Fuenferrada 3, the first Eocene mammal locality in the depression of Montalbán (Teruel, Spain), with some remarks on the fauna of Olalla 4A

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The rodent fauna of Fuenferrada contains two species of Theridomyidae and three species of Gliridae. It is compared with the Early Oligocene fauna of Olalla 4A, and with the Late Eocene fauna of Aguatón 2D. The absence of Cricetidae serves to determine its age as latest Eocene.

Contents

Introduction

In the area East of the village of Fuenferrada four localities have been sampled on the roadside: FF2A, FF2B, FF3A, and FF3B. FF2 and FF3 are about 300 m away from each other, and present the same sedimentary sequence; FF2A and FF3A represent probably the same bed, and the same goes for FF2B and FF3B. Their UTM co-ordinates are XL684262. No faunal differences have been detected. The sample FF3B is the largest one (6000 kg of sediment), and has yielded a collection of 178 specimens; FF2B has yielded an additional 17 specimens. The localities FF2A and FF3A have yielded fragments only.

The localities are poor and the collection is small, but quite important because it is the first proof of Eocene sediments in the Montalbán depression. The presence of Eocene deposits had been supposed by Martín Fernández et al. (1977) in the explanation of sheet 492 of the geological map of Spain, but until now no evidence was available.

Pérez et al. (1983) define five tectosedimentary units in the Montalbán area and Pérez García (1984) supposes an Eocene-Oligocene age for unit T1. This unit is exposed near Segura de los Baños on the northern border of the basin, and South of Martín del Río, on the southern border. In the area S of Martín del Río I have found an Early Oligocene locality, but no Eocene so far.

The Eocene localities of Fuenferrada lie in an area marked as TSU T3 (Lower Oligocene) by Pérez et al. (1983), interpreted as Miocene by Pérez García (1984).

Part of the material will be stored in the collections of the Museum of Paleontology of the University of Zaragoza, the other part (catalogue numbers RGM) belongs to the collections of the National Museum of Natural History, Leiden, The Netherlands.

Measurements are given in units of 0.1 mm.

The terminology of the cheek teeth of the Theridomyidae is basically after Wood & Wilson (1936), using metalophid instead of metalophulid, and hypolophid instead of hypolophulid, this being the form used by most authors. Entolophid instead of hypolophid, as used by various authors, is not recommendable as it has no homology with the entoloph of the upper molars. Incidentally I use the system of numbering crests and valleys as introduced by Stehlin & Schaub (1951). The terminology of the cheek teeth of the Gliridae is after de Bruijn (1967).

Abbreviations and codes

AGT2D	Aguatón 2D (Teruel, Spain)
FF2B	Fuenferrada 2B (Teruel, Spain)
FF3B	Fuenferrada 3B (Teruel, Spain)
OLA4A	Olalla 4A (Teruel, Spain)
MLB1D	Montalbán 1D (Teruel, Spain)
RGM	Rijksmuseum van Geologie en Mineralogie, Leiden, now National Museum of Natural History, Leiden, The Netherlands.

Measuring Theridomyidae teeth

Measuring length and width

Theridomyid teeth are difficult to measure, due to their shape, their hypsodonty, and their large size. Vianey-Liaud (1972) tried to solve this problem by measuring the wear surface instead of the entire crown length and width. This is possibly the best way to measure very hypsodont, tubular, teeth like those of *Issiodoromys*, but for moderately hypsodont teeth like those of *Theridomys* and *Pseudoltinomys* it gives a very wide range of measurements, the highest values corresponding to the most worn teeth. To minimize the undesirable effects of her measuring method, she divided her material in four wear classes. I measured a trial sample, and came to the conclusion that the difficulty of estimating the border of the wear surface may cause deviations of up to 13%. This together with the bias introduced by estimating the wear class makes measuring results so unreliable, that size differences between populations of less than 20% should be regarded as not significant. Measuring the overall length and width turned out to be much more reliable (measuring error obtained from repeatability tests generally less than 3%).

Of course hypsodont teeth cannot be measured by a system that uses an ocular micrometer, but any system based on projection on a movable stage is useful, provided the projection is perfectly vertical in order to permit refocusing. Such a system, based on a Leitz Ortholux microscope, was described by Freudenthal (1966). It has since then been digitalized, so that data are transmitted directly to a computer file for further processing. A similar system on the basis of a Wild M7S binocular microscope has been mentioned by Martín Suárez et al. (1993), and a Nikon monocular microscope by Daams et al. (1989). The Nikon system is the least advisable, because of its human-unfriendly design. The Wild system is the better one for measuring large specimens, because they are more easily oriented than on the Ortholux.

But even such a system fails when the two points that define the measurement cannot be made visible without changing the orientation of the specimen. This is the case for the width of the lower molars of *Theridomys*. Fig. 1a represents an $M_{1,2}$ seen in longitudinal view. The vertical lines are the delimiters for the width measurement of a specimen in occlusal orientation. Due to the fact that the labial wall is more curved than the lingual wall, the width may vary about 5% between the unworn and the worn stage of the same specimen (and slightly more than 5% if the wear surface undergoes an angular shift during abrasion). I tried to take measurements in the longitudinal orientation represented in Fig. 1a; the measurements are technically reliable (the measurement delimiters are unambiguous), but the result is worse than in occlusal view, because of the difficulty of orientation; a slight change of inclination of the specimen causes differences of over 10%. So the width of lower molars is taken as maximum visible crown width in occlusal orientation.

Fig. 1b represents an $M^{1,2}$ in longitudinal view; it shows that the width of the wear

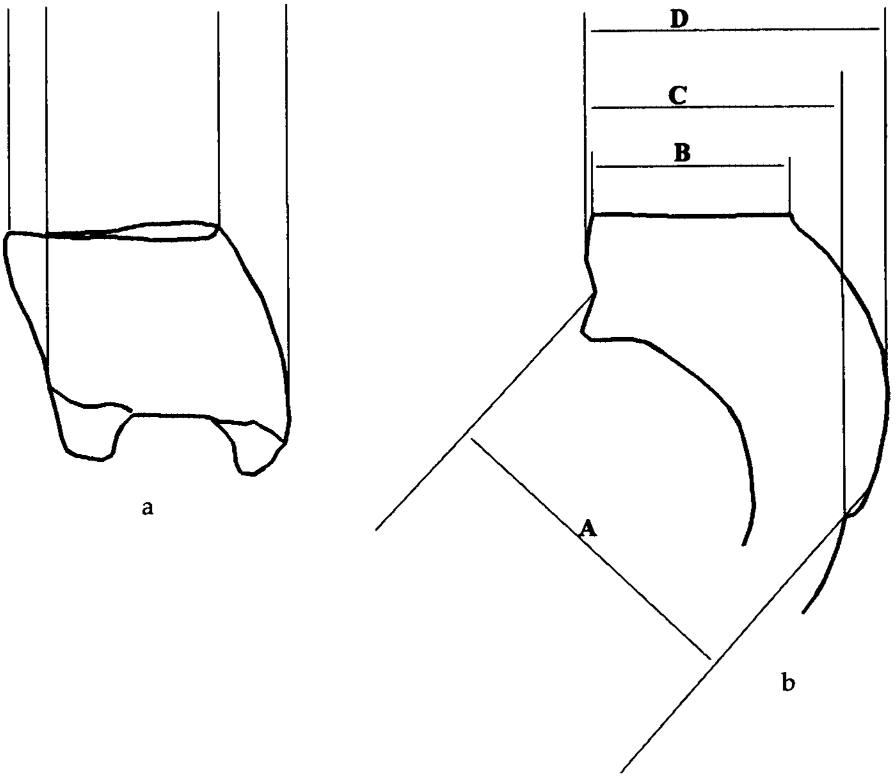

Fig. 1. Measurement definitions for Theridomorpha teeth.

surface of a worn specimen (A) may be more than double the width of the same specimen in an unworn stage (B), and such a result is evidently useless.

Theoretically the best measurement would be C, which is constant at all stages of wear; however, it is technically impossible: in unworn teeth it is not visible, and in worn teeth it is impossible to reconstruct the orientation of line C.

Measuring the maximum visible width gives a reasonable result: the width of the worn stage is the same as before (A), and the width of the unworn stage (D) differs less than 20% from the worn stage. The larger part of this 20% difference is caused by the rotation of the occlusal surface with respect to the basis of the tooth during the abrasion. Though this result is much better than measuring the dimensions of the wear surface, I still regard it to be insufficient, and one might consider to refrain from measuring the width of the upper molars. This agrees completely with the opinion of Mödden (1993), who rejects the usefulness of width measurements on the teeth of *Protechimys* and other semihypsodont theridomyids.

Mödden (1993) uses a lateral orientation for the length measurement of the upper molars of *Archaeomys*. This is probably a correct solution, and maybe the only one, but it presents the same problem of orientation that I encountered in the width measurements of the lower molars.

Only a measuring system with a sophisticated three-dimensional manipulating device, based on a cardanic suspension of the specimen, would be suitable to get useful results for measurements that cannot be taken reliably in occlusal view. With such a device one might orient each specimen in occlusal view, and take the desired measurements after a controlled rotation along the length or width axis.

The validity of the measurement method chosen in this paper is proven by the measurements tables: the variability coefficient V′ shows quite normal values for all parameters, except for the width of $M^{1,2}$.

Measuring hypsodonty

A frequently used coefficient of hypsodonty is height/length. Vianey-Liaud (1985) introduced the coefficient of hypsodonty CHY, defined as W+H/0.5L (where W = width, H = height, and L = length). From Anadón et al. (1987), it may be deduced that the formula should be written as CHY = (W+H)/0.5L. This may be written also as CHY = W/0.5L + H/0.5L, which means that CHY is not a coefficient, but a sum of two coefficients. Evidently dividing by 0.5L instead of by L only doubles the value of CHY, without any obvious reason. The histograms for H/L and CHY given by Vianey-Liaud (1985, fig. 2) seem to show that the range for CHY is more compressed than the range for H/L, but still the unworn specimens give the higher values and the worn teeth give the lower values.

Vianey-Liaud (1985, p. 164) states (translation by the present author), that 'the variability of CHY falls within the range of a normal variability for a fossil or recent rodent', implying that this permits the application of various statistical tests based on a normal distribution. However, it should be clear that, unless a normal distribution is proven, no test based on such a distribution may be applied reliably. That is precisely why Simpson's variability coefficient frequently fails to give useful results (see Freudenthal & Cuenca Bescós, 1984, Freudenthal & Martín Suárez, 1990). Since the values for length, width and height as measured by Vianey-Liaud are strongly influenced by the degree of wear, a normal distribution is per definition absent.

In my opinion, if one wishes to reduce the height to a hypsodonty coefficient, it may be divided by the overall crown length or width (or by length × width). The height should be measured in unworn or hardly worn specimens only. Of course this reduces the number of useful specimens, but at least the values obtained are meaningful.

Anyhow, height measurements are, in my experience, considerably less reliable than length or width measurements. This is due to the difficulty of orientation, the difficulty to locate the enamel border at the base of the tooth exactly, and the possibility that the apposition of enamel at the crown basis continues during some time after the wear process has started.

A general conclusion about measuring teeth of Theridomyidae is, that a slight difference in orientation of a specimen may result in important differences in the measurements, and that conclusions based on small size differences between populations are of questionable value.

Though the measurements published in this paper are taken as described before, size comparisons with measurements published in various publications by Vianey-Liaud, had to be based on measurements of the wear surface.

Taxonomic descriptions

Family Theridomyidae Alston, 1876
Genus *Theridomys* Jourdan, 1837

Theridomys sp. nov.
Fig. 2.

Material and measurements — See Table 1.

Characterization — This is a large *Theridomys* with a very simple dental pattern, without anteroconid in the lower molars, without any small extra crests, and without synclinid I in the lower molars. In comparison with the molars the D4 and P4 are relatively large. In view of the poor material I refrain from naming this new species; excavations in the Fuenferrada localities are being continued, and I hope sufficient material will be available in the near future.

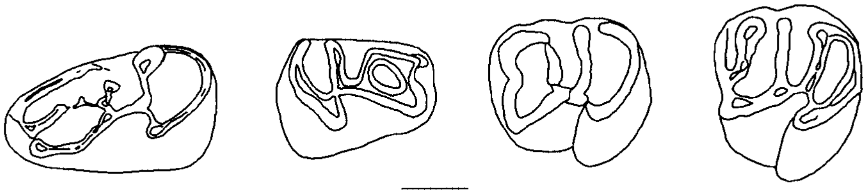

Fig. 2. *Theridomys* sp. nov. from Fuenferrada 3B. From left to right: D_4 sin., FF69; P_4 dext., RGM 417 820; M_2 sin., FF3B 75; M^2 dext., FF3B 90. Scale = 1 mm.

Table 1. Measurements of *Theridomys* sp. nov. (FF3B), *T. golpei* (Sant Cugat), and *T. calafensis* (Calaf 20).

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
D_4												
FF3B	4	30.4	32.10	34.4	12.35	1.677	6	17.8	18.18	18.7	4.93	0.293
S. Cugat	5	28.4	29.68	30.9	8.43	1.011	5	19.2	20.14	21.5	11.30	0.856
Calaf 20	0	—	—	—	—	—	1	19.2	19.20	19.2	—	—
P_4												
FF3B	3	33.4	35.10	36.8	9.69	1.700	5	21.0	24.20	26.1	21.66	1.996
S. Cugat	11	27.0	28.30	29.6	9.19	0.833	11	22.8	25.04	27.0	16.87	1.304
Calaf 20	2	33.4	33.45	33.5	0.30	0.070	3	22.3	24.50	26.0	15.32	1.947
$M_{1,2}$												
FF3B	11	22.7	25.43	29.3	25.38	1.715	13	22.0	24.11	26.0	16.67	1.163
S. Cugat	9	23.3	24.89	25.8	10.18	0.736	9	23.1	25.06	26.7	14.46	1.138
Calaf 20	8	22.4	24.80	26.3	16.02	1.343	8	22.1	24.58	27.7	22.49	1.905
M_3												
FF3B	6	23.2	25.15	27.0	15.14	1.490	6	19.6	22.05	23.2	16.82	1.311
S. Cugat	10	25.5	26.54	28.4	10.76	0.878	10	22.1	24.70	27.8	22.85	1.470
Calaf 20	2	22.0	24.85	27.7	22.94	4.031	2	24.1	24.25	24.4	1.24	0.212
D^4												
FF3B	3	25.6	26.57	27.5	7.16	0.950	3	21.7	22.97	25.1	14.53	1.858
S. Cugat	14	24.3	26.16	28.3	15.21	1.079	16	22.4	24.16	25.6	13.33	0.867
P^4												
FF3B	1	27.3	27.30	27.3	—	—	2	33.6	34.45	35.3	4.93	1.202
S. Cugat	13	22.1	24.20	25.3	13.50	0.997	13	24.6	28.82	31.3	23.97	1.829
Calaf 20	3	21.5	24.27	27.7	25.20	3.153	3	22.5	25.27	27.1	18.55	2.438
$M^{1,2}$												
FF3B	12	20.2	23.08	24.2	18.02	1.219	13	24.6	29.20	33.2	29.76	2.878
S. Cugat	30	21.9	23.03	25.1	13.62	0.735	29	26.0	29.23	33.9	26.38	1.779
Calaf 20	2	23.2	23.95	24.7	6.26	1.061	2	28.9	32.20	35.5	20.50	4.667
M^3												
FF3B	12	20.1	21.68	23.5	15.60	1.143	12	21.3	24.70	28.6	29.26	2.002
S. Cugat	12	22.3	23.83	26.1	15.70	1.015	11	27.6	29.21	31.9	14.45	1.502
Calaf 20	2	20.8	21.65	22.5	7.85	1.202	2	24.2	24.45	24.7	2.04	0.353

Description

D_4 — The anterior wall consists of two cusps, separated by a groove. One of these cusps bears a longitudinal crest, that may curve towards the lingual border, forming a closed synclinid I; in one specimen there is no crest inside the anterior valley. There is a continuous crest from mesolophid to anteroconid, without a trace of a protoconid, a constriction, or an interruption. This feature has been observed in eight specimens;

in two, very much worn, specimens (one from FF3B and one from FF2B) there is a slight indication of a protoconid. The mesolophid is complete, or somewhat interrupted near the lingual wall. It sends a spur forward.

P_4 — Very large, even larger than D_4. The metaconid forms a bulge on the antero-lingual corner of the tooth. The synclinid II is lingually closed, synclinid III is lingually open, synclinid IV is open or closed.

$M_{1,2,3}$ — There is no trace of an anteroconid or anterosinusid. There may be a posterior bulge or spur on the middle of the metalophid, but there is no closed synclinid I. The mesolophid may be low near the metaconid; synclinid II is closed, synclinid III is open; synclinid IV is in this respect intermediate between II and III, since the posterolophid meets the entoconid at mid-height in a number of cases.

D^4 — The dental pattern is fairly simple. Anteroloph, protoloph, mesoloph, metaloph, and posteroloph are easily recognized, and present no complications. In syncline I there is an oblique crest, that connects the middle of the protoloph with a cusp on the antero-labial border of the tooth.

P^4 — Very large teeth. Syncline I not fully closed. Paracone high and voluminous; mesoloph somewhat lower than the other crests.

$M^{1,2}$ — Considerably smaller than P^4. The dental pattern is very simple, without any longitudinal spurs. Syncline I and syncline III are equally long, or syncline I is longer. Syncline II is shorter than the other two. These three valleys are labially closed or slightly open. Syncline IV is small, and tends to disappear through the reduction of the posteroloph.

M^3 — Like $M^{1,2}$ but more rounded, and with a reduced posterior part. In a few specimens the sinus tends to get in contact with syncline I. In most specimens the posterior wall is concave, and there is no syncline IV, due to the reduction of the posteroloph. The mesoloph may be interrupted.

Discussion — This very large *Theridomys* is comparable in size to *T. golpei* Hartenberger, 1973, *T. calafensis* Vianey-Liaud & Hartenberger, 1987, and *T. major* Depéret, 1906, which are the largest species known within the genus. It is characterized by a very simple dental pattern, without any small extra crests, without anteroconid, and without synclinid I in the lower molars. The D_4 is very long, with a continuous crest between mesolophid and anteroconid, in which there is no protoconid cusp, nor an interruption. The anterior synclinid is either empty, or it bears one longitudinal crest.

The specimens are essentially of the same size as our material of *T. major* from Montalbán 1D, but the latter is characterized by the 100% presence of synclinid I in the lower molars. In FF3B there is no synclinid I, so the material cannot belong to *T. major*.

The measurements of *T. golpei* from Sant Cugat published by Vianey-Liaud (in Anadón et al., 1987) and by Vianey-Liaud & Ringeade (1993) show some discrepancies; therefore I measured all the material available in the collections of the Museum of Sabadell, and compared the results with the measurements of the material from FF3B. I also measured the material of *T. calafensis*. The molars of these three species are of the same size (the apparently deviant values for some elements of *T. calafensis* cannot be considered significant, because the material is very poor). The D_4 and P_4 from FF3B are significantly larger; the P_4 of *T. calafensis* is apparently larger than the P_4 of *T. golpei*.

T. golpei differs from the new species from FF3B by its considerably smaller D_4 and P_4. Furthermore the lower molars of *T. golpei* have a small, but distinct, anteroconid, which is absent in FF3B. The D_4 of *T. golpei* are characterized (five out of six specimens) by a strong stylid between protoconid and hypoconid. The crests of the lower molars of *T. golpei* are often irregular with small constrictions.

T. calafensis, according to the original description, is morphologically more evolved than *T. aquatilis,* but generally without synclinid I, and considerably larger, even somewhat larger than *T. major.* Several lower molars of *T. calafensis* show small longitudinal spurs, that are absent in our material from FF3B; the D_4 of *T. calafensis* (Anadón et al., 1987, fig. 4e, plus three fragments in the collection of Sabadell) has a different structure: the crest from mesolophid to anteroconid is interrupted, and there may be a protoconid cusp.

So, our material is different from all species of comparable size, and should be considered as representing a new species.

Vianey-Liaud & Hartenberger (in Anadón et al., 1987) suggest the lineage *T. aquatilis* — *T. calafensis* — *T. major,* or the alternative *T. golpei* — *T. calafensis* — *T. major.*

First of all, it seems worth while to note that *T. major* from Montalbán 1D shows a certain degree of enamel differentiation, comparable to, or even somewhat stronger than, the enamel differentiation in *Blainvillimys langei.* This feature is considered to be diagnostic for *Blainvillimys,* so either the value of this distinctive character should be reconsidered, or the generic attribution of *T. major* should be revised.

Secondly, we did not see the type material of *T. major* from Tárrega, and we cannot confirm whether it represents the same species as the one from Montalbán. If, as implied by Vianey-Liaud, 1972, the synclinid I is sometimes absent in the Tárrega material, there may be reason to revive the name *T. crusafonti* Thaler, 1970 for the population from Montalbán.

Some specimens from FF3B show a slight degree of enamel differentiation, which would imply incorporation in *Blainvillimys.* As said before, the diagnostic value of this feature is questionable: I observed it in *T. major* from Montalbán 1D, in *T. golpei* from San Cugat, and in *T. calafensis* from Calaf 20. It seems probable, that all lineages of *Theridomys* acquire — sooner or later — a certain degree of enamel differentiation, and that this feature cannot be used to distinguish genera. I therefore use the name *Theridomys* in a broad sense.

Hardly anything can be said about the phylogenetic relationships of this new species. Knowledge of *Theridomys* species from around the 'Grande Coupure' is rather scarce, and drawing phylogenetic lines seems to be premature. It might be the ancestor of *T. calafensis* (if the latter is not an immigrant), but that is just a mere guess, that cannot be substantiated. Anyway, the validity of the supposed lineage *T. aquatilis* — *T. calafensis* — *T. major* will have to be reconsidered.

Discussion of the D_4 of *Theridomys-Blainvillimys*

Comparison of our FF3B material with the three large *Theridomys* species mentioned before led to the observation that the D_4 in FF3B is quite different. I then compared the figured D_4 in the literature, and the material available in our collections, and came to the conclusion, that two different morphologies are found in the D_4 of *Theridomys-Blainvillimys*:

1. There is no protoconid, but an uninterrupted, longitudinal crest from mesolophid to anteroconid.
2. The crest between mesolophid and anteroconid is interrupted, and/or there is a protoconid cusp.

Table 2. *Theridomys* populations with a continuous crest between mesolophid and anteroconid of D_4.

Species	Locality	Publication
T. brachydens	Monac	Vianey-Liaud & Ringeade (1993) fig. 9a,i,j
B. civracensis	Ste Néboule	Vianey-Liaud & Ringeade (1993) fig. 20c-e
B. civracensis	Lascours	Vianey-Liaud & Ringeade (1993) fig. 21a-b
T. euzetensis	Fons 4	Hartenberger & Louis (1976) Pl.1, fig. 10
T. golpei	San Cugat	Hartenberger (1973) fig. 9b,c
T. golpei	Ste Croix	Vianey-Liaud & Ringeade (1993) fig. 11a
T. golpei	Lascours	Vianey-Liaud & Ringeade (1993) fig. 13a,b
T. aff. *golpei*	Gousnat	Vianey-Liaud & Ringeade (1993) fig. 16a,b
B. gousnatensis	Gousnat	Vianey-Liaud & Ringeade (1993) fig. 23a-b
T. perrealensis	La Débruge	Vianey-Liaud (1979) fig. 11c
T. pseudosiderolithicus	La Débruge	Vianey-Liaud (1979) fig. 11h
B. rotundidens	Baby 2	Vianey-Liaud & Ringeade (1993) fig. 27g-i
B. rotundidens	Ste Néboule	Hartenberger & Vianey-Liaud (1978) fig. 2c
T. sp.	AGT2D	unpublished material
T. sp.	Escamps	Vianey-Liaud (1974) fig. 11c
T. varleti	Fons 4	Hartenberger & Louis (1976) Pl.1, fig. 5

Table 3. *Theridomys* populations with a more or less interruped crest between mesolophid and anteroconid of D_4.

Species	Locality	Publication
T. aquatilis	Ronzon	Vianey-Liaud (1972) fig. 1g
T. bonduelli	Noisy-le-Sec	Vianey-Liaud (1972) fig. 1i
T. calafensis	Calaf	Anadón et al. (1987) fig. 4e
B. gemellus	La Plante 2	Vianey-Liaud (1989) fig. 10g-j
B. gregarius	MLB1D	unpublished RGM material
T. gregarius	Mas de Got	Vianey-Liaud (1969) fig. 4,3-5
T. gregarius	Mas de Got	Vianey-Liaud (1972) fig. 1c
T. gregarius	Lovagny	Vianey-Liaud (1972) fig. 20j,k
B. gregarius	La Plante 2	Vianey-Liaud (1989) fig. 10a-f
B. heimersheimensis	Heimersheim	Vianey-Liaud (1989) fig. 10k-l
B. helmeri	Les Chapelins	Vianey-Liaud (1972) fig. 1e
B. langei	Aubrelong	Vianey-Liaud (1972) fig. 1a, 13l,m
B. langei	OLA4A	unpublished RGM material
T. ludensis	Rigal-Jouet	Vianey-Liaud (1985) fig. 4c
T. major	MLB1D	unpublished RGM material
T. margaritae	Hoogbutsel	unpublished RGM material
T. margaritae	La Plante 2	Vianey-Liaud, 1989, fig. 4c

All published cases, and some unpublished material are listed in Tables 2 and 3.

A D_4 from Escamps, attributed to *B. rotundidens* by Vianey-Liaud (1974), was transferred to *Patriotheridomys* by Vianey-Liaud & Ringeade (1993), because the connection between mesolophid and anteroconid is interrupted.

Two D_4 from Escamps IV (Utrecht collections), attributed to *Patriotheridomys* by Vianey-Liaud (1974), were transferred to *Theridomys* by Vianey-Liaud & Ringeade (1993), because they present the same continuous crest.

The D_4 of *B. civracensis* from Civrac, figured by Vianey-Liaud & Ringeade (1993, fig. 18a) has a protoconid, and the crest in front of it is constricted; it may well belong to *Patriotheridomys*.

Both morphologies appear to be found in *T. rotundidens* from Baby 2 (MP20). Maybe some specimen (Vianey-Liaud & Ringeade, 1993, fig. 27j) belongs to *Patriotheridomys*, which is present in that locality.

A D_4 from the Hamstead Beds, attributed to *Isoptychus pseudosiderolithicus* by Bosma (1974) has a protoconid and an interrupted crest. This locality is post-'Grande Coupure', and the specific determination may be incorrect.

The group with continuous crest contains all the species older than the 'Grande Coupure', the second group contains the younger ones. A close examination of the variability of this feature is imperative, but, if the distinction materializes, one should envisage the possibility, that none of the younger species is derived from any of the known older ones. The simultaneous appearance of the same character in various lineages is far from probable. The post-'Grande Coupure' species may be immigrants, or there may be a relationship with the genus *Patriotheridomys*, which presents a similar D_4.

Comparison with *T. pseudosiderolithicus* from Aguatón 2D

Adrover et al. (1983) described a small collection of teeth from the locality 'Route de Aguatón'. We took nine samples at the same spot, and then concentrated on the level 2D, which turned out to be richest.

Among the species found in this locality there is a *Theridomys*, which is similar in size to the material from FF3B. Adrover et al. (1983) call it *T. golpei*. The latter species, however, is characterized by the presence of an anteroconid in the lower molars, which is absent in the material from AGT2D. The *Theridomys* from Aguatón 2D may well be *T. pseudosiderolithicus* de Bonis, 1964 (type-locality La Débruge).

T. calafensis Vianey-Liaud & Hartenberger, 1987 (in Anadón et al., 1987) is of the same size, but its D_4 has the morphology 2 (see above), with well-developed protoconid, whereas in AGT2D there is no protoconid.

It can neither be *T. perrealensis*, nor *T. golpei*, that have an anteroconid. In AGT2D the anteroconid is hardly indicated. The relative lengths of D_4, P_4, and $M_{1,2}$ are comparable to those of *T. pseudosiderolithicus*, their absolute size may be somewhat larger. D_4 and P_4 are relatively shorter than in FF3B. The $M_{1,2,3}$ are roughly of the same size in these two populations.

Small longitudinal spurs are frequent in the lower molars and present, though less frequent, in the upper molars. A comparable spur is seen in *T. pseudosiderolithicus* from La Débruge (Vianey-Liaud, 1979, fig. 11h). Such structures are absent in the material from FF3B, present in the material from La Débruge.

The little crest in the last synclinid of the D_4 of *T. pseudosiderolithicus*, mentioned by Vianey-Liaud (1979, p. 149), is present on all 3 specimens from AGT2D, and absent in FF3B.

Several specimens from AGT2D show a slight degree of enamel differentiation, like in FF3B. On the basis of this feature Vianey-Liaud & Ringeade (1993) place the species *pseudosiderolithicus* in *Blainvillimys*.

The locality of Aguatón 2D is supposed to be older than FF3B, but the *Theridomys* material gives no clue to reject or confirm this supposition.

Genus *Pseudoltinomys* Lavocat, 1951

Pseudoltinomys aff. *cuvieri* (Pomel, 1853)

The two species of Theridomyidae, found in the locality Fuenferrada 3B, are easily distinguished on the basis of size. *P.* aff. *cuvieri* is the smaller one of the two.

Anterosinusid and anteroconid are well developed. The entoloph presents a generally deep notch between protocone and mesoloph. The ectolophid may present a shallow notch between mesolophid and hypolophid, and a similar notch between hypolophid and hypoconid. The $M_{1,2}$ have two roots, the number of roots of M_3 is 2 or 3. The height measured in four unworn specimens of $M_{1,2}$ varies between 15.5 and 17.4, with a mean value of 16.8. The mesolophid of $M_{1,2}$ is high and firmly connected to the metaconid; in two specimens it is interrupted mid-way.

Measurements of the material from FF3B

	Length				Width			
	n	min.	mean	max.	n	min.	mean	max.
D_4	1	20.5	20.50	20.5	1	12.5	12.50	12.5
P_4	1	17.8	17.80	17.8	2	14.2	14.95	15.7
$M_{1,2}$	16	17.7	19.77	22.1	15	15.9	17.49	19.7
M_3	5	19.7	21.36	22.4	6	16.4	17.38	18.2
D^4	2	15.5	15.60	15.7	4	14.7	15.83	17.4
P^4	3	14.4	15.90	16.8	3	15.9	17.67	18.6
$M^{1,2}$	13	14.8	16.91	19.3	10	19.1	20.87	22.0
M^3	2	17.8	18.25	18.7	2	20.0	20.10	20.2

Description

D_4 — Apart from one complete specimen, there are several incomplete ones, and one complete specimen from FF2B. The anterior wall consists of two cusps, separated by a groove. There is a longitudinal crest in the anterior valley. The mesolophid is complete or interrupted. There is an extra crest, descending from the postero-lingual corner of the tooth into the posterior valley.

P_4 — There is a longitudinal crest in the anterior valley, or a bulge on the anterior wall of that valley. The mesolophid is complete or interrupted. The posterolophid is connected to the entoconid, either low or high.

$M_{1,2,3}$ — There is a well-developed anterosinusid. The mesolophid is slightly lower than the other crests. There is a shallow notch in the ectolophid of unworn specimens. In some specimens the posterolophid bears an anterior spur. M_3 has two or three roots.

Upper dentition — The notch in the entoloph is moderately to well developed, and may even be visible in very worn specimens. The mesoloph is lower than the other crests, interrupted in several specimens.

Discussion — Vianey-Liaud & Ringeade (1993) propose the evolutionary line *P. cuvieri* (Pomel, 1852) — *P. gaillardi* Lavocat, 1951 — *P. major* Vianey-Liaud, 1976, characterized by a very slight size increase, a moderate increase in hypsodonty, a progressive reduction of the anterosinusid, a progressive development of the mesoloph(id), and a progressive reduction of the entoloph and the ectolophid, so that the sinus(id) becomes ever more confluent with the opposite valley.

P. cuvieri is based on a single mandible from Montmartre, *P. gaillardi* on a small collection from Ronzon. Vianey-Liaud (1974) gives the measurements of the type specimen of *P. cuvieri* and some specimens from Ronzon. These data can only lead to the conclusion that this scarce material does not permit the distinction of two species. But, the same author publishes three fairly well documented populations, that are attributed to *P. cuvieri* (Escamps) and *P. gaillardi* (Aubrelong 1 and Ravet). Analysis of the measurement tables shows, that there is no difference between the populations from Escamps and Aubrelong (in some categories the Escamps- specimens are even larger), and this same result was obtained by Vianey-Liaud through a t-test (op. cit., p. 224). The same test gave a significant difference for the length of $M_{1,2}$ between the populations of Escamps and Ravet. However, applying this test on the data for *P. gaillardi* from Ravet and the population of *P. major* from La Plante 2, one finds that these two populations are not significantly different.

Furthermore, considering the difficulty to obtain reliable measurements for this kind of hypsodont specimens, the accidental distribution of worn and unworn specimens in each sample, the bias introduced by grouping the specimens in age classes (see Schmidt-Kittler, 1984, p. 466), and the danger of chronologically mixed faunas in fissure fillings, one should not lay too much value on these biometrical results. The mentioned material permits the distinction of two species at the most. *P. cuvieri* and *P. major* may be distinguished without too much difficulty, and a detailed analysis should make it clear whether *P. gaillardi* is a junior synonym of *P. cuvieri* or a senior synonym of *P. major*.

Comparison of *P.* aff. *cuvieri* from FF3B with *P. cuvieri* from Escamps

Vianey-Liaud gives a range of 15.9-20.6, and a mean value of 18.1 for the height of unworn and slightly worn $M_{1,2}$ of *P. cuvieri* from Escamps.

The height of our material from FF3B varies between 14.8 and 17.4, with a mean of 16.5. It seems to be less hypsodont than the material from Escamps.

Table 4. Measurements of *P. gaillardi* from OLA4A.

	Length						Width					
	n	min.	mean	max.	V'	s	n	min.	mean	max.	V'	s
D_4	3	20.1	20.50	20.8	3.42	0.361	5	12.6	12.92	13.3	5.41	0.278
P_4	16	20.0	20.96	22.3	10.87	0.705	16	13.7	15.41	17.4	23.79	0.926
$M_{1,2}$	58	18.6	20.43	22.8	20.29	0.920	58	16.7	18.70	20.7	21.39	1.080
M_3	22	19.7	22.76	25.7	26.43	1.406	24	15.8	18.31	20.5	25.90	1.223
D^4	3	16.7	17.57	18.3	9.14	0.808	2	16.1	16.85	17.6	8.90	1.061
P^4	10	16.8	18.37	20.4	19.35	1.052	9	18.3	19.51	21.6	16.54	1.052
$M^{1,2}$	43	15.9	18.45	20.1	23.33	0.988	44	17.7	20.83	24.9	33.80	1.471
M^3	29	15.0	18.23	20.7	31.93	1.447	31	17.8	20.29	23.3	26.76	1.389

The height could be measured in nine unworn specimens of $M_{1,2}$, and varies between 16.3 and 20.0, with a mean value of 17.7.

Comparison of *P.* aff. *cuvieri* from FF3B with *P. gaillardi* from Olalla 4A

In the sample from FF3B there are two species of Theridomyidae, that are very different in size; the small specimens are all attributed to *Pseudoltinomys* without any reasonable doubt.

We have quite an important collection of *Pseudoltinomys* material from OLA4A, but a statistical evaluation of its characters is bound to be biased by the previous decision on what specimens are included in it (see the chapter 'Remarks on the Theridomyidae from Olalla 4A').

The dental elements, especially D4 and P4, of *P. gaillardi* from OLA4A are on the average somewhat larger than those of *P.* aff. *cuvieri* from FF3B, but this difference cannot be considered fully convincing, due to the difficulty of measuring. They do seem to be more hypsodont, though only few data are available.

In Olalla 4A the anterosinusid and anteroconid of $M_{1,2}$ may have the same degree of development as in FF3B, but there also are specimens in which these structures are more reduced than in any of the FF3B specimens. On the other hand, the anteroconid may be clearly visible in specimens that are almost worn down to the roots. It is quite possible that the same range of variability exists in FF3B, but the material is much poorer than in OLA4A.

In OLA4A the mesolophid of $M_{1,2}$ is frequently low or interrupted near the metaconid. In spite of the scarcity of the material from FF3B one gets the impression, that the mesolophid is better developed in the latter locality. On the other hand, the mesolophid of D_4, and the mesoloph of the upper molars is low or interrupted in several cases, whereas it is nearly always high and complete in OLA4A.

The notch in the entoloph is deep in OLA4A. Unfortunately there are not sufficient unworn specimens in the FF3B sample that would permit an evaluation of this feature. Three specimens from FF2B (equivalent to FF3B) show a notch that is comparable in depth to the one in the OLA4A material.

The $M_{1,2}$ in OLA4A have two roots, as in FF3B; the M_3 in OLA4A has three roots, in FF3B the roots of M_3 are broken; besides specimens with three roots, there seems to be at least one specimen with only two roots.

So, there are size differences between the FF3B and the OLA4A samples; morphologically they are identical, except for the development of the mesolophid / mesoloph. OLA4A is younger than FF3B as demonstrated by Freudenthal (1996). The size and hypsodonty of the *Pseudoltinomys* material support this interpretation, but the degree of development of the mesolophid seems to indicate the opposite. For the moment this is interpreted as accidental, since the mesoloph is less developed in FF3B than in OLA4A.

Comparison of *P.* aff. *cuvieri* from FF3B with *P. major* from Montalbán

In MLB1D (the classic level of Montalbán) *Pseudoltinomys* is rare, but from the slightly lower level of MLB3C a rich collection is available. The height of unworn $M_{1,2}$ varies between 18.0 and 22.0. The length of $M_{1,2}$ varies between 20.4 and 23.6, clearly larger than in OLA4A. The entoloph shows a clear incision, and — to a lesser extent — the ectolophid too. The anterosinusid and anteroconid are fairly well developed, though less than in OLA4A. The notch in the ectolophid is deeper than in OLA4A.

In various younger levels of Montalbán the few specimens of *Pseudoltinomys* that are available appear to present the same morphology as in MLB3C, they are of the same size, and the maximum height found for $M_{1,2}$ is 22.8.

With some doubt, the MLB3C population may be attributed to *P. major*. The populations from the younger levels of Montalbán are not sufficiently known, but they may be attributed to *P. major* as well.

On the whole, hypsodonty of the Spanish specimens seems to be less than that of the French ones; this may lead to the hypothesis that we are dealing with separately evolved lineages (Freudenthal, 1996). A difference between these lineages may be the number of roots in M_3: in *P. cuvieri* from Escamps only 3 out of 20 M_3 have three roots, whereas in *P. gaillardi* from OLA4A the M_3 has nearly always three roots. In one $M^{1,2}$ from FF2B there is a tiny extra ridge between mesoloph and protoloph, like in *P. gliriformis* De Bruijn et al., 1979. This feature is also found in some specimens from OLA4A and MLB3C. It has not been mentioned for any of the French *Pseudoltinomys* populations. It may serve to find out whether or not French and Spanish populations represent separate evolutionary lineages.

Family Gliridae Muirhead, 1819
Genus *Glamys* Vianey-Liaud, 1989

Glamys olallensis Freudenthal, 1996
Pl. 1, figs. 8-16.

Type-locality — Olalla 4A (Teruel, Spain).

Measurements of the material from FF3B

	Length						Width					
	n	min.	mean	max.	V'	s	n	min.	mean	max.	V'	s
D_4	1	7.2	7.20	7.2	—	—	1	6.8	6.80	6.8	—	—
P_4	2	6.2	6.45	6.7	7.75	0.354	2	5.7	5.95	6.2	8.40	0.354
M_1	7	7.6	8.00	8.4	10.00	0.252	7	6.7	8.06	8.9	28.21	0.804
M_2	8	7.3	7.80	8.4	14.01	0.385	9	7.7	8.34	9.0	15.57	0.445
M_3	4	6.8	7.50	8.0	16.22	0.529	4	7.1	7.45	7.7	8.11	0.265
D^4	2	6.7	6.85	7.0	4.38	0.212	2	7.4	7.50	7.6	2.67	0.141
P^4	6	6.0	6.45	7.2	18.18	0.446	6	7.9	8.30	9.2	15.20	0.518
M^1	7	6.7	7.30	7.8	15.17	0.392	7	8.9	9.24	9.8	9.63	0.331
M^2	12	6.8	7.33	7.9	14.97	0.410	10	8.3	9.19	10.4	22.46	0.567
M^3	2	6.1	6.20	6.3	3.23	0.141	2	7.5	7.60	7.7	2.63	0.141

Description

P_4 — The four main cusps are well developed. The anterolophid is interrupted. There are no extra crests. The metalophid is connected high to the metaconid. The centrolophid is absent. The mesoconid lies on the labial border. In one specimen the mesolophid is absent, and there is a longitudinal crest from the metalophid towards the posterolophid. In the other one the mesolophid is well developed, pointing obliquely backwards, longer than half the width of the tooth.

M_1 — The anterolophid is not connected to the protoconid. There are no extra crests. The metalophid is connected to the base of the metaconid (6), or high to the metaconid (1). The centrolophid is absent (8). The mesoconid lies on the labial border (4), or more centrally (3). The mesolophid is of medium length, forming some small crests at its end in one case.

M_2 — The anterolophid is not connected to the protoconid.

There is no extra crest in the anterior valley. The metalophid is free (4), or connected to the base of the metaconid (4). The centrolophid is absent. The mesoconid lies on the labial border (5) or more centrally (4). The mesolophid is short (1), of medium length (5), or longer and directed towards the metaconid (1) or towards the entoconid (2). An extra crest in the posterior valley is absent (8), or present as a clear cusp (1).

M_3 — The anterolophid is not connected to the protoconid. There are no extra crests. The metalophid is free, or connected to the base of the metaconid. The centrolophid is absent. The mesostylid is absent. The mesoconid lies on the labial border or more centrally. The mesolophid is long, directed towards the entoconid.

D^4 — Triangular teeth with a long anterior centroloph, and a shorter posterior one. The anteroloph is long and low, the posteroloph is connected to the protocone.

P^4 — The anteroloph is long, not connected to the protocone. There are no extra crests. The protoloph is interrupted in one case. The anterior centroloph is long, connected to the paracone. In two cases the metaloph is connected to the paracone, and the centroloph is isolated in the central valley. The posterior centroloph is absent. The posteroloph is connected to the protocone, or separated.

M^1 — The anteroloph is lingually free. There are no extra crests. The anterior centroloph is long, and connected to the paracone (5), or placed centrally (3); in one of the latter cases it forms a mesostyl. The posterior centroloph is absent. The posteroloph is connected to the protocone or isolated lingually.

M^2 — The anteroloph is lingually free. There are no extra crests. The anterior centroloph is long, and connected to the paracone (9), or placed centrally (3). The posterior centroloph is absent. The posteroloph is connected to the protocone or lingually free.

M^3 — The anteroloph is lingually free. Anteroloph, protoloph, and posteroloph are high. The metaloph is much lower. There is one centrally placed centroloph, that is more or less connected to the metaloph. The posteroloph is slightly separated from the protocone.

Discussion — This small collection is identical to the material from Olalla 4A, both in size and morphology. It is distinguished from *G. priscus* (Stehlin & Schaub, 1951) by its smaller dimensions.

Bosma & de Bruijn (1979) describe *G. priscus* from the Isle of Wight. That occurrence is, biostratigraphically, in accordance with the presence of *G. priscus* in the fauna of Aguatón 2D. The occurrences of *G. olallensis* are younger than those of *G. priscus*. Whether or not this means that the larger *G. priscus* is the ancestor of the smaller *G. olallensis*, cannot be confirmed.

Genus *Gliravus* Stehlin & Schaub, 1951

Gliravus aff. *fordi* Bosma & de Bruijn, 1979
Pl. 1, figs. 1-7.

Measurements of the material from FF3B

	Length						Width					
	n	min.	mean	max.	V'	s	n	min.	mean	max.	V'	s
D_4	1	8.7	8.70	8.7	—	—	1	7.5	7.50	7.5	—	—
P_4	1	10.0	10.00	10.0	—	—	1	8.8	8.80	8.8	—	—
M_2	4	10.0	11.00	11.8	16.51	0.812	3	10.4	11.23	11.7	11.76	0.723
M_3	2	10.1	10.45	10.8	6.70	0.495	2	10.2	10.30	10.4	1.94	0.141
P^4	3	9.3	9.70	9.9	6.25	0.346	3	11.4	11.87	12.2	6.78	0.416
M^1	2	10.7	10.75	10.8	0.93	0.071	2	12.2	12.55	12.9	5.58	0.495
M^2	3	10.5	10.67	10.9	3.74	0.208	3	12.6	13.03	13.7	8.37	0.586
M^3	3	8.8	8.97	9.3	5.52	0.289	2	11.2	11.30	11.4	1.77	0.142

Description

D_4 — Protoconid and metaconid are connected along the anterior border. The metalophid is connected to the metaconid at a low level. There is neither a mesoconid, nor a mesolophid, but there are three irregular crests in the central valley. The entoconid and hypoconid are well developed.

P_4 — The protoconid occupies 1/3 of the anterior border and the metaconid the other 2/3. The cusps are in contact without a connecting crest. The metalophid surrounds the metaconid, and is connected to its postero- lingual wall. There is an extra cusp on the labial border, between protoconid and mesoconid. Entoconid and hypoconid are well developed. There are three thick, longitudinal crests in the central valley.

M_2 — The anterolophid is connected to the protoconid (1), or not connected (1). The metaconid occupies about 1/3 of the anterior border of the tooth. The anterior extra crest is formed by several cusps. The metalophid is connected to the metaconid, either low or high. There is no centrolophid. The mesolophid forms the basis of a number of tangled crests in the central valley. The main branch of the mesolophid is curved backwards in three of the four specimens.

M_3 — The anterolophid is not connected to the protoconid. The metaconid occupies less of the anterior border of the tooth than in M_2, and the anterolophid is longer. The anterior extra crest is formed by two separate parts. The metalophid is not connected to the metaconid, or connected to it. There is a long centrolophid. The posterior cingulum of the metaconid is very long. The mesolophid is ramified, the posterior extra crest is well developed. Either the mesolophid, or the posterior extra crest is connected to a cusp on the postero-lingual border, between entoconid and posterolophid.

D^4 — See description of D^4 of *Bransatoglis parvus*.

P^4 — The anteroloph is of medium length or long. There are two centrolophs and an extra crest descending from the paracone, between protoloph and centroloph. The centrolophs may be broken up in two or more parts. The posteroloph is connected to the protocone or separated from it. In some specimens there is a longitudinal connection between anteroloph and protoloph.

M^1 — The anteroloph is isolated from the protocone. In one specimen the protoloph is interrupted near the paracone. There are basically two centrolophs and one or two extra crests inside the trigone. These three or four crests are broken up and interconnected, which makes their interpretation difficult. The posteroloph is free from the metacone, and not fully connected to the protocone.

M^2 — The anteroloph is isolated from the protocone. The protoloph is interrupted near the paracone. There are basically three crests inside the trigone, broken up and interconnected like in M^1 in one specimen, more continuous and regular in the other ones. In two specimens the posterior centroloph bears a mesostyl, that is more or less separated from the metacone. The posteroloph is free from metacone and protocone.

M^3 — The anteroloph is connected to the protocone. There are at least three crests inside the trigone, that form an intricate pattern, and fill the valley completely. The posteroloph is connected to the protocone or incompletely connected.

Discussion — Bosma & de Bruijn (1979) describe two new species of *Gliravus* from the Isle of Wight (UK), *G. devoogdi* from the Bembridge Beds, and *G. fordi* from the Hamstead Beds. *G. devoogdi* is smaller, and morphologically more simple; it is thought to be the ancestor of *G. fordi*. Whether or not this group is derived from *G. priscus* is open to doubt. The transition of *G. devoogdi* to *G. fordi* coincides more or less with the 'Grande Coupure'.

Vianey-Liaud (1994) recognizes *G. devoogdi* in Hoogbutsel (Belgium), and gives several possible interpretations of the evolution of this group.

Our specimens from FF3B are larger than *G. devoogdi*, and more complicated; they seem to be slightly smaller and somewhat less complicated than *G. fordi*. Especially in the lower molars the webbed pattern of little cusps and crests around the mesolophid is less developed than in *G. fordi* from the Isle of Wight.

The FF3B material confirms hypothesis number 2 or 3 of Vianey-Liaud (1994, fig. 26, p. 152), as it means that *G. devoogdi* exists (in Belgium) after the 'Grande Coupure', while *G. fordi* appears (in Spain) before the 'Grande Coupure'. On pure morphological grounds one might draw the evolutionary lineage *G. devoogdi* — *G.* aff. *fordi* — *G. fordi*, but that would be a hazardous simplification, in view of the geographical distance between the English and Spanish localities.

In Spain *G. fordi* has been reported from the Lower Oligocene of Calaf 6 and 7 (Anadón et al., 1987). Its oldest occurrence so far is probably a yet unpublished locality in the Sierra Palomera, that is slightly older than FF3B.

Genus *Bransatoglis* Hugueney, 1967

Bransatoglis parvus Freudenthal, 1996
Pl. 2, figs. 1-10.

Type-locality — Olalla 4A (Teruel, Spain).

Measurements of the material from FF3B

	Length						Width					
	n	min.	mean	max.	V'	s	n	min.	mean	max.	V'	s
D_4	1	7.9	7.90	7.9	—	—	1	6.4	6.40	6.4	—	—
P_4	5	8.2	8.92	10.2	21.74	0.760	4	7.2	7.78	8.8	20.00	0.704
M_1	3	10.4	10.93	11.6	10.91	0.611	4	10.1	10.75	11.6	13.82	0.656
M_2	5	10.2	10.72	11.3	10.23	0.507	5	9.9	10.94	12.4	22.42	0.940
M_3	5	9.7	10.22	10.6	8.87	0.432	5	9.7	10.12	10.6	8.87	0.370
D^4	1	9.0	9.00	9.0	—	—	1	10.1	10.10	10.1	—	—
P^4	8	7.0	7.64	8.0	13.33	0.325	9	8.6	9.54	10.8	22.68	0.800
M^1	8	9.1	10.30	10.9	18.00	0.548	8	10.7	11.34	11.8	9.78	0.334
M^2	4	9.9	10.10	10.2	2.99	0.141	1	12.5	12.50	12.5	—	—
M^3	3	9.1	9.37	9.9	8.42	0.462	3	10.8	11.23	11.5	6.28	0.379
D_4	4	7.8	8.00	8.2	5.00	0.183	4	6.4	6.68	6.9	7.52	0.206
P_4	10	7.6	8.68	10.2	29.21	0.681	10	6.6	7.64	8.8	28.57	0.599
M_1	11	10.4	10.83	11.6	10.91	0.385	12	9.7	10.50	11.6	17.84	0.510
M_2	11	10.2	10.92	11.5	11.98	0.449	11	9.9	11.18	12.4	22.42	0.701
M_3	14	9.4	10.36	11.1	16.59	0.561	14	9.1	9.93	10.6	15.23	0.450
D^4	4	7.1	7.92	9.0	23.60	0.854	4	7.4	8.25	10.1	30.86	1.245
P^3	1	6.3	6.30	6.3	—	—	1	6.9	6.90	6.9	—	—
P^4	14	7.0	7.71	8.3	16.99	0.405	15	8.6	9.62	10.8	22.68	0.696
M^1	15	9.1	10.47	11.0	18.91	0.467	15	10.2	11.27	12.0	16.22	0.459
M^2	11	9.9	10.41	11.1	11.43	0.324	8	11.6	12.39	13.0	11.38	0.482
M^3	8	8.6	9.16	10.1	16.04	0.550	8	9.7	10.73	11.5	16.98	0.656

Description

D_4 — Protoconid and metaconid are connected along the anterior border, and through the metalophid; in one case the metalophid is interrupted. The entoconid is a well-developed cusp or a longitudinal crest. There are some cuspules in the central valley, with a tendency to form a longitudinal crest.

P_4 — The anterior accessory crest is absent, the posterior one is present. The anterolophid is connected to protoconid and metaconid (4), or interrupted in front of the protoconid (3). The metalophid is connected to the metaconid, either high (5) or low (2); in two cases it is not connected to the protoconid. The centrolophid is long and connected to the metaconid; labially it is connected to the metalophid, to the mesolophid, or it ends free. The mesolophid is connected to the entoconid, or directed towards that cusp.

M_1 — The anterolophid is not connected to the protoconid. The anterior extra crest is a thick cusp or a thick crest, sometimes vaguely developed. The metalophid is connected to the metaconid (6) or free (6); the centrolophid is long and connected to the metaconid (9), or short and isolated from the metaconid (3); it is never connected to the protoconid or the metalophid. The mesolophid is directed towards the entoconid (3), connected to the entoconid (5), or it ends in front of the entoconid (5). The posterior extra crest is well developed, never connected to hypoconid or entoconid.

M_2 — The anterolophid is not connected to the protoconid. The anterior extra crest is absent (5), small (5), or large (1). The metalophid is connected to the metaconid (9), or it ends at its base (2); the centrolophid is long, connected to the metaconid; it is not connected to the protoconid or to the metalophid at its labial end. The mesolophid is connected to the entoconid (8), directed towards that cusp (3), or directed to the lingual border in front of the entoconid; in one case it is curved forward and connected to the centrolophid. The posterior extra crest is strongly developed, isolated, or labially connected to the posterolophid.

M_3 — The anterolophid is connected to the protoconid (3), or not connected (8). The anterior extra crest is absent (4), small (5), or long (1). The metalophid is connected to the metaconid (7) or not connected (4); the centrolophid is of medium length, generally connected to the metaconid, not connected in two cases. The mesolophid is connected to the entoconid. The posterior extra crest is of medium length or long, isolated, or lingually connected to the posterolophid; in one case it is short, and in one case absent. The posterolophid is separated from the entoconid.

D^4 — The anteroloph is long, and in one specimen it forms, together with the posteroloph, a continuous ridge, that separates the protocone from the lingual border of the tooth. The anterior centroloph is longer and stronger than the posterior one, which may be absent.

The largest specimen (FF3B 40, Pl. 3, fig. 7) is a triangular tooth with anteroloph of medium length, two centrolophs, and a posteroloph that is connected to protocone and metacone. The posterior centroloph is longer than the anterior one. There is a longitudinal connection between the anteroloph and the protoloph; such a connection is present in some P^4 of *G.* aff. *fordi*. That fact, and the size of the tooth, make it possible that it belongs to *G.* aff. *fordi*.

P^3 — One specimen (FF3B 166) has the same morphology as the P^4, but is considerably smaller. It is interpreted as a P^3.

P^4 — Rounded teeth. The anteroloph is of medium length or long. The anterior centroloph is long and connected to the paracone; the posterior one is absent (10), or very vague (3). The posteroloph is connected to protocone and metacone.

M^1 — The anteroloph is isolated from the protocone, or connected to it. There is an anterior extra crest between anteroloph and protoloph in 8 out of 15 specimens; it may be weak or fairly strong, or consisting of a series of small cusps. There are two long centrolophs, that may unite in the center of the tooth; they are connected to the paracone and the metacone respectively. There are no extra crests inside the trigone. The posteroloph is connected to the protocone (10), or not connected (2).

M^2 — The anteroloph is isolated from the protocone, or connected to it. There is a weak extra crest between anteroloph and protoloph in 1 out of 11 specimens (this specimen may be a M^1). There are two long centrolophs connected to paracone and metacone respectively, they may unite in the center of the tooth, and in one specimen there are two connections. In five specimens there is an extra crest inside the trigone, branching off from the anterior centroloph, and forming a complicated pattern with the two centrolophs. The posteroloph is connected to the protocone, or not connected.

M^3 — The anteroloph is connected to the protocone. There is no anterior extra crest between anteroloph and protoloph. There are two centrolophs, that may unite in the center of the tooth, and — in 2 specimens — a strong extra crest between protoloph and anterior centroloph, that may easily be mistaken for a centroloph. The paracone shows a tendency to split off a mesostyl, which bears the anterior centroloph. In two out of seven specimens there is a strong transverse crest between centroloph and protoloph. There is no clear metacone cusp. There may be an extra crest in the posterior valley. The posteroloph is connected to the protocone.

Discussion — In size and morphology this material resembles the type-population of *B. parvus* very much. Maybe the typical *Bransatoglis* pattern of quadrangular lower molars with long, straight, parallel crests is somewhat less pronounced than in the type-population.

Remarks on the Theridomyidae from Olalla 4A

The rich rodent fauna of Olalla 4A has recently been described by Freudenthal (1996). The main subjects of that publication were the Cricetidae and the Gliridae. The Theridomyidae were treated in a more superficial way, since they seemed to bring little news. While comparing the Theridomyidae from FF3B with those of Olalla 4A, I came to the conclusion that the OLA4A fauna is considerably more complex than it seemed to be at first sight, and therefore decided to add a paragraph on the Olalla theridomyids to this paper.

The locality of Olalla 4A has yielded over 3500 theridomyid teeth. Among them there is quite a good collection of *Pseudoltinomys* material, which was attributed to *P. gaillardi* by Freudenthal (1996). It is accompanied by a few specimens of *Elfomys* sp., a few specimens of *Sciuromys cayluxi*, and a huge amount of specimens of *Blainvillimys langei*.

Elfomys sp. is easily distinguished on the basis of size. It is larger than *E. nanus* from Montalbán 1D, and may therefore be attributed to *E. medius* Vianey-Liaud, 1976.

The lower molars of *Sciuromys cayluxi* are easily recognized, the upper molars are not certain.

The vast majority of the theridomyid material from OLA4A is attributed to *Blainvillimys langei,* which overlaps the size range of *Pseudoltinomys gaillardi.*

Distinction of the upper teeth of the latter two species is based on the absence/presence of a notch in the entoloph. Upper teeth cannot be distinguished when they are worn down too far, and this is the reason why there are less $M^{1,2}$ than $M_{1,2}$. Maybe on the average the bottom of the sinus is nearer to the crown basis in *Blainvillimys* than in *Pseudoltinomys,* but there are *Blainvillimys* specimens with shallow sinus, and *Pseudoltinomys* specimens with deep sinus, so this feature cannot be used to classify worn upper molars.

A distinctive feature of the M^3 may be the position of the posteroloph: in *Blainvillimys* this crest is always curved backwards towards the posteroloph, whereas in *Pseudoltinomys* it is frequently — though not always — transverse.

All specimens that are not evidently *Pseudoltinomys* are put in *Blainvillimys.* This means, that the *Pseudoltinomys* population appears to be quite homogeneous, whereas the *Blainvillimys* population may be a waste basket.

Distinction of the lower molars of *Pseudoltinomys* and *Blainvillimys* is based on the absence/presence of an anteroconid. The lower teeth at first seemed easy to separate, since they all present a well-developed anterosinusid and anteroconid, even in a very advanced stage of wear, and a slight notch in the ectolophid. However, during a second inspection of the huge amount of teeth attributed to *Blainvillimys,* a small number of specimens turned up, that have a clear notch in the ectolophid, but no trace whatsoever of an anterosinusid or anteroconid. I do not think these specimens can be attributed to *P. gaillardi,* because in that case one would expect to find specimens with an intermediate degree of development of the anteroconid, which is not the case, and moreover the notch in the ectolophid of typical *Pseudoltinomys* teeth in OLA4A is shallower, or almost non-existent.

Among these few specimens (5 $M_{1,2}$ and 7 M_3) the M_3 are equal in length to the $M_{1,2}$ or shorter, whereas in *Pseudoltinomys* the M_3 are in general longer than the $M_{1,2}$. Furthermore the M_3 with preserved roots have two roots, whereas the unambiguous *Pseudoltinomys* M_3 have three roots. In the unworn specimens the hypolophid is interrupted near the hypoconid, causing a communication between the sinsusid and synclinid IV. The corresponding upper molars are unknown, probably because they can not be distinguished from those of *P. gaillardi.*

It is worthwhile noting, that among both the upper molars and the lower ones of *B. langei* there is a large number of specimens with a very slight notch in the ectolophid/entoloph. These specimens show some differentiation in the enamel thickness and are considered to belong to the *B. langei* population. The previously mentioned specimens with the deep notch in the ectolophid show some enamel differentiation too, so they may belong to *B. langei* as well. Among the unambiguous *P. gaillardi* specimens there may be a very slight degree of enamel differentiation in a few specimens, but this is almost negligible.

It is, however, more probable that these few lower molars with a deep notch represent another lineage, which is neither *Pseudoltinomys gaillardi* nor a *Blainvillimys.* It probably belongs to the Issiodoromyinae, and it may be a new species of *Pseudoltino-*

mys or even an *Issiodoromys*, if one accepts that the supposed lineage *Elfomys* — *Issiodoromys* is not necessarily correct.

The faunal list of Theridomyidae for Olalla 4A is now constituted as follows:
Blainvillimys langei Vianey-Liaud, 1972
Pseudoltinomys gaillardi Lavocat, 1951
Elfomys medius Vianey-Liaud, 1976
Issiodoromyinae gen. et sp. indet.
Sciuromys cayluxi Schlosser, 1884

Biostratigraphy

The faunal list of FF3B is as follows:
Theridomys sp. nov.
Pseudoltinomys aff. *cuvieri* (Pomel, 1853)
Bransatoglis parvus Freudenthal, 1996
Gliravus aff. *fordi* Bosma & de Bruijn, 1979
Glamys olallensis Freudenthal, 1996

The most important characteristic of the Fuenferrada faunules is the absence of Cricetidae. This is sufficient reason to date them as Eocene (pre- 'Grande Coupure').

The collections from Fuenferrada are small (195 specimens altogether, of which 178 specimens are from FF3B), and it cannot be excluded, that in a larger collection *Atavocricetodon* would be represented. However, we think the absence of this taxon is real, because even among the hundreds of tooth fragments from this locality not a single one could be attributed to *Atavocricetodon*.

The oldest locality with cricetids in the area is Olalla 4A (Freudenthal, 1996). In that locality cricetids are very abundant, much more so than glirids, and in all younger localities in the area too, cricetids dominate over glirids. So, even if FF3B is post-'Grande Coupure' it must be older than Olalla 4A, because glirids are frequent, and cricetids — if they ever show up — are bound to be very rare.

The Eocene/Oligocene boundary is defined at 19 m above the basis of the Massignano section near Ancona in Italy, coinciding with the extinction of the Hantkeninidae, top of zone P17 (Premoli et al., 1988). Since the Rupelian has been accepted as a global stratigraphic unit (Janssen, 1992) the lower limit of the Rupelian is per definition equivalent to the Eocene/Oligocene boundary.

The fossil mammal locality of Hoogbutsel is located in a continental intercalation in the upper part of the Tongrian, correlated with the Lower Rupelian (pers. comm. A.W. Janssen). Since Hoogbutsel is one of the oldest localities after the 'Grande Coupure', this faunal break coincides probably quite well with the Eocene/Oligocene boundary. Therefore it seems justified to attribute the pre-'Grande Coupure' faunas to the Eocene, unless a strong diachrony of this phenomenon be proven (see Berggren & Prothero, 1992; Legendre, 1987; Legendre & Hartenberger, 1992).

On the other hand, Prothero & Emry (1996) place the Eocene/Oligocene boundary in Chron C13r, at 33.7 Ma, and the 'Grande Coupure' in Chron 13n, at about 33 Ma.

Theridomys sp. nov. from FF3B (and FF2B) cannot be compared with any theridomyid from OLA4A.

Pseudoltinomys aff. *cuvieri* from FF3B seems to be less hypsodont than the *Pseudoltinomys* from OLA4A, and slightly smaller. This may serve to place the populations from FF3B and OLA4A in an ancestor-descendant relationship, and confirm the older age of FF3B.

Blainvillimys langei is the most frequent theridomyid in OLA4A, and no comparable species has been found in FF3B. *B. langei* is supposed to be derived from *B. rotundidens* (Vianey-Liaud & Ringeade, 1993), but in *B. rotundidens* (from Escamps IV, Utrecht collections) the enamel differentiation is strongly developed, much more so than in *B. langei* from OLA4A. So, instead of being a descendant of *B. rotundidens*, *B. langei* may be the first step of a new lineage, not directly related with *B. rotundidens*; in that case its absence in FF3B and presence in OLA4A may be of biostratigraphic importance.

Two of the Gliridae from FF3B and OLA4A are identical. The only difference is, that *Glamys olallensis* is relatively more frequent in FF3B than in OLA4A.

On the other hand, *Gliravus* aff. *fordi* is relatively frequent in FF3B, and absent in the rich sample of OLA4A. This certainly means that this taxon disappears from the area in the time span between the deposition of these two localities.

The other components of the OLA4A fauna are not known from FF3B, but that doesn't mean anything, because they are very rare in OLA4A, and one wouldn't expect to find them in the poor sample from FF3B.

FF3B has not a single taxon in common with the Late Eocene locality of Aguatón 2D. Its *Theridomys* is similar in size to *T. pseudosiderolithicus* from AGT2D, but it is morphologically quite different.

Bransatoglis sp. nov. from AGT2D differs from *B. parvus* from FF3B, but a phylogenetic interpretation would be premature.

The *Glamys* from AGT2D, *G. priscus*, is larger than *G. olallensis* from FF3B; their phylogenetic relationship is unknown.

The presence of archaic taxons like *Paradelomys*, *Pseudosciurus*, and *Treposciurus* in AGT2D demonstrates that it must be older than FF3B.

So, FF3B is younger than the Eocene locality of AGT2D, and older than the Oligocene locality OLA4A. It must probably be placed in the latest Eocene, close to the Eocene / Oligocene boundary.

The recent discovery in the Sierra Palomera of a locality with *Atavocricetodon* opens possibilities to locate the Eocene / Oligocene boundary in that area, where lithological correlations are much easier than in the area around Fuenferrada, and to make an effort to confirm the biostratigraphic correlation of FF3B.

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Plate 1

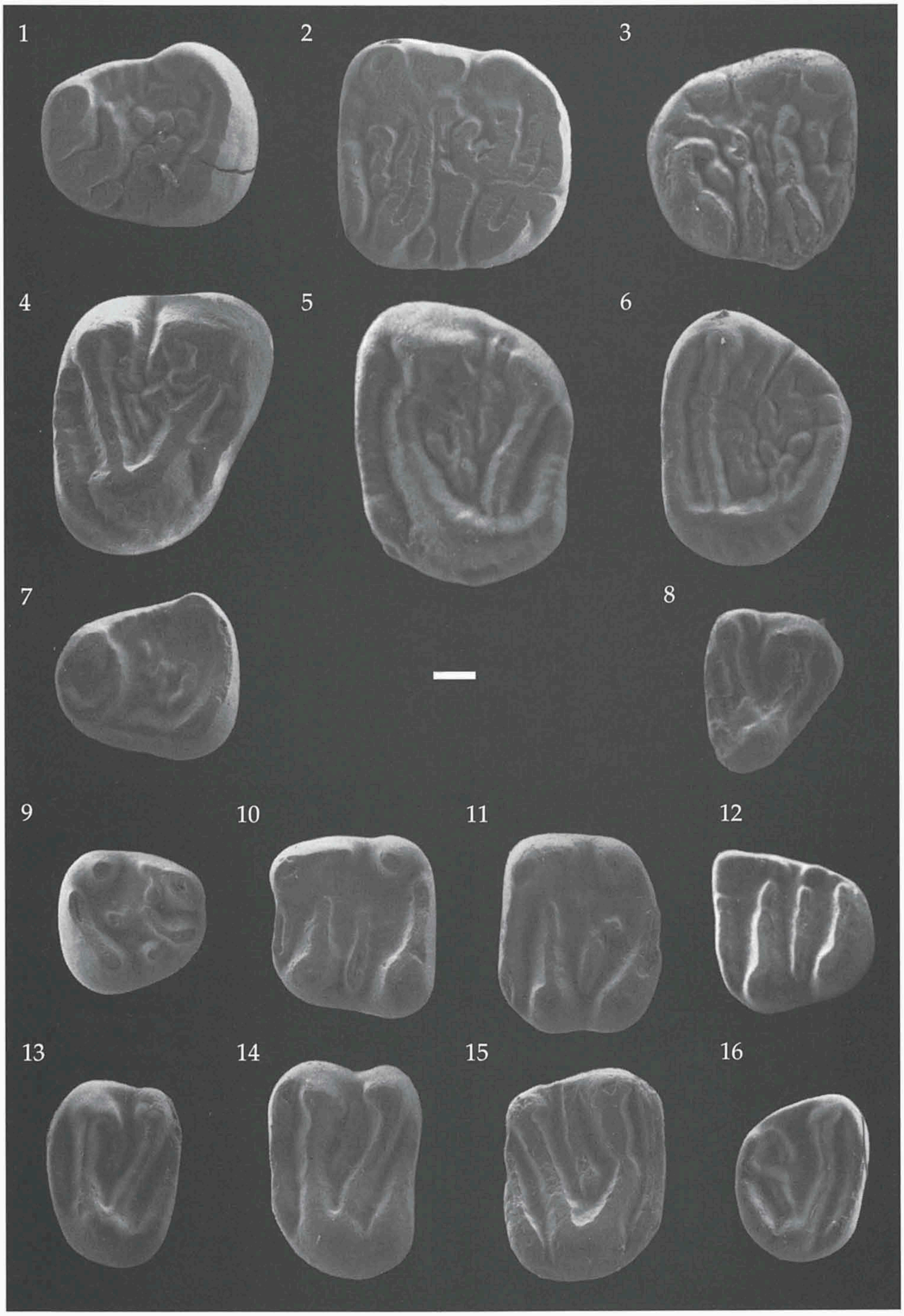
Figs. 1-7. *Gliravus* aff. *fordi* Bosma & de Bruijn, 1979 from Fuenferrada 3B.

1: P_4 sin., FF3B 57.
2: M_2 sin., FF3B 58.
3: M_3 dext., FF3B 63.
4: P^4 dext., FF3B 67.
5: M^2 sin., RGM 417 790.
6: M^3 sin., FF3B 68.
7: D_4 sin., RGM 417 786.

Figs. 8-16. *Glamys olallensis* Freudenthal, 1996 from Fuenferrada 3B.

8: D^4 dext., FF3B 12.
9: P_4 dext., RGM 417 776.
10: M_1 sin., FF3B 4.
11: M_2 sin., FF3B 8.
12: M_3 sin., RGM 417 778.
13: P^4 sin., FF3B 13.
14: M^1 sin., FF3B 17.
15: M^2 dext., FF3B 23.
16: M^3 dext., FF3B 24.

Scale bar is 200 μm.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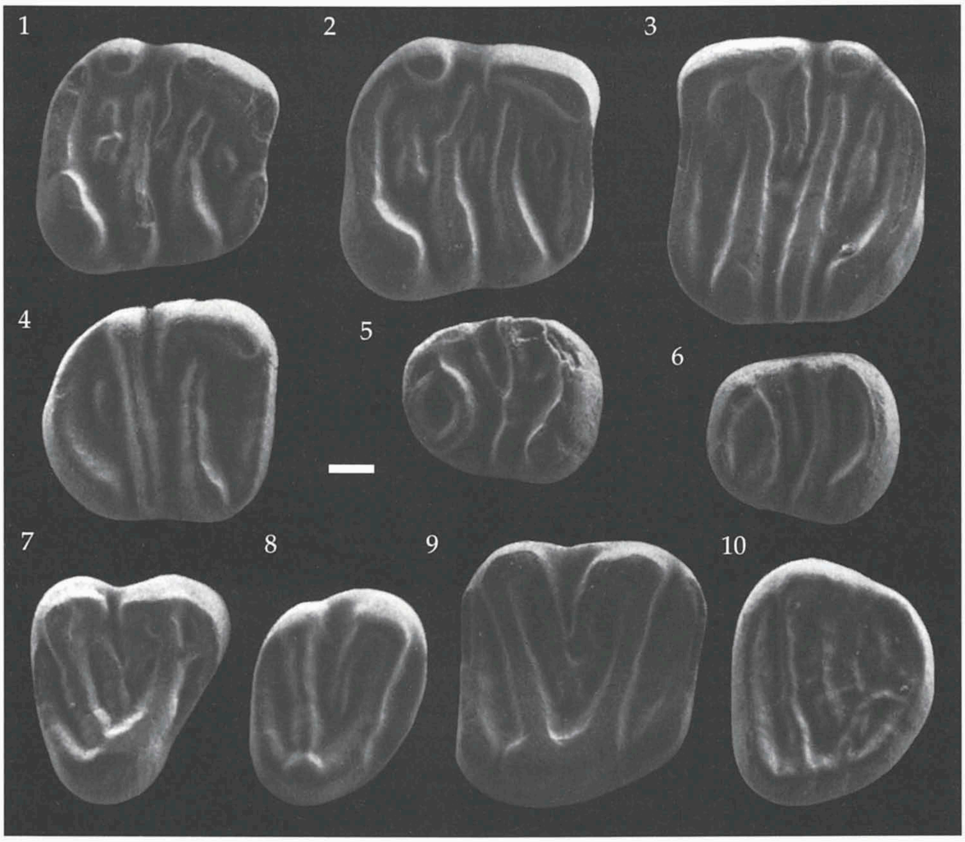

Plate 2

Figs. 1-10. *Bransatoglis parvus* Freudenthal, 1996 from Fuenferrada 3B.

1: M_1 dext., RGM 417 797.
2: M_1 dext., RGM 417 798.
3: M_2 sin., FF3B 31.
4: M_3 dext., FF3B 39.
5: D_4 sin., FF3B 28.
6: P_4 sin., FF3B 29.
7: D^4 dext., FF3B 40.
8: P^4 dext., FF3B 46.
9: M^1 dext., FF3B 50.
10: M^3 sin., FF3B 54.

Scale bar is 200 μm.