Glirinae (Gliridae, Rodentia) from the type area of the Aragonian and adjacent areas (provinces of Teruel and Zaragoza, Spain)

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Daams, R. Glirinae (Gliridae, Rodentia) from the type area of the Aragonian and adjacent areas (provinces of Teruel and Zaragoza, Spain). — Scripta Geol., 77: 1-20, 9 figs., 2 pls, Leiden, July 1985.

This paper, the first in a series of monographs on the mammal faunas from the type area of the Aragonian and adjacent areas in the provinces of Teruel and Zaragoza, deals with the description and palaeoenvironmental interpretation of the Glirinae (Gliridae: dormice).

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Introduction

In the summers of 1976-1983 extensive collections from micromammal-bearing localities have been made in the type-area of the Aragonian and adjacent areas in the provinces of Zaragoza and Teruel. Preliminary reports on these faunas have been published by Daams & Freudenthal (1981) and Daams & van der Meulen (1983). Detailed taxonomic studies did not appear hitherto, however. This study on the Glirinae is the first contribution to the detailed investigation of the various groups. All other groups of the micro- and macromammals are presently under study by various students from Spain and The Netherlands.

For the stratigraphic order of the localities and more complete information on the faunas, the reader is referred to the above mentioned publications.

The nomenclature of the cheek teeth is after Daams (1981). The teeth have been measured using a Leitz Orthoplan Microscope (ocular 10 ×, objective 4 ×) with mechanical stage and measuring clocks. All measurements are given in 0.1 mm units.

STORAGE OF THE MATERIAL

The material is stored in the following collections:
Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands:
Bañon 2, Bañon 5, Bañon 11A, Borjas, Carrilanga 1, La Dehesa, Olmo Redondo 2, Olmo Redondo 3, Las Planas 5K, Las Planas 5L, Ramblar 1, San Roque 1, Solera, Toril, Valalto 1, Valdemoros 3E, Vargas 1A.
State University of Utrecht, The Netherlands:
Bouzigues, Buñol, Manchones, Pedregueras 2C, Villafeliche 2A.
Museo de Ciencias Naturales, Madrid:
Ramblar 3B, Ramblar 5A, Ramblar 7, Valhondo 1.

Acknowledgements

This study has been made possible by the cooperation of the following institutions and persons: the 'Comisión Nacional de Geología' (Spain), the 'Instituto Geológico y Minero de España (I.G.M.E.)', Dr N. Lopez Martínez (Madrid) and Dr M. Freudenthal (Leiden). The excavations have been financed by the State University of Groningen (The Netherlands), the Rijksmuseum van Geologie en Mineralogie (Leiden, the Netherlands), the Netherlands Organization for the Advancement of Pure Research (Z.W.O), and I.G.M.E. We gratefully acknowledge these contributions. Furthermore we want to thank many Spanish colleagues and students, and several Dutch students for their help in the excavations.

Systematic descriptions

Glirudinus modestus (Dehm, 1950)
Pl. 1, figs. 2-6, 8,9.

Description — For material and measurements see Tables 1-7.

M^1 — The anteroloph is isolated from the protocone in all specimens. The labial part of the anteroloph may or may not be connected to the paracone (Table 8). The long anterior centroloph is longer than the posterior centroloph. In some cases these two ridges fuse at their lingual ends. The anterior centroloph may or may not be connected to the metacone (Table 8). The posteroloph is lingually connected to the protocone in all specimens, and labially it may be isolated from the metacone (Table 7). The anterior extra ridge is always present. Up to four extra ridges may be present.

In the M^1 four morphotypes have been distinguished. The first one has one well-developed extra ridge, situated between the protoloph and the anterior centroloph. The second type has one additional extra ridge, which may be situated either inside or outside the trigone. The third morphotype has three extra ridges, of which one is situated outside the trigone. The fourth type has four extra ridges (Fig. 1). Differences between older and younger assemblages are not obvious.

MORPHOTYPES M¹ / LOCALITIES					N
BUÑOL		1	1		2
VILLAFELICHE 2A	4	2		3	9
SAN ROQUE 1	2	6	1	1	10
OLMO REDONDO 2	1	2	1	3	7
BAÑON 2	3	3			6
BAÑON 5	2				2
RAMBLAR 5A	1				1
RAMBLAR 7	3	1		1	5
BOUZIGUES	5	3	4	1	13

Fig. 1. Distribution of morphotypes of the M¹ of *Glirudinus modestus* in the Miocene of Spain and Bouzigues (France).

MORPHOTYPES M² / LOCALITIES						N
BUÑOL		1		3	3	7
VILLAFELICHE 2A		2	2	6		10
SAN ROQUE 1	1		2	1	1	5
OLMO REDONDO 3			1			1
OLMO REDONDO 2	1	1	2	3		7
BAÑON 2			1	2		3
BAÑON 5	1	2	2			5
RAMBLAR 5A				1		1
RAMBLAR 7		1		1		2
RAMBLAR 1		2		1		3
BOUZIGUES	5	9	2	5	2	23

Fig. 2. Distribution of morphotypes of the M² of *Glirudinus modestus* from the Miocene of Spain and Bouzigues (France).

M² — The anteroloph may lingually be isolated, it may have a narrow and low connection to the protoloph, or it may form a complete endoloph with the protocone (Table 10). For the other characters the reader is referred to Table 9. In the M² five morphotypes have been distinguished. The first four types correspond to the ones of the M¹, the fifth type has five, six, or seven extra ridges. As in the M¹, differences between older and younger assemblages are not clear (Fig. 2).

M³ — A continuous endoloph is present. The anteroloph is labially connected to the paracone. The anterior centroloph is long but it does not reach the endoloph. Up to

two extra ridges may be present. The anterior accessory ridge is always present, the other one may be situated inside or outside the trigone. In some specimens the posterior part of the tooth forms a reticulate pattern. The posteroloph is lingually connected to the endoloph, and labially to the metacone.

P_4 — The five main ridges are present. The anterolophid is connected to the protoconid. Two extra ridges are present, one in the anterior valley and one in the posterior valley.

M_1 and M_2 — The five main ridges and two extra ridges are always present. The extra ridge in the anterior valley may or may not be connected to the metaconid (Tables 11, 12). On either or both sides of the largest extra ridge in the anterior valley a small accessory ridge may be present. The long centrolophid may or may not be connected to the metaconid (Tables 11, 12), and it never reaches the labial border of the tooth. The posterior extra ridge may be connected to the entoconid or to the hypoconid or to both.

In the M_1 and M_2 three morphotypes have been distinguished. The most simple one has one large extra ridge in the anterior valley, the other two types have two and three extra ridges in the anterior valley respectively (Figs. 3, 4). Although the material is poor, it is evident that the more complicated morphotypes predominate in the younger assemblages.

M_3 — This element has basically the same pattern as the M_1 and M_2 although the number of extra ridges never exceeds three.

Discussion — By the scarcity of the material clear evolutionary trends cannot be observed in *Glirudinus modestus* from the Miocene of Spain. Some slight differences can be seen, however, between the older and the younger associations. In the Ramblar localities, for instance, the anterior centroloph of the M^2 does not reach the endoloph, whereas in the younger localities it sometimes does. In the older localities (Ramblar 1, Ramblar 7 and Bañon 5) a continuous endoloph is not present in the M^2, whereas in the younger localities specimens with continuous endolophs do occur. Other differences between older and younger associations lie in the number of extra ridges in the M_1 and M_2. Specimens with three anterior accessory ridges are only present in the younger localities. In the upper molars similar differences cannot be observed. Size trends are absent.

Mayr (1979) synonymized *Glirudinus bouziguensis* (Thaler, 1966) with *G. modestus*, demonstrating that the size and dental pattern of the former species fall within the range of variation of that of the latter species. This is not entirely true for *G. modestus* from Spain, as the M_1 and M_2 of this species tend to be more complicated than those of *G. modestus* from Bouzigues (Figs. 3, 4). On the other hand, the M^1 and M^2 of the Spanish and the French species have a similar dental pattern (Figs. 1, 2). The present author does not consider these slight differences to be of great taxonomic importance, and supports therefore Mayr's (1979) proposal to synonymize *G. bouziguensis* with *G. modestus*, the latter one prevailing.

Glirudinus sp.
Pl. 1, fig. 1.

Material — M_3 (10.3 × 8.7).

Locality — Bañon 11A.

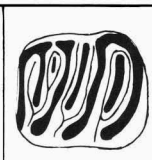
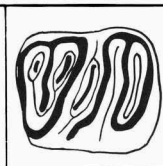
MORPHOTYPES / M_1 / LOCALITIES				N
BUÑOL		1	3	4
VARGAS 1A	1			1
VILLAFELICHE 2A	2	1		3
SAN ROQUE 1	1	3		4
OLMO REDONDO 3		1		1
OLMO REDONDO 2	2	7	1	10
BAÑON 2	2	2		4
BAÑON 5	4	1		5
LA DEHESA	1			1
VALHONDO 1	2			2
RAMBLAR 7	1			1
RAMBLAR 1	3			3
BOUZIGUES	12	1		13

Fig. 3. Distribution of morphotypes of the M_1 of *Glirudinus modestus* from the Miocene of Spain and Bouzigues (France).

MORPHOTYPES / M_2 / LOCALITIES				N
BUÑOL			3	3
VILLAFELICHE 2A		6	1	7
SAN ROQUE 1		4	3	7
OLMO REDONDO 2	2	6		8
BAÑON 2	3	2	1	6
BAÑON 5	1	1		2
VALHONDO 1	1			1
RAMBLAR 3B		2		2
RAMBLAR 1	1			1
BOUZIGUES	15	1	1	17

Fig. 4. Distribution of morphotypes of the M_2 of *Glirudinus modestus* from the Miocene of Spain and Bouzigues (France).

Description — The labial part of the anterolophid is connected to the metalophid. The centrolophid is long but it does not reach the labial border of the tooth. The mesolophid is separated from the posterolophid at the entoconid by a shallow and narrow furrow. Nine extra ridges are present. Four of these are situated between the anterolophid and metalophid, one behind the metalophid, one behind the centrolophid, and three in the posterior valley. The central extra ridge in the posterior valley is labially connected to the posterolophid. Most of the ridges make an angle of c. 65° with the longitudinal axis of the tooth, the four anterior extra ridges and the metalophid are slightly sigmoidally curved.

Discussion — The M_3 from Bañon 11A is larger than the same element of *G. modestus* from the other Spanish localities and it has a much more complicated dental pattern. It is of the same size and similar complexity as the M_3 of *G. gracilis* (Dehm, 1950) and *G. undosus* Mayr, 1979 from the Bavarian 'Süsswassermolasse'.

Myoglis meini (de Bruijn, 1966)
Pl. 1, figs. 7, 10-12.

Description

P^4 (Solera, 13.5 × 14.5 and Borjas, 16.4 × 17.8) — The two specimens have an identical dental pattern. The four main transverse ridges are present. An isolated centroloph is present in the central valley. A narrow and low extra ridge is present in the posterior valley.

M^1 (Toril, 18.0 × 18.4) — At the labial side all ridges end freely. The anterior centroloph is as high and as wide as the main ridges, but the posterior centroloph is shorter, more narrow and lower. Tiny accessory ridges are present between the protoloph and the anterior centroloph, and in the posterior valley.

P_4 (Villafeliche 9, 13.9 × 13.6) — The dental pattern is simple. Anterolophid and metalophid form a composite ridge. Mesolophid and posterolophid are isolated ridges.

M_1 (Solera, 16.6 × 15.8 and 17.4 × 16.4) — All ridges are isolated. The anterolophid, metalophid, mesolophid, and posterolophid are present. Between the metalophid and

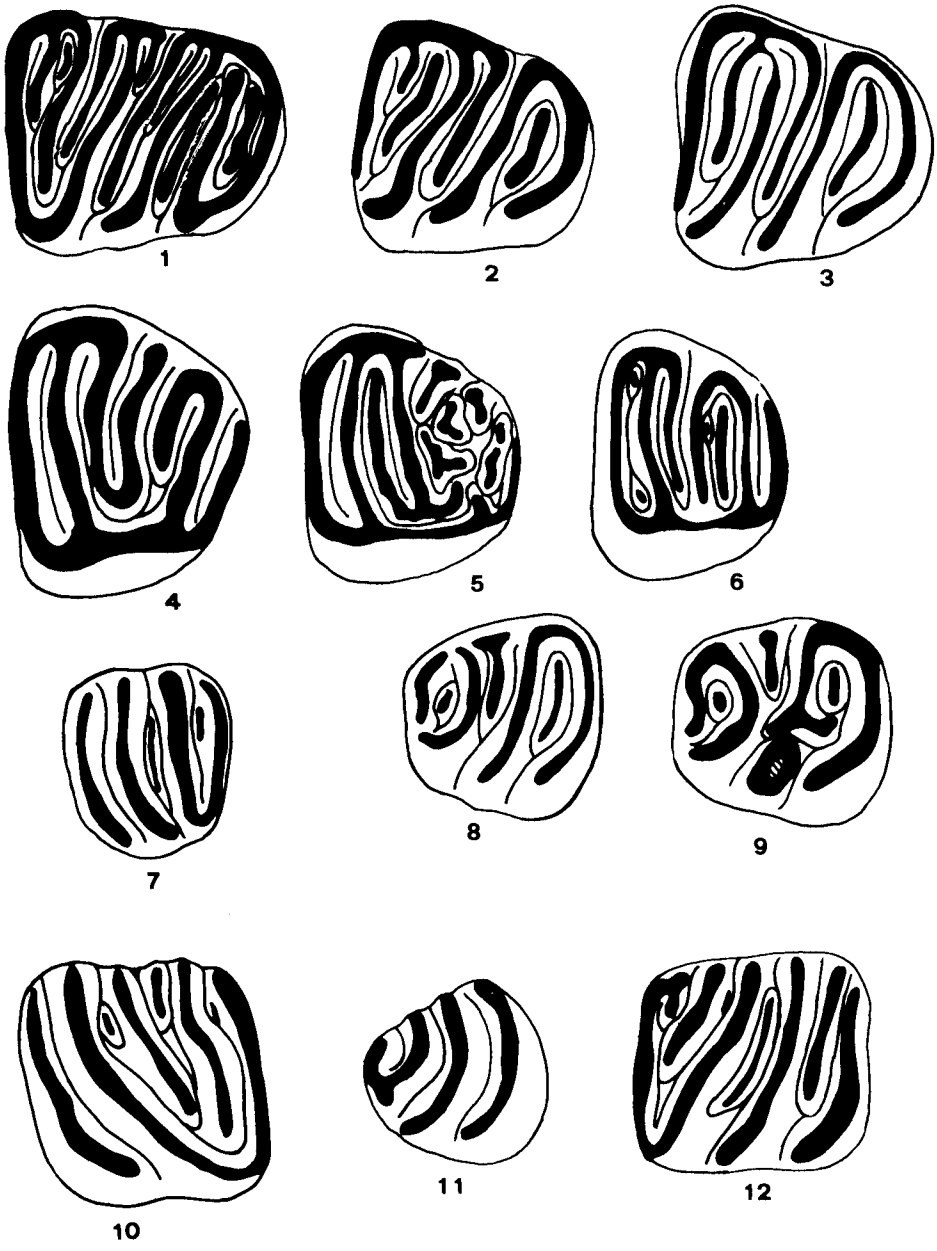
Plate 1

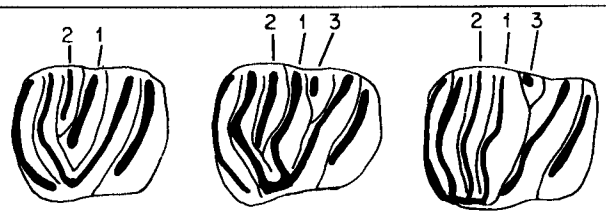
Glirudinus sp. (approx. × 36)
Fig. 1. M_3 sin (Bañon 11A), RGM 336 435.

Glirudinus modestus (Dehm, 1950) (approx. × 36)
Fig. 2. M_3 dex (inverse), San Roque 1, RGM 336 647.
Fig. 3. M_3 sin, Bañon 2, RGM 336 444.
Fig. 4. M^3 sin, Bañon 5, RGM 253 680.
Fig. 5. M^3 sin, San Roque 1, RGM 336 624.
Fig. 6. M^3 dex (inverse), Olmo Redondo 2, RGM 336 659.
Fig. 8. P_4 sin, Bañon 2, RGM 336 445.
Fig. 9. P_4 dex (inverse), Bañon 5, RGM 268 558.

Myoglis meini (de Bruijn, 1966) (approx. × 18)
Fig. 7. P^4 sin, Solera, RGM 255 847.
Fig. 10. M^1 sin, Toril, RGM 253 525.
Fig. 11. P_4 sin, Villafeliche 9, RGM 265 575.
Fig. 12. M_1 dex (inverse), Solera, RGM 255 850.

Plate 1





LOCALITIES	RIDGE 1		RIDGE 2		RIDGE 3		N	*M. thaleri*	*M. hispanicus*
	short	long	short	long	present	absent			
PEDREGUERAS 2C	4	16	20		8	12	20		+
CARRILANGA 1	2	3	5		5		5		+
TORIL		1	1		1		1	+	
LAS PLANAS 5K		1	1		1		1	+	
MANCHONES	1		1		1		1	+	
VALALTO 1	1		1		1		1	+	

Fig. 5. Numbers of M^1 of several *Muscardinus* assemblages with the anterior centroloph either short or long reaching the lingual border (1), of M^1 with a short or long posterior centroloph (2), and M^1 with or without an extra ridge (3) (emended after van de Weerd, 1976).

anterolophid three extra ridges are present. The two anterior ones of these are wide, the third one is low and narrow. The centrolophid and the posterior extra ridge are also more narrow and lower than the main ridges.

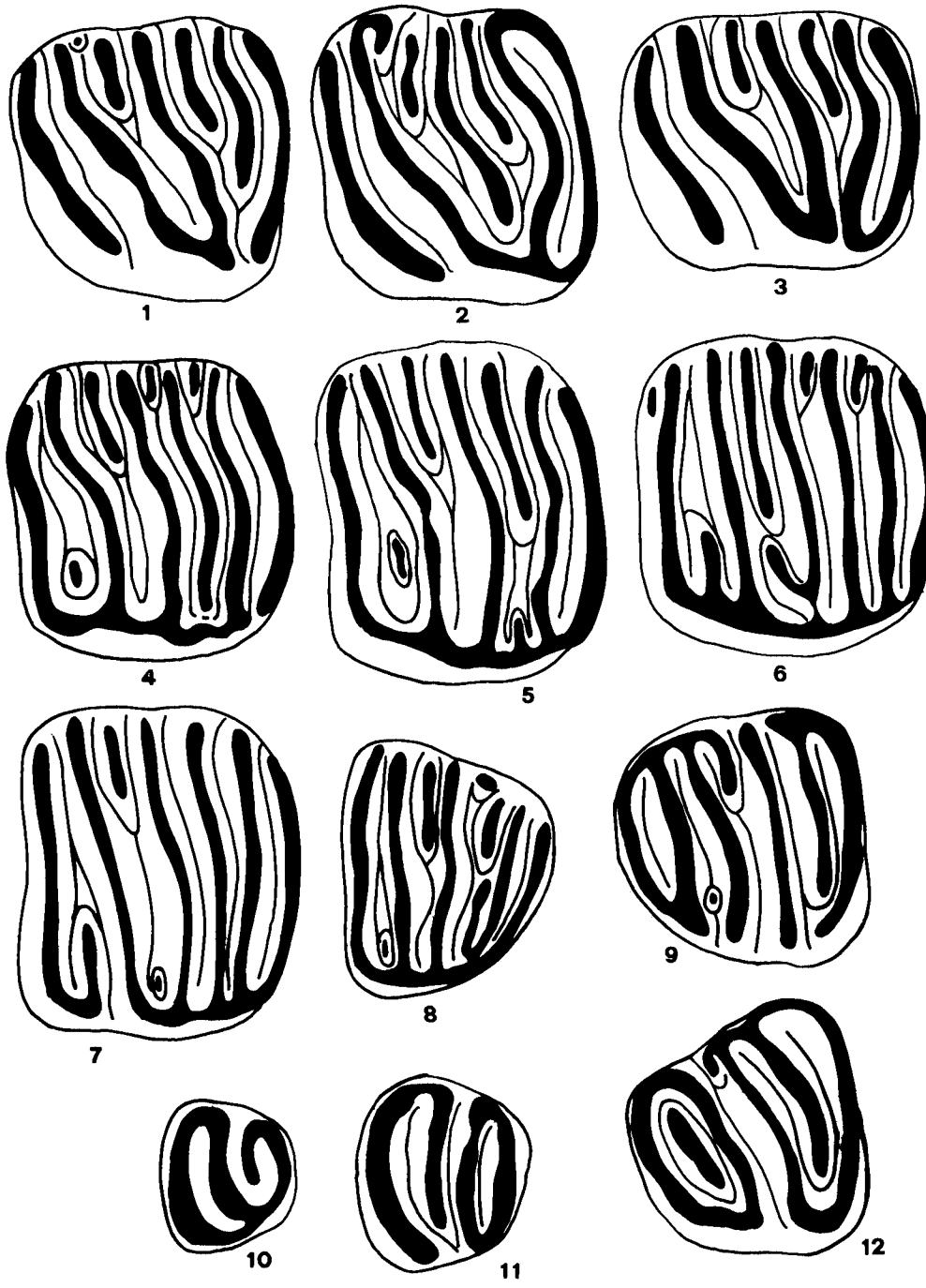
Discussion — *Myoglis* is a rare taxon in the Spanish Miocene. The first evidence of this genus is in Zone B from Rubielos de Mora (de Bruijn & Moltzer, 1974) from where *Myoglis* sp. has been described. Its appearance in the Calatayud-Teruel Basin is in Zone G, where it is represented by *Myoglis meini*.

Plate 2

Muscardinus thaleri de Bruijn, 1966 (approx. × 36).
Fig. 1. M^1 sin, Toril, RGM 253 522.
Fig. 2. M^1 sin, Valalto 1, RGM 253 212.
Fig. 4. M^2 sin, Toril, RGM 253 524.
Fig. 5. M^2 dex (inverse), Toril RGM 253 523.
Fig. 6. M^2 dex (inverse), Las Planas 5K, RGM 252 470.
Fig. 11. P_4 dex, Valalto 1, RGM 253 209.
Fig. 12. M_3 dex, Las Planas 5L, 254 503.

Muscardinus hispanicus de Bruijn, 1966 (approx. × 36).
Fig. 3. M^1 sin, Carrilanga 1, RGM 336 401.
Fig. 7. M^2 dex (inverse), Carrilanga 1, RGM 336 404.
Fig. 8. M^3 sin, Carrilanga 1, RGM 336 409.
Fig. 9. M_3 dex, Carrilanga 1, RGM 336 421.
Fig. 10. P_4 sin (inverse), Carrilanga 1, RGM 336 411.

Plate 2



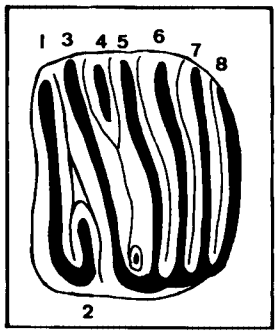


Fig. 6. Nomenclature of the ridges of the M^2 of *Muscardinus*.

Muscardinus thaleri de Bruijn, 1966
Pl. 2, figs. 1, 2, 4-6, 11, 12.

Muscardinus hispanicus de Bruijn, 1966
Pl. 2, figs. 3, 7-10.

Material and measurements — See Tables 13, 14.

Upper dentition — In the M^1 the variation of the length or the presence/absence of three ridges has been tabled (Fig. 5). The only slight morphological differences between the two species is that in the M^1 of *M. hispanicus* from Pedreguerras 2C ridge no. 3 is absent in 12 out of 20 specimens. But in *M. hispanicus* from Carrilanga 1 this extra ridge is still present. Furthermore the M^1 of *M. thaleri* is more or less as long as wide, whereas the M^1 of *M. hispanicus* is longer than wide.

In order to facilitate the description of the M^2, the traditional nomenclature of the ridges is abandoned in this case, and the ridges have been numbered (Fig. 6).

In the M^2 of both species ridges 1, 3, 5, 7, and 8 are complete. Ridge 2 is small and tends to be isolated in *M. thaleri*, whereas it is longer and connected to the lingual side of the tooth in *M. hispanicus*. Ridge 6 may be incomplete in *M. thaleri* (Pl. 2, figs. 4, 5), and it is always complete in *M. hispanicus*. Small extra ridges at the labial side are more frequent in *M. thaleri* than in *M. hispanicus*. The endoloph is always complete in *M. thaleri*, but in *M. hispanicus* it may be interrupted at various places, as well anteriorly (Pl. 2, fig. 7) as posteriorly.

Of *M. thaleri* M^3 is not available. The only M^3 of *M. hispanicus* from Carrilanga 1 has been figured at Pl. 2, fig. 8.

Lower dentition — In the M_1 and M_2 three morphotypes have been distinguished (Figs. 7, 8). The first morphotype has seven ridges. The second ridge is of medium length, and the fourth, lingually situated, ridge is small. The second morphotype lacks the small fourth ridge, and in the third type the second ridge is complete.

It is evident that in *M. thaleri* the second ridge is never complete, and that the fourth small ridge may be present. In *M. hispanicus* the dental pattern consists of 6 complete transverse ridges, which tend to arch forward.

In the M_3 of *M. hispanicus* the posterior extra ridge is connected to both labial and lingual side of the tooth, whereas it is an isolated ridge in *M. thaleri*.

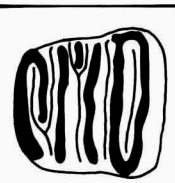
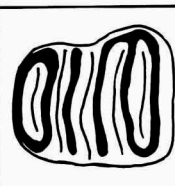
MORPHOTYPES M_1 / LOCALITIES				N	M. THALERI	M. HISPANICUS
PEDREGUERAS 2C			19	19		*
CARRILANGA 1			5	5		*
TORIL	2	2		4	*	
LAS PLANAS 5K		3		3	*	
MANCHONES		1		1	*	
VALDEMOROS 3E		1		1	*	

Fig. 7. Distribution of morphotypes of the M_1 of *Muscardinus thaleri* in the Aragonian and of *Muscardinus hispanicus* in the Lower Vallesian of the Daroca-Villafeliche area.

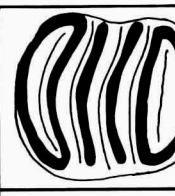
MORPHOTYPES M_2 / LOCALITIES				N	M. THALERI	M. HISPANICUS
PEDREGUERAS 2C			20	20		*
CARRILANGA 1			5	5		*
TORIL	5			5	*	
LAS PLANAS 5K	5	1		6	*	
MANCHONES		1		1	*	
VALALTO 1	1			1	*	

Fig. 8. Distribution of morphotypes of the M_2 of *Muscardinus thaleri* in the Upper Aragonian and of *Muscardinus hispanicus* in the Lower Vallesian of the Daroca-Villafeliche area.

Discussion — *Muscardinus thaleri* from the Aragonian of the Daroca-Villafeliche area differs from *Muscardinus hispanicus* from the Lower Vallesian of Carrilanga 1 and Pedregueras 2C from the same area in the following features:

The second transverse ridge of the M_1 and M_2 does not reach the labial border in *M. thaleri*, whereas this ridge is complete in *M. hispanicus*.

Between the third and the fourth ridge of M_1 and M_2 of *M. thaleri* a small accessory, lingually situated ridge may be present. In *M. hispanicus* this ridge has not been observed. This feature is more evident in the M_2 than in the M_1.

The M_1 and M_2 of *M. thaleri* are relatively shorter than those of *M. hispanicus*. Moreover the M_2 of *M. thaleri* is narrower posteriorly than anteriorly, whereas in *M. hispanicus* the anterior and posterior width tend to be the same.

The transverse ridges of M_1 and M_2 of *M. thaleri* tend to be straight, whereas these ridges of the same elements arch strongly forward in *M. hispanicus*.
In the upper molars differences are less evident, because M^1 and M^2 of *M. thaleri* are not well represented. A slight difference may be observed in the presence of some small accessory ridges in *M. thaleri*.

It appears that *M. thaleri* and *M. hispanicus* are closely related, as already mentioned by de Bruijn (1966a). *M. thaleri* is considered to be the ancestor of *M. hispanicus*, which is consistent with de Bruijn's (1966b) interpretation.

Aguilar (1982) assumes *Eomuscardinus sansaniensis* (Lartet, 1851) to be the ancestor of *M. thaleri*. As the first evidence of *M. thaleri* is from older levels (Valdemoros 3E, zone D, MN Zone 4), this assumption does not seem justified. It is doubtful if the ancestor of *Muscardinus* must be sought in the older *Glirudinus* stock. These doubts are based on the following arguments:
All modern *Glirudinus* species have more complicated dental patterns than *M. thaleri*. A possible ancestry would imply that a trend towards complication in *Glirudinus* would be reserved in a trend towards simplification in the *Muscardinus* lineage.
Glirudinus has a slightly concave occlusal surface, and an oblique masticatory stroke. In *Muscardinus* the occlusal surface is completely flat and the masticatory stroke is longitudinal.

As yet, no intermediates between these two types have been found, leaving the descendance of *Muscardinus* to be an open question.

M. thaleri is supposed to be an immigrant into Spain, where it remained endemic until the close of the Aragonian.

Muscardinus crusafonti Hartenberger, 1966 from Can Llobateres resembles much *M. hispanicus* from Carrilanga 1 and Pedregueras 2C. In the original diagnosis of the former species Hartenberger (1966) points out that the M^1 of *M. crusafonti* is shorter than in *M. hispanicus*. Considering the measurements of both species, it appears that these values are not significantly different. The ratio average length/average width of the M_1 results to be 1.17 in *M. hispanicus* from Pedregueras 2C, 1.12 in the same species from Carrilanga 1, and 1.14 in *M. crusafonti* from Can Llobateres.

The M^2, M_1 and M_3 of both species are similar in size and in dental pattern. The only difference between the two species seems to be that the two M_2 of *M. crusafonti* from Can Llobateres are as wide as long, whereas the M_2 of *M. hispanicus* from Carrilanga 1 and Pedregueras 2C are more elongated. This slight difference does not warrant the distinction of two species, and these are therefore synonymized, *M. hispanicus* prevailing. Moreover, the faunas of Pedregueras 2C and Can Llobateres are considered to be of more or less the same age, not making it probable that *M. crusafonti* would be the ancestor of *M. hispanicus*, as suggested by Hartenberger (1966).

Conclusions

Glirinae are dormice with a flat or slightly concave occlusal surface. The entire subfamily is considered to have inhabited forested areas (van der Meulen & de Bruijn, 1982; Daams & van der Meulen, in press). As representatives of this subfamily are rare in the Miocene of the Calatayud-Teruel Basin, longlasted extensive forested areas are supposed to have been absent in this area during that time.

It is striking that the appearance or relative flourishing of *Glirudinus modestus* in the Calatayud-Teruel Basin coincides with the peaks of relative abundance of *Peridyro-*

Continental stages	Local zones	N of M^1M^2 of Gliridae	*Peridyromys murinus*	*Myomimus dehmi*	*Glirudinus modestus*	*Myoglis meini*	*Muscardinus thaleri*	*Muscardinus hispanicus*	*Microdyromys*
Vall.	I	252		49				25	
	H	137		82				16	
	G	273		*		1	13		84
Aragonian	E/F	59							92
	D	967	1				*		46
	C	775	3		1				48
	B	1894	40		5				8
	A	712	51		4				3
?	Z	2882	67		1				1

Fig. 9. Distribution and relative frequency (in percentages) of the Glirinae, and of some other dormice. *Armantomys* and *Praearmantomys* have been omitted calculating the relative frequency of the Gliridae. All material is from the Calamocha-Daroca-Villafeliche area in the Calatayud-Teruel Basin. Asterisks indicate frequencies below one percent. Vall. means Vallesian.

mys murinus (Fig. 9). These peaks have been interpreted by Daams & van der Meulen (1983) as representing relatively cool periods. Therefore *Glirudinus*, which is more abundant in Northern and Central European Miocene faunas, is supposed to be an immigrant into Spain from the north during cooler periods.

Muscardinus thaleri on the other hand appears in zone D, when temperatures are supposed to have been relatively high. Afterwards, during the Late Aragonian and Early Vallesian *M. thaleri* and *M. hispanicus* respectively are relatively abundant. During this time humidity increased and temperatures declined (Daams & van der Meulen, 1983).

References

Aguilar, J.P., 1982. Contributions à l'étude des Micromammifères du gisement Miocène supérieur de Montredon (Hérault). 2. Les Rongeurs. — Palaeovertebrata, 12, 3: 81-117.

Aguilar, J.P., J. Agusti & J. Gibert, 1979. Rongeurs Miocènes dans le Vallés-Penedés. 2. Les rongeurs de Castell de Barbera. — Palaeovertebrata, 9, 1: 17-31.

Bruijn, H. de, 1966a. Some new Miocene Gliridae (Rodentia, Mammalia) from the Calatayud area (Prov. Zaragoza, Spain). — Proc. Kon. Ned. Akad. Wet., B, 69, 1: 58-71, 2 pls.

Bruijn, H. de, 1966b. On the Mammalian fauna of the *Hipparion*-beds in the Calatayud-Teruel Basin (Prov. Zaragoza, Spain). — Proc. Kon. Ned. Akad. Wet., B, 69, 3: 367-387, 2 pls.

Bruijn, H. de, 1967. Gliridae, Sciuridae y Eomyidae (Rodentia, Mammalia) miocenos de Calatayud (Provincia de Zaragoza, España) y su relación con la bioestratigrafia del área. — Bol. Inst. Geol. Min. España, 78: 178-373, 11 pls.

Bruijn, H. de & J.G. Moltzer, 1974. The rodents from Rubielos de Mora; the first evidence of the existence of different biotopes in the Early Miocene of Eastern Spain. — Proc. Kon. Ned. Akad. Wet., B, 77, 2: 129-145, 3 pls.

Daams, R., 1976. Miocene rodents (Mammalia) from Cetina de Aragon (Prov. Zaragoza) and Buñol (Prov. Valencia), Spain. — Proc. Kon. Ned. Akad. Wet., B, 79, 3: 152-182, 5 pls.

Daams, R., 1981. The dental pattern of the dormice *Dryomys, Myomimus, Microdyromys* and *Peridyromys*. — Utrecht Micropal. Bull., Spec. Publ. 3: 1-115, 5 pls.

Daams, R. & M. Freudenthal, 1981. Aragonian: the Stage concept versus Neogene Mammal Zones. — Scripta Geol., 62: 1-17.

Daams, R. & A.J. van der Meulen, 1983. Paleoecological interpretation of micromammal faunal successions in the Upper Oligocene and Miocene of Spain. — R.C.M.N.S. Interim-Coll. on Mediterranean Neogene continental paleoenvironments and paleoclimatic evolution, Montpellier, 1983, Abstracts.

Daams, R. & A.J. van der Meulen, (in press). Paleoenvironmental and paleoclimatic interpretation of micromammal faunal successions in the upper Oligocene and Miocene of North-Central Spain. — Proc. R.C.M.N.S. Interim-Coll. on Mediterranean Neogene continental paleoenvironments and paleoclimatic evolution, Montpelier, 1983.

Dehm, R., 1950. Die Nagetiere aus dem Mittel-Miozän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. — N. Jb. Miner. Geol. Paläont., Abh., B, 91: 321-428.

Hartenberger, J.L., 1966. Les rongeurs du Vallésien (Miocène supérieur) de Can Llobateres (Sabadell, Espagne): Gliridae et Eomyidae. — Bull. Soc. géol. France, 7, 8: 596-604.

Mayr, H., 1979. Gebissmorphologische Untersuchungen an miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands. — Doctor's Thesis, Univ. München: 1-380, 1-17 pls.

Meulen, A.J. van der & H. de Bruijn, 1982. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2. The Gliridae. — Proc. Kon. Ned. Akad. Wet., B, 85, 4: 485-524.

Thaler, L., 1966. Les Rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. — Mém. Mus. Natl. Hist. Nat., C, 17: 1-295, 27 pls.

Weerd, A. van de, 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. — Utrecht Micropal. Bull., Spec. Publ. 2: 1-216, 16 pls.

Weerd, A. van de & R. Daams, 1978. Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications. — Proc. Kon. Ned. Akad. Wet., B, 81, 4: 448-473.

Manuscript received 28 March 1984.

Table 1. Measurements of the M^1 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France). Measurements from Buñol have been taken from Daams (1976) and those of Villafeliche 2A from de Bruijn (1967).

	length				width			
	min	mean	max	n	min	mean	max	
Buñol	8.0	8.5	8.8	3/1	—	9.2	—	
Villafeliche 2A	7.7	9.1	10.2	20	9.1	10.4	11.2	(M^1 M^2)
San Roque 1	8.1	9.0	9.6	9	9.3	10.2	10.9	
Olmo Redondo 2	8.7	9.2	9.6	3	9.6	9.9	10.0	
Bañon 2	9.3	9.5	9.6	5	11.1	11.3	11.6	
Bañon 5	9.9	10.0	10.1	3/2	10.6	11.1	11.6	
Ramblar 5A	—	9.9	—	1	—	10.1	—	
Ramblar 7	9.1	9.2	9.3	3	10.8	11.2	11.5	
Bouzigues	8.5	9.1	10.0	16/13	9.3	10.1	11.0	

Table 2. Measurements of the M^2 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France). Measurements from Buñol have been taken from Daams (1976) and those of Villafeliche 2A from de Bruijn (1967).

	length				width			
	min	mean	max	n	min	mean	max	
Buñol	8.4	8.8	9.1	8	9.0	9.8	10.3	
Villafeliche 2A	7.7	9.1	10.2	20	9.1	10.4	11.2	(M^1 M^2)
San Roque 1	8.8	9.1	9.6	7	10.2	10.7	11.1	
Olmo Redondo 3	—	9.2	—	1	—	10.8	—	
Olmo Redondo 2	8.6	8.9	9.0	6/5	10.2	10.5	10.9	
Bañon 2	9.5	9.7	9.8	4	11.3	11.9	12.4	
Bañon 5	9.7	10.1	10.4	5	11.0	12.3	13.1	
Ramblar 5A	—	9.3	—	1	—	11.6	—	
Ramblar 7	—	9.6	—	1	—	11.5	—	
Ramblar 1	8.5	9.0	9.4	2	10.4	10.9	11.4	
Bouzigues	8.4	9.0	9.6	20/19	10.1	10.7	11.9	

Table 3. Measurements of the M^3 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France). Measurements from Buñol have been taken from Daams (1976) and those of Villafeliche 2A from de Bruijn (1967).

	length				width		
	min	mean	max	n	min	mean	max
Buñol	7.2	7.7	8.1	3	9.7	9.8	9.8
Villafeliche 2A	6.7	7.7	8.6	9	9.1	9.8	10.2
San Roque 1	7.6	8.0	8.3	2	9.1	9.3	9.4
Olmo Redondo 2	7.1	7.3	7.5	2	9.0	9.8	10.5
Bañon 5	8.6	8.7	8.8	2	11.1	11.2	11.2
Bouzigues	6.9	7.4	8.0	5/4	9.1	9.7	10.5

Table 4. Measurements of the P_4 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France). Measurements from Buñol have been taken from Daams (1976) and those of Villafeliche 2A from de Bruijn (1967).

	length				width		
	min	mean	max	n	min	mean	max
Buñol	6.4	6.5	6.5	2	6.1	6.3	6.5
La Dehesa	—	7.1	—	1	—	7.4	—
Bañon 2	—	7.5	—	1	—	7.5	—
Bañon 5	—	8.2	—	1	—	7.8	—
Ramblar 7	—	7.0	—	1	—	7.0	—
Bouzigues	6.4	7.0	7.6	2	6.5	6.9	7.3

Table 5. Measurements of the M_1 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France). Measurements from Buñol have been taken from Daams (1976) and those of Villafeliche 2A from de Bruijn (1967).

	length				width		
	min	mean	max	n	min	mean	max
Buñol	8.6	9.1	9.6	5	8.2	8.6	9.2
Vargas 1A	—	10.0	—	1	—	8.6	—
Villafeliche 2A	8.6	9.2	10.0	8	8.1	8.6	9.0
San Roque 1	9.3	9.6	9.8	2/3	8.3	8.7	9.1
Olmo Redondo 3	—	9.6	—	1	—	9.1	—
Olmo Redondo 2	8.7	9.4	10.4	8/7	8.3	8.7	9.1
Bañon 2	9.5	9.9	10.1	4	9.0	9.4	9.8
Bañon 5	9.7	10.8	11.5	4/2	10.0	10.3	10.5
La Dehesa	—	9.8	—	1	—	9.6	—
Valhondo 1	9.5	9.6	9.6	2	8.9	8.9	8.9
Ramblar 7	—	9.6	—	1	—	9.6	—
Ramblar 1	9.2	9.3	9.5	3	8.5	8.6	8.8
Bouzigues	9.1	9.4	9.8	12/11	8.3	9.0	9.8

Table 6. Measurements of the M_2 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France). Measurements from Buñol have been taken from Daams (1976) and those of Villafeliche 2A from de Bruijn (1967).

	length				width		
	min	mean	max	n	min	mean	max
Buñol	9.6	9.7	9.8	3	9.0	9.2	9.4
Villafeliche 2A	9.1	9.9	10.4	7	8.4	9.3	9.8
San Roque 1	8.9	9.6	10.0	7	8.0	8.8	9.2
Olmo Redondo 2	8.8	9.6	10.0	8	8.6	8.9	9.2
Bañon 2	10.1	10.5	10.8	6	9.7	10.2	10.5
Bañon 5	10.6	10.8	10.9	2	10.4	10.5	10.5
Valhondo 1	—	9.4	—	1	—	9.3	—
Ramblar 3B	—	10.2	—	1	—	9.3	—
Ramblar 1	—	8.9	—	1	—	9.0	—
Bouzigues	8.9	9.4	10.1	16/18	8.7	9.4	10.0

Table 7. Measurements of the M_3 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France). Measurements from Buñol have been taken from Daams (1976) and those of Villafeliche 2A from de Bruijn (1967).

	length				width		
	min	mean	max	n	min	mean	max
Buñol	7.4	7.9	8.4	2/1	—	7.6	—
Vargas 1A	—	8.6	—	1	—	8.7	—
Villafeliche 2A	7.7	8.5	9.5	11	6.7	8.2	8.8
San Roque 1	—	8.9	—	1	—	8.5	—
Olmo Redondo 2	—	8.2	—	1	—	8.3	—
Bañon 2	8.9	9.1	9.2	2	9.0	9.4	9.8
Valhondo 1	—	8.2	—	1	—	8.7	—
Ramblar 7	—	8.8	—	1	—	9.3	—
Ramblar 1	—	7.7	—	1	—	7.1	—
Bouzigues	8.0	8.2	8.5	5	7.7	8.1	8.5

Table 8. Some variable features of the dental pattern of the M^1 of *Glirudinus modestus* from the Miocene of Spain and of Bouzigues (France).

	anteroloph connected to paracone		anterior centroloph connected to paracone		posterior centroloph connected to metacone		posteroloph connected to metacone	
	yes	no	yes	no	yes	no	yes	no
Buñol	2	1	2	1	3	0	3	0
Villafeliche 2A	7	2	6	3	8	1	9	0
San Roque 1	5	3	3	5	7	1	7	1
Olmo Redondo 2	1	2	1	2	3	0	3	0
Bañon 2	2	4	6	0	4	2	5	1
Bañon 5	0	1	1	1	1	1	1	1
Ramblar 5A	1	0	1	0	1	0	1	0
Ramblar 7	2	1	1	2	3	0	2	1
Bouzigues	7	6	8	4	9	2	9	3

Table 9. Some variable features of the dental pattern of the M^2 of *Glirudinus modestus* from the Miocene of Spain and Bouzigues (France).

	anteroloph connected to paracone		anterior centroloph connected to paracone		posterior centroloph connected to metacone		posteroloph connected to metacone		anterior centroloph connected to endoloph	
	yes	no	yes	no	yes	no	yes	no	yes	no
Buñol	7	0	4	2	6	1	6	0	4	4
Villafeliche 2A	7	1	5	3	8	0	6	2	0	8
San Roque 1	5	1	1	5	5	1	5	1	5	2
Olmo Redondo 3	1	0	0	1	1	0	1	0	0	1
Olmo Redondo 2	4	1	3	2	4	0	2	1	1	6
Bañon 2	3	0	3	0	3	0	1	2	0	3
Bañon 5	4	0	4	0	4	0	5	0	2	3
Ramblar 5A	1	0	1	0	1	0	1	0	0	1
Ramblar 7	1	0	0	1	1	0	1	0	0	2
Ramblar 1	2	0	2	0	2	0	2	0	0	2
Bouzigues	20	3	18	5	18	3	18	2	0	23

Table 10. Variation of the endoloph in the M^2 of *Glirudinus modestus* from the Miocene of Spain and Bouzigues (France).

	endoloph absent	endoloph incomplete	endoloph continuous
Buñol	0	5	3
Villafeliche 2A	2	3	2
San Roque 1	1	1	4
Olmo Redondo 3	0	0	1
Olmo Redondo 2	2	0	4
Bañon 2	3	0	1
Bañon 5	2	3	0
Ramblar 7	1	0	0
Ramblar 1	1	1	0
Bouzigues	3	4	16

Table 11. Some variable features of the dental pattern of the M_1 of *Glirudinus modestus* from the Miocene of Spain and Bouzigues (France).

	Large anterior extra ridge connected to metaconid		centrolophid connected to metaconid		posterior extra ridge connected to entoconid		posterior extra ridge connected to hypoconid		posterior extra ridge connected to both entoconid and hypoconid	endolophid present
	yes	no	yes	no	yes	no	yes	no		
Buñol	3	1	0	5	0	5	3	2	0	0
Villafeliche 2A	1	2	1	2	1	2	0	3	0	0
San Roque 1	3	0	2	2	1	2	0	3	1	1
Olmo Redondo 3	1	0	1	0	0	1	0	1	0	0
Olmo Redondo 2	10	0	2	8	2	3	0	5	5	0
Bañon 2	1	3	4	0	0	3	0	3	1	0
Bañon 5	2	2	2	1	0	3	1	2	1	0
La Dehesa	0	1	0	1	0	1	0	1	0	0
Valhondo 1	1	2	3	0	0	3	1	1	0	0
Ramblar 7	0	1	0	1	0	1	0	1	0	0
Ramblar 1	0	3	3	0	0	3	0	3	0	1
Bouzigues	4	9	12	1	1	6	3	4	4	1

Table 12. Some variable features of the dental pattern of the M_2 of *Glirudinus modestus* from the Miocene of Spain and Bouzigues (France).

	Large anterior extra ridge connected to metaconid		centrolophid connected to metaconid		posterior extra ridge connected to entoconid		posterior extra ridge connected to hypoconid		posterior extra ridge connected to both entoconid and hypoconid	endoloph present
	yes	no	yes	no	yes	no	yes	no		
Buñol	3	0	2	1	0	3	3	0	0	0
Villafeliche 2A	6	1	5	2	6	1	1	7	0	1
San Roque 1	5	2	5	2	1	6	0	7	0	0
Olmo Redondo 2	4	4	7	1	3	5	0	8	0	2
Bañon 2	3	3	6	0	2	3	0	5	1	1
Bañon 5	1	1	1	1	0	2	1	1	0	0
Valhondo 1	0	1	1	0	0	1	0	1	0	0
Ramblar 3B	2	0	0	1	0	2	1	1	0	0
Ramblar 1	0	1	1	0	0	0	0	0	1	0
Bouzigues	0	17	16	1	0	16	2	14	2	5

Table 13. Measurements of the upper molars of *Muscardinus* from the Aragonian and Lower Vallesian of the Daroca-Villafeliche area.

		length				width			*M. thaleri*	*M. hispanicus*
		min	mean	max	n	min	mean	max		
M^1	Pedregueras 2C	11.7	13.0	14.1	21	10.1	11.1	12.0		+
	Carrilanga 1	10.8	12.0	13.2	5	10.4	10.7	11.6		+
	Toril	—	10.9	—	1	—	11.0	—	+	
	Las Planas 5K	—	11.9	—	1	—	11.6	—	+	
	Manchones	11.9	12.3	12.6	2	11.6	11.9	12.3	+	
	Valalto 1	—	10.8	—	1	—	11.8	—	+	
M^2	Pedregueras 2C	10.0	10.8	12.5	21	10.1	11.3	12.3		+
	Carrilanga 1	10.5	11.4	12.4	5/6	11.8	12.3	13.0		+
	Toril	10.7	10.9	11.1	2	11.9	12.7	13.5	+	
	Las Planas 5K	—	12.0	—	1	—	12.4	—	+	
	Manchones	—	12.6	—	1	—	13.7	—	+	
M^3	Pedregueras 2C	6.8	7.6	9.4	20	8.0	9.8	11.0		+
	Carrilanga 1	8.6	8.7	8.8	2/1	—	10.2	—		+
	Manchones	—	9.5	—	1	—	11.2	—	+	

Table 14. Measurements of the lower cheek teeth of *Muscardinus* from the Aragonian and Lower Vallesian of the Daroca-Villafeliche area.

		length				width				
		min	mean	max	n	min	mean	max	*M. thaleri*	*M. hispanicus*
P_4	Pedregueras 2C	4.3	4.9	5.2	17	5.0	5.8	6.2		+
	Carrilanga 1	—	5.6	—	1	—	6.1	—		+
	Toril	—	6.5	—	1	—	7.2	—	+	
	Valalto 1	—	6.8	—	1	—	7.7	—	+	
M_1	Pedregueras 2C	10.6	12.3	13.4	20	8.6	9.9	10.8		+
	Carrilanga 1	11.6	11.9	12.3	3	9.8	10.3	10.8		+
	Toril	10.0	10.7	11.6	6	10.4	11.0	11.7	+	
	Las Planas 5K	10.0	10.9	11.6	6	10.3	11.0	11.5	+	
	Valdemoros 3E	—	10.8	—	1	—	10.5	—	+	
M_2	Pedregueras 2C	10.0	12.1	12.9	20	10.4	11.1	12.0		+
	Carrilanga 1	11.9	12.4	13.2	5/6	10.0	11.1	12.1		+
	Toril	10.8	11.0	11.3	3	11.0	11.4	11.8	+	
	Las Planas 5K	—	11.6	—	1/2	10.1	10.7	12.2	+	
	Manchones	—	11.9	—	1	—	12.3	—	+	
	Valalto 1	—	11.7	—	1	—	11.9	—	+	
M_3	Pedregueras 2C	7.0	8.4	9.8	20	8.2	8.7	10.0		+
	Carrilanga 1	9.3	9.7	10.0	2/3	9.3	9.8	10.6		+
	Las Planas 5K	—	—	—	0/1	—	9.4	—	+	
	Las Planas 5L	—	9.5	—	1	—	10.0	—	+	
	Borjas	—	10.2	—	1	—	10.3	—	+	
	Manchones	9.8	10.5	10.9	3	9.8	10.1	10.5	+	
	Valalto 1	—	9.4	—	1	—	9.2	—	+	