Geología y Paleontología del Eoceno de la Pobla de Segur (Lleida)

Dra. Nieves LOPEZ MARTINEZ,
Universidad Complutense de Madrid.

Dr. Jorge CIVIS LLOVERA,
Universidad de Salamanca.

Dra. Mª Lourdes CASANOVAS CLADELLAS,
Institut de Paleontologia "Miguel Crusafont", Sabadell.

Dr. Remmert DAAMS,
Universidad Complutense de Madrid.

(Eds.)

Universitat de Lleida

INSTITUT D'ESTUDIS ILERDENCS
Fundació Pública de la Diputació de Lleida

licions de la Universitat de Lleida, 1998
Los autores
Institut d'Estudis Ilerdencs
Universitat de Lleida

aquetación: Montse Corderroure / Servei de Publicacions de la UdL
seño de portada: Gabriela Latapí

BN 84-89727-60-0
L. Z-3536-97

Contenido de la edición

The Gliridae from the Upper Eocene of Sossís, Roc de Santa and Claverol (Lleida, Spain)

*by Jan van Dam**

Abstract

Three species of *Gliravus* (*G. priscus* Stehlin and Schaub, 1951, *G. meridionalis* Hartenberger, 1971 and *G. hispanicus* n. sp., Gliridae, Rodentia) from the Upper Eocene sections of Sossís, Roc de Santa and Claverol (Tremp Basin, Lleida, Spain) are described and discussed. *G. hispanicus* n. sp. is a *Gliravus* of medium size and is more advanced than *G. priscus* and is more primitive than *G. meridionalis*, to which it is closely related. *G. hispanicus* and *G. meridionalis* may be descendants of the small-sized *G. robiacensis*-type ancestor (the model of Hartenberger 1971), or they may be directly traced back to the middle-sized *Eogliravus* stock.

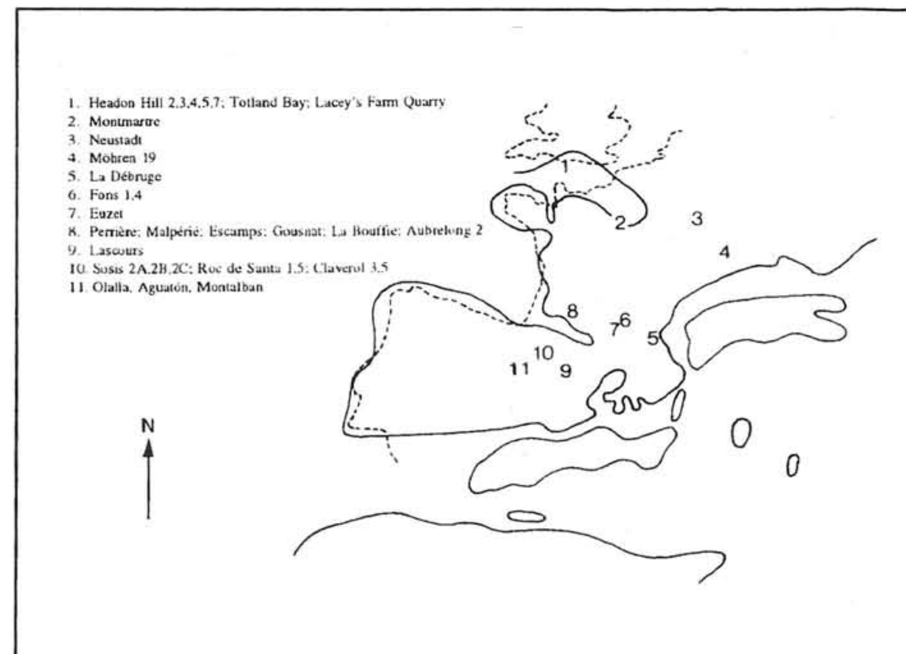


Figure 1. *Late Eocene and Early Oligocene localities with* Gliravus. *(Paleogeographical reconstruction for the Eocene-Oligocene boundary (35 Ma) after Dercourt et al. 1986.)*

* Authors' adress: J.A.van Dam, Instituut voor Aardwetenschappen, Rijksuniversiteit Utrecht, postbus 80021, 3508 TA, Utrecht, Netherlands. E-mail: jdam@earth.ruu.nl

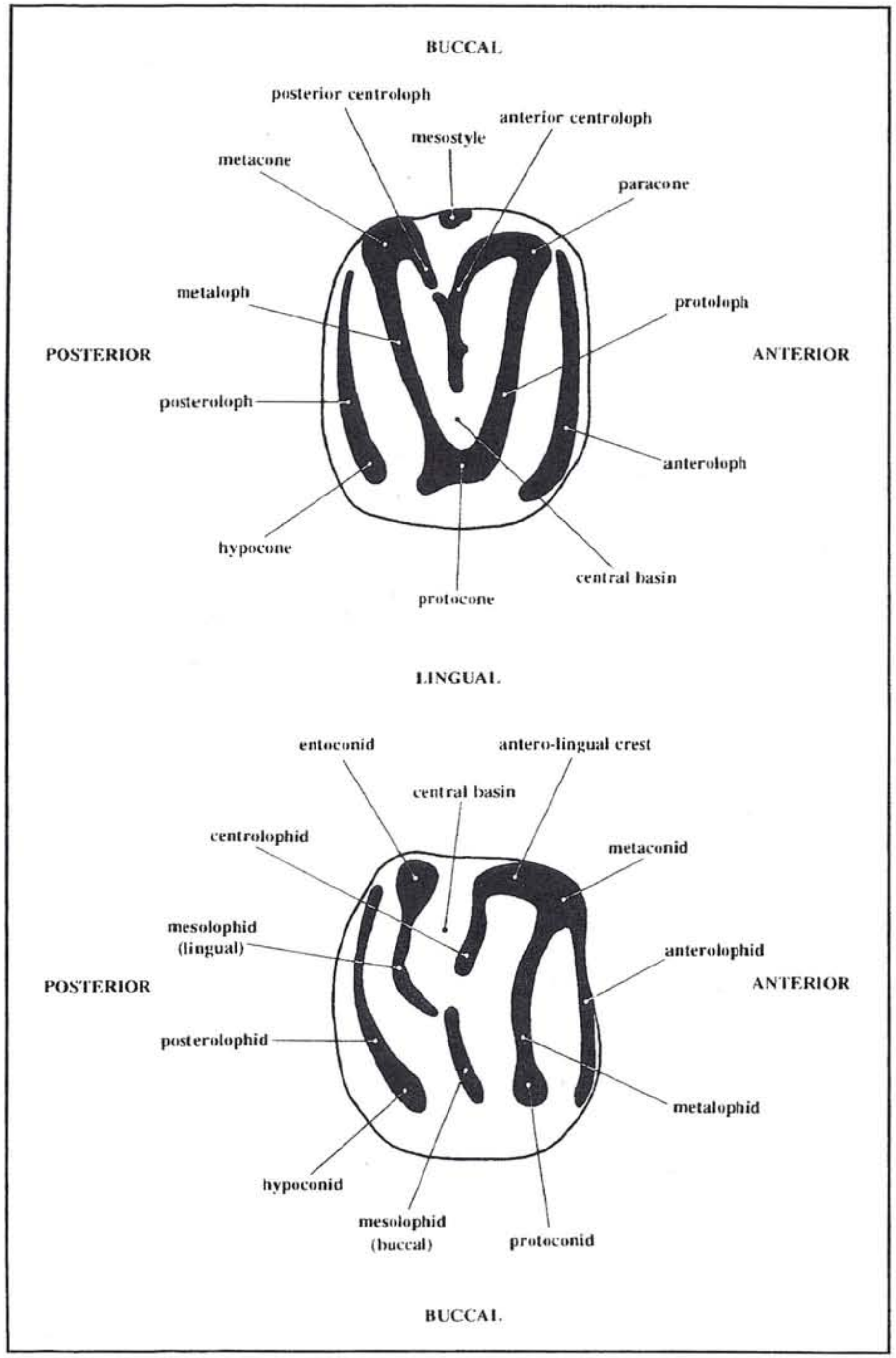


Figure 2. *Nomenclature used for the upper and lower cheek teeth of* Gliravus *(based on de Bruijn 1967).*

A new measuring method is proposed to discriminate dental elements on the basis of their general outline. With this method the M^1 and the M^2 of the studied *Gliravus* species can be much better discriminated than with the traditional length-width measurements.

Detailed measurements on the shape of the trigone and on the centroloph length of the upper cheek teeth allow quantification of morphological trends a) within toothrows, and b) within the stratigraphic interval studied. Evolutionary stages and relative abundances of the glirids allow correlations between the Sossís, Roc de Santa and Claverol sections (which is not possible on the basis of lithostratigraphy).

Introduction

Glirids form an important part of Late Eocene and Early Oligocene rodent associations in western Europe. The genus *Gliravus*, to which most of the primitive glirid species belong, was widespread in this time interval and has been found in many localities in western and south-western Europe (figure 1).

This paper decribes the glirid material from the Upper Eocene sections of Sossís, Roc de Santa and Claverol, which are located in the Tremp Basin in the province of Lleida in Spain.

The material described consists of 772 isolated cheek teeth from seven levels. These levels are named Sossís 2A, 2B and 2C (coded by SS2A, SS2B and SS2C), Roc de Santa 1 and 5 (coded by ROS1 and ROS5) and Claverol 3 and 5 (coded by CLA3 and CLA5).

Nomenclature and methods

Figure 2 shows the nomenclature used in the description of the occlusal surfaces of the cheek teeth. Measurements were taken with a Reflex three-dimensional measuring microscope, connected to a personal computer. For a detailed description of the measuring methods, the reader is referred to the penultimate chapter.

The figures of the plates were made with a Cambridge stereo-scan electron microscope.

Acknowledgements

I am indebted to Prof. N. López-Martínez of the Universidad Complutense de Madrid for the loan of the material. Sincere thanks are due to Dr. A. J. van der Meulen, Dr. H. de Bruijn and Dr. R. Daams for their willingness to discuss the material and to critically read the manuscript, to Dr. P. Pelaez-Campomanes for his valuable suggestions, to W. den Hartog for taking the photographs, to J. Luteyn for preparing the plates and to J. Luteyn and T. van Hinte for making and beautifying part of the illustrations.

Taxonomy

Family Gliridae Thomas, 1897
Subfamily Gliravinae Schaub, 1958
Genus *Gliravus* Stehlin and Schaub, 1951

Original reference: Stehlin and Schaub 1951, p. 136-139, 298-300, 368.

Type-species: *Gliravus majori* Stehlin and Schaub, 1951.

Emended diagnosis (Bosma and de Bruijn 1979): Cheek teeth with prominent main cusps. Hypocone not well delimited as in *Eogliravus*. Mesolophid low, narrow, and usually not extending to the entoconid. Trigone approximately symmetrical.

Remark:

In recent publications on dormice (Holden 1993 and Wahlert *et al.* 1993) the family name Myoxidae is preferred over the name Gliridae. Gliridae has been generally used during the last fifty years (Simpson, 1945) and Myoxidae has become obsolete. We therefore consider the re-introduction of the name Mioxidae against the purpose of the Code: "The Principle of Priority is to be used to promote stability and is not intended to be used to upset a long-accepted name in its accustomed meaning through the introduction of an unused name that is its senior synonym." (International Commission on Zoological Nomenclature 1985, p. 47)

Gliravus priscus Stehlin and Schaub, 1951
(Plate 1: figures 1-10)

Original reference: Stehlin and Schaub 1951, p. 136-137, 298-300, 368.

Emended diagnosis (Bosma and de Bruijn 1979): The cheek teeth of *G. priscus* are small and concave. The metalophid, the protoloph and the metaloph are uninterrupted smooth crests. The M^{1-2} usually have one centroloph.

Type locality: La Débruge (France).

Holotype (designated by Bosma and de Bruijn 1979): One isolated M_2, kept in the "Naturhistorisches Museum Basel" (Db. 486C), illustrated by Stehlin and Schaub 1951, figure 513.

Type-level: MP 17 (Schmidt-Kittler 1987), Late Eocene.

Material available:

90 isolated cheek teeth from 7 levels:

Claverol 5: 1 M^1;

Claverol 3: 2 M^3;

Roc de Santa 5: 1 M_1, 1 M_3;

Roc de Santa 1: 1 P^4, 6 M^1, 3 M^2, 2 M^3, 4 P_4, 5 M_1, 4 M_2;

Sossís 2C: 2 P^4, 5 M^1, 1 M^2, 1 P_4, 4 M_1, 6 M_2, 1 M_3;

element		n	length (mm.)				width (mm.)				area (mm.^{2})			
			min	max	m	sd	min	max	m	sd	min	max	m	sd
P^4	SS2A	2	.63	.75	.69	.09	.70	.80	.75	.07	.37	.47	.42	.07
	ROS1	1	.63	.63	.63	.00	.78	.78	.78	.00	.41	.41	.41	.00
M^1	SS2A	1	.79	.79	.79	.00	.84	.84	.84	.00	.56	.56	.56	.00
	SS2B	2	.80	.80	.80	.00	.89	.91	.90	.02	.61	.62	.61	.01
	SS2C	4	.71	.82	.79	.05	.81	.96	.91	.07	.51	.64	.60	.01
	ROS1	6	.70	.79	.75	.03	.86	.94	.91	.03	.51	.61	.56	.03
	CLA3	1	.79	.79	.79	.00	.90	.90	.90	.00	.60	.60	.60	.00
M^2	SS2B	6	.77	.84	.80	.03	.87	.95	.92	.03	.57	.68	.62	.04
	SS2C	1	.74	.74	.74	.00	.94	.94	.94	.00	.59	.59	.59	.00
	ROS1	2	.75	.78	.76	.02	.85	.92	.88	.05	.53	.61	.57	.06
M^3	ROS1	2	.64	.67	.65	.02	.76	.82	.79	.05	.38	.43	.40	.04
	CLA3	6	.75	.76	.76	.00	.89	.89	.89	.00	.53	.53	.53	.00
P_4	SS2C	1	.70	.70	.70	.00	.63	.63	.63	.00	.36	.36	.36	.00
	ROS1	4	.68	.72	.69	.01	.62	.65	.63	.02	.33	.36	.35	.01
M_1	SS2A	2	.75	.84	.79	.06	.78	.79	.78	.01	.50	.56	.53	.04
	SS2B	10	.75	.89	.81	.05	.76	.88	.81	.04	.49	.66	.57	.05
	SS2C	4	.83	.86	.84	.01	.82	.86	.84	.01	.60	.62	.61	.01
	ROS1	5	.81	.85	.83	.02	.80	.88	.84	.03	.56	.62	.59	.02
	ROS5	1	.84	.84	.84	.00	.83	.83	.83	.00	.61	.61	.61	.00
M_2	SS2A	3	.81	.87	.85	.03	.90	.92	.91	.01	.64	.68	.65	.02
	SS2B	11	.75	.88	.83	.04	.85	.92	.89	.02	.56	.71	.65	.05
	SS2C	6	.80	.86	.83	.03	.85	.89	.87	.02	.61	.69	.65	.03
	ROS1	4	.75	.86	.82	.05	.77	.94	.88	.08	.51	.71	.63	.09
M_3	SS2B	1	.78	.78	.78	.00	.81	.81	.81	.00	.50	.50	.50	.00
	SS2C	1	.71	.71	.71	.00	.72	.72	.72	.00	.43	.43	.43	.00

SS= Sosis ROS=Roc de Santa CLA= Claverol

Table 1. *Length, width and area measurements for* Gliravus priscus *(n=number, min=minimum value, max=maximum value, m=average, sd=standard deviation).*

zone	locality	l	w	reference
MP19	Escamps	.97	.91	Vianey-Liaud, 1974
MP18	La Debruge *	.94	.94	Stehlin and Schaub, 1951
MP18	Headon Hill 3	.86	.94	Bosma and de Bruijn, 1979
MP17/18?	Totland Bay	.85	.92	Bosma and de Bruijn, 1979
MP17	Headon Hill 2	.87	.93	Bosma and de Bruijn, 1979
MP17	Sosis 2C	.83	.89	this paper
MP17	Sosis 2B	.81	.87	this paper

* Measured from figure 513 (holotype)

Table 2. *Average length (l) and width (w) for M_2 of* Gliravus priscus *from a number of localities.*

Sossís 2B: 2 M^1, 8 M^2, 12 M_1, 12 M_2, 1 M_3;

Sossís 2A: 1 M^2, 2 M_1, 2 M_3.

Measurements: See table 1.

Description:

P^4

The occlusal surface has a subrounded circumference. The anteroloph is very short. The low and short centroloph is a curved crest running from the paracone or a position between paracone and metacone to a position on the protoloph just lingually of the paracone.

M^{1-2}

The first and second upper molars are characterized by a pattern consisting of four main cusps and five transverse crests. In comparison with the rectangular M^2, the M^1 are asymmetric and have their antero-lingual part reduced. The buccal side of the occlusal surface bends strongly upward to form a slope from which the paracone and metacone protrude prominently. The paracone is the largest cusp. In M^1 the protocone is located in the middle of the lingual part, whereas in M^2 it lies slightly more anteriorly. Although incorporated in the posteroloph, the hypocone is a distinct cusp. The protocone and hypocone are either separated by,a depression or connected by a low and narrow crest. The relatively short anteroloph is isolated from the protocone and ends at the base of the paracone. The metaloph and protoloph are the highest crests and they form a V-shaped trigone. The M^{1-2} have one centroloph, which in most cases is the anterior one. The posteroloph is shorter than the anteroloph and does not reach the lingual border. Three roots are present.

M^3

The paracone is the most prominent cusp, the metacone and hypocone are indistinct. The anteroloph and the protoloph are the widest and highest crests. The protocone is connected to the hypocone. In one specimen posteroloph and endoloph form one uninterrupted crest.

P_4

Compared to the lower molars the lower premolars are characterized by a reduced anterolophid and a reduced metalophid. Three of the four specimens have their metalophid and mesolophid connected on the buccal side of the occlusal surface. The mesolophid does not reach the entoconid in these specimens. In one specimen a short but relatively straight centrolophid is present, which is connected to the antero-lingual crest. Two roots are present.

M_{1-2}

The M_{1-2} have four main cusps and four transverse crests. All four cusps are well-developed. The metaconid is the highest cusp. This cusp is incorporated in an antero-lingual crest, which is separated from the entoconid by an incision. The anterolophid is connected to the metaconid, but not to the protoconid. One M_2 has a mesolophid which is not running to the entoconid, but to the posterior end

of the antero-lingual crest. The posterolophid is the highest transverse crest. Two roots are present.

M_3

The third lower molars are represented by three worn specimens. They differ from M_{1-2} in that the posterior end is more rounded, and in their more prominent mesolophid, which extends to the lingual side of the tooth.

Discussion:

Gliravus priscus had a large geographical distribution and is known from many localities in western and south-western Europe. Its temporal distribution is also large: from MP17 (Late Eocene) to MP23 (Middle Oligocene) (zonation of Schmidt-Kittler 1987). In table 2, the mean length and width of the second lower molar from our richest localities Sossís 2B and 2C are compared with the values of some other localities for a number of localities assigned to the zones MP 17-19. It can be observed from this table, that the average values of the Sossís localities are low and fit well in a general trend towards larger size.

Given this size increase, it is probable that the few teeth of "très petite taille" from Sossís recorded as *Gliravus* species indet. by Hartenberger 1971 belong to *Gliravus priscus*. The hypothesis of Bosma and de Bruijn 1982, p. 370) that these teeth may belong to *G.* minor Bosma and de Bruijn, 1982 is therefore rejected. In addition, the latter species is characterized by a continuous endoloph in most of the first and second molars, a feature which is not observed in any of the teeth of Sossís.

Vianey-Liaud 1989 made *G. priscus* the type species of a new genus *Glamys*, on the basis of the possession of a myomorphous skull from Mas de Got (from the Middle Oligocene of the Quercy, France). This skull is different from the protrogomorphous skull of the type species of *Gliravus*, *G. majori* and that of *G. itardiensis* Vianey-Liaud, 1989. Although this is an important result, we think that it is better not to use the skull morphology as a diagnostic character in genera of the Gliravinae. The main reason is practical: skulls of representatives of this subfamily are, and probably will remain very rare. On the other hand numerous teeth have been found, that have proved to be very suitable for taxonomic purposes. Using skull morphology as diagnostic character causes serious problems, if one wants to identify populations from which only teeth are known (which is the overwhelming majority).

Gliravus meridionalis Hartenberger, 1971

(Plate 2: figures 1-11)

Original reference: Hartenberger 1971, p. 124.

Diagnosis (translated from French): Smaller than *G. majori*; high anteroloph, and metaloph and protoloph forming a 'U' in the upper molars; in the lower molars the centrolophid is always present.

Type locality: Fons 4 (France).

Holotype: One isolated M^1 or M^2, kept in the "Faculté des Sciences de Montpellier" (Fs 4833) (plate 4 - figure 6 in Hartenberger 1971).

Type-level: MP 17 (Schmidt-Kittler 1987), Late Eocene.

Material available:

101 isolated cheek teeth from 5 levels:

Claverol 3: 1 M^3;

Roc de Santa 1: 4 M^2, 1 M_1, 1 M_2, 2 M_3;

Sossís 2C: 7 M^1, 2 M^2, 2 M^3, 1 P_4, 2 M_1, 1 M_2, 1 M_3;

Sossís 2B: 2 P^4, 16 M^1, 12 M^2, 5 M^3, 4 P_4, 8 M_1, 8 M_2, 8 M_3.

Sossís 2A: 1 M^1, 1 M^2, 2 M^3, 3 M_1, 4 M_2, 2 M_3;

Measurements: See table 3.

Description:

P^4

The occlusal surface has a sub-rectangular circumference. The anteroloph is a true crest and is connected to the curved protoloph. Lingually of this connection the anteroloph continues as a cingulum.

M^{1-2}

The first and second upper molars are characterised by a pattern consisting of four main cusps and five transverse crests. The paracone is the largest cusp. In the M^1 the protocone is located in the middle of the lingual part, whereas in the M^2 it lies slightly more anteriorly. The hypocone is a distinct cusp, although it is incorporated into the posteroloph. The protocone and hypocone are either separated by a depression or connected by a low and narrow crest. The anteroloph is well-developed and almost as high as the trigone. The metaloph and protoloph form a U-shaped trigone in the M^2, and an asymmetric V or U-shaped trigone in the M^1. Most specimens have one centroloph, which mostly is the anterior one. Three roots are present.

M^3

The paracone is the most prominent cusp, the metacone and hypocone are small. The protocone is connected to the hypocone. The anteroloph and the protoloph are the main crests. In most specimens the central basin contains at least one well-developed centroloph that usually reaches the buccal side, where it ends in a cuspule. This cuspule may be isolated or incorporated in a ridge, which connects paracone and metacone and is irregular in height. A second centroloph is usually present, and also a third centroloph may be present.

P_4

The lower premolars are more or less trapezium-shaped. The specimens strongly differ among each other in morphology. The broad metalophid is connected to the entoconid in two of the five specimens. The protoconid and the mesoconid, and the mesoconid and the hypoconid may be connected by narrow ridges.

element		n	length (mm.)				width (mm.)				area (mm.²)			
			min	max	m	sd	min	max	m	sd	min	max	m	sd
M^1	SS2A	1	1.07	1.07	1.07	.00	1.19	1.19	1.19	.00	1.06	1.06	1.06	.00
	SS2B	14	.99	1.09	1.03	.03	1.14	1.26	1.20	.03	.96	1.14	1.04	.05
	SS2C	4	.98	1.04	1.02	.03	1.15	1.20	1.18	.02	.96	1.06	1.03	.05
M^2	SS2A	1	1.02	1.02	1.02	.00	1.22	1.22	1.22	.00	1.01	1.01	1.01	.00
	SS2B	8	1.01	1.17	1.08	.06	1.23	1.37	1.29	.05	1.07	1.35	1.19	.10
	SS2C	2	1.00	1.04	1.02	.03	1.20	1.28	1.24	.06	1.02	1.11	1.07	.06
M^3	SS2A	1	.94	.94	.94	.00	1.11	1.11	1.11	.00	.82	.82	.82	.00
	SS2B	5	.88	1.02	.96	.07	1.04	1.20	1.13	.06	.72	.99	.86	.10
	SS2C	2	.86	.95	.91	.06	1.07	1.09	1.08	.01	.75	.81	.78	.04
	CLA3	1	.93	.93	.93	.00	1.07	1.07	1.07	.00	.78	.78	.78	.00
P_4	SS2B	4	.95	1.01	.98	.03	.81	.89	.86	.04	.65	.74	.69	.04
	SS2C	1	1.01	1.01	1.01	.00	.83	.83	.83	.00	.68	.68	.68	.00
M_1	SS2A	2	1.08	1.13	1.11	.04	1.05	1.10	1.07	.04	.97	1.01	.99	.03
	SS2B	8	1.07	1.16	1.11	.04	1.12	1.21	1.17	.03	1.00	1.16	1.08	.05
	SS2C	2	1.10	1.14	1.12	.03	1.13	1.13	1.13	.01	1.09	1.11	1.10	.01
	ROS1	1	1.09	1.09	1.09	.00	1.10	1.10	1.10	.00	1.03	1.03	1.03	.00
M_2	SS2A	3	1.03	1.14	1.09	.06	1.10	1.23	1.17	.07	1.00	1.18	1.11	.10
	SS2B	8	1.04	1.12	1.08	.03	1.15	1.26	1.22	.03	1.08	1.21	1.14	.05
	SS2C	1	1.13	1.13	1.13	.00	1.25	1.25	1.25	.00	1.24	1.24	1.24	.00
	ROS1	1	1.12	1.12	1.12	.00	1.23	1.23	1.23	.00	1.19	1.19	1.19	.00
M_3	SS2A	2	1.05	1.10	1.07	.03	1.04	1.18	1.11	.09	.87	1.05	.96	.13
	SS2B	6	1.03	1.12	1.07	.04	1.03	1.10	1.07	.03	.88	.99	.94	.04
	SS2C	1	1.06	1.06	1.06	.00	1.04	1.04	1.04	.00	.88	.88	.88	.00
	ROS1	2	.99	1.20	1.10	.14	.98	1.15	1.07	.12	.80	1.10	.95	.21

SS= Sosis ROS=Roc de Santa CLA= Claverol

***Table 3.** Length, width and area mesurements for* Gliravus meridionalis *(n=number, min=minimum value, max=maximum value, m=average, sd=standard deviation).*

M_{1-2}

The M_{1-2} have four main cusps and four or five transverse crests. The metaconid is the highest cusp. This cusp is incorporated in a antero-lingual crest, that is separated from the entoconid by a small incision. The anterolophid is connected to the metaconid, and in a few specimens a very low connection with the protoconid is present. Often mesolophid and centrolophid fuse at about a position half-way the width of the tooth. The centrolophid either has an irregular shape, or is reduced to one or more small cuspules or short ridges. The mesolophid reaches the entoconid in the majority of the specimens.

M_3

The M_3 are rounded at the posterior end with the maximum curvature at a position about half-way the width. The posteroloph is very robust. The centrolophid and the mesolophid may run parallel or may bifurcate. The mesolophid reaches the entoconid.

Discussion:

A comparison with the type material of Fons 4 can only be made tentatively because of the small quantity of material from this locality (only 15 teeth, and the M^{1-2} are not separated). Nevertheless, our *G. meridionalis* is larger than the type material: amongst our lower molars only one M_1 and one M_3 have sizes within the ranges of the *G. meridionalis* from Fons 4. The differences in size may be due to geographical and/or temporal variation.

Gliravus hispanicus n. sp.
(Plate 3: figures 1-10, plate 4: figures 1-10)

Diagnosis:

G. hispanicus is a *Gliravus* of medium size. The trigone has the shape of a sharp or obtuse V. The M^{1-2} have either one or two centrolophs, which may be fused. The centrolophs and the anteroloph in the M^{1-2} are lower than the other transverse crests. In the lower molars a centrolophid may be present, which may be fused with the mesolophid.

Differential diagnoses:

G. hispanicus differs from *G. robiacensis* Hartenberger, 1965 from the Upper Eocene of Robiac (France) by its larger size and by its relatively smaller protocone. Furthermore, *G. robiacensis* has a mesolophid that never reaches the entoconid, not even in the M_3, and it has no centrolophid.

G. hispanicus differs from *G. priscus* Stehlin and Schaub, 1951 by its larger size, by its less concave occlusal surface, and by its relatively lower main cusps. Furthermore, it differs from this species by its longer mesolophid and the presence of a centrolophid in the lower cheek teeth, and by its less distinct hypocone and its more complex centroloph pattern in the upper cheek teeth.

G. hispanicus is much larger than *G. minor* Bosma and de Bruijn, 1982. In addition, *G. hispanicus* has either no connection or a low and narrow connection between the hypocone and the protocone. In *G. minor* this connection is almost always a firm loph.

G. hispanicus differs from *G. daamsi* Bosma and de Bruijn, 1982 in its smaller size, and in its mesolophid, which does not reach the entoconid in the M_{1-2}.

G. hispanicus has a lower and narrower anteroloph and a shorter, lower and more irregular centroloph than *G. meridionalis* Hartenberger, 1971. The M^2 of *G. hispanicus* have a V-shaped trigone, whereas those of *G. meridionalis* have a U-shaped trigone. In contrast with the lower molars of *G. meridionalis*, those of *G. hispanicus* not always have a centrolophid.

G. hispanicus differs from *Bransatoglis bahloi* Bosma and de Bruijn, 1982 by its shorter centroloph(s) and by the absence of an extra crest between anterolophid and metalophid in M_{1-2}. Moreover, the mesolophid of M_{1-2} of *G. hispanicus* reaches the entoconid in a few specimens, whereas in *Bransatoglis bahloi* it is always connected to the entoconid.

Derivatio nominis: Named after the country of Spain.

Type-locality: Sossís 2B.

Holotype: An isolated right M^2, kept at the Universidad Complutense de Madrid (SS2B-309) (plate 3 - figure 4)

Type-level: MP 17 (zonation in Schmidt-Kittler 1987), Late Eocene.

Material from the type locality:

313 isolated cheek teeth:

1 D^4, 38 P^4, 49 M^1, 39 M^2, 11 M^3, 1 D_4, 24 P_4, 52 M_1, 65 M_2, 33 M_3.

Other material available:

268 isolated cheek teeth from 6 levels:

Claverol 5: 1 P^4, 2 M^1, 4 M^2, 1 M^3, 1 P_4, 1 M_1, 3 M_2, 4 M_3;

Claverol 3: 8 P^4, 10 M^1, 9 M^2, 4 P_4, 9 M_1, 10 M_2, 12 M_3;

Roc de Santa 5: 3 P^4, 6 M^1, 1 M^2, 4 M^3, 3 P_4, 9 M_1, 3 M_2;

Roc de Santa 1: 3 P^4, 8 M^1, 8 M^2, 1 M^3, 2 D_4, 5 P_4, 8 M_1, 12 M_2, 9 M_3;

Sossís 2C: 1 D^4, 3 P^4, 16 M^1, 17 M^2, 8 M^3, 1 D_4, 3 P_4, 16 M_1, 16 M_2, 10 M_3;

Sossís 2A: 1 D^4, 3 P^4, 1 M^1, 1 D_4, 5 M_1, 1 M_2, 1 M_3.

Measurements: See table 4.

Description of the type material:

D^4

The single specimen present (plate 3 - figure 2) contains a short, isolated but prominent anteroloph. The centroloph is isolated. A mesostyle is present.

P^4

Occasionally the hypocone is recognisable as a clear cusp (plate 4 - figure 1). The anteroloph is short to very short. All P^4 have one centroloph, which in most cases is connected to the paracone. In a few specimens the centroloph is connected to the metaloph. Three roots are present.

M^{1-2}

The dental pattern is characterised by the presence of four main cusps and five, or in some specimens six, main transverse crests. In most M^1 the protocone is situated slightly posteriorly of the middle of the lingual side of the tooth, whereas in most M^2 it is situated slightly anteriorly of the middle of the lingual side.

The protocone and the hypocone either are separated by a depression, or connected by a low and narrow crest. The hypocone is not a distinct cusp. The protoloph, the metaloph and the posteroloph are the highest crests. The anteroloph is isolated from the protocone, but connected to the paracone in most specimens. The protoloph and the metaloph form a V-shaped trigone, the V being either sharp or obtuse. The centrolophs are low, narrow crests. Most specimens have one anterior centroloph, but they may also have a posterior one, or they may have both. If there are two centrolophs present, they are usually fused. The centrolophs may be

element		n	length (mm.)				width (mm.)				area (mm.^{2})			
			min	max	m	sd	min	max	m	sd	min	max	m	sd
D^4	SS2A	1	.89	.89	.89	.00	.88	.88	.88	.00	.58	.58	.58	.00
	SS2B	1	1.02	1.02	1.02	.00	.85	.85	.85	.00	.65	.65	.65	.00
P^4	SS2A	3	.86	.87	.86	.01	.89	1.10	1.02	.12	.57	.82	.66	.06
	SS2B	33	.72	.90	.81	.04	.86	1.09	.99	.05	.52	.82	.66	.06
	SS2C	2	.82	.84	.83	.01	.97	.99	.98	.01	.63	.67	.65	.02
	ROS1	2	.77	.84	.81	.05	.97	1.02	.99	.04	.60	.70	.65	.07
	ROS5	3	.73	.86	.80	.06	.93	1.01	.97	.04	.59	.65	.63	.04
	CLA3	7	.75	.82	.79	.03	.90	.99	.96	.03	.61	.64	.62	.02
	CLA5	1	.73	.73	.73	.00	.94	.94	.94	.00	.58	.58	.58	.00
M^1	SS2B	39	.87	1.06	1.00	.04	1.06	1.22	1.13	.04	.81	1.03	.94	.05
	SS2C	13	.88	1.03	.98	.04	1.03	1.18	1.13	.04	.79	1.01	.92	.06
	ROS1	7	.93	.99	.97	.02	1.04	1.11	1.07	.03	.83	.91	.86	.03
	ROS5	7	.90	1.05	.97	.05	.99	1.14	1.07	.05	.75	.98	.86	.08
	CLA3	10	.88	.97	.92	.07	1.08	1.08	1.08	.00	.80	.89	.84	.06
	CLA5	2	.88	.97	.92	.07	1.08	1.08	1.08	.00	.80	.89	.84	.06
M^2	SS2B	31	.91	1.04	.98	.03	1.15	1.29	1.20	.04	.94	1.12	1.01	.05
	SS2C	9	.94	1.06	1.01	.04	1.16	1.30	1.22	.04	.91	1.15	1.03	.08
	ROS1	4	.95	1.06	1.00	.04	1.14	1.22	1.19	.04	.93	1.04	1.00	.05
	ROS5	2	.90	1.04	.97	.10	1.11	1.20	1.16	.06	.87	1.04	.96	.12
	CLA3	8	.88	.97	.93	.04	1.09	1.21	1.16	.04	.82	.98	.91	.06
	CLA5	3	.90	.99	.96	.05	1.17	1.18	1.17	.01	.90	.99	.95	.04
M^3	SS2B	11	.73	.89	.82	.04	.97	1.07	1.03	.04	.60	.75	.68	.05
	SS2C	4	.77	.91	.85	.06	.98	1.04	1.02	.03	.59	.72	.67	.06
	ROS1	1	1.01	1.01	1.01	.00	1.11	1.11	1.11	.00	.86	.86	.86	.00
	CLA5	1	.88	.88	.88	.00	1.04	1.04	1.04	.00	.70	.70	.70	.00
D_4	SS2A	1	.94	.94	.94	.00	.75	.75	.75	.00	.57	.57	.57	.00
	SS2B	1	1.01	1.01	1.01	.00	.80	.80	.80	.00	.62	.62	.62	.00
	SS2C	1	.98	.98	.98	.00	.82	.82	.82	.00	.63	.63	.63	.00
	ROS1	2	.86	.97	.92	.08	.67	.77	.72	.07	.43	.57	.50	.10
P_4	SS2B	23	.79	.97	.89	.05	.70	.90	.80	.05	.46	.67	.56	.05
	SS2C	3	.84	.87	.85	.02	.68	.79	.74	.05	.45	.53	.49	.04
	ROS1	4	.81	.98	.90	.08	.76	.84	.81	.04	.50	.65	.58	.07
	ROS5	3	.84	.91	.89	.07	.73	.87	.80	.07	.49	.65	.56	.08
	CLA3	4	.83	.88	.86	.02	.77	.85	.80	.04	.50	.57	.52	.03
	CLA5	1	.89	.89	.89	.00	.82	.82	.82	.00	.57	.57	.57	.00
M_1	SS2A	5	1.02	1.12	1.08	.04	1.04	1.15	1.10	.05	.95	1.16	1.04	.08
	SS2B	46	.97	1.15	1.05	.04	.96	1.11	1.05	.04	.85	1.06	.95	.05
	SS2C	14	1.00	1.07	1.03	.02	.93	1.09	1.05	.04	.79	.98	.92	.05
	ROS1	5	1.01	1.05	1.03	.02	1.03	1.10	1.05	.03	.90	.95	.93	.02
	ROS5	5	1.03	1.15	1.07	.03	1.02	1.08	1.05	.03	.93	1.00	.96	.03
	CLA3	6	.91	1.02	.98	.05	.95	1.03	.99	.03	.74	.90	.83	.06
	CLA5	1	1.03	1.03	1.03	.00	1.03	1.03	1.03	.00	.91	.91	.91	.00

Table 4. *Length, width and area mesurements for* Gliravus hispanicus *(n=number, min=minimum value, max=maximum value, m=average, sd=standard deviation).*

connected to the paracone, to the metacone, to both of them, or to none of them. The posteroloph reaches the base of the metacone. A mesostyle may be present (for example: plate 4 - figure 4). Three roots are present.

element		n	length (mm.)				width (mm.)				area (mm.^{2})			
			min	max	m	sd	min	max	m	sd	min	max	m	sd
M_2	SS2A	1	1.05	1.05	1.05	.00	1.17	1.17	1.17	.00	1.08	1.08	1.08	.00
	SS2B	46	.98	1.13	1.05	.04	1.05	1.29	1.14	.04	.91	1.22	1.04	.06
	SS2C	11	.98	1.10	1.05	.04	1.09	1.21	1.15	.04	.97	1.13	1.06	.07
	ROS1	6	1.01	1.12	1.05	.04	1.10	1.15	1.13	.02	.98	1.10	1.03	.05
	ROS5	1	1.01	1.01	1.01	.00	1.14	1.14	1.14	.00	.98	.98	.98	.00
	CLA3	9	.94	1.06	1.01	.03	1.06	1.15	1.09	.03	.90	1.07	.97	.05
	CLA5	3	.99	1.01	1.00	.02	1.10	1.11	1.11	.00	.94	1.00	.96	.03
M_3	SS2A	1	1.03	1.33	1.03	.00	1.15	1.15	1.15	.00	1.01	1.01	1.01	.00
	SS2B	25	.87	1.05	.98	.04	.94	1.12	1.01	.05	.68	.97	.81	.08
	SS2C	9	.94	1.07	1.01	.04	.96	1.11	1.05	.04	.77	.95	.87	.05
	ROS1	6	.97	1.04	1.01	.03	.97	1.09	1.02	.05	.79	.92	.85	.05
	ROS5	4	.98	1.13	1.07	.07	1.02	1.10	1.07	.04	.84	1.00	.95	.08
	CLA3	12	.86	.97	.93	.03	.89	1.03	.96	.04	.65	.80	.74	.04
	CLA5	4	.97	1.00	.98	.01	.95	1.08	1.00	.05	.77	.84	.80	.03

SS= Sosis ROS=Roc de Santa CLA= Claverol

Table 4. *(continued).*

M^3

The paracone is the most prominent cusp. The protoloph and the anteroloph are the broadest and highest ridges. The anteroloph is connected to both the paracone and the protocone. The posteroloph is connected to the metacone, and the hypocone to the protocone. The hypocone, and in most specimens also the metacone, are indistinct. In a number of specimens an uninterrupted ring of crests is present, which consists of the anteroloph, endoloph, posteroloph and a buccal ridge connecting paracone and metacone. In most specimen, the centroloph is connected to the metacone. In a number of specimen a centroloph branch is running to a position at the buccal side between paracone and metacone, where it may end in a cuspule.

D_4

Compared to the P_4, the single D_4 available has a circumference which is more pointed anteriorly, and has lower ridges. The posterolophid and the anteriorlingual crest are the most prominent crests. The central basin contains a short and low mesolophid and a low transverse ridge that reaches the entoconid (plate 3 - figure 7).

P_4

The P_4 have a reduced anterior part, resulting in a very short anterolophid and a short metalophid. Many specimens have a short extra crest that connects the lingual cuspule situated between metaconid and entoconid with the metalophid at a position about half-way this crest. Many specimens have a buccal connection between metalophid and mesolophid. Two roots are present.

M_{1-2}

Four main cusps and four main transverse crests are present. The metaconid is the highest cusp; in most specimens it forms the anterior end of a short but well-developed crest, which is situated along the anterior part of the lingual border. Usually this crest contains a cuspule at its posterior end, but it may also be isolated. The protoconid is incorporated into the metalophid, but is recognisable as a distinct cusp. The hypoconid is incorporated into the posterolophid and is usually indistinct.

The anterolophid is a thin crest connected to the base of the metaconid. The metalophid narrows when it approaches the metaconid and may be connected to it. The mesolophid-centrolophid complex is highly variable. The mesolophid may end in the central basin or may ditkan worden overgeplakt run in the direction of the entoconid, A centrolophid may be present, which runs in the direction of the cuspule at the posterior end of the antero-lingual crest. The mesolophid and the centrolophid may be fused. The posterolophid is the broadest and highest transverse crest. It ends at the base of the entoconid, to which it is either connected or almost connected. The M_{1-2} have two roots.

M_3

The mesolophid is generally longer than in the M_{1-2}. In a number of specimens it reaches the lingual side. Mesolophid and centrolophid may run parallel or fuse. In some specimens a low and short extra crest is present between the anterolophid and the metalophid.

Comparison of the assemblage of the type locality with those of the other localities:

The differences between the *G. hispanicus* assemblages are discussed in the next two chapters.

Discussion:

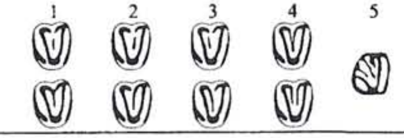
Hartenberger 1971 mentions some teeth from Sossís who resemble *G. priscus*, but are somewhat larger. This author ascribes them to *G.* aff. *priscus*. From the scatter diagrams of figure 13 and 14 in Hartenberger 1971 it appears that the size of these teeth is within the range of *G. hispanicus*. On this basis, there are reasons to believe that these teeth can be assigned to *G. hispanicus*.

The evolutionary relationship of *G. hispanicus* with a number of other Gliravinae is discussed in the last chapter.

Discrete variation: morphotypes

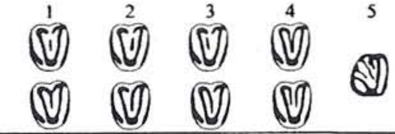
Introduction

Four series of standard morphotypes are defined for inter- and intraspecific comparison. The largest assemblage, Sossís 2B, is chosen to analyse morphological differences between the three *Gliravus* species as well as between different elements within the upper and lower toothrows of one species. Morphological differences between the localities are analysed in detail only for the first and



locality	morphotype (%) 1	2	3	4	5	tot	n
Claverol 5	100.0	.0	.0	.0	.0	100	1
Claverol 3	50.0	30.0	20.0	.0	.0	100	10
Roc de Santa 5	22.2	44.4	33.3	.0	.0	100	9
Roc de Santa 1	57.1	28.6	14.3	.0	.0	100	7
Sosis 2C	30.8	46.2	15.4	7.7	.0	100	13
Sosis 2B	28.3	50.0	17.4	4.4	.0	100	46
Sosis 2A	.0	100.0	0.0	.0	.0	100	1
total	33.3	44.8	18.4	3.5	.0	100	87

Table 5. *Distribution of the morphotypes 1-5 in the* M^1 *of* Gliravus hispanicus.

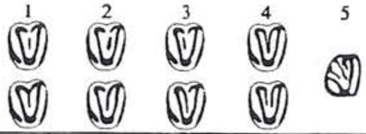


locality	morphotype (%) 1	2	3	4	5	tot	n
Claverol 5	25.0	75.0	.0	.0	.0	100	4
Claverol 3	62.5	.0	37.5	.0	.0	100	8
Roc de Santa 5	.0	100.0	.0	.0	.0	100	2
Roc de Santa 1	.0	42.9	28.6	28.6	.0	100	7
Sosis 2C	15.4	46.2	38.5	.0	.0	100	13
Sosis 2B	15.6	62.5	12.5	9.4	.0	100	32
Sosis 2A	.0	.0	.0	.0	.0	100	0
total	19.7	51.5	21.2	7.6	.0	100	66

Table 6. *Distribution of the morphotypes 1-5 in the* M^2 *of* Gliravus hispanicus.

second molars of *G. hispanicus*, because, on the average, these elements are the best represented. It must be remarked that the order of the localities shown in the tables referred to in this and the next chapters is not arbitrary. (The stratigraphy will be discussed in the last chapter.)

This chapter only deals with the analysis of morphotypes, which are discrete classes. The analysis of the features which are measured on a continuous scale is described in the next chapter.



element	morphotype (%) 1	2	3	4	5	tot	n
<u>G. priscus</u>							
M^1	.0	100.0	.0	.0	.0	100	2
M^2	12.5	62.5	25.0	.0	.0	100	8
<u>G. meridionalis</u>							
P^4	.0	100.0	.0	.0	.0	100	1
M^1	26.7	46.7	26.7	.0	.0	100	15
M^2	10.0	50.0	20.0	20.0	.0	100	10
M^3	.0	.0	20.0	40.0	40.0	100	5
<u>G. hispanicus</u>							
D^4	100.0	.0	.0	.0	.0	100	1
P^4	11.4	85.7	2.9	.0	.0	100	35
M^1	28.3	50.0	17.4	4.4	.0	100	46
M^2	15.6	62.5	12.5	9.4	.0	100	32
M^3	25.0	.0	50.0	25.0	.0	100	8

***Table 7**. Distribution of the morphotypes 1-5 in the upper cheek teeth of the three* Gliravus *species from Sossís 2B.*

locality	morphotype (%) A	B	C	tot	n
Claverol 5	.0	100.0	.0	100	2
Claverol 3	11.1	88.9	.0	100	9
Roc de Santa 5	.0	100.0	.0	100	9
Roc de Santa 1	57.1	42.9	.0	100	7
Sosis 2C	33.3	66.7	.0	100	12
Sosis 2B	40.5	59.5	.0	100	42
Sosis 2A	100.0	.0	.0	100	1
total	32.9	67.1	.0	100	82

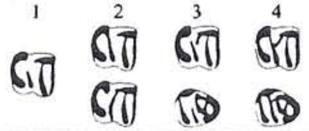
***Table 8**. Distribution of the morphotypes A-C in the M^1 of* Gliravus hispanicus.

locality	morphotype (%) A	B	C	tot	n
Claverol 5	33.3	66.6	.0	100	3
Claverol 3	37.5	62.5	.0	100	8
Roc de Santa 5	.0	100.0	.0	100	3
Roc de Santa 1	71.4	28.6	.0	100	7
Sosis 2C	30.0	70.0	.0	100	10
Sosis 2B	32.1	67.9	.0	100	28
Sosis 2A	.0	.0	.0	100	0
total	39.3	60.7	.0	100	59

***Table 9**. Distribution of the morphotypes A-C in the M^2 of* Gliravus hispanicus.

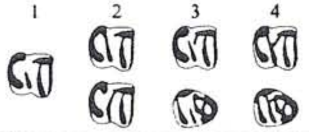
element	morphotype (%) A	B	C	tot	n
<u>G. priscus</u>					
M^1	50.0	50.0	.0	100	2
M^2	37.5	62.5	.0	100	6
<u>G. meridionalis</u>					
P^4	.0	100.0	.0	100	1
M^1	46.7	53.3	.0	100	15
M^2	66.7	33.3	.0	100	9
M^3	20.0	60.0	20.0	100	5
<u>G. hispanicus</u>					
D^4	100.0	.0	.0	100	1
P^4	24.1	75.9	.0	100	29
M^1	40.5	59.5	.0	100	42
M^2	32.1	67.9	.0	100	28
M^3	.0	71.4	28.6	100	7

***Table 10**. Distribution of the morphotypes A-C in the upper cheek teeth of the three* Gliravus *especies from Sossís 2B.*



locality	morphotype (%)							n
	1	2	3	4	5	6	tot	
Claverol 5	.0	.0	.0	100.0	.0	.0	100	1
Claverol 3	60.0	20.0	20.0	0.0	.0	.0	100	5
Roc de S. 5	20.0	40.0	40.0	.0	.0	.0	100	5
Roc de S. 1	80.0	20.0	.0	.0	.0	.0	100	5
Sosis 2C	35.7	28.6	21.4	14.3	.0	.0	100	14
Sosis 2B	58.3	25.0	6.3	10.4	.0	.0	100	48
Sosis 2A	40.0	20.0	20.0	.0	.0	20.0	100	5
total	51.8	25.3	12.1	9.6	.0	1.2	100	83

Table 11. *Distribution of the morphotypes 1-6 in the* M_1 *of* Gliravus hispanicus.



locality	morphotype (%)							n
	1	2	3	4	5	6	tot	
Claverol 5	33.3	33.3	.0	.0	33.3	.0	100	3
Claverol 3	50.0	25.0	.0	25.0	25.0	.0	100	8
Roc de S. 5	.0	100.0	.0	.0	.0	.0	100	1
Roc de S. 1	28.6	42.9	28.6	.0	.0	.0	100	7
Sosis 2C	10.0	70.0	20.0	.0	.0	.0	100	10
Sosis 2B	49.0	35.3	3.9	9.8	2.0	.0	100	51
Sosis 2A	.0	.0	.0	100.0	.0	.0	100	1
total	40.0	34.0	8.0	15.0	3.0	.0	100	81

Table 12. *Distribution of the morphotypes 1-6 in the* M_2 *of* Gliravus hispanicus.

The upper cheekteeth

The number and the direction of the centrolophs

Five morphotypes are defined in order to classify the upper cheek teeth according to the pattern of centrolophs (tables 5-7):

1. a type with one complete or incomplete centroloph, not running in the direction of the paracone or in the direction of the metacone;

2. a type with one complete or incomplete centroloph, running in the direction of the paracone;
3. a type with one complete or incomplete centroloph, running in the direction of the metacone;
4. a type with two centrolophs;
5. a type with three centrolophs.

The tables 5 and 6 show the morphotypes of M^1 and M^2 and their distribution within the seven *Gliravus hispanicus* populations. It can be observed that the morphological variation in the M^1 from Sossís 2B, 2C and Roc de Santa 5 is similar and is characterised by the dominance of morphotype 2 over morphotype 1. In Roc de Santa 1 and Claverol 3 morphotype 1 is more frequent than morphotype 2, but these assemblages contain only 7 and 10 teeth respectively.

Sossís 2B and 2C differ in the frequencies of the morphotypes 2 and 3 in the M^2. Sossís 2C contains many specimen with a posterior centroloph, whereas in Sossís 2B the type with an anterior centroloph prevails. The distribution in Claverol 3 differs from the others because morphotype 2 is not represented there.

Table 7 shows the distributions for all the upper elements from Sossís 2B. As can be seen from this table, dental patterns are progressively more complex in the more posterior elements. The M^3 may even show secondary crests outside the trigone (in *G. meridionalis*).

It can be seen from table 7 that *G. hispanicus* and *G. meridionalis* have about the same distributions per element. Because *G. priscus* is poorly represented, its proportions are not very reliable.

Protocone-hypocone connection

Three morphotypes are defined to describe the state of the protocone-hypocone connection (tables 8-10):

A. a type with the protocone-hypocone connection absent;

B. a type with the presence of a low and narrow connection between the protocone and the hypocone;

C. a type with the presence of a high and broad connection between the protocone and the hypocone.

The stratigraphic distribution of the morphotypes of the M^{1-2} is shown in the tables 8 and 9 respectively. On the average, most specimens are of type B, with maximum proportions in the M^1 from Roc de Santa 5 and Claverol 3 and 5, and in the M^2 from Roc de Santa 5. In contrast, Roc de Santa 1 contains relatively many specimen without the protocone-hypocone connection, especially in the M^2.

Table 10 shows that a high and broad protocone-hypocone connection (type C) is present only in the M^3. It can further be seen, that *G. meridionalis* has a larger proportion of M^2 without this connection, compared to the other two species.

element	morphotype (%) 1	2	3	4	5	6	tot	n
<u>G. priscus</u>								
M_1	.0	80.0	20.0	.0	.0	.0	100	10
M_2	60.0	20.0	20.0	.0	.0	.0	100	10
M_3	.0	100.0	.0	.0	.0	.0	100	1
<u>G. meridionalis</u>								
P_4	.0	100.0	.0	.0	.0	.0	100	1
M_1	12.5	25.0	12.5	50.0	.0	.0	100	8
M_2	14.3	.0	14.3	57.1	14.3	.0	100	7
M_3	.0	.0	.0	50.0	33.3	16.7	100	6
<u>G. hispanicus</u>								
D_4	.0	.0	.0	100.0	.0	.0	100	1
P_4	9.5	38.1	14.3	19.1	9.5	9.5	100	21
M_1	58.3	25.0	6.3	10.4	.0	.0	100	48
M_2	49.0	35.3	3.9	9.8	2.0	.0	100	51
M_3	.0	15.4	15.4	34.6	30.8	3.9	100	32

Table 13. *Distribution of the morphotypes 1-6 in the lower cheek teeth of the three* Gliravus *especies from Sossís 2B.*

locality	morphotype (%) A	B	tot	n
Claverol 5	100.0	.0	100	1
Claverol 3	40.0	60.0	100	5
Roc de Santa 5	40.0	60.0	100	5
Roc de Santa 1	40.0	60.0	100	5
Sosis 2C	28.6	71.4	100	14
Sosis 2B	39.1	60.9	100	46
Sosis 2A	80.0	20.0	100	5
Total	40.7	59.3	100	81

Table 14. *Distribution of the morphotypes A-B in the M_1 of* Gliravus hispanicus.

locality	morphotype (%) A	B	tot	n
Claverol 5	.0	100.0	100	2
Claverol 3	14.3	85.7	100	7
Roc de Santa 5	100.0	.0	100	1
Roc de Santa 1	28.6	71.4	100	7
Sosis 2C	60.0	40.0	100	10
Sosis 2B	34.0	66.0	100	50
Sosis 2A	.0	100.0	100	1
Total	34.6	65.4	100	78

Table 15. *Distribution of the morphotypes A-B in the M_2 of* Gliravus hispanicus.

element	morphotype (%) A	B	tot	n
<u>G. priscus</u>				
M_1	30.0	70.0	100	10
M_2	50.0	50.0	100	10
M_3	.0	100.0	100	1
<u>G. meridionalis</u>				
P_4	.0	100.0	100	4
M_1	12.5	87.5	100	8
M_2	25.0	75.0	100	8
M_3	33.3	66.7	100	6
<u>G. hispanicus</u>				
D_4	.0	100.0	100	1
P_4	4.6	95.5	100	22
M_1	39.1	60.9	100	46
M_2	34.0	66.0	100	50
M_3	19.2	80.8	100	26

Table 16. *Distribution of the morphotypes A-B in the lower cheek teeth of the three* Gliravus *species from Sossís 2B.*

The lower cheekteeth

The mesolophid-centrolophid complex and the number of crests

The pattern of the mesolophid-centrolophid complex is highly variable. Six morphotypes are distinguished (tables 11-13):

1. a type with one short mesolophid;
2. a type with one long mesolophid or one long centrolophid;
3. a type with an incomplete mesolophid and an incomplete centrolophid;
4. a type with a joining mesolophid and centrolophid;
5. a type with a parallel mesolophid and centrolophid;
6. a type as 4 or 5, but with another extra crest.

The tables 11 and 12 show the variation in *G. hispanicus* in the M_1 and the M_2 respectively. In both elements the simple morphotype 1 occurs most frequently, although it is more dominant in the M_1 than in the M_2. The relative frequencies of the morphotypes fluctuate from one locality to another, but a large part of these fluctuations must be ascribed to the statistical uncertainty associated with the small numbers of teeth. However, the low proportions (especially in M_2) of morphotype 1 in Sossís 2C and the high proportion in the M_1 of Roc de Santa 1 seem to be real.

The frequencies for the different species and elements are compared in table 13. *G. hispanicus* is the only species, which has the P_4 well represented. It can be seen that this element has a highly variable crest pattern, with every morphotype present. Furthermore, also in the lower toothrow of *G. meridionalis* and *G. hispanicus* a gradient of increasing complexity in posterior direction can be observed. A similar gradient was observed in the upper toothrow (see the preceding paragraph).

Table 13 shows clearly that the three species have a different distribution of the morphotypes. In *G. hispanicus* type 1 (one short mesolophid) and to a lesser degree type 2 (one long mesolophid or centrolophid) dominate in both the first and second lower molar. In *G. priscus* most M_1 are of type 2, while the majority of M_2 are of type 1. In *G. meridionalis* the bifurcated type (type 4) is dominant.

The metaconid-metalophid connection

Two morphotypes are distinguished on the basis of the state of the metaconid-metalophid connection (tables 14-16):

A. a type with the metalophid reaching the metaconid;

B. a type with the metalophid not reaching the metaconid.

Table 14 shows the distribution of the two types of M_1 in *G. hispanicus*. In most localities type B prevails (although the statistical uncertainty is large for some localities). According to table 15 the average frequency of type B is slightly higher in the M_2 than in the M_1. The M_2 from Sossís 2C do not have the average distribution of morphotypes with type A being dominant.

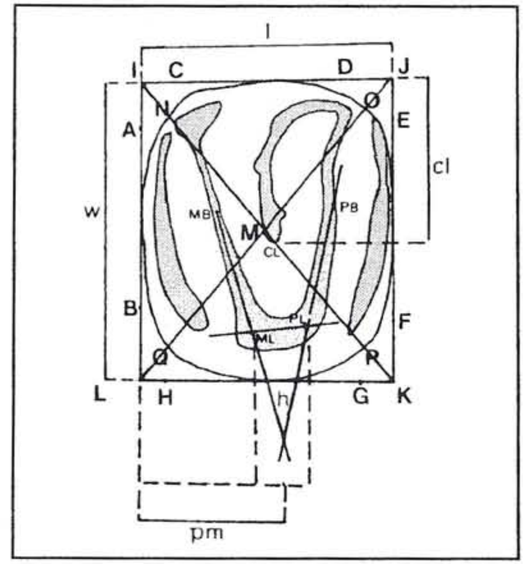


Figure 3. *Measurements on the upper cheek teeth of* Gliravus. *Explanation: see text.*

Table 16 shows that the metalophid and metaconid of M_1 and M_2 are more often connected in *G. meridionalis* than in the other two species.

The localities compared

Summarising, on the basis of the analysis of morphotypes it may be concluded that the morphology of the cheek teeth was not constant during the studied interval. More specifically, the localities from the Roc de Santa and Claverol sections tend to have similar distributions of morphotypes in the upper cheek teeth. The lower teeth seem to have a less variable morphology, although at least one locality (Sossís 2C) clearly differs from the others.

Continuous variation: measurements

Introduction

In this chapter the results of the measurements on the cheek teeth of the three *Gliravus* species are described. The next paragraph deals with tooth size and contains results of length, width and area measurements. It is followed by a paragraph, in which a new measuring method is described, which discriminates specimens on the basis of their general outlines. The method is illustrated with first and second upper molars of *Gliravus*. The last two paragraphs deal with measurements on the position of the protocone and on the relative length of the centroloph complex.

element	size ranking (1 = smallest, __ = same size)						
	1	2	3	4	5	6	7
P^4	CLA5	CLA3	ROS5	ROS1 —	SS2C	SS2B —	SS2A
M_1	CLA3	CLA5	SS2C	ROS1	SS2B	ROS5	SS2A
M_2	CLA5	CLA3	ROS5	ROS1	SS2B	SS2C	SS2A
M_3	CLA3	CLA5	SS2B	ROS1	SS2C	ROS5	SS2A

Table 17a. *Locality rankings for the size of 4 elements of* Gliravus hispanicus *(size is measured as the average area of the occlusal surface).*

locality	sum of rankings
CLA5	6
CLA3	6
ROS1	16.5
ROS5	18
SS2C	19
SS2B	19.5
SS2A	28

Table 17b. *Totals of the locality rankings in table 17a. (In case two localities as equal ranking in table 17a, both get the average value)*

Length, width and area

Measuring method

In order to measure length and width, the teeth were orientated so that width could be measured parallel to an anterior or a posterior facet. In both upper and lower teeth, the posterior facet was chosen for D4, P4 and M1 and the anterior facet was chosen for M2 and M3. A rectangle was defined to enclose the occlusal surface with the anterior and posterior sides of this rectangle running parallel to the chosen facet (see figure 3). Length (l) and width (w) were defined as the sides of this rectangle.

In order to calculate length and width two arbitrary points are measured along each side of the rectangle (points A-H in figure 3). (The coordinates of these points are the measured images of a light diode of the 'Reflex' measuring microscope.) Next, the the corner points I-L, which are the intersections of the four lines through the points A-H, are calculated. The distances between these corner points are the length and width.

Area was measured in the horizontal plane by "moving" the light diode image around the occlusal outline. The precision of this area measurement is high: a series of 5 trials yielded a standard deviation in the range of 5 micron.

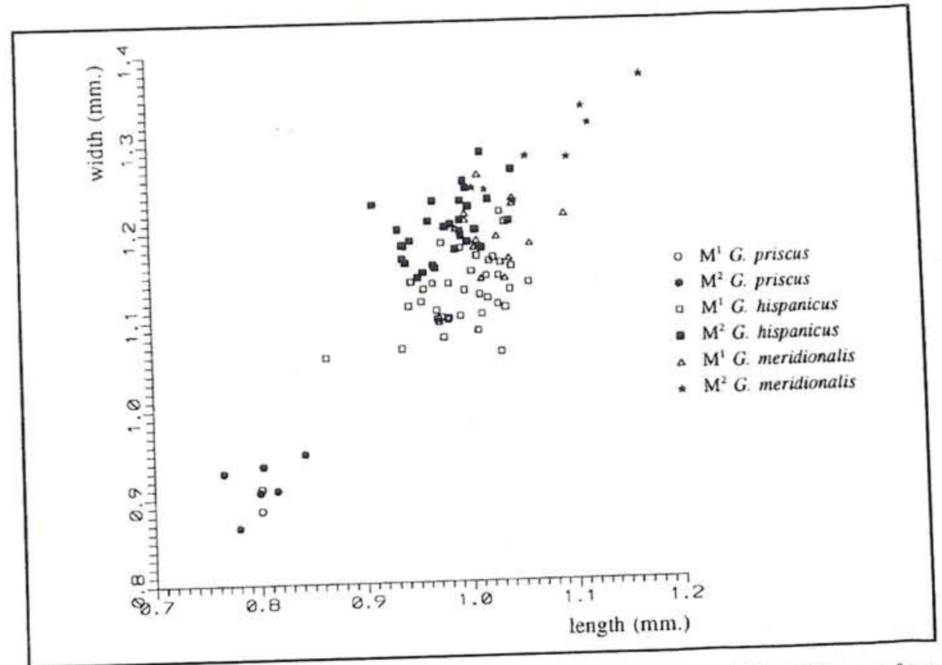


Figure 4. *Scatter diagram showing length and width of the* M^1 *and* M^2 *of* Gliravus *from Sossís 2B.*

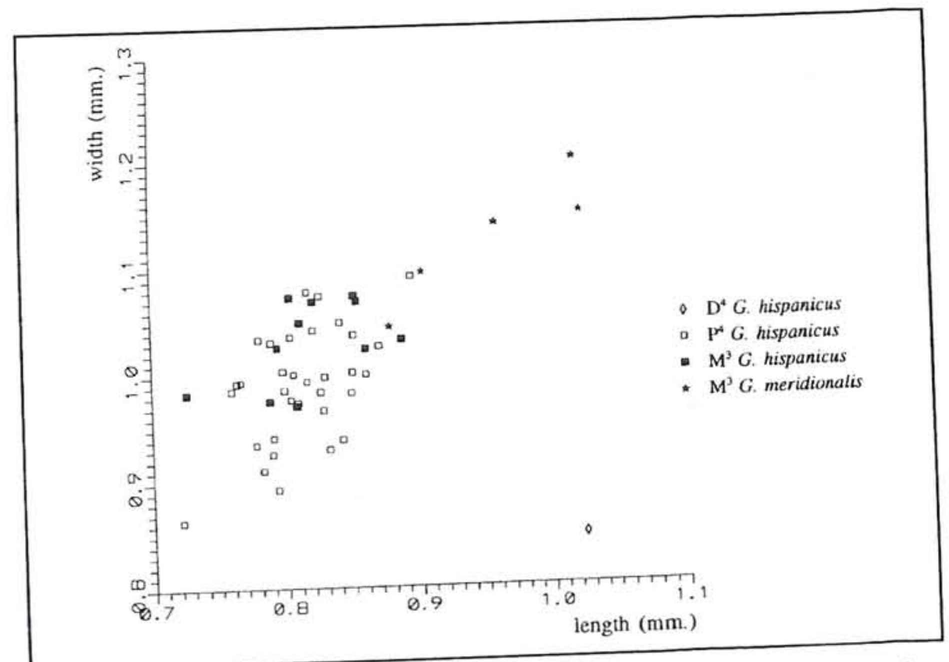


Figure 5. *Scatter diagram showing length and width of the* D^4, P^4 *and* M^3 *of* Gliravus *from Sossís 2B.*

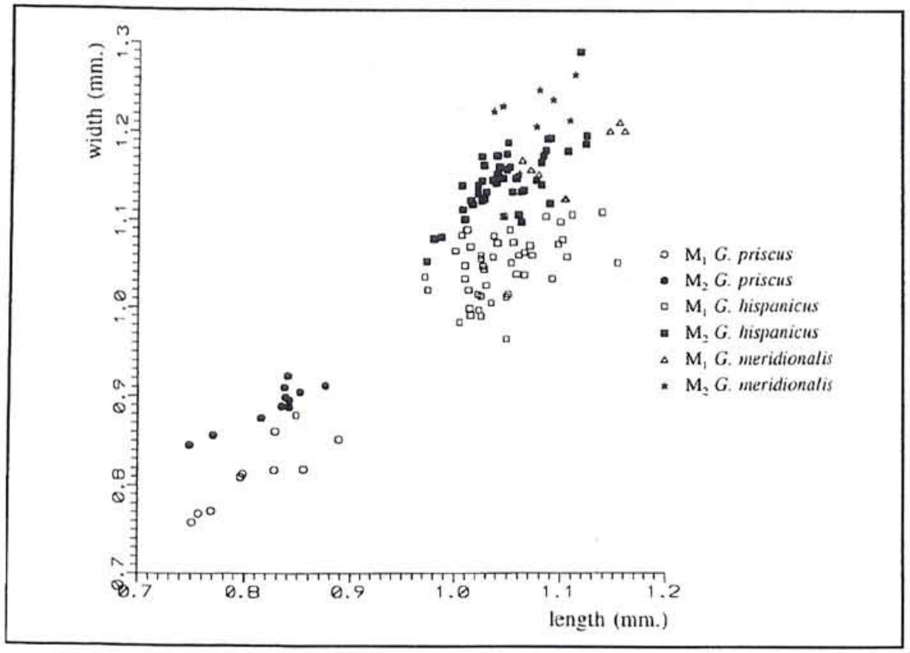


Figure 6. *Scatter diagram showing length and width of the M_1 and M_2 of* Gliravus *from Sossís 2B.*

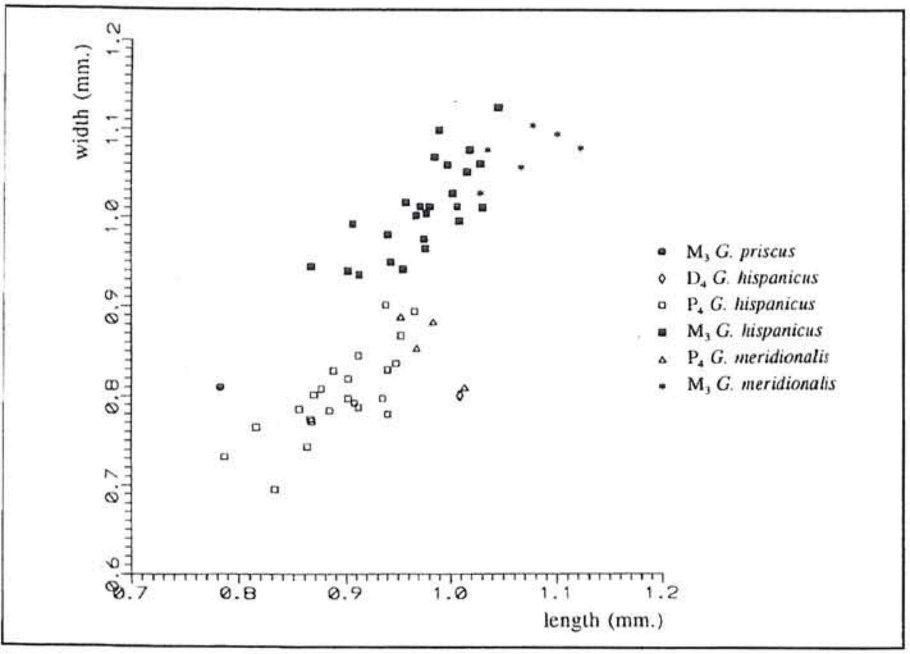


Figure 7. *Scatter diagram showing length and width of the D_4, P_4 and M_3 of* Gliravus *from Sossís 2B.*

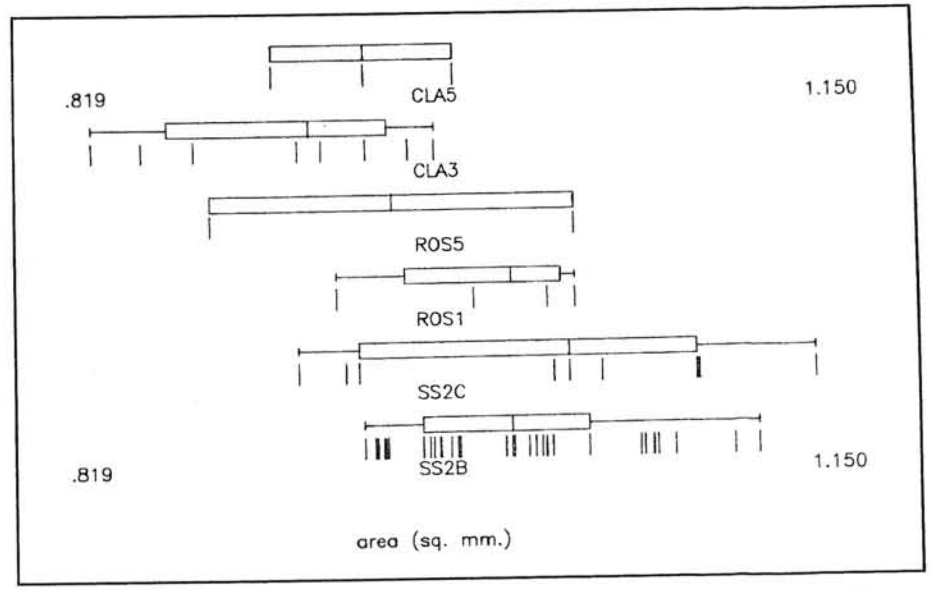


Figure 8. *Diagram showing the spread of the area of the occlusal surface of M^2 of* Gliravus hispanicus. *Explanation of the box plots: The line in the middle of the box represents the median, the box extends from the 25th percentile to the 75th percentile and the lines emerging from the box extend to values three-halves the interquartile range rolled back to where there is data.*

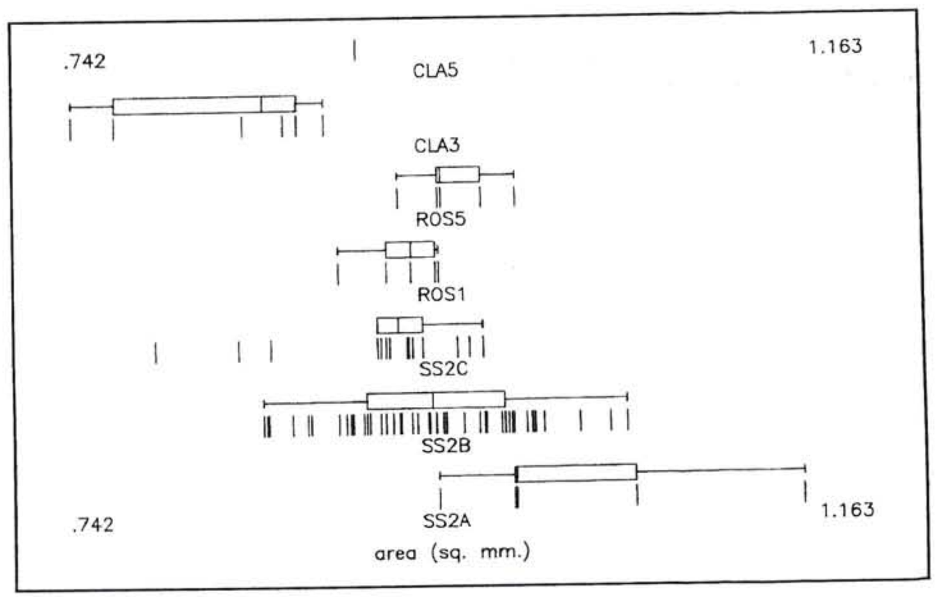


Figure 9. *Diagram showing the spread of the area of the occlusal surface of M_1 of* Gliravus hispanicus. *Explanation of the box plots: see caption of figure 8.*

General results

General statistics for all elements of all seven assemblages are shown in the tables 1, 3 and 4. The most important results will be discussed below.

Length-width relation

Length-width plots for Sossís 2B are shown in the figures 4-7. *G. priscus* can be easily distinguished from the two other species by its small size. The *G. meridionalis* and *G. hispanicus* clusters show a small overlap.

Spread of area, localities compared

Table 4 was used to construct table 17a, which per element ranks the localities according to the average tooth area of *G. hispanicus*. Only those elements are included, that occur in all seven faunas (P^4 and $M_{1\text{-}3}$). In order to average out statistical errors of size per element and in order to obtain one overall size score for each locality, the rankings were added up (table 17b). (It must be remarked however, that the scores for the individual elements may not be independent, because elements may belong to the same individuals).

Table 17b shows that the Claverol localities have a very low score, which means that they contain a relatively small *Gliravus hispanicus*. The largest *G. hispanicus* is from Sossís 2A. The other Sossís levels and the Roc de Santa levels have about equal scores.

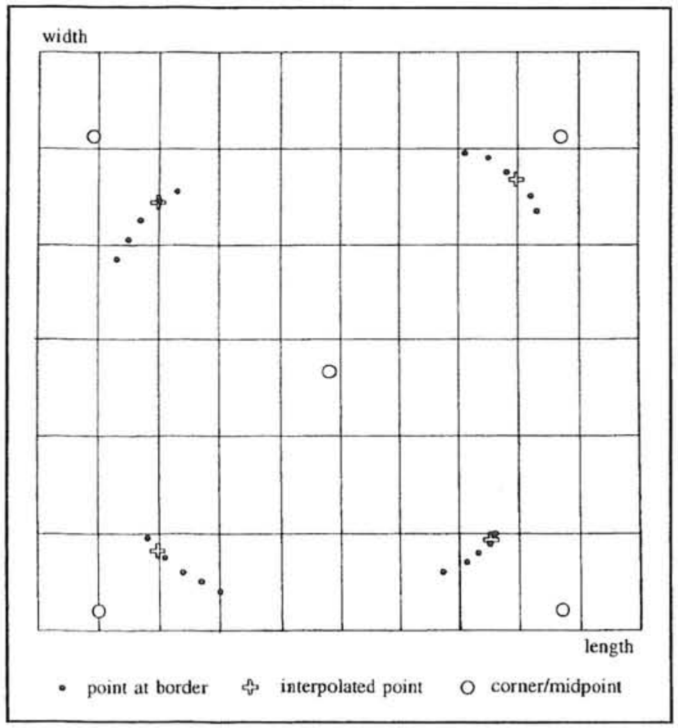


Figure 10. *Illustration of the method used to make measurements diagonally across the occlusal surface.*

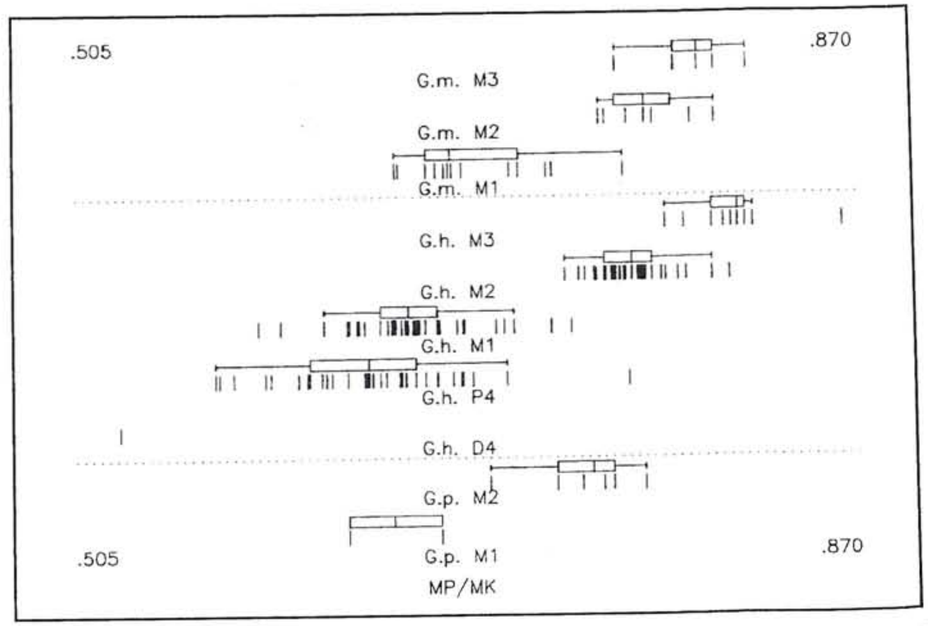


Figure 11. *Diagram showing the spread of the quotient MP/MK in the upper cheek teeth of Gliravus from Sossís 2B. The distances MP and MK are explained in figure 3. Explanation of the box plots: see caption of figure 8. G.p.=*Gliravus priscus, *G.h.=*Gliravus hispanicus, *G.m.=*Gliravus meridionalis.

The figures 8 and 9 show the spread of the area of the occlusal surface of M^2 and M_1 in *G. hispanicus* from the seven assemblages.

Diagonal measurements

Measuring method

Diagonal measurements were taken in order to describe the general outline of the teeth, and to investigate the possibility to discriminate better between elements than can be done by the method of measuring length and width. Measurements were done for the upper teeth only.

The method's first step is the calculation of the coordinates of the corners I-L of the length-width rectangle (figure 3). Next, the center M of the rectangle is calculated as the intersection of the two diagonals I-K and J-L The following step would be the calculation of the distances of the center M to the points N, O, P and Q situated along the border of the tooth. However, it is not possible to measure these distances directly, because one cannot observe the exact position of the points M-Q through the measuring microscope. To solve this problem, an indirect method was devised (figure 10). At each corner five points are measured along the border of the tooth. Next, a computer program determines the particular pair of points between which the diagonal runs. Finally, a linear interpolation between

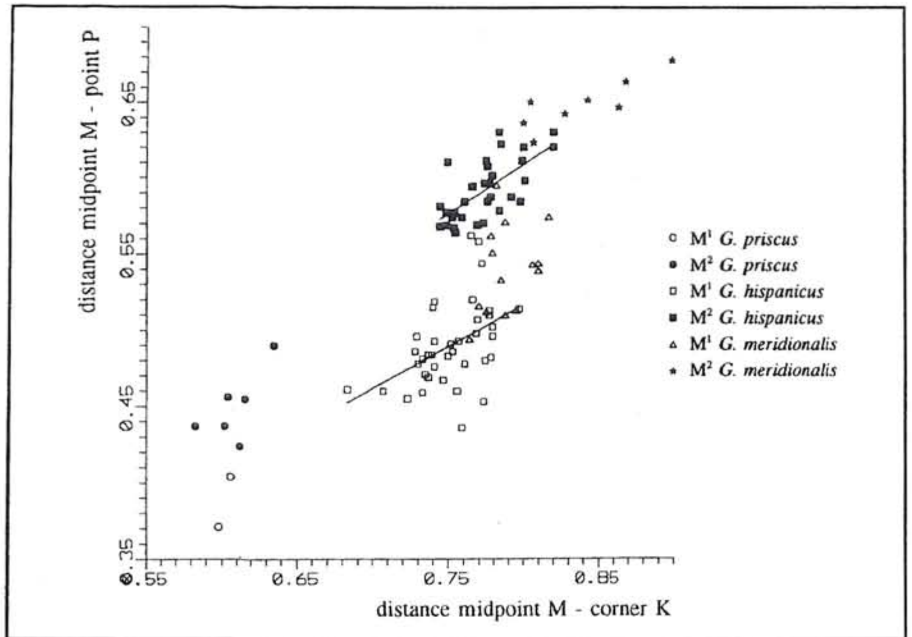


Figure 12. *Scatter diagram showing MK and MP in the upper check teeth of* Gliravus *from Sossís 2B. The distances MP and MK are explained in figure 3. Linear regressions lines are drawn for* Gliravus hispanicus.

these two points is made to estimate the points M-Q (indicated by the crosses in figure 10).

The antero-lingual corner of the upper teeth

As an illustration of this method, the variability in the shape of the antero-lingual corner of the upper elements in Sossís 2B is analysed.

Figure 11 shows the variability in the quotient of the distance between the center and the border of the occlusal surface, measured in the direction of the antero-lingual corner of the length-width rectangle (distance MP) on the one hand, and the distance between the center and this corner (MK) on the other hand. An extreme low value of MP/MK is attained in D^4. This is understandable given the triangular shape of this element. However, a more remarkable result is the clear discrimination of the M^{1-2} in all three species. Figure 12 shows the same result in a scatter diagram of MP and MK. For *G. hispanicus* two linear regression lines are added. These lines show that for the same center-to-corner distance, the M^1 show have on the average some 0.08 mm. reduction of the antero-lingual corner with respect to the M^2. When we compare figure 12 to figure 4, it is clear that it is much more difficult to discriminate between the first two upper molars of these *Gliravus* species on the basis of length and width.

element	locality	PML		h (in °)		CLW	
		n	mean	n	mean	n	mean
G. priscus							
P^4	SS2A	2	.54	2	43	2	.46
	ROS1	1	.57	1	40	1	.62
M^1	SS2A	1	.48	1	42	1	.57
	SS2B	2	.42	2	47	2	.60
	SS2C	4	.49	4	37	4	.60
	ROS1	6	.51	4	39	4	.55
	CLA5	1	.49	1	35	1	.62
M^2	SS2B	6	.54	8	38	6	.63
	SS2C	1	.56	1	32	1	.69
	ROS1	2	.55	2	31	2	.61
M^3	ROS1	2	.60	2	33	2	.58
	CLA3	2	.53	2	26	2	.45
G. meridionalis							
P^4	SS2B			1	19		
M^1	SS2A	1	.47	1	39	1	.63
	SS2B	13	.48	15	39	13	.66
	SS2C	4	.46	6	35	4	.70
M^2	SS2A	1	.50	1	27	1	.76
	SS2B	8	.55	10	31	8	.70
	SS2C	2	.56	2	26	2	.71
	ROS1	4	.57	4	25	4	.66
M^3	SS2A	2	.55	2	34	2	.73
	SS2B	5	.57	5	32	5	.72
	SS2C	2	.51	2	38	2	.67
	CLA3	1	.56	1	36	1	.73
G. hispanicus							
D^4	SS2A	1	.53	1	55	1	.48
	SS2B	1	.30	1	65	1	.65
P^4	SS2A	2	.57	2	35	2	.61
	SS2B	29	.54	31	46	29	.61
	SS2C	2	.48	3	44	2	.64
	ROS1	2	.54	2	43	2	.56
	ROS5	3	.57	3	49	3	.59
	CLA3	7	.56	8	49	7	.58
	CLA5	1	.70	1	51	1	.53
M^1	SS2B	34	.46	43	36	34	.64
	SS2C	12	.44	13	43	12	.63
	ROS1	7	.45	7	43	7	.59
	ROS5	7	.46	9	36	7	.61
	CLA3	9	.44	9	43	9	.62
	CLA5	2	.44	2	42	2	.59
M^2	SS2B	31	.54	35	32	31	.67
	SS2C	9	.53	14	32	9	.66

Table 18. *Average values of the relative position of protocone (PML), the protoloph-metaloph angle (h) and the relative width of the centroloph complex (CLW) in the three* Gliravus *species. Mesurement method: see text and figure 3.*

element	locality	PML		h (in °)		CLW	
		n	mean	n	mean	n	mean
	ROS1	4	.56	7	37	4	.66
	ROS5	2	.54	3	36	2	.61
	CLA3	8	.54	8	35	8	.63
	CLA5	3	.57	4	33	3	.65
M^3	SS2B	10	.61	10	31	10	.61
	SS2C	4	.59	7	33	4	.68
	ROS1	1	.65	1	33	1	.63
	CLA3	1	.56	1	36	1	.74
	CLA5	1	.62	1	37	1	.62

SS= Sosis ROS= Roc de Santa CLA= Claverol

***Table 18.** (continued).*

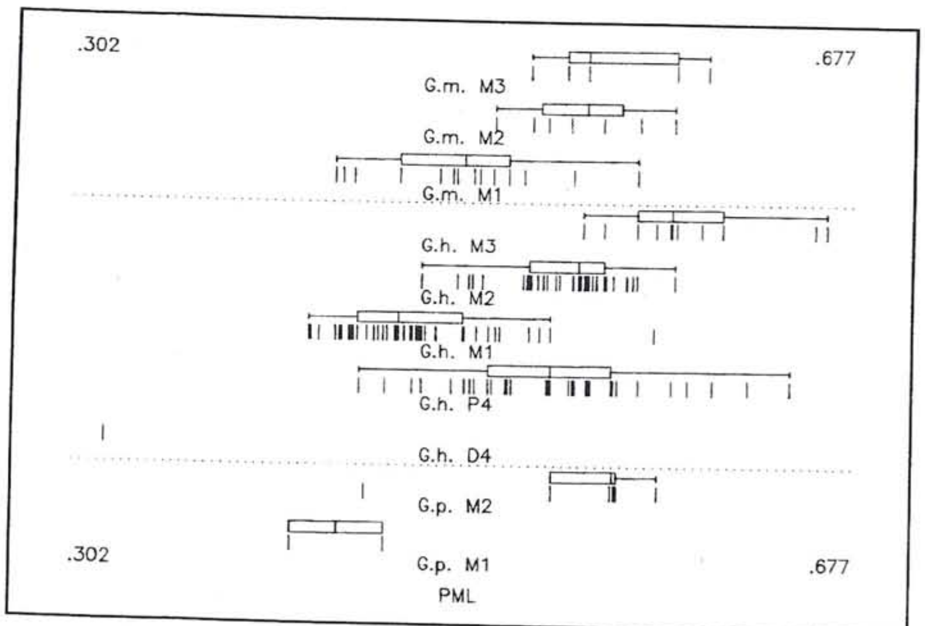


***Figure 13.** Diagram showing the spread of the quotient PML in the upper cheek teeth of* Gliravus *from Sossís 2B. PML is the quotient of the distance between the protocone and the posterior border (=pm) and the length (=l) (see figure 3). Explanation of the box plots: see caption of figure 8. G.p.=* Gliravus priscus, *G.h.=* Gliravus hispanicus, *G.m.=* Gliravus meridionalis.

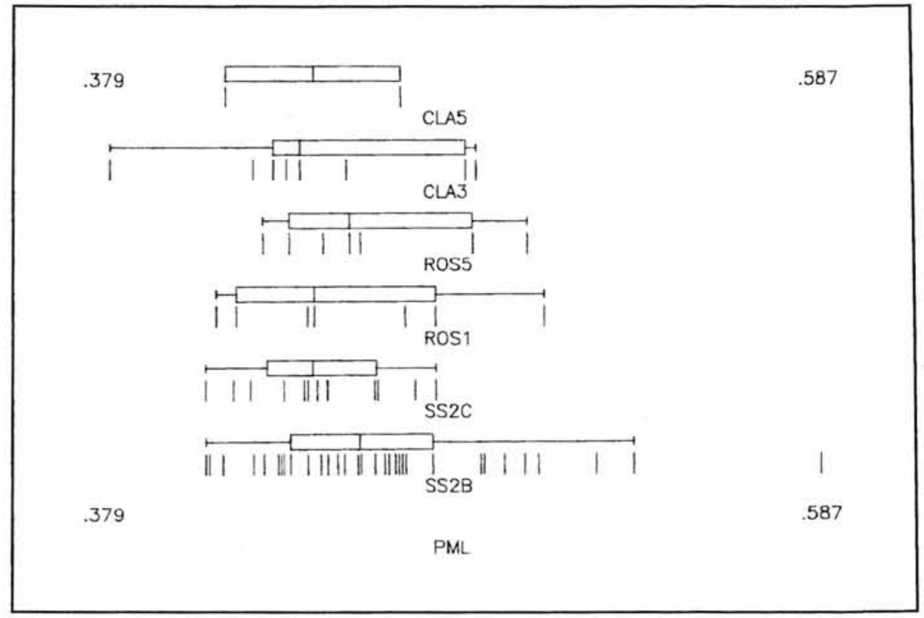


***Figure 14.** Diagram showing the spread of the quotient PML in the M^1 of* Gliravus hispanicus. *PML is the quotient of the distance between the protocone and the posterior border (=pm) and the length (=l) (see figure 3). Explanation of the box plots: see caption of figure 8.*

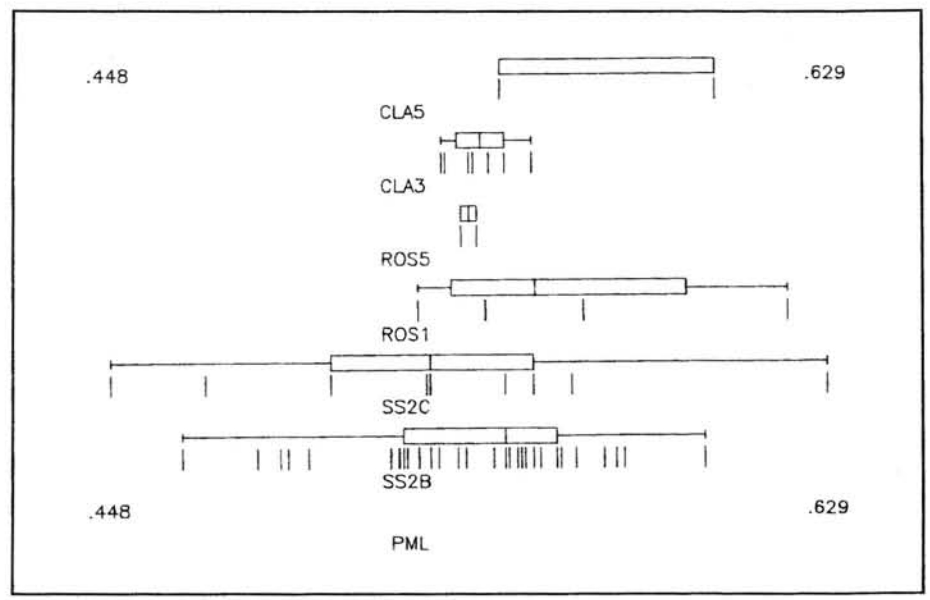


***Figure 15.** Diagram showing the spread of the quotient PML in the M^2 of* Gliravus hispanicus. *PML is the quotient of the distance between the protocone and the posterior border (=pm) and the length (=l) (see figure 3). Explanation of the box plots: see caption of figure 8.*

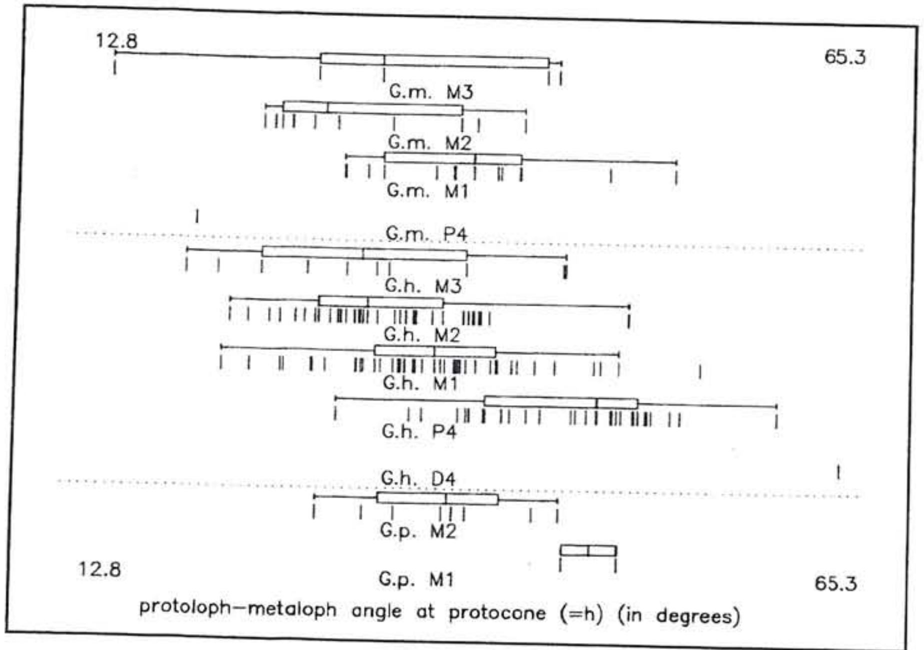


Figure 16. *Diagram showing the spread of the angle h between the protoloph and the metaloph in the upper cheek teeth of* Gliravus *from Sossís 2B. The angle h is measured in degrees and is indicated in figure 3. Explanation of the box plots: see caption of figure 8. G.p.*=Gliravus priscus, *G.h.*=Gliravus hispanicus, *G.m.*=Gliravus meridionalis.

Shape and symmetry of the trigone

Measuring method

In order to measure the asymmetry of the trigone the position of the protocone was measured (see figure 3). Because the protocone is elongated, its position is defined to be the mid of the line between the points PL and ML. The index PML is calculated as the quotient of the length (in the horizontal plane) of the perpendicular from the protocone to the posterior side I-L of the rectangle (pm) and the total length l. Thus, a tooth with a PML larger than 0.5 can be said to have its protocone situated in an anterior rather than in an posterior position.

A related variable is the angle of the V-shape of the trigone. This angle (called h) is calculated as the angle between the lines PL-PB and MP-MB, PB and MB being the points of the (usually present) inflection of proto- and metaloph (figure 3).

The position of the protocone

A clear morphological trend in the toothrow of *G. hispanicus* was observed for the (average) position of the protocone. Starting from M^3 and going to M^1 this position becomes more posteriorly (see figure 13 and table 18). For instance

element	ranking of PML (1: protocone most anteriorly, __ = equal value)					
	1	2	3	4	5	6
P^4	CLA5	ROS5	CLA3	ROS1—SS2B		SS2C
M^1	ROS5—SS2B		ROS1	CLA5—CLA3—SS2C		
M^2	CLA5	ROS1	CLA3—ROS5—SS2B			SS2C
	ranking of h (1: widest proto-metaloph angle, __ = equal value)					
	1	2	3	4	5	6
P^4	CLA5	CLA3—ROS5		SS2B	SS2C	ROS1
M^1	CLA3—ROS1		CLA5—SS2C		SS2B	ROS5
M^2	ROS5	CLA3	CLA5	ROS1—SS2C—SS2B		
	ranking of CLW (1: smallest relative width of centroloph complex, __ = equal value)					
	1	2	3	4	5	6
P^4	CLA5	ROS1	CLA3	ROS5	SS2B	SS2C
M^1	CLA5—ROS1		ROS5	CLA3	SS2B—SS2C	
M^2	ROS5	CLA3	CLA5—ROS1—SS2C—SS2B			

Table 19a. *Locality rankings for the relative position of protocone (PML) protoloph-metaloph angle (h) and the relative width or the centroloph complex (CLW) in* Gliravus hispanicus. *Mesurement method: see text and figure 3.*

locality	PML	h	CLW
CLA5	7	7.5	6
CLA3	12	5.5	9
ROS5	7.5	9.5	8
ROS1	9.5	12	7
SS2C	17	13.5	16
SS2B	10	14	15

Note: Sosis 2A is not included, because only P^4 and no M^{1-2} are present in this locality.

Table 19b. *Totals of the rankings in table 17a. (In case two localities have an equal ranking in table 19a, both get the average value).*

the average PML values for Sossís 2B are 61, 54 and 46 respectively). D^4 may be said to continue this trend (with a PML value of 30). The P^4 do not fit in quite well. On the average they have a more posterior position of the protocone compared to M^1 (PML=. 54) and their variability is large.

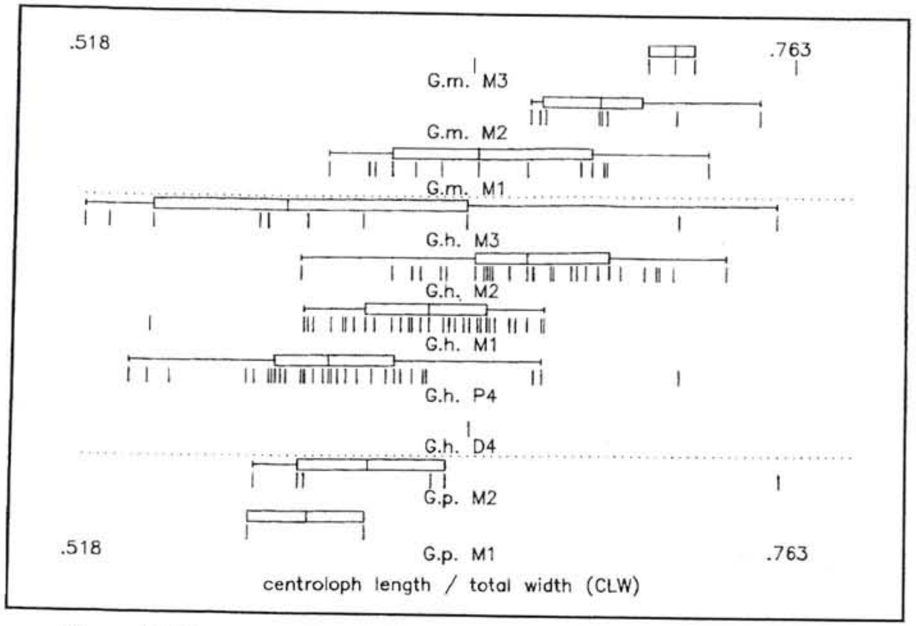


Figure 17. *Diagram showing the spread of the quotient CLW in the upper cheek teeth of* Gliravus *from Sosis 2B. CLW is the quotient of the distance from the buccal border to the most lingual progression of the centroloph complex (=cl) and the width (=w) (see figure 3). Explanation of the box plots: see caption of figure 8. G.p.*=Gliravus priscus, *G.h.*=Gliravus hispanicus, *G.m.*=Gliravus meridionalis.

The same trends were observed in the other two species.

Table 19a and b show the ranking of assemblages based on the PML of *G. hispanicus*. (The M^3 are excluded, because of their low numbers.) The high score of Sossís 2C in table 19b indicates that, on the average, the protocone is situated more posteriorly in the upper elements of *G. hispanicus* than in the other levels. The elements from Claverol 5 and Roc de Santa 5 have their protocone situated in a more anterior position.

Figure 14 and 15 visualise the results for the M^1 and M^2.

Protoloph-metaloph angle

Generally, the angle between protoloph and metaloph decreases in the posterior direction. In *G. hispanicus* from Sossís 2B the average value ranges from 65 degrees (D^4), 46 (P^4), 43 (M^1), 32 (M^2) up to 31 degrees (M^3) (table 18, figure 16). The M^2 of *G. meridionalis* have smaller average angles than those of *G. hispanicus* in all the assemblages where both are present.

The other assemblages show a similar toothrow gradient in the angle between protoloph and metaloph as was observed for Sossís 2B. The mean angles of the M^2 are very close to each other (table 18). The same holds for the M^3. The M^1 from Sossís 2B and Roc de Santa 5 have a smaller mean angle than the M^1 of the other assemblages.

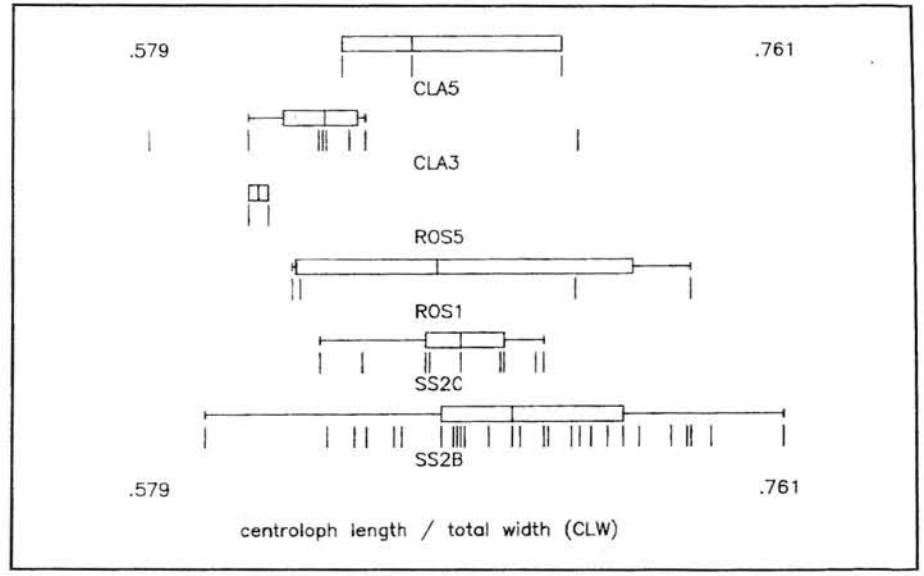


Figure 18. *Diagram showing the spread of the quotient CLW in the M^2 of* Gliravus hispanicus. *CLW is the quotient of the distance from the buccal border to the most lingual progression of the centroloph complex (=cl) and the width (=w) (see figure 3). Explanation of the box plots: see caption of figure 8.*

Table 19b shows that, on the average, the Claverol localities have the widest, and the Sossís localities have the smallest angle between the protoloph and the metaloph.

Centroloph length

Measurement method

The length of the centroloph "complex" (cl) is measured as the shortest distance from the lingual end of the farthest reaching central crest (CL in figure 3) to the buccal side of the tooth. To obtain the relative measure CLW, this distance is divided by the total width w.

Results

In general, the M^2 and M^3 have the largest lingual progression of a centroloph (table 18). The P^4 have the smallest values. The CLW of the M^3 of *G. hispanicus* from Sossís 2B is highly variable (figure 17), which can be explained by the variable pattern of centrolophs. In almost all localities and elements *G. priscus* has the shortest and *G. meridionalis* the longest centroloph.

Table 19b shows that the localities can be divided in two groups: on the one hand the Sossís localities with long centrolophs and at the other hand the other four localities with short centrolophs. Figure 18 shows the spread of the length of the centroloph complex in the M^2 from the six localities that contain second upper molars.

It is interesting to note that analysis of the protoloph-metaloph angle and the centroloph length in the M^2 result in a similar sequence of localities. An obvious explanation would be one in terms of the available space for the centroloph(s) to develop. However, in P^4 and M^1 the relation between the two features is not so evident.

Discussion

Evolutionary relationships

Among the three species discussed, *G. priscus* is the most primitive. *G. meridionalis* is a little more advanced than *G. hispanicus*. These conclusions are based on the following dental features:

1. The concavity of the occlusal surface

The cheek teeth of *G. priscus* have a more concave occlusal surface than those of the other two species. In their ecological characterization of recent and fossil glirids, Van der Meulen and de Bruijn 1982 call flatness a derived character (probably related to a change towards a more longitudinal power stroke).

2. The importance of cusps versus crests

The paracone, metacone, hypocone and metaconid are less high in *G. hispanicus* and *G. meridionalis* than in *G. priscus*. It is a trend in the Gliravinae and in the Gliridae in general that cusps disappear and become integral parts of ridges. (However: some living genera like *Eliomys* and *Graphiurus* have clear, pointed cusps, which is probably related to their partly insectivorous diet.)

3. The mutual similarity of the transverse crests

G. meridionalis shows the largest mutual similarity of the transverse crests, particularly in the upper cheek teeth: the anteroloph is almost as high as the trigone and the centroloph is a long straight crest. In contrast, primitive forms like *G. priscus* and *G. robiacencis* only have the protoloph, metaloph and posteroloph well-developed.

4. The complexity of the crest pattern in the lower cheek teeth

G. priscus has a relatively empty central basin in the lower cheek teeth, whereas *G. hispanicus* and *G. meridionalis* have basins with more and/or better developed central crests. The presence of a complicated crest pattern can be considered an advanced character in the early Gliravinae. For example, in the *G. priscus-G. fordi* lineage, Bosma and de Bruijn 1982 observe an increase in the presence of extra crests and cuspules in the central basins of both lower and upper teeth.

As was shown in the previous chapter, *G. hispanicus* is larger than *G. priscus* and *G. meridionalis* is again larger than *G. hispanicus*. These results might suggest that small size is a more primitive state than large size. In fact, this is what seems to be confirmed by most of the literature on *Gliravus*: early forms such as *G. robiacensis*, *G. priscus* and *G.* minor are small, while a number of Oligocene species are very large (for example *G. bravoi* Hugueney, Adrover and Moissenet 1985). Also the *G. priscus-fordi* lineage (Bosma and de Bruijn 1979) is

characterized by an increase of size. However, there are exceptions: for instance, a relative large *Gliravus* (*G. daamsi* Bosma and the Bruijn, 1982) is already known from MP17 (Late Eocene). In brief, although it may give a general indication, size is not a very reliable character to infer the primitive or advanced state of a *Gliravus* species.

In the reconstruction of the phylogeny by Hartenberger 1971 (figure 16) the small-sized *G. robiacensis* is the ancestor of three lineages containing *G. priscus*, *G. meridionalis* and *G. bruijni* respectively. The time of the radiation is supposed to be the Late Eocene. We agree with this author that *G. robiacensis* is probably the ancestor of *G. priscus*. However, given the new Spanish material, we are less sure about the proposed descent of *G. meridionalis* from *G. robiacensis*. We think that another possible scheme would be a descent of *G. meridionalis* direct from the Middle Eocene *Eogliravus* stock, characterised by a similar size as *G. meridionalis*. (The primitive genus *Eogliravus* is separated from the rest of the Gliravinae by Hartenberger 1971). From the morphological point of view a development from *Eogliravus* to *G. meridionalis* is not difficult to imagine: The most important morphological change would be the further development of the transverse ridges of upper and lower cheek teeth.

The question may be posed how *G. hispanicus* n. sp. fits in this scheme. As was shown in the chapter on the morphotypes, this species is characterised by a shorter and lower centroloph (complex) and a lower anteroloph, and generally also a less developed centrolophid-mesolophid complex, compared with *G. meridionalis*. Given this, the possibility of an *Eogliravus* - *G. hispanicus* - *G. meridionalis* type of lineage must be considered. The first evolutionary stage would be an anagenesis from *Eogliravus* to *G. hispanicus* or a form close to it, characterised by the straightening of the protoloph and the metaloph, and the development of a centroloph, mesolophid and centrolophid. The next step would be a cladogenesis, resulting in two branches. One branch would lead to *G. meridionalis* by means of anagenesis, and would be characterised by the further development of the central crests, and by the development towards a higher anteroloph, whereas in the other branch *G. hispanicus* would change only a little, if at all. Unfortunately, it is difficult to test this hypothesis, because of the scanty fossil record of glirids. After an interval characterised by the presence of *Eogliravus* (found in the localities Mas de Gimel (MP10) and Bouxwiller (MP13) in France, and the locality Casa Ramón (MP 11 - 12) in Spain (see Pelaez - Campomanes 1993) glirids seem to become relatively rare. Those that are known are small-sized: *G. robiacensis* from the French reference localities of La Livinière 2 (MP15) and Robiac (MP 16), and *G.* cf. *robiacensis*, from the Spanish locality of Laguarrès (Huesca) (Pelaez-Campomanes 1993), which is represented by a few teeth only. Until no middle-sized *Gliravus* is found, which could be placed in the lineage from *Eogliravus* to *G. hispanicus*/*G. meridionalis*, the hypothesis of Hartenberger 1971 assuming a small *G. robiacensis*-type ancestor for all other *Gliravus* species cannot be rejected.

Although we do not know the exact evolutionary pattern relating the early *Gliravus* forms, we do know that it resulted in different types of Late Eocene as-

locality	G.p.	G.m.	G.h.	total	%G.p.	%G.m.	%G.h.
SS2A	6	9	7	22	27	41	32
SS2B	34	44	205	283	12	16	72
SS2C	16	12	65	93	17	13	70
ROS1	18	6	36	60	30	10	60
ROS5	1	0	19	20	5	0	95
CLA3	0	0	38	38	0	0	100
CLA5	1	0	10	11	9	0	91
total				527			

G.p. = Gliravus priscus
G.m. = Gliravus meridionalis
G.h. = Gliravus hispanicus

Table 20. *Total numbers of* M^{1-2} *and* M_{1-2} *of the three* Gliravus *species.*

semblages in France on the one hand and Spain on the other in the late Late Eocene. MP 17 assemblages of *Gliravus* from Spain and France differ in a number of aspects, such as the absence of *G. hispanicus* in France and the size difference in *G. meridionalis*. Differences at the species level between Spain on the hand and Languedoc and Quercy on the other hand have also been observed in several other mammal groups in this period. At the generic level, however, there seem to be no differences between the two areas (Russell *et al.* 1982, p. 40).

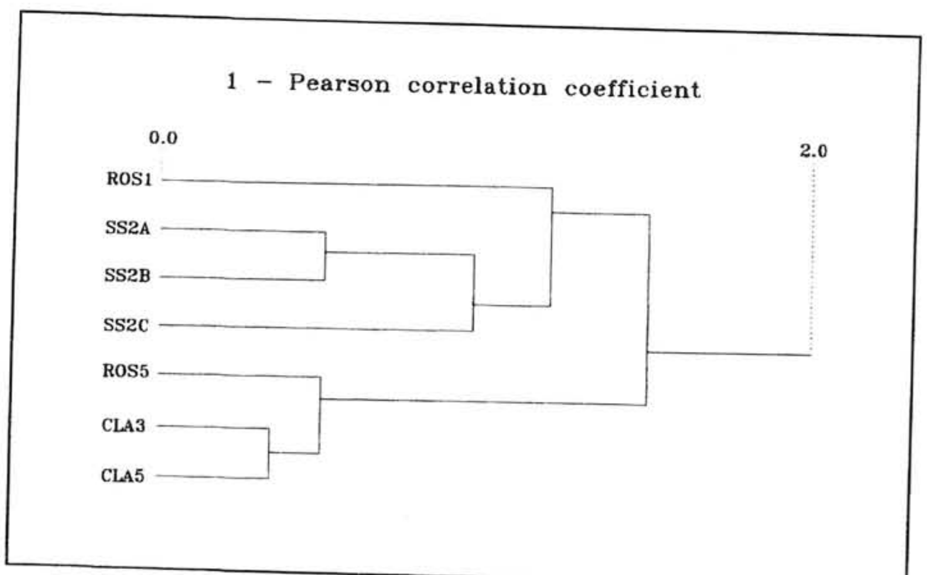


Figure 19. *Dendrogram resulting from an UPWGA clusteranalysis connecting the seven localities. Explanation: see text.*

	CLA5	CLA3	ROS5	ROS1	SS2C	SS2B	SS2A
CLA5	1.00						
CLA3	.65	1.00					
ROS5	.59	.44	1.00				
ROS1	-.05	-.38	-.36	1.00			
SS2C	-.49	-.29	-.48	-.38	1.00		
SS2B	-.62	-.42	-.17	-.35	.23	1.00	
SS2A	-.72	-.93	-.55	.34	-.17	.49	1.00

Table 21. *Pearson correlation coefficient matrix for the seven localities. Variables used: see text.*

	1	2	3
CLA5	-.90	-.23	.00
CLA3	-.88	.21	.08
ROS5	-.72	.07	-.56
ROS1	.24	-.88	.28
SS2C	.38	.71	.57
SS2B	.61	.47	-.54
SS2A	.88	-.36	-.32
% expl. variation	49	25	16

Table 22. *Q-mode principal component scores based on the correlations in table 21.*

	1	2	3
% G. priscus	.40	-1.36	1.09
% G. meridionalis	.59	-.07	-.30
% G. hispanicus	-2.02	.48	-.55
size ranking	.59	.19	-.98
PML ranking	-.17	1.14	1.70
h ranking	.72	.06	-.52
CLW ranking	.73	1.61	-.57

Note: Some morphotype proportions were excluded from the analysis because of the small amount of specimens in some localities. This is the reason why scores could not be calculated for the four morphotype variables.

Table 23. *Q-mode principal component loadings based on the correlations of table 21.*

Local biostratigraphical correlations

Unfortunately, the geological setting around the Sossís, Roc de Santa and Claverol sections is such, that lithostratigraphic correlations between these sections are difficult to establish. However, differences between the glirid assemblages may give some indication about the relative stratigraphic positions.

Table 20 shows the distribution of the M1-2 of the three species in the seven localities. A number of interesting differences can be observed. As can be seen from this table, Claverol 3, 5 and Roc de Santa 5 contain more than 90% *G. hispanicus*, and contain no first and second molars of *G. meridionalis*. (Claverol 3 contains one upper third molar of this species.) On the other hand, the assemblage of Sossís 2A is relatively equitable and contains a proportion of *G. hispanicus* less than 50%. Sossís 2B and 2C and Roc de Santa 1 have intermediate proportions of this species, ranging from 60% up to 72%. Furthermore, it can be observed that in both the Sossís and Roc de Santa sections the proportion of *G. hispanicus* increases higher up in the section (from Sossís 2A to 2B to 2C, and from Roc de Santa 1 to 5).

At this point we make the assumption that similar distributions of the three species in two localities imply similar ages (which is debatable, because the possibility of cyclical patterns can not be excluded). The assumption would lead to a biostratigraphic sequence with Claverol 3 and 5 having high and Sossís 2A, 2B and 2C having low stratigraphic positions. The position of Roc de Santa 1 would lie closer to that of the Sossís localities, whereas the position of Roc de Santa 5 would lie closer to that of the Claverol localities.

In order to explore further this hypothesis, data on the intraspecific variation of *G. hispanicus* were used. The following features were selected:

1. The average proportion of morphotype 1 for M^{1-2} (table 5 and 6);
2. The average proportion of morphotype A for M^{1-2} (table 8 and 9);
3. The average proportion of morphotype 1 for M_{1-2} (table 11 and 12);
4. The average proportion of morphotype A for M_{1-2} (table 14 and 15);
5. The ranking of size (table 19b);
6. The ranking of PML, the antero-posterior position of the protocone (table 19b);
7. The ranking of h, the angle between the protoloph and the metaloph (table 19b);
8. The ranking of CLW, the relative length of the (longest) centroloph (table 19b).

A data matrix was constructed that consisted of the scores of the localities on these variables and on the three relative abundances:

9. The number of M1 and M2 of *G. priscus* divided by the total number of M1 and M2 (table 20);
10. The number of M1 and M2 of *G. meridionalis* divided by the total number of M1 and M2 (table 20);
11. The number of M1 and M2 of *G. hispanicus* divided by the total number of M1 and M2 (table 20).

The eleven variables were standardized and used in a UPWGA Clusteranalysis and a Q-mode Principal Component Analysis (PCA). Values for the features 1-4 were entered as 'missing', in case the total number of specimens was less than 5.

Table 21 shows the Pearson correlation coefficients between the eleven variables that were used as input for the Clusteranalysis. The resultant dendrogram is shown in figure 19.

It shows two clusters: one distinct cluster containing the localities Claverol 3, 5 and Roc de Santa 5, and an other one containing the Sossís localities. Roc de Santa 1 is associated with the Sossís localities. Thus, on the basis of the quantitative clustering of the different levels using both relative frequencies and intraspecific variation, we have no reason to reject the initial hypothesis on the relative stratigraphic positions of the levels.

Table 22 shows the loadings on the first component of a Q-mode PCA analysis. It can be seen that the arrangement of localities in the table is consistent with a) the (ascending) order of loadings on the first component, b) the correct lithostratigraphic order of the localities within each of the three sections, and c) the above mentioned hypothesis. Therefore we interpret the first axis as a "time" axis, and arrange the localities accordingly: from old (Sossís 2A) to young (Claverol 5). The first column in table 23 shows the scores of the variables on the first axis.

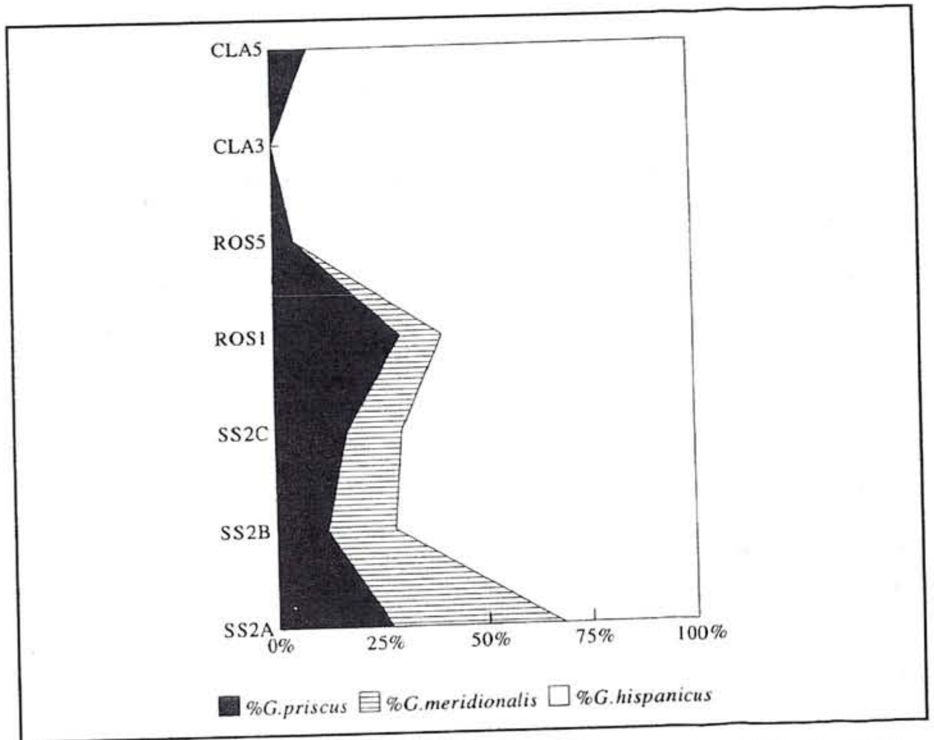


Figure 20. *Diagram showing the relative abundances of* Gliravus priscus, Gliravus meridionalis *and* Gliravus hispanicus. *The stratigraphic order of the localities is explained in the text.*

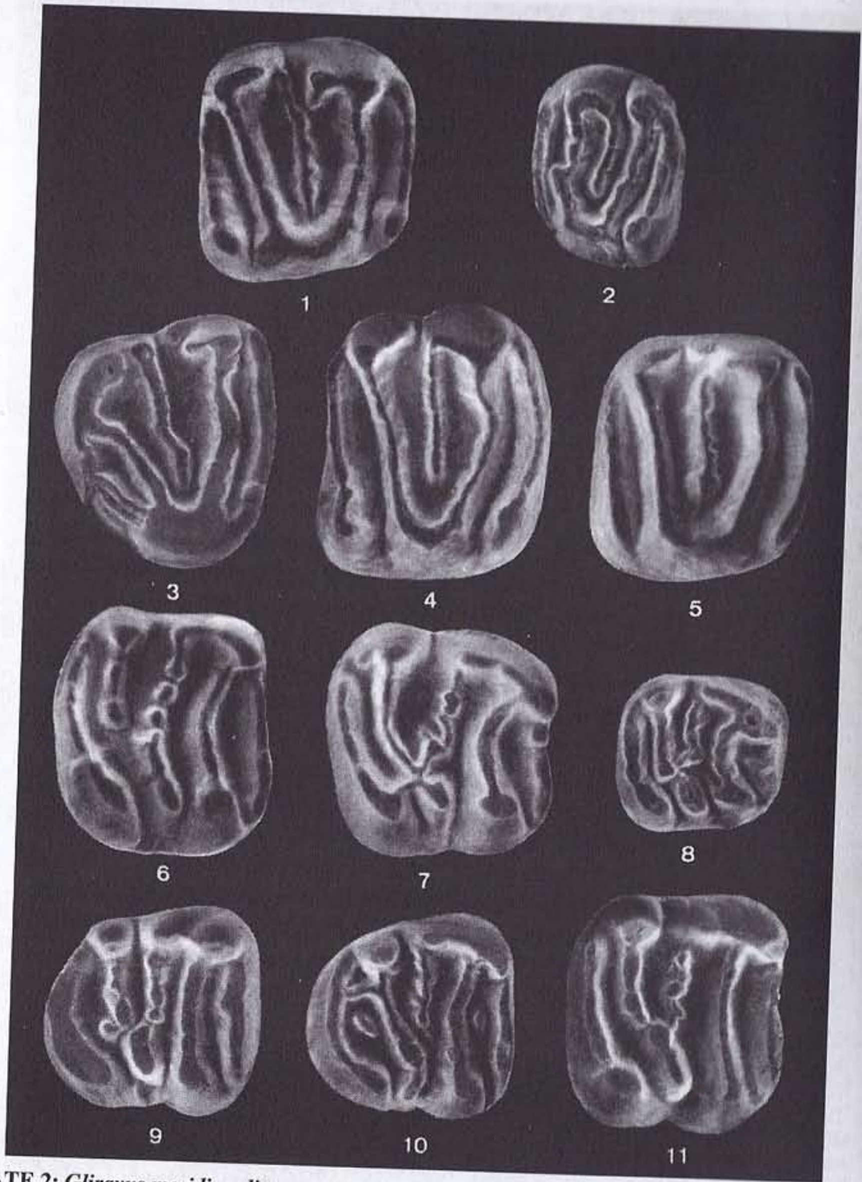


PLATE 2: *Gliravus meridionalis*
(enlargement about x 30)

1	*SS2B-G330:*	*M^1 dex.*	
2	*SS2B-G276:*	*P^4 sin.*	*(in reverse)*
3	*SS2B-G420:*	*M^3 sin.*	*(in reverse)*
4	*SS2B-G379:*	*M^2 sin.*	*(in reverse)*
5	*SS2C-G120:*	*M^2 sin.*	*(in reverse)*
6	*SS2B-G117:*	*M_2 dex.*	
7	*SS2B-G 62:*	*M_1 dex.*	
8	*SS2B-G 24:*	*P_4 sin.*	*(in reverse)*
9	*SS2B-G185:*	*M_3 dex.*	
10	*SS2B-G186:*	*M_3 dex.*	
11	*SS2B-G149:*	*M_3 sin.*	*(in reverse)*

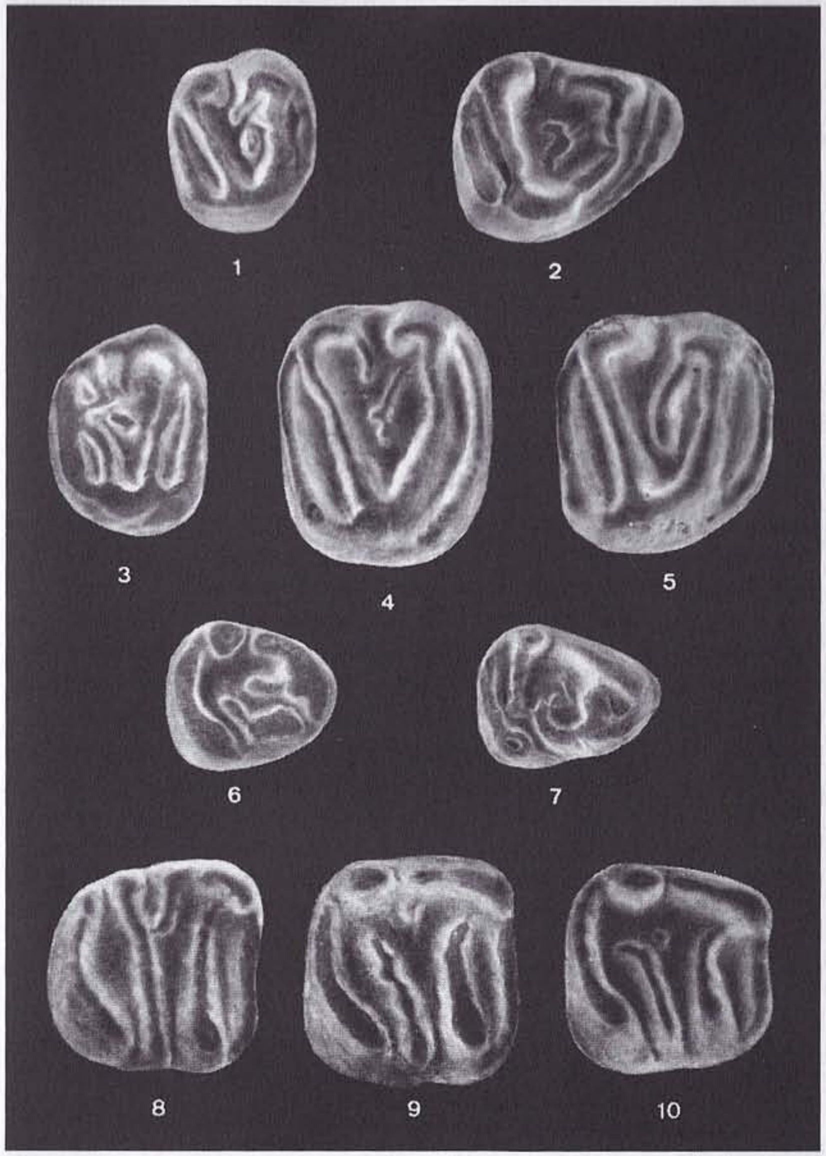


PLATE 3: *Gliravus hispanicus* n. sp.
(enlargement about x 30)

1	*SS2B-G250:*	*P^4 dex.*	
2	*SS2B-G232:*	*D^4 dex.*	
3	*SS2B-G423:*	*M^3 sin.*	*(in reverse)*
4	*SS2B-G309:*	*M^2 dex.*	*(holotype)*
5	*SS2B-G289:*	*M^1 dex.*	
6	*SS2B-G 16:*	*P_4 dex.*	
7	*SS2B-G 6:*	*D_4 dex.*	
8	*SS2B-G190:*	*M_3 dex.*	
9	*SS2B-G135:*	*M_2 dex.*	
10	*SS2B-G 48:*	*M_1 dex.*	

It appears that the proportion *G. hispanicus* and to a lesser degree the morphological variables h (protoloph-metaloph angle) and CLW (relative length of centroloph) have the most extreme values, which means that they change through time significantly. Accepting this sequence of the localities, it appears that h increases gradually during the interval, whereas CLW decreases suddenly between Sossís 2C and Roc de Santa 1 (table 19b). In contrast to these two variables, the range of values of the variable PML (the antero-posterior position of the protocone) does not show a clear pattern.

A number of other patterns can be observed (table 22 and 23), which we regard as superimposed on this time pattern. They reflect other, less important differences between the localities. For instance, the second component separates Roc de Santa 1 from Sossís 2B and 2C. Table 23 indicates that these assemblages differ in the proportion of *G. priscus* and the variables CLW (relative length centroloph) and PML (anterior-posterior position of the protocone). The third axis separates Sossís 2C from Sossís 2A and 2B. The most important associated variable is PML (table 23), that shows a peak in Sossís 2C (see table 19b).

In conclusion, on the basis of a) the lithostratigraphic positions within the three sections, b) the abundances and the morphological characteristics of the glirids from these sections, and c) the assumption that similar evolutionary stages of species as well as of assemblages imply similar ages, the following stratigraphical order is proposed (from top to bottom):

Claverol 5
Claverol 3
Roc de Santa 5
Roc de Santa 1
Sossís 2C
Sossís 2B
Sossís 2A

The proposed stratigraphic sequence implies the following changes and trends within the glirids studied:

- a sudden decrease in the length of the centroloph(s) (CLW) in the interval between Sossís 2C and Roc de Santa 1 (table 19b);
- an overall gradual increase in the angle h between protoloph and metaloph during the interval (table 19b);
- a reduction in the size of *G. hispanicus* (table 17b);
- a gradual increase in the proportion of *G. hispanicus* during the interval (with a temporary decline in Sossís 2C and especially in Roc de Santa 1), and the gradual disappearance of *G. meridionalis* during the interval (figure 20, table 20).

Plates

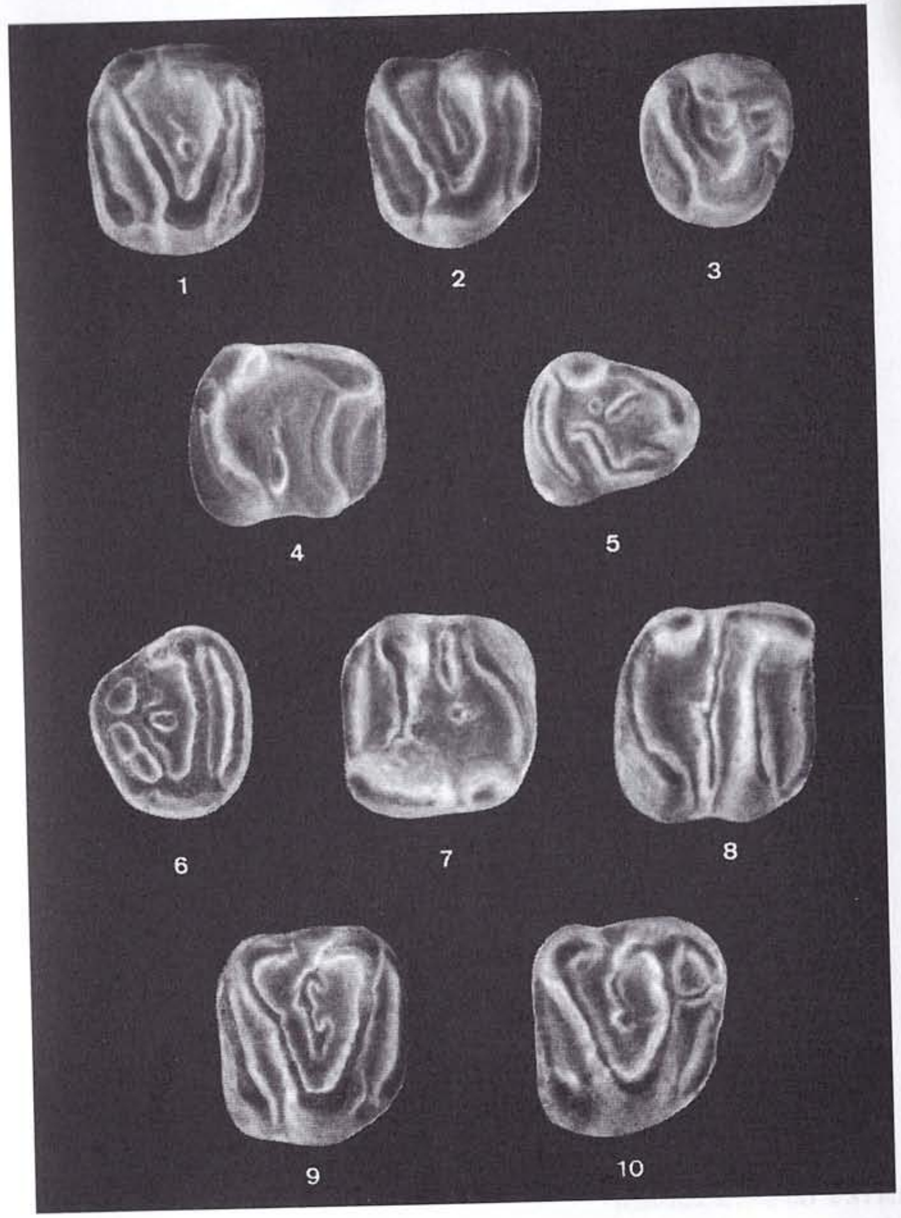


PLATE 1: ***Gliravus priscus*** **(enlargement about x 30)**

1	*SS2B-G480:*	*M^2 sin.*	*(in reverse)*
2	*SS2A-G 46:*	*M^1 sin.*	*(in reverse)*
3	*SS2C-G157:*	*P^4 sin.*	*(in reverse)*
4	*SS2C-G141:*	*M_1 dex.*	
5	*ROS1-G 6:*	*P_4 dex.*	
6	*ROS1-G108:*	*M^1 sin.*	*(in reverse)*
7	*SS2C-G453:*	*M_2 dex.*	
8	*ROS1-G 47:*	*M_3 sin.*	*(in reverse)*
9	*ROS1-G102:*	*M^2 sin.*	*(in reverse)*
10	*ROS1-G 81:*	*M^1 sin.*	*(in reverse)*

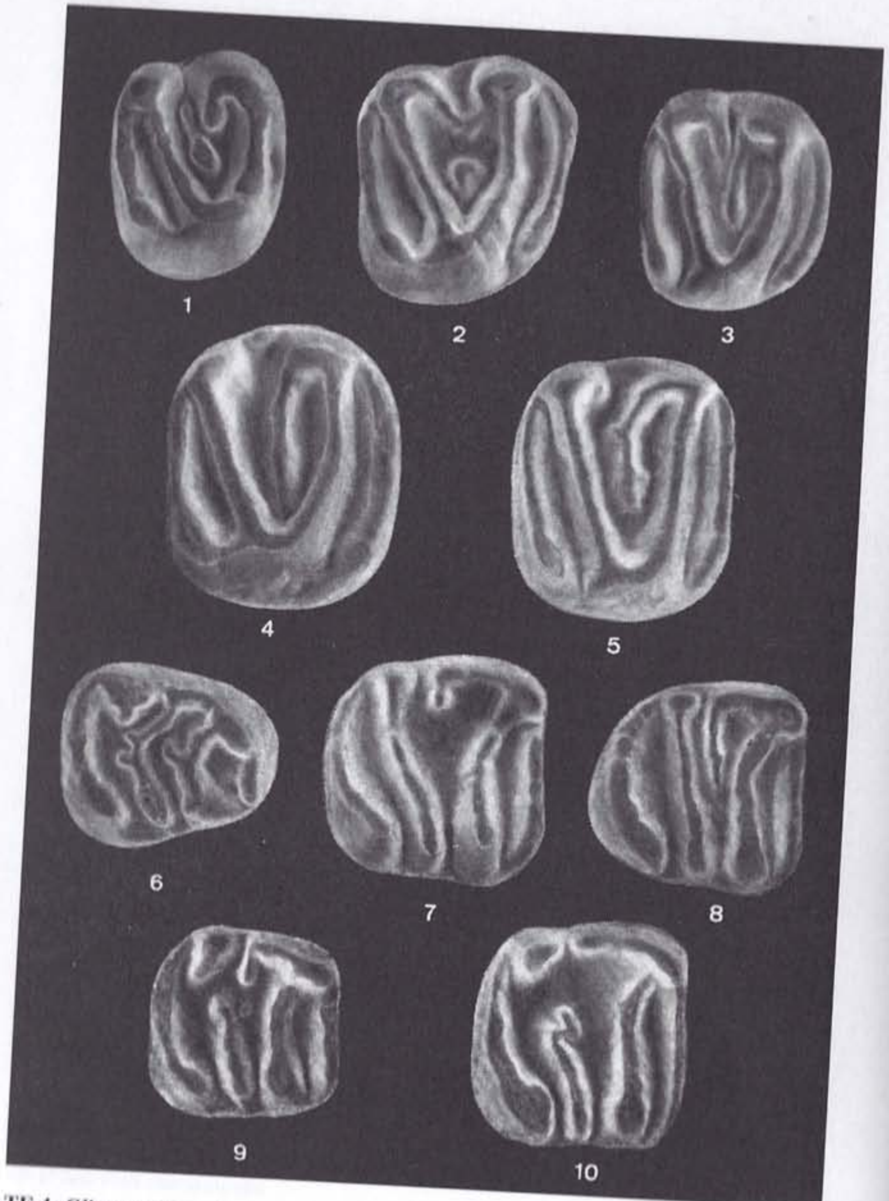


PLATE 4: ***Gliravus hispanicus*** **n. sp.**
(enlargement about x 30)

1	*SS2B-G246:*	*P^4 dex.*
2	*SS2B-G281:*	*M^1 dex.*
3	*SS2C-G 79:*	*M^1 dex.*
4	*SS2C-G100:*	*M^2 dex.*
5	*ROS1-G 91:*	*M^2 dex.*
6	*ROS1-G 2:*	*P^4 dex.*
7	*SS2B-G 99:*	*M_2 dex.*
8	*SS2B-G192:*	*M_3 dex.*
9	*ROS5-G 7:*	*M_1 dex.*
10	*CLA5-G 4:*	*M_2 dex.*

References

BOSMA, A. A. & DE BRUIJN, H. (1982): "Eocene and Oligocene Gliridae (Rodentia, Mammalia) from the isle of Wight, England". Part II. *Gliravus minor* n. sp., *Gliravus daamsi* n. sp., and *Bransatoglis bahloi* n. sp. *Kon. Ned. Akad. Wetensch. Proc. B*, 85: 365-380.

BOSMA, A. A. & DE BRUIJN, H. (1979): "Eocene and Oligocene Gliridae (Rodentia, Mammalia) from the isle of Wight, England". Part I. The *Gliravus priscus - Gliravus fordi* lineage. *Kon. Ned. Akad. Wetensch. Proc. B*, 812: 367-384.

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.

DERCOURT, J.; ZONENSHAIN, L. P.; RICOU, L. E.; KAZMIN, V. G.; LE PICHOU, X.; KNIPPER, A. L.; GRANDJACQUET, C.; SBORTSHIKOW, I. M.; GEYSSANT, J.; LEPVRIER, C.; PECHERSKY, D. H.; BOULIN, J.; SIBUET, J. C.; SAVOSTIN, L. A.; SOROTHKIN, O.; WESTPHAL, M.; BAZHENOW, M. L.; LAUER, J. P. & BIJU-DUVAL, B. (1986): "Geological evolution of the Tethys belt from the Atlantic to the Pamirs since the Lias". In: AUBOUIN, J; LE PICHON, X. & MONIN, A. S. (eds.): "Evolution of the Tethys". *Tectonophysics*, 123: 241-315.

HARTENBERGER, J. L. (1965): "*Gliravus robiacensis* n. sp., nouveau rongeur (Gliridae) de l'Éocène supérieure du Languedoc". *C. R. somm. Soc. Geol. France*, 10: 326-327.

HARTENBERGER, J. L. (1971): "Contribution a l'étude des genres *Gliravus* et *Microparamys* (Rodentia) de l'Éocène d'Europe". *Palaeovertebrata*, 4: 97-135.

HOLDEN, M. E. (1993): Myoxidae. In: WILSON, D. E. & REEDER, D. M. (eds.): *Mammal species of the world*. Smithsonian Inst. Press., Washington D. C.

HUEGENEY, M.; R. ADROVER & MOISSENET, E. (1985): "*Gliravus bravoi* nov. sp., la plus grande espèce du genre *Gliravus* (Mammalia, Rodentia, Gliridae) dans l'Oligocène supérieure d'Espagne". *Geobios*, 18: 251-256.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (1985): *International Code of Zoological Nomenclature*. International Trust for Zoological Nomenclature, London, 338 pp.

PELAEZ-CAMPOMANES, P. (1993): *Micromamníferos del Paleógeno continental español: Sistemática, Biocronología y Paleoecología*. Thesis, Universidad Complutense de Madrid, 388 pp.

SCHMIDT-KITTLER, N. (ed.) (1987): "International symposium on mammalian biostratigraphy and paleoecology of the European Paleogene. European reference levels and correlation tables". *Müncher Geowissenschaftliche Abhandlungen*, 10: 13-32.

RUSSELL, D. E.; HARTENBERGER, J. L.; POMEROL, C.; SEN, S.; SCHMIDT-KITTLER, N. & VIANEY-LIAUD, M. (1982): "Mammals and stratigraphy: the Paleogene of Europe". *Paleovertebrata*, Memoire extraordinaire: 1-77.

SCHAUB, S. (1958): "Simplicidenta (Rodentia)". In: PIVETAU, J.: *Traité de Paleontologie*, 6: 659-818. Masson et Cie., Paris.

SIMPSON, G. G. (1945): "The principles of classification and a classification of mammals". *Bull. Am. Mus. Nat. Hist.*, 85: xvi+350 pp.

STEHLIN, H. G. & SCHAUB, S. (1951): "Die Trigonodontie der Simplicidentaten Nager". *Schweiz. Paläont. Abh.*, 67: 1-385.

VIANEY-LIAUD, M. (1989): "Parallelism among Gliridae (Rodentia): the genus *Gliravus* Stehlin and Schaub". *Historical biology*, 2: 213-226.

WAHLERT, J. H.; SAWITZKE, S. L. & HOLDEN, M. E. (1993): "Cranial Anatomy and Relationships of Dormice (Rodentia, Myoxidae)". *Am. Mus. Novitates*, 3061: 1-32.

Los Pseudoesciuridos (Rodentia) del Eoceno Superior de la cuenca lacustre de Sossís (Pirineos)

Gloria Cuenca Bescós. Departamento de Geología (Paleontología). Facultad de Ciencias, Universidad de Zaragoza.

Introducción

Los Pseudoesciuridae son roedores exclusivamente fósiles, de gran tamaño, con la dentición braquidonta y bunodonta. Se distribuyen desde el Eoceno Inferior hasta el Oligoceno inferior en el terciario continental europeo.

En la Cuenca lacustre de Sossís (Robles y Ardevol,1984) se encuentran, en 12 niveles fosilíferos estratificados cuya situación en la columna estratigráfica es conocida, uno de los más completos registros de pseudoesciúridos de Europa (Crusafont, 1965, Crusafont y Golpe, 1968, 1973, Hartenberger, 1973), representados por cinco especies: *Treposciurus mutabilis, T. intermedius, Paradelomys crusafonti, P. cf. quercy* y *Sciuroides cf. siderolithicus* de las cuales *T. mutabilis* es la más abundante. El material ha sido obtenido en dos perfiles estratigráficos próximos entre sí y denominados respectivamente Claverol-Roc de Santa y Sossís. El perfil de Sossís podría estar situado entre los niveles de Claverol 6 y Roc de Santa 1.

Objetivos y método

El principal objetivo de este trabajo es el estudio sistemático de las especies *T. mutabilis, T. intermedius, P. cf. quercy* y *S. cf. siderolithicus* de la cuenca lacustre de Sossís. La especie de Pseudosciuridae restante, *P. crusafonti*, será estudiada por J.I. Lacomba.

El material estudiado se encuentra en el Departamento de Paleontología de la Universidad Complutense de Madrid y está compuesto por piezas aisladas de la dentición (a escepción del de Claverol 3 1/2). Están sigladas con la abreviatura de cada uno de los yacimientos:

Claverol (CL)
Claverol 6: CL 6 1-56
Claverol 5: CL 5 1-27
Claverol 4: CL 4 pieza única
Claverol 3 1/2: CL 3 1/2 Serie dental única
Claverol 3: CL 3 1-88, 11'-14'
Claverol 2: CL 2 1-2

Sossís (SS)
Sossís 2C: SS 2C 1-73