. 8: m1 (NHMW 1997z0198/0002/8);
fig. 9: m2 (NHMW 1997z0198/0002/9);
fig. 10: m3 (NHMW 1997z0198/0002/10).

Figs. 1–10 from Oberdorf 4.

Hylopetes hoeckarum from Oberdorf

- Figs. 11 and 12: M1/2 (Holotype, NHMW 1997z0199/0001/1 and NHMW 1997z0199/0002/1); fig. 13:
M3 (NHMW 1997z0199/0001/2); fig. 14: m1 (NHMW 1997z0199/0001/3).

Figs. 11, 13, and 14 from Oberdorf 3.

Fig. 12 from Oberdorf 4.

Plate 5

Glis minor complicatus from Oberdorf

- Fig. 1: P4 (NHMW 1997z0200/0001/1);
figs 2 and 3: M1–2 (NHMW 1997z0200/0001/2 and holotype, NHMW 1997z0200/0002/1);
fig. 4: m1 (NHMW 1997z0200/0001/3);
fig. 5: m2 (NHMW 1997z0200/0001/4);
fig. 6: m3 (NHMW 1997z0200/0001/5).

Figs. 1, 2, 4–6 from Oberdorf 3.

Fig. 3: from Oberdorf 4.

Seorsumuscardinus alpinus from Oberdorf

- Fig. 7: P4 (NHMW 1997z0201/0002/2);
fig. 8: M1 (Holotype, NHMW 1997z0201/0002/1);
fig. 9: M2 (NHMW 1997z0201/0002/3);
fig. 10: M3 (NHMW 1997z0201/0001/1);
fig. 11: P4 (NHMW 1997z0201/0002/4);
fig. 12: m1 (NHMW 1997z0201/0002/5);
fig. 13: m2 (NHMW 1997z0201/0002/6);
fig. 14: m3 (NHMW 1997z0201/0002/7).

Fig. 10 from Oberdorf 3.

Figs. 7, 8, 9, 11, 12, 13 and 14 from Oberdorf 4.

Glirudinus minutus from Oberdorf

- Fig. 15: M1 (NHMW 1997z0202/0001/1);
fig. 16: M2 (NHMW 1997z0202/0002/1);
fig. 17: m1 (NHMW 1997z0202/0002/2);
fig. 18: m2 (NHMW 1997z0202/0002/3);
fig. 19: m3 (NHMW 1997z0202/0002/4).

Fig. 15 from Oberdorf 3.

Figs. 16, 17, 18, and 19 from Oberdorf 4.

Plate 6

Glirulus (Glirulus) lissiensis from Oberdorf

Figs 1 and 2: M1–2 (NHMW 1997z0203/0002/1 and 2);
fig. 3: M3 (NHMW 1997z0203/0002/3);
figs 4 and 5: m1 (NHMW 1997z0203/0002/4 and 5);
fig. 6: m2 (NHMW 1997z0203/0002/6);
fig. 7: m3 (NHMW 1997z0203/0001/1).

Fig. 7 from Oberdorf 3.

Figs. 1, 2, 3, 4, 5, and 6 from Oberdorf 4.

Glirulus (Paraglrulus) sp. from Oberdorf

Figs 8 and 9: M1–2 (NHMW 1997z0204/0002/1 and NHMW 1997z0204/0001/1).

Fig. 8 from Oberdorf 4.

Fig. 9 from Oberdorf 3.

Microdyromys hildebrandti from Oberdorf

Fig. 10: M1–2 (NHMW 1997z0207/0001/1) from Oberdorf 3.

Peridyromys murinus form Oberdorf

Fig. 11: M1–2 (NHMW 1997z0205/0001/1) from Oberdorf 4.

Microdyromys cf. legidensis from Oberdorf

Fig. 12: m2 (NHMW 1997z0206/0002/1) from Oberdorf 4.

Bransatoglis fugax from Oberdorf

Figs 13–16: M1–2 (NHMW 1997z0208/0002/1–4);
fig. 17: M3 (NHMW 1997z0208/0001/1);
fig. 18: m1 (NHMW 1997z0208/0001/2);
fig. 19: m2 (NHMW 1997z0208/0001/3);
fig. 20: m3 (NHMW 1997z0208/0001/4).

Figs. 17, 18, 19, and 20 from Oberdorf 3.

Figs. 13, 14, 15, and 16 from Oberdorf 4.

Bransatoglis cf. astaracensis from Oberdorf

Fig. 21: m3 (NHMW 1997z0209/0002/1) from Oberdorf 4.

