

# Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain)

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## RESUMEN

FREUDENTHAL, M. Gliridae (Rodentia, Mammalia) del Eoceno y Oligoceno en la Sierra Palomera (Teruel, Spain).

En este trabajo se hace una revisión taxonómica de los Gliridae pertenecientes a los géneros *Glamys* y *Gliravus* a partir de material obtenido en la Sierra Palomera y en el área de Montalbán (Teruel, España). Esta revisión lleva a una definición más precisa del género *Glamys*; a una limitación del género *Gliravus*, que incluye la especie-tipo y algunas especies estrechamente relacionadas; y a la definición de un género nuevo, *Schizoglravus*. Con esta nueva clasificación se soluciona el problema del género *Gliravus*, que se había convertido en un refugio en donde meter todas las especies que no cabían en otro género.

Se proponen términos adicionales en la nomenclatura de los dientes de los Gliridae.

Se describen dos especies nuevas: *Glamys umbriae* y *Schizoglravus montisalbani*, la especie-tipo del nuevo género *Schizoglravus*.

Dentro del género *Glamys* se pueden reconocer al menos tres líneas, supuestamente adaptadas a condiciones ambientales diferentes.

**Palabras clave:** Gliridae, Mammalia, Eoceno, Oligoceno, España.

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**ABSTRACT**

On the basis of material from the Sierra Palomera and the area of Montalbán (Teruel, Spain) the glirid genera *Glamys* and *Gliravus* are revised. This leads to a better definition of the genus *Glamys*, restriction of the genus *Gliravus* to its type-species and some closely related species, and the creation of a new genus, *Schizoglriravus*, which reduces considerably the waste-basket function, that the genus *Gliravus* had until now.

Two new species are described, *Glamys umbriae* and *Schizoglriravus montisalbani*, the type-species of the new genus *Schizoglriravus*.

Within the genus *Glamys* at least three lineages are recognized, that are supposed to be adapted to different environmental conditions.

**Key words:** Gliridae, Mammalia, Eocene, Oligocene, Spain.

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## INTRODUCTION

The Sierra Palomera (Teruel, Spain) is a syncline of Jurassic limestones, with a cover of Paleogene and Neogene continental sediments in its center. The studied area is located on the topographical map of Spain 1:50,000: Monreal del Campo (26-20), Santa Eulalia (26-21), and Alfambra (27-21).

The first fossil mammals from the Paleogene of the Sierra Palomera were published by Adrover et al. (1983), and proved the hitherto unknown presence of Late Eocene sediments in that depression.

The Tertiary sedimentation is divided into two parts: the older sediments, strongly affected by the NNW-SSE directed tectonics, are attributed to the Late Eocene and the Eocene/Oligocene transition. This sedimentation ends somewhere in the Early Oligocene, and an important hiatus separates it from the second sedimentary phase. This second phase starts quite late in the Late Oligocene, and apparently continues uninterrupted into the Miocene.

The deposits are very poor in fossils, and in order to obtain statistically reliable collections, we sampled between 10,000 and 20,000 kg of sediment per locality, an activity that has taken us more than 12 years. The fossil material of the older phase is characterized by Theridomorpha and Gliridae, with a minor presence of Pseudosciuridae, and some other groups of rodents, insectivores and marsupials, and the almost complete absence of macromammals.

The Gliridae from the older phase belong to the genera *Glamys*, *Bransatoglis*, *Gliravus*, and *Microdyromys*. The subject of this paper is the genus *Glamys* (Gliridae), and all the species that have been attributed to that genus, whether that attribution is correct or not. The type-species of *Glamys* is *G. priscus* Stehlin & Schaub, 1951. It has been reported from an extremely long stratigraphic range, from Mormont-Entreroches (MP16) to Aubenas-les-Alpes (MP25, Vianey-Liaud, 1994). However, the cited author changes the classification of the youngest occurrences to *G. garouillensis* in that same paper. With that change the youngest occurrence of *G. priscus* appears to be Itardies (MP23), the stratigraphic range still being one of the longest – if not the longest – known for a fossil rodent. Maybe more than one species are lumped together, due to the simple dental pattern that offers few details for discrimination, and the poor amount of material known in most of its localities. On the other hand, most post-“Grande Coupure” citations are from fissure fillings, and in these cases of course the possibility of mixture of material of various ages cannot be excluded.

Several localities in the Sierra Palomera have yielded good collections of *Glamys* that permit for the first time a statistical treatment of this group. This treatment reveals the existence of several lineages of *Glamys*, and a more complex evolutionary pattern than assumed until now.

In the course of this study, when trying to delimit *Glamys* against *Gliravus*, it became clear that *Gliravus* had to be redefined. This led to a narrower definition of that genus, and the creation of a new genus, *Schizoglriravus*, to house a number of species that used to be placed in *Gliravus* previously.

## GEOLOGICAL SETTING

The Sierra Palomera consists of a syncline of Jurassic limestones, with an Eocene/Oligocene cover in its center. The axis of the syncline has a NNW-SSE direction, typical of the Celtiberian Chains.

The structure of the basin is a syncline with a smooth eastern flank, lying unconformably on the Jurassic limestones, and a very steep, at some places overturned, western flank, due to the Eastward thrust of the Palomera block. West-East compression is very strong in the north of the syncline, much less in the south. The intense faulting makes correlation of the fossiliferous localities quite difficult. The sedimentation in most of the basin is very irregular; beds taper out at short distances and their thickness varies considerably.

The Late Eocene sedimentation starts with up to 200 m of yellow conglomerates, well exposed along the road from Torrelacárcel to Aguatón, just W of Aguatón, and along the eastern and southern flank of the Jurassic block of Palomera and Medio Monte. They represent paleochannels discharging towards E and NE, and are absent on the Eastern flank of the basin. An intercalated marl bed is fairly rich in mammal fossils.

Next follows a maximum of 60 m of variegated marls, well exposed in the Bco. de la Peña Blanca, S of Aguatón, which are probably Upper Eocene too, but so far no fossil mammals have been found. They represent flood plain conditions.

Next come 40 m of limestones alternating with gray and black marly clays at the base and green marly clays in the middle and at the top, with many fossil mammal localities, attributed to the Lowest Oligocene. Most beds are rich in gastropods, but unfortunately these do not support our sieving techniques. This unit represents deposition in a probably persistent lake, with hardly any sediment inflow.

On top of this sequence we find, in the southern part of the depression, a lignitic clay or even a real lignite, maximum 8 m thick in the Bco. de Villarroso SE of the Masía Baja, sufficiently thick for it to have been exploited in the past. It forms the top of the Lower Oligocene sediments, cut off by an unconformity that is not evident in the field. The lignite level has been recognized at several places in the northern part of the basin, where it may be only a few centimeters thick. It is interpreted as a phase of drying up of the lake. Adrover et al. (1983) mention the presence of *Theridomys aquatilis* in the fossiliferous site Palomera B, in yellow marls of their Veguillas Fm., in the Bco. de la Fuente Umbría. I have not been able to locate this site, but the yellow marls in that area belong to the lignite level, which is dated as Early Oligocene (pre-“Grande Coupure”, no cricetids).

The Veguillas marls, up to 100 m thick, are a lateral equivalent of the Serretilla limestones. Several beds of green marls at its basis and up to the middle of the series are now attributed to the upper part of the Upper Oligocene, thanks to the recent discovery of *Allocricetodon*, *Pseudocricetodon*, *Eomys*, *Issiodoromys*, *Archaeomys*, etc. in the new locality SER5 (Serretilla 5). The limestones and intercalated marls represent lacustrine conditions with a considerably higher amount of sediment inflow than in the previously mentioned lake.

The last formation attributed to the Paleogene is a unit of 80 m of yellow marls with some limestone intercalations. It has delivered a fauna with the same character-

ristics as the previously mentioned one. The marls indicate flood plain conditions, and the fossiliferous locality represents a small ephemeral lake.

The lignite level is dated as very Early Oligocene, the locality SER5, lithostratigraphically about ten meters higher, belongs to the upper part of the Upper Oligocene. This implies, that there is an important unconformity, not obvious in the field, but undeniable through paleontological evidence, and that the major part of the Oligocene is missing. On IGME map 27-21 unit 16 is indicated as L. Oligocene. It is now clear, that it belongs to the upper part of the Upper Oligocene. Table 1 gives the new interpretation of the age of the units on the IGME maps.

Description	Max.	Near	IGME 26-21	IGME 27-21	Age
Yellow marls with limestone intercalations	80 m	Cerro del Rodal		19	U. Olig., MP28
White limestones/green marls	50 m	Serretilla	24	18	U. Olig., MP27
Red and white sands and clays	50 m	Fuente Umbría	23	16	U. Olig., MP27
Lignite	8 m	Villarrosano			L. Olig., MP 21
White limestones/green marls	60 m	Aguatón	22	15	Eoc./Olig., MP20/21
Variegated marls	60 m	Bco. de la Peña	21,22	14	U. Eoc., MP19?
Yellow conglomerates	200 m	Aguatón	21	14	U. Eoc., MP19

Table 1. Stratigraphy of the Sierra Palomera Paleogene.

Tabla 1. Estratigrafía del Paleógeno de la Sierra Palomera.

## ABBREVIATIONS

### Institutions:

IRSNB Institut Royal des Sciences Naturelles de Belgique

RGM The geological collections of the National Museum of Natural History, Leiden, The Netherlands (formerly **R**ijksmuseum van **G**eologie en **M**ineralogie). Naturalis continues using the code RGM for its geological collections.

RUU University Utrecht, The Netherlands.

### Localities:

AGT2D Aguatón 2D

AGT5A Aguatón 5A

AGT5B Aguatón 5B

AGT6 Aguatón 6

BOULDC Bouldnor Cliff

CF Calaf

CHR2D Barranco del Chorrillo 2D

CHR5A Barranco del Chorrillo 5A

CHR5B Barranco del Chorrillo 5B

CHR6C Barranco del Chorrillo 6C

FF3B Fuenferrada 3B

HB Hoogbutsel

HH Headon Hill

OLA4A Olalla 4A

SOS Sossís

UMB1B Fuente Umbría 1B

VRS15A Villarrosano 15A

VRS15B Villarrosano 15B

VRS17A Villarrosano 17A

Bco. Barranco (=ravine)

V' is the variability coefficient as defined by Freudenthal & Cuenca (1984).

MV is Morphology value, a quantification of morphology, proposed by Freudenthal (1976), and defined in a slightly different way in this paper.

## PALEONTOLOGY

### Nomenclature of parts of the cheek teeth

De Bruijn (1966) proposed a nomenclature for the crests of the teeth that has been fully accepted, and is being used generally. However, in trying to describe the homologies between the crests of M<sup>1</sup>, M<sup>2</sup>, and M<sup>3</sup> of various glirid populations terms like “anterior accessory crest” and “anterior extra crest inside the trigone” turned out to be so cumbersome, that the need for short single-word terms was felt. We propose the following terminology (see Fig. 1):

Anteroloph, protoloph, metaloph and posteroloph are used as always for the upper molars, with the suffix -id for the lower molars, nor does the terminology of the cusps change.

Accessory crests are denominated “trope” in the upper molars, and “tropid” in the lower ones (trope from the Greek *tropis* = keel, ridge). The accessory crests accompanying the anteroloph and posteroloph are called anterotrope and posterotrope respectively. The corresponding crests in the lower molars are called anterotropid and posterotropid. Inside the trigone the extra ridge behind the protoloph is called prototrope, the one in front of the metaloph is called metatrope. Anterior and posterior centroloph are called precentroloph and postcentroloph respectively. In case only one – centrally placed – centroloph is present, it is called midcentroloph, when it cannot be decided whether it is originally a precentroloph or a postcentroloph.

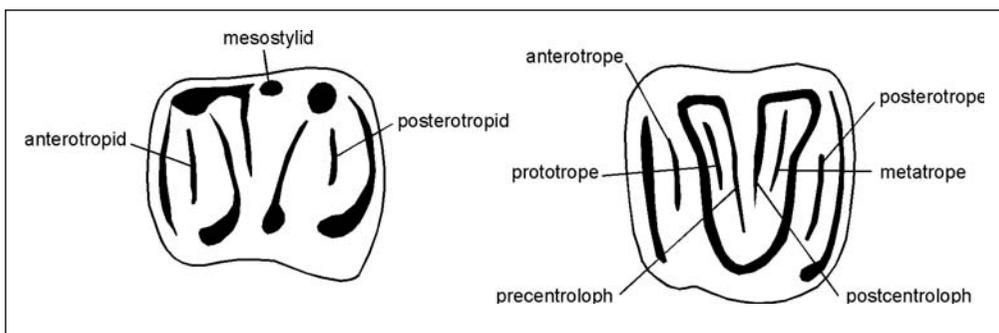


Fig. 1. Nomenclature of parts of the cheek teeth. The term midcentroloph does not appear in the figure, because it automatically replaces both precentroloph and postcentroloph. Only the new or unusual terms are explained. The figures are drawn as left-hand molars.

Fig. 1. Terminología utilizada en la descripción de las piezas dentarias. El término “midcentroloph” no aparece en la figura, porque reemplaza automáticamente a “precentroloph” y “postcentroloph”. Sólo aparecen los términos nuevos e inusuales. Los dibujos representan molares izquierdos.

These new terms facilitate a more concise description of the dental pattern, and in most cases are quite sufficient, though in extreme cases (like *Glamys fordi*) they fail to be a complete descriptive tool.

In the descriptions subscript and superscript are used as usual, to designate upper and lower molars, respectively. P4, M1 etc. are used to designate both upper and lower teeth at the same time.

## Methods

### *Distinction of M1 and M2*

M<sub>1</sub> and M<sub>2</sub> are easily distinguished, and in fact most authors nowadays describe them separately. M<sup>1</sup> and M<sup>2</sup> are much more difficult to distinguish, but I tried to do so anyway. In a number of cases the wrong decision may have been made, but I think it is better to separate them, accepting the risk of some mistakes, than treat them together. If the possibility exists, that M<sup>1</sup> and M<sup>2</sup> are metrically or morphologically different, the usual statistical methods can not be applied when they are not distinguished, and in view of this disadvantage, one should try to separate them as well as possible.

Still, in order to make our measurements compatible with published data, M1 and M2 are represented separately and grouped together in various tables.

### *Measurements and orientation*

Measurements were taken, partly with a Leitz Ortholux, partly with a Wild M8, equipped with a mechanical stage with electronic sensors, connected to a computer through a Sony Magnescale measuring unit. The measurement data were processed by a private computer program. Measurements are given in units of 0.1 mm with one decimal. Mean length and width in the tables are represented with two decimals, except for data taken from the literature, where often only one decimal is available.

The orientation of the specimens for measuring length and width is as follows:

*D<sub>4</sub> and P<sub>4</sub>* – Length along a line through the middle of the posterior wall, parallel to the bisectrix of labial and lingual wall; width perpendicular to length, over hypoconid and entoconid.

*M<sub>1</sub> and M<sub>2</sub>* – Length along a line through the middle of the anterior and posterior wall; width perpendicular to length, either over protoconid and metaconid, or over hypoconid and entoconid, whatever is largest.

*M<sub>3</sub>* – Length perpendicular to the anterior border; width parallel to the anterior border, over protoconid and metaconid. In a few cases the anterior and labial border are not perpendicular, and the specimen is reoriented to measure the width over protoconid and metaconid.

*D<sup>4</sup>* – Length over the foremost and backmost point of the borders, or somewhat lingually of the foremost point. Length and width are formed by the circumscribed rectangle.

*P<sup>4</sup>* – Width along a line over the anterior slope of the metacone and the posterior border of the protocone (sometimes over the middle of the metacone). Length and width are formed by the circumscribed rectangle.

$M^1$  and  $M^2$  – Width parallel to the bisectrix of the posterior border and the labial part of the anterior border; or parallel to the posterior border; length perpendicular to the width.  
 $M^3$  – Width parallel to the anterior border; length perpendicular to the width.

### Computer programs

Several computer programs have been written to facilitate the study of the material:

A measurements program takes care of the communication between the measuring microscope and the computer. The computer receives the data from the measurement equipment, and the program transforms them into text files with the standard format of the RGM collection database. Thus, no errors are introduced by copying measurements manually, or by incorrect rounding.

The morphology program stores the morphological data of all specimens, that I have been able to observe personally, in a morphological database, as described by Freudenthal (1996). The morphological data base program performs all kinds of statistical calculations, and can transform the data into a readable text, that forms the basis of the final description of each population.

In a number of cases I have captured measurement data from published length/width diagrams of other authors, through a program that projects a co-ordinate grid on a scanned image of such a plot, and interprets each mouse click as a length/width datum. By clicking all points in a plot, one can recover the original measurements. Tests on my own plotted material have shown an almost 100% precision.

### The contents of the genus *Glamys* Vianey-Liaud, 1989

Vianey-Liaud (1989) created the genus *Glamys* for *Gliravus priscus* Stehlin & Schaub, 1951. It is based on the shape of the infraorbital foramen of a fragmentary skull, MGB 99, from Mas de Got B (coll. Montpellier). Vianey-Liaud (1974) interpreted its foramen infraorbitale as protrogomorphous (op. cit., p. 237), and later (Vianey-Liaud, 1994) she figured and described the same specimen and called it sciuromorphic or pseudo-myomorphic. Apparently the morphology of the specimen is open to various interpretations, and until this ambiguity be solved, this character is better not used to diagnose the genus.

The second diagnostic feature given by Vianey-Liaud, is the absence of  $P^3$ . However, in her 1994 publication she places *Gliravus robiacensis* Hartenberger, 1965 in *Glamys*, although that species is known to have a  $P^3$  (cf. Hartenberger, 1971). Moreover, in our collection from AGT2D we found a few  $P^4$  of *G. priscus* with a possible facet for  $P^3$  on the anterior wall. Apparently,  $P^3$  has not completely disappeared in *Glamys*, and this feature is not useful either, at least not as a primary diagnostic feature. On the other hand, among some 20  $P^4$  of *G. majori* from Mirambueno not a single specimen presents an anterior facet for  $P^3$ . The absence of a facet does not mean the absence of  $P^3$ , but it seems reasonable to believe, that  $P^3$  may have been either absent or present in both *G. majori* and *G. priscus*.

Since the diagnosis of the subfamily Glamyinae is based on the same ambiguous features as that of the genus, it seems better, for the moment, to consider Glamyinae a synonym of Gliravinae.

Van Dam (1998) rejects the use of the genus name *Glamys*, but his statement, that skull morphology be better not used as a diagnostic character holds no ground. Any good criterion should be used, and skull morphology is certainly a good criterion. His argument that skull morphology causes serious problems, if one wants to identify populations from which only teeth are known, lacks any sense of reality. Tooth morphology serves perfectly to distinguish taxons at the species level, but may well be insufficient to distinguish taxonomic units of higher rank, especially when parallel evolutions are involved.

Daams & de Bruijn (1995) propose a classification of the Gliridae, based exclusively on tooth morphology, and (op. cit., p. 3) state that this leads to the undesirable "synonymy" of *Glamys* and *Gliravus*, and on p. 39 "but as our classification is exclusively based on the dental pattern, we cannot avoid that *Glamys* becomes a junior synonym of *Gliravus*." I interpret, that these authors in fact support the difference between these two genera, but that they are victims of a too rigid application of their self-imposed rules. They just present a piece of classification, technically correct, but undesirable because it does not reflect the complete knowledge available, that would turn it into systematics.

For the time being, it seems best to base the genus *Glamys* on dental morphology, and in fact, in this case, tooth morphology alone is sufficient to distinguish it from *Gliravus*. The dental pattern of *Glamys priscus*, the type species of *Glamys*, and that of *Gliravus majori*, the type species of *Gliravus*, really are quite distinct:

In *Glamys (priscus)* the P<sup>4</sup> is triangular, and relatively long, with a moderately developed anteroloph; in the molars there is usually only one – anterior - centroloph; when two centrolophs are present, the anterior one is dominant. The centrolophid is generally absent. The mesolophid is of variable length, often bifurcated in the center of the molar; a posterotropid is frequently present, either connected to the mesolophid or separated from it. Posterotropid and mesolophid together often form an irregular pattern of crests. The labial end of the mesolophid usually reaches the labial border of the molar.

In *Gliravus (majori)*, on the other hand, the shape of P<sup>4</sup> is more or less rectangular, with a very reduced and often absent anteroloph, relatively shorter than in *Glamys*; in the molars there is one centroloph, which is the posterior one. The lower molars of *G. majori* are not known from the type-locality. In fact, the holotype of *G. majori* is the only specimen that can be attributed to this species without any doubt. However, several species are known (*G. alvarezae* Lacombe & Morales, 1987; *G. caracensis* Daams, Freudenthal, Lacombe & Alvarez, 1989), that are evidently very closely related to *G. majori*, and in our material from Mirambueno *G. majori* or a closely related species is found. Even if none of these populations is the true *G. majori*, it may be assumed that they give a good idea of what the lower dentition of that species looked like: a centrolophid may be present; the posterotropid is absent or very small; the mesolophid is a simple crest, with its labial end frequently withdrawn from the labial border of the molar. In the upper molars there is a postcentroloph; two centrolophs may be present, but then the postcentroloph is the dominant one.

What really brings together *Gliravus majori*, *G. alvarezae*, and *G. caracensis* is the (tendency towards a) union of anteroloph and posteroloph, along the lingual border, separating the protocone from the border. This feature is observed, in different degrees of development, in the mentioned three species, and in unpublished material from Mirambueno (see Freudenthal, 1997a).

In my opinion, it must be one of the basic elements of the diagnosis of *Gliravus*, and the genus should be restricted to species having this tendency. It then comprises *Gliravus majori* Stehlin & Schaub, 1951, *Gliravus alvarezae* Lacomba & Morales, 1987, *Gliravus caracensis* Daams, Freudenthal, Lacomba & Alvarez, 1989, and *Gliravus* (aff.) *majori* in Freudenthal (1997a).

*G. daamsi*, *G. tenuis*, *G. garouillensis*, *G. itardiensis*, *G. bruijni*, *G. bravoii*, and *G. hispanicus* do not belong to the genus *Gliravus* (nor to *Glamys*), and should be transferred to a new genus, to be described hereafter.

A problem is, which other glirid species, if any, should be transferred to *Glamys*. Vianey-Liaud (1994) transferred *Gliravus devoogdi* and *G. fordi* to the genus *Glamys*, on the basis of supposed evolutionary relationships. These supposed relationships are not certain at all, and their dental morphology is quite different from that of *G. priscus*. But, in the restricted concept of *Gliravus*, as proposed above, the mentioned two species evidently do not fit in that genus, and there are no serious objections against transferring them to *Glamys*, at least for the time being.

Vianey-Liaud (1994) created the new genus *Miniglis* on the basis of *Gliravus minor* Bosma & de Bruijn, 1982 from Headon Hill 2. The dental pattern of this species is not fundamentally different from that of *G. priscus*, and until new data that prove a difference, are available, it is most logical to classify it in the genus *Glamys*. Bosma & de Bruijn (1982) say that *G. minor* differs from *G. priscus* by the connections between protocone and anteroloph and posteroloph. It is true that the protocone-posteroloph connection may be slightly better developed in the material from HH2, but among the six available specimens in the RUU collection, none has an anteroloph-protocone connection.

*G. robiacensis* Hartenberger, 1965 was placed in *Glamys* by Vianey-Liaud (1994). Consequently, the absence of P<sup>3</sup> in the diagnosis of the genus (Vianey-Liaud, 1994) is no longer tenable, but *G. robiacensis* may well be a *Glamys*.

*G. meridionalis* Hartenberger, 1971 and *G. hispanicus* van Dam, 1998 may be related (see van Dam, 1998, p. 109), and the disposition of centroloph, mesolophid, and some complications of the dental pattern of the lower molars, point towards *Glamys*. On the other hand, the specimens of *G. meridionalis* from Sossís 1, figured by Agustí & Arcas (1997) do not support this idea.

## Genus *Gliravus* Stehlin & Schaub, 1951

### *Type-species*

*Gliravus majori* Stehlin & Schaub, 1951

### *Diagnosis*

The shape of P<sup>4</sup> is a rectangle, with a very reduced, or absent anteroloph. Lingual and labial lengths are very similar, and the exit of the sinus lies in the middle of the tooth. In the upper molars there is one centroloph, which is the posterior one. When there are two centrolophs, the postcentroloph dominates. There is a (tendency towards

a) union of anteroloph and posteroloph, along the lingual border, separating the protocone from the border. In the lower molars a centrolophid may be present; the posterotropid is absent or very small; the mesolophid is a simple crest, with a labial end frequently withdrawn from the labial border of the molar.

#### *Differential diagnosis*

See the diagnosis of *Glamys*.

The P<sup>4</sup> of *Gliravus* is quite different from that of other Gliridae: The anteroloph is variable, but the most frequent situation is a short anteroloph, situated in front of the protocone, and not in front of the paracone, augmenting the lingual length of the tooth, so that it is more or less equal to the labial length. In *Glamys* and many other Gliridae, on the other hand, the anteroloph lies in front of the paracone, augmenting the labial length, and giving the tooth a triangular shape; the anteroloph may continue until in front of the protocone, but the labial length is larger than the lingual length.

#### *Attributed species*

*Gliravus alvarezae* Lacomba & Morales, 1987

*Gliravus caracensis* Daams, Freudenthal, Lacomba & Alvarez, 1989

*Gliravus* (aff.) *majori* in Freudenthal (1997a)

*Gliravus* aff. *bruijni* from Gandesa in Agustí et al. (1985)

The material from Mas de Got, and several other localities in the Quercy, described by Vianey-Liaud (1969) as *Gliravus* aff. *majori*, does not fit the genus diagnosis, and is excluded.

### **Genus *Schizoglravus* gen. nov.**

#### *Type-species*

*Schizoglravus montisalbani* sp. nov.

#### *Derivatio nominis*

From the Greek verb *schizein*, to divide, being this genus a result of the subdivision of the genus *Gliravus* in its previous sense.

#### *Attributed species*

*Bransatoglis micio* (Misonne, 1957) in Vianey-Liaud (1994), pro parte

*Gliravus bruijni* Hugueneu, 1967

*Gliravus tenuis* Bahlo, 1975

*Gliravus daamsi* Bosma & de Bruijn, 1982

*Gliravus bravoii* Hugueneu, Adrover & Moissenet, 1985

*Gliravus itardiensis* Vianey-Liaud, 1989  
 ?*Gliravus garouillensis* Vianey-Liaud, 1994  
*Gliravus hispanicus* van Dam, 1998

### Diagnosis

P<sup>4</sup> triangular like in *Glamys* with a fairly well developed anteroloph. Upper molars with two centrolophs that are frequently connected lingually, or with one single centroloph, which may be the precentroloph or the postcentroloph; extra crests practically absent. In the lower molars the anterotropid is absent to rare, the centrolophid varies between absent and frequent, but is not very well developed, the posterotropid may be frequent. The postero-lingual corner of M<sub>3</sub> is strongly reduced.

### Differential diagnosis

*Schizoglravus* differs from *Bransatoglis* by the triangular P<sup>4</sup> (oval in *Bransatoglis*), and by the less complete and more irregular crests. It differs from *Glamys* and *Gliravus* by the frequently double centrolophs. It differs from *Glamys* by the more reduced postero-lingual corner of M<sub>3</sub>. It differs from *Gliravus* by the frequent and better-developed posterotropid, and the shape of P<sup>4</sup> (see diagnosis of *Gliravus*).

### The position of *Peridyromys micio* and *Gliravus itardiensis*

Vianey-Liaud (1989) created *G. itardiensis* for a population from Itardies, and in 1994 she synonymized it with *P. micio*, and transferred this species to *Bransatoglis*. Whether *G. itardiensis* and *P. micio* are synonymous or not, I think they are better not placed in that genus. In the oldest *Bransatoglis* known (*B. bahloi*) the anterotropid is already frequently present, and in the somewhat younger material from AGT2D this crest never fails, and the dental pattern is characterized by long, parallel, regular crests, M<sub>2</sub> being more advanced than M<sub>1</sub>. Except for the very oldest populations, those that don't have an anterotropid should not be attributed to *Bransatoglis*. According to the figures and the description by Vianey-Liaud (1989) *G. itardiensis* does not have an anterotropid. Most of the material of *G. itardiensis* (and/or *P. micio*) fits perfectly well in *Schizoglravus*, though some specimens may belong to another species and genus; e.g. the P<sup>4</sup> ITD183 (op. cit., fig.7e) looks more like a true *Gliravus*.

Vianey-Liaud (1994) designated the M<sub>2</sub> dext. IRSNB M 1683 as the holotype of *Peridyromys micio*. According to art. 74.5 of the International Code of Zoological Nomenclature this designation is invalid (a subsequent author can only designate a lectotype, never a holotype), "unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series...". Since that condition is fulfilled, the specimen M 1683 is the valid lectotype of *P. micio* (the correct catalogue number of that specimen is Ct.M. 1143, and not M 1683). The code contains no rule, that the first figured specimen should be the lectotype, as stated by Vianey-Liaud (1994, p. 138). There is only recommendation 74B, which, "other things being equal", expresses a preference for a figured syntype, and that is nothing but a recom-

mentation, not an obligation. In practice, one is free to choose anyone of the syntypes, if the choice is based on good arguments.

Fig. 14k in Vianey-Liaud (1994) gives the impression, that the lectotype specimen of *P. micio* is a *Bransatoglis*, because of the presence of an anterotripid; however, detailed observation of the specimen showed that this is an incorrect interpretation, and there is no anterotripid. The lectotype specimen of *Peridyromys micio* is a *Schizoglriravus*, and *S. itardiensis* may well be a junior synonym of *S. micio*, as supposed by Vianey-Liaud (1994).

*Gliravus garouillensis* Vianey-Liaud, 1994 is not attributed to this genus with certainty. The populations attributed to this species were originally attributed to *Glamys priscus*, Vianey-Liaud herself doubts whether it is a *Glamys* or a *Gliravus*, the material is too poor to define a species reliably, and the only measurement given ( $M^2$ , 9.1 x 8.5) is apparently incorrect, because the  $M^2$  are usually shorter than broad.

### *Choice of the type-species*

When looking for the best type-species for this new genus, I discarded *G. itardiensis*, because it is insufficiently known, and the author of that species synonymized it with *P. micio*. *G. bruijni* and *G. bravoii* have a peculiar mesolophid, that is certainly not characteristic of *Schizoglriravus*. *G. daamsi* is the oldest species known, and has not yet acquired some typical features; moreover it is based on a very poor material. *G. tenuis* is from a time-interval, that is hardly known, except for its type-locality Heimersheim. *G. garouillensis* is based on very poor material, and will be impossible to recognize when differences between species rely on relative frequencies of characters, and it may even not be a *Schizoglriravus*.

So, I decided to base the genus on the very rich material of a new species from Montalbán 1D, an already classical locality, and a locality that offers – for the time being – unlimited possibilities to collect more material. Furthermore MLB1D lies in a stratigraphic sequence of fossiliferous localities.

### ***Schizoglriravus montisalbani* sp. nov.**

Plate 1, Fig. 1-20

#### *Type-locality*

Montalbán 1D (MLB1D, Teruel, Spain)

#### *Derivatio nominis*

From the ancient name of Montalbán, Monte Albano.

#### *Holotype*

$M_1$  sin., MLB1D 1050, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza (Plate 1, fig. 5).

### *Objective synonymy*

*Gliravus tenuis* in Vianey-Liaud (1994) from Montalbán S  
*Gliravus* aff. *itardiensis* in Freudenthal (1997a)

### *Other localities*

Montalbán 3X, Montalbán 8, Montalbán 3C, Montalbán 7, Montalbán 9, Montalbán 10, Montalbán 11, Montalbán 12.

### *Diagnosis*

Upper molars with two, generally long, centrolophes of about the same importance, connected lingually or midway in about 50% of the cases, and generally connected to paracone and metacone respectively. Extra crests are very rare. Lower molars with a well-developed metalophid that stays free from the metaconid in 50% of the specimens. Anterotropid very rare, and small to very small when present; posterotropid frequent, best developed in  $M_1$ . Centrolophid frequently present, but generally not very well developed. Mesolophid well developed, in the majority of the cases long, either directed towards the metaconid, or to the entoconid; in  $M_2$  it may be connected to the entoconid, and in  $M_3$  this is the rule.

### *Differential diagnosis*

Of the size of *S. tenuis* and *S. hispanicus*, and smaller than other *Schizoglriravus*. Dental pattern more complicated than that of *S. tenuis* and *S. hispanicus*: centrolophid and mesolophid better developed, presence of posterotropid, frequently two centrolophes in  $P^4$ , and nearly always in  $M^{1,2}$ .

### *Material and measurements*

See Table 2a and 2b.

### *Description of Schizoglriravus montisalbani from Montalbán 1D*

$D_4$  –The shape is anteriorly pointed. The anterolophid is interrupted (2) or continuous (10). The anterotropid is absent (12). The metalophid is free (1), low connected to the metaconid (5), or high connected to that cusp (5). The centrolophid is absent (10) or short (2). The centrolophid-metaconid connection is absent. The mesoconid is absent (3), placed on the labial border (7), or more centrally (2). The mesolophid is absent (3), of medium length and interrupted (3), of medium length (2), or directed towards the entoconid (4). The posterotropid is absent (9) or very small (3).

*P*<sub>4</sub> -The shape is anteriorly blunt (30) or pointed (2). The anterolophid is interrupted (18) or continuous (14). The anterotropid is absent (30) or very small (2). The metalophid is free (1), low connected to the metaconid (14), or high connected to that cusp (14). The centrolophid is absent (17), short (9), of medium length (4), or long (2). The centrolophid-metaconid connection is normally absent; it may be low (4), or high (2). The mesostylid is absent (33). The mesoconid is placed on the labial border (24) or more centrally (8). The mesolophid is short (2), curved forward (2), directed towards the metaconid (5), directed towards the entoconid (18), connected to the entoconid (1), long and straight (2), or it reaches the lingual border (1). The posterotropid is absent (31) or very small (1).

*M*<sub>1</sub> -The anterolophid is labially free (40) or labially connected (2). The anterotropid is absent (36), very small (2), or small (2). The metalophid is free (20), low connected to the metaconid (17), or high connected to that cusp (2). The centrolophid is absent (22), short (11), of medium length (5), or long (2). The centrolophid-metaconid connection is normally absent, low in 1 case. The mesostylid is absent (42). The mesoconid is placed on the labial border (40) or more centrally (2). The mesolophid is of medium length (6), directed towards the metaconid (15), connected to the metaconid (5), directed towards the entoconid (12), connected to the entoconid (1), or long and straight (3). The posterotropid is absent (13), very small (7), small (8), of medium length (6), or long (5).

*M*<sub>2</sub> -The anterolophid is labially free. The anterotropid is absent (50), very small (3), or small (1). The metalophid is free (41) or low connected to the metaconid (9). The centrolophid is absent (27), short (15), of medium length (7), or long (3). A low centrolophid-metaconid connection is present in 3 cases only. The mesostylid is absent. The mesoconid is placed on the labial border (51) or more centrally (3). The mesolophid is of medium length (7), curved forward (1), directed towards the metaconid (17), connected to the metaconid (1), directed towards the entoconid (19), connected to the entoconid (7), or long and straight (2). The posterotropid is absent (20), very small (15), small (10), or of medium length (5).

*M*<sub>3</sub> -The anterolophid is labially free. The anterotropid is absent (58) or small (1). The metalophid is free (38), low connected to the metaconid (15), or high connected to that cusp (3). The centrolophid is absent (16), short (25), of medium length (14), or long (3). When a centrolophid is present, the centrolophid-metaconid connection is absent (14), low connected (23), or high connected (4). The mesostylid is absent. The mesoconid is placed on the labial border (58) or more centrally (1). The mesolophid is connected to the metaconid (1), directed towards the entoconid (10), or connected to the entoconid (48). The posterotropid is absent (37), very small (8), small (11), or of medium length (2).

*D*<sup>4</sup> - There are no extra crests. The anteroloph is of medium length (4) or long (12). The anterotrope is absent. The precentroloph is absent (7), short (3), of medium length (2), or long (4). The postcentroloph is absent (9) or long (7). The centrolophs are not connected (16). The endoloph is formed by the protocone only (14) or anteriorly interrupted (2). The lingual border is smooth (16).

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*P*<sup>4</sup> - There are no extra crests. The anteroloph is absent (1), short (7), of medium length (23), or long (14). The precentroloph is absent (1), short (3), of medium length (9), or long (36). The postcentroloph is absent (29), short (4), of medium length (8), or long (8). The centrolophs are not connected (49) or connected (1). The endoloph is formed by the protocone only (39) or anteriorly interrupted (4). The lingual border is smooth.

*M*<sup>1</sup> -The anteroloph is lingually free (55). The anterotrope is absent (53), short (1), or of medium length (1). The precentroloph is absent (3), short (2), of medium length (11), or long (37); when present, it is connected to the paracone (39), free from the paracone (10), or connected to a mesostyl (1). The postcentroloph is absent (3), short (2), of medium length (7), or long (41); when present, it is connected to the metacone (27), free from the metacone (17), or placed centrally (4). The prototrope is absent (46), short (3), or of medium length (1). Metatrope and posterotrope are absent. The centrolophs are not connected (27), connected lingually (18), or connected midway (7). The endoloph is formed by the protocone only. The lingual border is smooth.

*M*<sup>2</sup> -The anteroloph is lingually free (31) or lingually low connected (6). The anterotrope is absent (39) or short (1). The precentroloph is absent (3), short (2), of medium length (4), or long (29); when present it is connected to the paracone (23), free from the paracone (12), or placed centrally (1). The postcentroloph is absent (1), short (2), of medium length (5), or long (31); when present it is connected to the metacone (34), or free from the metacone (4). The prototrope is absent (38) or short (1). The metatrope is absent (38) or short (1). The centrolophs are not connected (18), connected lingually (8), connected midway (8), or there are two connections (3). The posterotrope is absent (40). The endoloph is formed by the protocone only (25), anteriorly interrupted (11), or complete (1). The lingual border is smooth (37) or crenulated (3).

*M*<sup>3</sup> -The anteroloph is lingually free (16), lingually low connected (11), or lingually high connected (17). The anterotrope is absent. Crests inside the trigone: one crest (2), two crests (39), or three crests (17). The mesostyl is absent (58) or present (1). The posterotrope is absent (56) or short (2). The endoloph is formed by the protocone only (11), anteriorly interrupted (15), posteriorly interrupted (2), or complete (16). The lingual border is smooth.

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
D <sub>4</sub>												
VIV	4	10.0	10.53	11.2	11.4	0.51	5	7.3	8.02	9.3	24.9	0.80
SOS2B	1		10.10				1		8.00			
ITA	4	8.6	8.9	9.1	5.6	0.24	4	7.7	8.1	8.7	12.3	0.43
MLB1D	12	7.7	8.19	8.7	12.2	0.33	12	6.3	7.02	7.6	18.5	0.44
HB	17	7.8	8.4	9.3	17.9	0.44	17	6.3	6.9	7.8	21.7	0.44
P <sub>4</sub>												
VIV	3	10.8	12.53	13.8	23.9		3	9.9	11.53	12.7	24.3	
COD	1		10.9				1		9.7			
SOS2B	23	7.9	8.95	9.7	20.1	0.45	23	7.0	8.03	9.0	24.9	0.49
ITA	6	9.4	10.0	10.9	15.0	0.60	6	8.8	9.5	10.5	17.9	0.67
MLB1D	31	7.6	8.23	9.1	18.2	0.37	32	6.8	7.52	8.3	20.0	0.36
HEIM	6	8.0	8.68	9.4	16.1	0.49	6	7.1	7.62	8.0	11.8	0.33
HB	31	7.9	9.2	10.3	26.1	0.57	31	7.1	8.4	9.4	27.4	0.63
M <sub>1</sub>												
VIV	14	14.0	14.81	15.7	11.5	0.55	11	14.1	14.98	16.1	13.3	0.74
SOS2B	46	9.7	10.47	11.5	17.2	0.39	46	9.7	10.48	11.1	13.4	0.35
ITA	14	10.1	11.6	12.4	19.8	0.57	14	10.1	11.6	12.6	21.6	0.64
MLB1D	42	8.8	10.00	11.3	25.0	0.49	42	9.4	10.39	11.5	20.2	0.54
HEIM	11	8.2	9.54	10.9	28.3	0.68	11	8.6	10.05	11.4	27.8	0.74
M <sub>2</sub>												
VIV	15	13.1	14.68	15.7	17.7	0.78	15	13.9	15.89	17.1	20.1	0.89
WIGHT	2	12.0	12.30	12.6	4.9		2	12.6	13.05	13.5	6.9	
SOS2B	46	9.7	10.50	11.3	15.2	0.36	46	10.5	11.46	12.9	20.9	0.39
ITA	16	11.1	11.8	12.8	14.4	0.58	16	11.8	12.4	12.9	8.9	0.34
MLB1D	54	9.2	10.06	11.1	18.9	0.41	55	9.4	10.72	12.1	25.2	0.56
HEIM	17	9.2	10.06	10.9	16.9	0.45	17	10.3	11.05	12.0	15.4	0.50
M <sub>1,2</sub>												
VIV	29	13.1	14.74	15.7	17.6	0.67	26	13.9	15.51	17.1	20.6	0.94
COD	9	11.2	12.4	13.1	15.3		9	11.5	13.1	14.0	19.1	
WIGHT	2	12.0	12.30	12.6	4.9		2	12.6	13.05	13.5	6.9	
SOS2B	92	9.7	10.49	11.5	17.2	0.37	92	9.7	10.97	12.9	29.2	0.62
ITA	30	10.1	11.71	12.8	23.1		30	10.1	12.03	12.9	23.3	
MLB1D	96	8.8	10.03	11.3	24.9	0.45	97	9.4	10.58	12.1	25.5	0.57
HEIM	28	8.2	9.85	10.9	27.4	0.60	28	8.6	10.66	12.0	31.9	0.77
HB	101	10.3	11.6	13.0	23.3	0.52	101	9.8	12.0	14.1	35.8	0.80
M <sub>3</sub>												
VIV	17	13.5	14.34	15.3	12.6	0.48	17	13.3	14.05	15.3	14.2	0.49
COD	6	11.5	12.3	13.1	13.0		6	11.6	12.3	13.4	14.6	
WIGHT	2	10.3	11.30	12.3	17.7		2	11.5	11.60	11.7	1.7	
SOS2B	25	8.7	9.74	10.5	18.5	0.44	25	9.4	10.12	11.3	18.8	0.52
ITA	8	9.9	10.7	11.5	15.0	0.59	8	9.5	10.5	11.3	17.1	0.61
MLB1D	57	8.2	9.23	10.5	24.9	0.47	56	8.2	9.21	10.3	22.8	0.56
HEIM	7	8.9	9.39	9.8	9.6	0.33	7	8.9	9.50	10.1	12.6	0.42
HB	36	10.3	11.8	12.7	20.3	0.61	36	9.8	11.1	12.2	21.6	0.56

Table 2a. Measurements of the lower dentition of various species of *Schizoglyiravus*. VIV = *S. bravoii* from Vivel del Río; COD = *S. bruijini* from Coderet; WIGHT = *S. daamsi* from Isle of Wight; SOS2B = *S. hispanicus* from Sossís 2B; ITA = *S. itardiensis* from Itardies; MLB1D = *S. montisalbani* from Montalbán 1D; HEIM = *S. tenuis* from Heimersheim; HB = *B. micio* from Hoogbutsel.

Tabla 2a. Medidas de la dentición inferior de varias especies de *Schizoglyiravus*. VIV = *S. bravoii* de Vivel del Río; COD = *S. bruijini* de Coderet; WIGHT = *S. daamsi* de la isla de Wight; SOS2B = *S. hispanicus* de Sossís 2B; ITA = *S. itardiensis* de Itardies; MLB1D = *S. montisalbani* de Montalbán 1D; HEIM = *S. tenuis* de Heimersheim; HB = *B. micio* de Hoogbutsel.

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
D <sup>4</sup>												
VIV	3	10.6	11.23	11.6	8.9		4	11.6	11.90	12.6	8.4	0.48
WIGHT	1		11.30				1		11.20			
SOS2B	1		10.20				1		8.50			
MLB1D	16	7.3	7.71	8.2	11.7	0.31	16	7.7	8.34	9.1	16.8	0.33
HEIM	1		8.30				1		9.10			
HB	20	7.3	8.0	9.1	22.5	0.41	20	8.2	9.0	9.9	18.9	0.48
P <sup>4</sup>												
VIV	8	10.3	11.20	12.4	18.7	0.72	8	13.6	15.58	16.7	19.9	1.02
COD	5	8.8	9.5	11.1	24.2		5	11.4	13.3	14.4	22.6	
WIGHT	1		9.20				1		10.90			
SOS2B	33	7.2	8.13	9.0	22.1	0.36	33	8.6	9.92	10.9	23.2	0.54
ITA	8	7.9	8.6	9.5	18.6	0.51	8	8.9	10.0	11.4	25.0	0.91
MLB1D	49	6.0	6.97	7.9	27.3	0.44	49	8.4	9.41	10.6	23.4	0.54
HEIM	11	6.4	7.39	8.1	23.0	0.56	11	8.3	9.56	10.4	22.0	0.63
HB	25	8.2	8.7	9.4	13.8	0.33	25	10.2	10.9	11.8	14.7	0.39
M <sup>1</sup>												
VIV	14	11.9	13.62	15.1	23.5	0.86	14	14.4	16.66	18.1	22.2	1.13
SOS2B	37	8.7	9.97	10.6	19.1	0.38	37	10.6	11.29	12.2	14.2	0.38
ITA	11	9.9	10.8	12.0	19.4	0.51	11	10.5	11.5	12.3	15.7	0.48
MLB1D	53	8.8	9.71	10.8	20.6	0.46	53	10.0	11.22	12.4	21.4	0.64
HB	57	10.0	11.0	11.9	17.3	0.41	57	10.9	12.2	13.3	19.7	0.51
M <sup>2</sup>												
VIV	17	12.8	13.89	15.5	19.4	0.68	19	15.4	17.35	19.9	25.9	1.02
WIGHT	1		11.60				1		14.20			
SOS2B	29	9.1	9.80	10.4	13.3	0.32	29	11.5	12.04	12.9	11.6	0.36
ITA	14	10.0	11.0	11.9	17.3	0.61	14	11.7	12.8	14.2	19.5	0.72
MLB1D	38	8.7	9.54	10.2	15.7	0.40	37	10.9	11.64	12.4	12.9	0.38
HB	50	10.0	11.3	13.1	27.4	0.55	50	12.1	13.1	14.2	16.0	0.51
M <sup>1,2</sup>												
VIV	31	11.9	13.77	15.5	26.1	0.76	33	14.4	17.05	19.9	32.2	1.11
COD	15	10.9	12.2	13.1	18.0		15	12.9	14.2	16.2	23.2	
WIGHT	5	11.3	11.62	11.8	4.3	0.19	5	13.8	14.16	14.8	7.1	0.38
SOS2B	66	8.7	9.90	10.6	19.2	0.36	66	10.6	11.62	12.9	19.8	0.53
ITA	25	9.9	10.91	12.0	19.2		25	10.5	12.23	14.2	30.3	
MLB1D	91	8.7	9.64	10.8	21.8	0.44	90	10.0	11.39	12.4	21.1	0.58
HEIM	29	9.1	10.06	10.9	17.9	0.52	29	10.3	11.55	13.0	23.4	0.60
HB	107	10.0	11.1	13.1	27.9	0.50	107	10.9	12.6	14.2	26.2	0.66
M <sup>3</sup>												
VIV	20	11.0	12.16	13.6	21.4	0.72	21	13.7	14.71	15.9	15.0	0.74
COD	3	10.1	10.7	11.4	12.1		3	12.0	12.3	12.4	3.3	
SOS2B	11	7.3	8.19	8.9	19.5	0.43	11	9.7	10.35	10.8	10.6	0.39
ITA	6	9.1	9.8	10.9	18.4	0.67	6	9.5	10.7	12.0	23.4	1.02
MLB1D	58	7.2	8.09	8.9	21.0	0.49	58	8.7	9.86	10.9	22.3	0.50
HEIM	5	8.3	9.36	10.2	20.3	0.78	5	8.9	10.64	11.8	27.3	1.46
HB	33	8.4	10.0	11.3	29.0	0.65	33	10.8	11.9	12.8	16.8	0.51

Table 2b. Measurements of the upper dentition of various species of *Schizoglivrus*. For explanation see Table 2a.

Tabla 2b. Medidas de la dentición superior de varias especies de *Schizoglivrus*. Para explicación véase Tabla 2a.

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## Genus *Glamys* Vianey-Liaud, 1989

*Type-species*

*Gliravus priscus* Stehlin & Schaub, 1951

*Synonymy*

*Miniglis* Vianey-Liaud, 1994

*Emended diagnosis*

P<sup>4</sup> is rounded triangular, with a fairly well developed anteroloph; the labial length is greater than the lingual length, the exit of the central valley lies behind the middle of the tooth. In the upper molars there is generally only one centroloph, which is the precentroloph; when two centrolophs are present, the anterior one is dominant. In the lower molars the centrolophid is generally absent. The mesolophid is of variable length, often bifurcated in the center of the molar; the posterotropid is frequently present, participating in the irregular pattern formed by the mesolophid.

*Differential diagnosis*

In contrast with *Gliravus* the P<sup>4</sup> is relatively long; the centroloph is anterior, anteroloph and posteroloph are not connected along the lingual border.

*Glamys* differs from *Schizoglriravus* by having only one – anterior – centroloph, and by the irregular pattern of crests in the lower molars.

*Attributed species:*

*Gliravus priscus* Stehlin & Schaub, 1951  
*Gliravus robiacensis* Hartenberger, 1965  
 ?*Gliravus meridionalis* Hartenberger, 1971  
*Gliravus devoogdi* Bosma & de Bruijn, 1979  
*Glamys fordi* Bosma & de Bruijn, 1979  
*Gliravus minor* Bosma & de Bruijn, 1982  
*Glamys olallensis* Freudenthal, 1996  
*Glamys umbriae* sp. nov.

Apart from the type-species, *Gliravus priscus* Stehlin & Schaub, 1951, at least one species belongs to this genus: *G. olallensis* Freudenthal, 1996 from Olalla 4A and Fuenferrada 3B. *G. olallensis* is smaller than *G. priscus*, and morphologically very similar.

The position of the other species in the preceding list is less certain. They are, however, closer to *Glamys* than to *Gliravus* or *Schizoglriravus*.

*Gliravus meridionalis* Hartenberger, 1971 was placed in *Bransatoglis* by Vianey-Liaud (1994). This may be correct, but there are no arguments to prove it, or to deny it.

## Diagnostic features in *Glamys*

In the following an attempt is made to analyze several features of the dental pattern, in order to find out, which ones serve to compare various *Glamys* species.

### *Morphology values (MV)*

In several cases morphology values (MV) have been calculated (see Freudenthal (1976) and Daams & Freudenthal [1988, p. 41]). The definition has been changed, so that values always range between 0 and 1, according to the equation

$$MV = \Sigma(n-1) f_n / (C-1) \Sigma f_n,$$

where C is the number of character states, and  $f_n$  is the observed frequency for the nth character state.

MV is typically useful for classes, that in fact have a continuous size representation, e.g. for a length: absent – short – medium – long, and is an approximation of actually measuring each specimen, and calculating the mean of the measurements. It may be calculated on actual numbers of specimens, or on percentages; in the latter case  $\Sigma f_n = 100$ .

	AGT2D	CHR5A	VRS15B	AGT6	AGT5A	CHR6C	UMB1B	OLA4A
N	159	45	42	68	53	118	6	115
P <sub>4</sub>	7.7	11.1	22.2	13.3	12.5	13.8	0.0	0.0
M <sub>1</sub>	13.7	11.8	14.3	46.2	27.3	27.8	0.0	4.0
M <sub>2</sub>	7.4	12.5	28.6	22.2	50.0	48.0	83.3	3.1
M <sub>3</sub>	40.9	70.6	100.0	91.6	60.0	95.8	0.0	24.3

Table 3. Percentages of the presence of a mesostylid. N is the sum of the specimens of the various elements.  
Tabla 3. Porcentajes de presencia del mesostilido. N es la suma de especímenes de los elementos.

### *Mesostylid*

In the lower molars of *Glamys* the metaconid has developed a posterior flange, along the molar border. The hind part of this flange may get isolated, and form a more or less individualized cusp, that may be called a mesostylid in view of its topographic position, without entering in a discussion about homologies. Table 3 gives the percentages of this feature in the lower dentition, and the total number of specimens. The order of the localities from left to right corresponds to their stratigraphic position from old to young. Apart from the irregularities, that may be expected in such a distribution, there appears to be a tendency towards higher values to the right of the table, except for Olalla 4A, which presents the lowest values of all. In my opinion the mesostylid is a derived character, and the distribution in Table 3 shows its evolution during the time before the “Grande Coupure”. *G. olallensis* from Olalla 4A, the only locality later than the “Grande Coupure”, represents a total break in this tendency,

meaning that *G. olallensis* is not a descendant of the *G. priscus*-lineage present in the preceding localities.

The published *G. priscus* material from other European areas is not abundant enough, or the published data do not give sufficient details, to permit a comparison with our material. Nevertheless, the presence of a mesostylid is proven in the material from the Isle of Wight (Bosma & de Bruijn, 1979, p. 374, and pl. 1), Escamps (Vianey-Liaud, 1974, fig. 20), and Mormont-Entreroches (Stehlin & Schaub, 1951).

### *Anterolophid of M<sub>1</sub>-M<sub>3</sub>*

There are two different morphologies in the anterolophid of the lower molars: 1) it descends continuously from the metaconid to its labial end, or 2) it first descends steeply, and then continues almost horizontally, with a tendency towards interruption at the inflexion point. The first case is frequent in our *G. priscus* material, the second case is more frequent in *G. olallensis*. I have not been able to quantify this feature, because it is difficult to observe objectively, and successive observations did not meet the required repeatability. Interruptions of the anterolophid are very frequent in the *G. devoogdi-fordi* group. This feature appears to be linked to the position of the labial end of the anterolophid: In *G. olallensis* from OLA4A the anterolophid frequently ends before it reaches the antero-labial corner of the tooth, and the separation from the protoconid is wide. In *G. devoogdi* from Hoogbutsel the anterolophid is frequently discontinuous, the anterolophid continues to the antero-labial corner, and the separation between anterolophid and protoconid is extremely narrow. In *G. priscus* the situation is intermediate.

### *Anterotropid*

In *G. priscus* from AGT2D and in *G. olallensis* from OLA4A there is never an anterotropid in M<sub>3</sub>. In the other populations varying numbers of anterotropids in various degrees of development are found. There is no apparent relation with the stratigraphic position of the localities (see Table 4).

Anterotropid N	AGT2D 24	CHR5A+B 16	VRS15B 7	AGT6 24	AGT5A 10	CHR6C 26	OLA4A 35
absent	100.0	81.3	42.9	20.8	40.0	80.8	100.0
very small	0.0	6.3	0.0	8.3	0.0	11.5	0.0
small	0.0	0.0	28.6	29.2	20.0	0.0	0.0
medium	0.0	12.5	14.3	29.2	40.0	3.8	0.0
long	0.0	0.0	14.3	12.5	0.0	3.8	0.0

Table 4. Frequency of an anterotropid in M<sub>3</sub> (in percentages).

Tabla 4. Frecuencia del anterotrópido en M<sub>3</sub> (en porcentajes).

Metalophid	AGT2D	CHR5A+B	VRS15B	AGT6	AGT5A	CHR6C	OLA4A
P <sub>4</sub> N =	27	19	7	15	16	29	21
free	33.3	10.5	28.6	13.3	18.8	27.7	14.3
to mcd base	29.6	10.5	0.0	13.3	12.5	27.6	14.3
to mcd high	37.0	78.9	71.4	73.3	68.8	44.8	71.4
M <sub>1</sub> N =	52	18	15	14	11	36	23
free	23.1	5.6	0.0	14.3	0.0	19.4	8.7
to mcd base	25.0	77.8	46.7	50.0	27.3	61.1	52.2
to mcd high	51.9	16.7	53.3	35.7	72.2	19.4	39.1
M <sub>2</sub> N =	58	9	8	19	16	25	29
free	31.0	55.6	12.5	0.0	0.0	32.0	10.3
to mcd base	53.4	22.2	62.5	78.9	68.8	52.0	58.6
to mcd high	15.5	22.2	25.0	21.1	31.1	16.0	31.0
M <sub>3</sub> N =	22	16	7	24	10	23	33
free	36.4	75.0	71.4	45.8	20.0	82.6	51.5
to mcd base	59.1	18.8	28.6	54.2	70.0	13.0	30.3
to mcd high	4.5	6.3	0.0	0.0	10.0	4.3	18.2
MV P <sub>4</sub>	0.52	0.84	0.71	0.80	0.75	0.59	0.79
MV M <sub>1</sub>	0.64	0.56	0.77	0.61	0.86	0.50	0.65
MV M <sub>2</sub>	0.42	0.33	0.56	0.61	0.66	0.42	0.60
MV M <sub>3</sub>	0.34	0.16	0.14	0.27	0.45	0.11	0.33

Table 5. Percentages of character states of the metalophid. mcd = metaconid; MV = morphology value for the degree of development of the metalophid.

Tabla 5. Porcentajes de los "character states" del metalófidio. mcd = metacónido; MV = valor morfológico del grado de desarrollo del metalófidio.

### *Metalophid*

Table 5 gives the percentages and the morphology values MV for the degree of development of the metalophid (see definition earlier in this chapter): a free metalophid scores 0, a low connection scores 0.5 and a high connection scores 1.

Generally MV values decrease from P<sub>4</sub> to M<sub>3</sub>. In other words, the metalophid is progressively less developed from P<sub>4</sub> to M<sub>3</sub>. On the other hand, there is no correlation of the MV with the stratigraphic order of the localities in the table (left to right = old to young). Nevertheless, a well-developed metalophid should be considered an advanced character, since it is poorly developed in the oldest Gliridae known. This would mean that P<sub>4</sub> is the most advanced element of the lower dentition, and M<sub>3</sub> the most conservative one.

### *Length of the mesolophid*

The morphological database distinguishes a large number of character states for the mesolophid. In Table 6 several categories have been lumped together, to facilitate

the evaluation. For the calculation of MV: “absent” scores a 0, “short” scores 0.25, “medium” = 0.5, “long” = 0.75, and “very long” scores a 1.

In all populations the mesolophid is progressively longer from M<sub>1</sub> to M<sub>3</sub>, but, surprisingly, in P<sub>4</sub> it is as long as in M<sub>3</sub>. A well-developed mesolophid is supposed to be a derived character, since it is poorly developed in the oldest Gliridae known. According to the values obtained M<sub>1</sub> would be the most conservative molar, and M<sub>3</sub> the most advanced one. This result is just opposite the situation found for the metalophid. I have no explanation for this fact, but apparently one must be extremely careful when drawing evolutionary conclusions on the basis of the degree of development of one single character.

The values of MV for P<sub>4</sub> are the most variable, and very low in OLA4A. In M<sub>1</sub> and M<sub>2</sub> the values are surprisingly similar, with the exception of the low values in OLA4A. The MV for M<sub>3</sub> are almost identical in all populations.

Mesolophid	AGT2D	CHR5A+B	VRS15B	AGT6	AGT5A	CHR6C	OLA4A
P <sub>4</sub> N =	27	19	9	16	17	29	23
absent	0.0	0.0	0.0	0.0	0.0	0.0	17.4
short	11.1	5.3	11.1	6.3	0.0	20.7	26.1
medium	0.0	0.0	0.0	0.0	5.9	3.4	4.3
long	81.5	47.7	88.9	62.5	88.2	72.4	52.2
very long	7.4	47.4	0.0	31.3	5.9	3.4	0.0
M <sub>1</sub> N =	52	18	15	13	11	38	23
absent	0.0	0.0	0.0	0.0	0.0	0.0	0.0
short	1.9	0.0	0.0	0.0	0.0	0.0	8.7
medium	38.5	50.0	33.3	30.8	27.3	21.1	91.3
long	57.7	44.4	60.0	69.2	72.7	73.7	0.0
very long	1.9	5.6	6.7	0.0	0.0	5.3	0.0
M <sub>2</sub> N =	62	9	9	21	18	27	33
absent	0.0	0.0	0.0	0.0	0.0	0.0	0.0
short	0.0	0.0	0.0	0.0	0.0	0.0	3.0
medium	25.8	0.0	0.0	14.3	16.7	3.7	57.6
long	64.5	8	88.9	71.4	72.2	85.2	33.3
very long	9.7	1	11.1	14.3	11.1	11.1	6.1
M <sub>3</sub> N =	23	17	7	25	10	25	35
absent	0.0	0.0	0.0	0.0	0.0	0.0	0.0
short	0.0	0.0	0.0	0.0	0.0	0.0	0.0
medium	0.0	0.0	0.0	0.0	0.0	0.0	2.9
long	73.9	58.8	71.4	68.0	90.0	84.0	62.9
very long	26.1	41.2	28.6	32.0	10.0	16.0	34.3
MV P <sub>4</sub>	0.71	0.84	0.69	0.80	0.75	0.65	0.48
MV M <sub>1</sub>	0.65	0.64	0.68	0.67	0.68	0.71	0.48
MV M <sub>2</sub>	0.71	0.78	0.78	0.75	0.74	0.77	0.61
MV M <sub>3</sub>	0.82	0.85	0.82	0.83	0.78	0.79	0.83

Table 6. Length of the mesolophid (in percentages).  
Tabla 6. Longitud del mesolófido (en porcentajes).

### Height of the mesolophid

The height of the mesolophid, taken at its highest point, which is usually the labial end (mesoconid), is considered “low” when it is lower than half the height of the hypoconid, “medium” when it is about half the height of the hypoconid, and “high” when its height is (almost) equal to the height of the hypoconid (see Table 7). In all populations the height of the mesolophid increases from  $M_1$  to  $M_3$ , confirming the developmental trend found for the length of this crest. In AGT2D and other populations attributed to *G. priscus* the height of the mesolophid in  $M_{2,3}$  is usually medium, and in  $M_3$  it is medium or high. In OLA4A, on the other hand, the mesolophid in  $M_{1,2}$  is usually low, and less frequently medium. In  $M_3$  it is on the average higher than in  $M_{1,2}$ , but lower than in the other populations.

Mesolophid	AGT2D	CHR5A+B	VRS15B	AGT6	AGT5A	CHR6C	OLA4A
$M_1$ N =	52	13	15	13	11	36	22
low	11.5	7.7	6.7	7.7	9.1	16.7	68.2
medium	88.5	92.3	93.3	92.3	90.9	83.3	31.8
high	0.0	0.0	0.0	0.0	0.0	0.0	0.0
$M_2$ N =	58	9	10	23	18	29	34
low	10.3	22.2	10.0	8.7	5.6	3.4	58.8
medium	89.7	77.8	70.0	87.0	77.8	96.6	41.2
high	0.0	0.0	20.0	4.3	16.7	0.0	0.0
$M_3$ N =	26	17	7	22	10	23	34
low	0.0	0.0	0.0	0.0	0.0	0.0	32.4
medium	65.4	52.9	42.9	50.0	30.0	56.5	64.7
high	34.6	47.1	57.1	50.0	70.0	43.5	2.9

Table 7. Height of the mesolophid (in percentages).

Tabla 7. Altura del mesolofido (en porcentajes).

### Entoconid

The entoconid presents itself in either of two ways: 1) the entoconid is round, with steep walls, and more or less isolated from the posterolophid, or 2) it is more elongated antero-posteriorly, and more or less integrated in the posterolophid. The distribution of this character in the tooth row, and throughout the stratigraphic sequence seems to be completely random. It may be a useful character, but it certainly is difficult to evaluate objectively. Furthermore the height and the volume of the entoconid are very variable. For the entoconid of  $M_3$  see the next paragraph.

### Reduction of $M_3$

As in a large variety of rodents, the  $M_3$  is more or less reduced in comparison with the other molars. In *Glamys* the degree of reduction is quite variable.

One factor in the reduction is the length: the longest  $M_3$  are nearly as long as the longest  $M_2$ , but the shortest  $M_3$  are considerably shorter than the shortest  $M_2$ .

The second factor is the postero-lingual corner (see Table 8): in some specimens the labial and lingual border of the tooth are almost parallel, to such an extent that there may be doubt whether the specimen is an  $M_2$  or an  $M_3$ ; in others the borders converge, the entoconid is displaced labially, and the posterior width of the specimen (over the entoconid-hypoconid) is smaller than the anterior width (over metaconid-protoconid).

The third factor is the entoconid itself: round and high, with steep walls, or low, elongated, and integrated in the posterolophid (see previous paragraph). In  $M_3$  it may disappear as an individualized cusp. The latter situation is frequent in *G. olallensis* from OLA4A (18 out of 28 specimens) and *G. umbriae* sp. nov.

Borders of $M_3$	AGT2D	CHR5A+B	VRS15B	AGT6	AGT5A	CHR6C	OLA4A
N =	27	17	7	25	10	25	34
parallel	37.0	47.1	42.9	28.0	40.0	40.0	14.7
convergent	63.0	52.9	57.1	72.0	60.0	60.0	85.3

Table 8. Reduction of  $M_3$  (in percentages).

Tabla 8. Reducción del  $M_3$  (en porcentajes).

### *The centrolophs*

The presence or absence of one or two centrolophs may be a fundamental datum in the study of the gliroid dentition. Table 9 gives the morphological data of the centroloph of  $M^1$  and  $M^2$  for the *G. priscus* and *G. olallensis* populations in our material. My hypothesis was, that a precentroloph connected to the paracone is the original situation, and that it tends to shift backwards and loose contact with the paracone.

The centroloph-paracone connection is represented in Table 10, which is an extract of Table 9, with the data for  $P^4$  added. In the majority of the cases the single centroloph present is the precentroloph, and also in most cases this precentroloph is connected to the paracone. It may, however, be disconnected, placed more centrally, there may be a postcentroloph instead of the precentroloph, or it is unclear which centroloph is present (in that case it is called midcentroloph). If the centroloph-paracone connection is the original situation, and the other character states are derived,  $P^4$  is the most conservative element, and  $M^2$  is most modernized.  $M^3$  has not been analyzed, because its pattern cannot be interpreted reliably. *G. olallensis* from OLA4A is the only population in which the number of connections is higher in  $M^2$  than in  $M^1$ . This is not the only character of the centroloph that distinguishes OLA4A from the *G. priscus* populations: in OLA4A the centroloph is much lower, with respect to the other crests, than it is in the other populations, though its length is the same.

The data shed no light on the evolution of the centroloph in time: There is no correlation with the stratigraphic position of the localities (left to right in Table 9 = old to young). On the contrary, the percentages for CHR5A+B are so extremely low (caused by the fact, that the majority of the specimens has a midcentroloph) and those for VRS15B so high, that one comes to the conclusion, that we are dealing with more than one single species (or lineage).

On the other hand, in the population from HH3, certainly older than our oldest population, a number of specimens has two centrolophs, a feature practically unknown in our material.

	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
M <sup>1</sup>														
precentroloph	38		13		10		17		10		34		28	
absent	11	28.9	8	61.5	1	10.0	4	23.5	1	10.0	5	14.7	1	3.6
long	27	71.1	5	38.5	9	90.0	13	76.5	9	90.0	29	85.3	27	96.4
precentroloph	37		13		10		15		9		33		25	
absent	11	29.7	8	61.5	1	10.0	4	26.7	1	11.1	6	18.2	1	4.0
paracone	22	59.5	3	23.1	9	90.0	10	66.7	5	55.6	20	60.6	10	40.0
free	2	5.4	1	7.7	0	0.0	1	6.7	2	22.2	6	18.2	4	16.0
central	0	0.0	1	7.7	0	0.0	0	0.0	1	11.1	1	3.0	8	32.0
mesostyl	2	5.4	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	8.0
midcentroloph	37		13		10		17		10		33		27	
absent	27	73.0	5	38.5	9	90.0	13	76.5	9	90.0	29	87.9	27	100
long	10	27.0	8	61.5	1	10.0	4	23.5	1	10.0	4	12.1	0	0.0
postcentroloph	39		15		10		17		10		35		27	
absent	38	97.4	13	86.7	10	100.0	16	94.1	10	100.0	34	97.1	27	100
long	1	2.6	2	13.3	0	0.0	1	5.9	0	0.0	1	2.9	0	0.0
postcentroloph	39		14		10		17		10		35		27	
absent	38	97.4	13	92.9	10	100.0	16	94.1	10	100.0	34	97.1	27	100
metacone	1	2.6	1	7.1	0	0.0	1	5.9	0	0.0	1	2.9	0	0.0
M <sup>2</sup>														
precentroloph	54		14		5		17		13		27		30	
absent	20	37.0	5	35.7	0	0.0	4	23.5	1	7.7	0	0.0	1	3.3
long	34	63.0	9	64.3	5	100.0	13	76.5	12	92.3	27	100.0	29	96.7
precentroloph	54		13		4		16		13		27		27	
absent	21	38.9	5	38.5	0	0.0	4	25.0	1	7.7	0	0.0	1	3.7
paracone	25	46.3	3	23.1	2	50.0	7	43.8	5	38.5	17	63.0	14	51.9
free	3	5.6	3	23.1	2	50.0	2	12.5	4	30.8	5	18.5	6	22.2
central	2	3.7	2	15.4	0	0.0	2	12.5	3	23.1	3	11.1	3	11.1
mesostyl	3	5.6	0	0.0	0	0.0	1	6.3	0	0.0	2	7.4	3	11.1
midcentroloph	54		9		1		17		13		0		30	
absent	35	64.8	2	22.2	0	0.0	13	76.5	11	84.6	0	0.0	29	96.7
medium	0	0.0	0	0.0	0	0.0	0	0.0	1	7.7	0	0.0	1	3.3
long	19	35.2	7	77.8	1	100.0	4	23.5	1	7.7	0	0.0	0	0.0
postcentroloph	54		13		4		16		13		28		30	
absent	52	96.3	13	100.0	4	100.0	16	100.0	13	100.0	27	96.4	30	100
long	2	3.7	0	0.0	0	0.0	0	0.0	0	0.0	1	3.6	0	0.0
postcentroloph	54		13		4		16		13		28		30	
absent	52	96.3	13	100.0	4	100.0	16	100.0	13	100.0	27	96.4	30	100
metacone	1	1.9	0	0.0	0	0.0	0	0.0	0	0.0	1	3.6	0	0.0
central	1	1.9	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0

Table 9. Character states of the centrolophs.

Tabla 9. "Character states" de los centrolofos.

	AGT2D	CHR5A+B	VRS15B	AGT5A	AGT6	CHR6C	OLA4A
N	130	45	20	43	60	83	75
P <sup>4</sup>	92.0	100.0	100.0	100.0	100.0	100.0	69.6
M <sup>1</sup>	59.5	23.1	90.0	55.6	66.7	60.6	40.0
M <sup>2</sup>	46.3	23.1	50.0	38.5	43.8	63.0	51.9

Table 10. Percentages of the presence of a centroloph-paracone connection. N is the sum of the specimens of the various elements.

Tabla 10. Porcentajes de la presencia de la conexión centrolofo-paracono. N es la suma de los especímenes de los elementos.

### *Shape of M<sup>1</sup>*

One gets the impression, that the anterior and posterior border of M<sup>1</sup> are more parallel in *G. olallensis* than in the other populations, but the difference is too small to quantify reliably.

## ***Glamys priscus* Stehlin & Schaub, 1951**

### *Lectotype*

M<sub>2</sub> sin., Db 486C Naturhistorisches Museum Basel, fig. 513 in Stehlin & Schaub (1951).

Remark: Bosma & de Bruijn (1979) designate this specimen as holotype. According to art. 74.5 of the rules of zoological nomenclature it can only be a lectotype. The conditions of art. 74.5 are fulfilled, so the lectotype designation may be considered valid (see the remarks on the lectotype of *Peridyromys micio* earlier in this paper).

### *Type-locality*

La Débruge (Vaucluse, France)

According to Stehlin & Schaub (1951) the upper molar of *G. priscus* from La Débruge has a centroloph, which is more or less connected to the metacone, and completely separated from the paracone (postcentroloph in our terminology). This is certainly not the rule among the populations that have been published as *G. priscus*. In our material from the Sierra Palomera the postcentroloph is practically absent. However, I did observe specimens with a postcentroloph instead of a precentroloph in the population from Totland Bay (Wight).

Table 11. Measurements of *Glamys*. OLA4A and FF3B = *G. olallensis*; CHR5A and CHR5B = *G. sp. nov.* 1; UMB1B = *G. sp. nov.* 2; ROBIAC = *G. robiacensis*; SOS1 = *G. aff. robiacensis*; rest is *G. priscus*.

Tabla 11. Medidas de *Glamys*. OLA4A y FF3B = *G. olallensis*; CHR5A y CHR5B = *G. sp. nov.* 1; UMB1B = *G. sp. nov.* 2; ROBIAC = *G. robiacensis*; SOS1 = *G. aff. robiacensis*; los demás son *G. priscus*.

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
D <sub>4</sub>												
OLA4	6	6.8	7.20	7.8	13.7	0.40	6	5.4	5.68	6.3	15.4	0.33
FF3B	1		7.20				1		6.80			
CHR6C	6	6.9	7.33	7.8	12.2	0.33	6	5.9	6.12	6.4	8.1	0.19
AGT5A	1		7.60				1		6.90			
AGT6	1		7.50				1		6.10			
VRS15B	1		7.80				1		6.60			
CHR5B	1		7.90				1		6.30			
AGT2D	10	7.0	7.40	7.9	12.1	0.35	10	5.8	6.21	6.8	15.9	0.32
DEBRUG	1		7.7				1		7.6			
P <sub>4</sub>												
OLA4	22	6.4	6.92	7.3	13.1	0.25	22	5.8	6.24	7.0	18.8	0.31
FF3B	2	6.2	6.45	6.7	7.8		2	5.7	5.95	6.2	8.4	
UMB1B	2	7.6	7.70	7.8	2.6		2	7.0	7.20	7.4	5.6	
CHR6C	29	7.0	7.61	8.4	18.2	0.33	30	6.2	6.92	7.9	24.1	0.40
AGT5A	18	7.0	7.78	8.5	19.4	0.44	17	5.9	6.92	7.6	25.2	0.50
AGT6	15	7.0	7.66	8.6	20.5	0.47	15	6.1	6.86	7.4	19.3	0.43
VRS15B	9	7.1	7.46	8.0	11.9	0.32	9	6.2	6.74	7.1	13.5	0.28
CHR5B	4	7.4	7.83	8.4	12.7	0.42	4	7.0	7.50	8.0	13.3	0.44
CHR5A	15	7.2	7.91	9.0	22.2	0.45	14	6.3	7.27	8.1	25.0	0.50
AGT2D	26	6.9	7.65	8.4	19.6	0.38	27	6.4	7.06	8.1	23.4	0.48
DEBRUG	2	7.9	8.25	8.6	8.5		2	7.3	7.45	7.6	4.0	
SOS1	58	6.9	8.10	8.9	25.3		58	5.9	6.70	8.1	31.4	
ROBIAC	9	6.7	7.28	7.9	16.4	0.39	9	6.1	7.06	8.4	31.7	0.66
M <sub>1</sub>												
OLA4	25	7.6	8.08	8.8	14.6	0.32	26	7.4	8.14	8.7	16.1	0.29
FF3B	7	7.6	8.00	8.4	10.0	0.25	7	6.7	8.06	8.9	28.2	0.80
UMB1B	1		9.60									
CHR6C	37	7.8	8.54	9.9	23.7	0.40	33	8.0	8.68	10.1	23.2	0.41
AGT5A	11	8.3	8.84	9.5	13.5	0.41	11	7.6	8.60	9.3	20.1	0.54
AGT6	13	8.2	8.82	9.5	14.7	0.37	12	7.8	8.55	9.3	17.5	0.43
VRS15B	15	7.9	8.50	9.1	14.1	0.37	12	7.9	8.39	9.0	13.0	0.33
CHR5B	5	8.5	8.96	9.5	11.1	0.37	4	8.7	8.90	9.3	6.7	0.27
CHR5A	13	8.5	9.07	9.3	9.0	0.29	12	8.2	8.95	9.4	13.6	0.37
AGT2D	52	8.0	8.88	9.7	19.2	0.39	52	7.8	8.63	9.4	18.6	0.38
DEBRUG	1		9.3				1		9.0			
SOS2B	10	7.5	8.13	8.9	17.1	0.45	10	7.6	8.15	8.8	14.6	0.40
SOS1	51	7.4	8.20	8.8	17.3		51	7.0	8.10	8.9	23.9	
ROBIAC	20	8.2	8.88	9.6	15.7	0.42	20	7.8	8.30	9.0	14.3	0.32

	Length						Width						
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$	
M <sub>2</sub>													
OLA4	32	7.2	7.98	8.6	17.7	0.33	32	7.1	8.36	9.2	25.8	0.48	
FF3B	8	7.3	7.80	8.4	14.0	0.39	9	7.7	8.34	9.0	15.6	0.44	
UMB1B	5	9.0	9.40	9.9	9.5	0.38	4	9.0	9.65	10.1	11.5	0.51	
CHR6C	27	8.0	8.60	9.1	12.9	0.28	26	8.2	8.93	9.8	17.8	0.41	
AGT5A	14	7.9	8.76	9.3	16.3	0.41	16	8.5	9.25	9.8	14.2	0.40	
AGT6	18	8.0	8.69	9.4	16.1	0.39	19	8.0	8.87	9.5	17.1	0.39	
VRS15B	12	8.1	8.55	9.4	14.9	0.34	9	8.5	8.98	9.5	11.1	0.33	
CHR5B	1		8.40				1		9.20				
CHR5A	8	8.9	9.22	9.5	6.5	0.19	8	9.0	9.45	10.0	10.5	0.35	
AGT2D	58	8.0	8.93	9.6	18.2	0.35	57	8.2	9.13	10.2	21.7	0.40	
DEBRUG	1		9.2				1		9.1				
SOS2B	11	7.5	8.25	8.7	14.8	0.36	11	8.4	8.91	9.2	9.1	0.23	
SOS1	56	6.6	8.00	8.8	28.6		56	7.4	8.50	9.4	23.8		
ROBIAC	23	8.0	8.86	9.4	16.1	0.37	23	8.4	8.99	9.6	13.3	0.31	
M <sub>1,2</sub>													
OLA4	57	7.2	8.02	8.8	20.0	0.33	58	7.1	8.26	9.2	25.8	0.42	
FF3B	15	7.3	7.89	8.4	14.0	0.33	16	6.7	8.22	9.0	29.3	0.62	
UMB1B	6	9.0	9.43	9.9	9.5	0.35	4	9.0	9.65	10.1	11.5	0.51	
CHR6C	64	7.8	8.57	9.9	23.7	0.35	59	8.0	8.79	10.1	23.2	0.43	
AGT5A	25	7.9	8.79	9.5	18.4	0.40	27	7.6	8.99	9.8	25.3	0.56	
AGT6	31	8.0	8.75	9.5	17.1	0.38	31	7.8	8.75	9.5	19.7	0.43	
VRS15B	27	7.9	8.52	9.4	17.3	0.35	21	7.9	8.64	9.5	18.4	0.44	
CHR5B	6	8.4	8.87	9.5	12.3	0.40	5	8.7	8.96	9.3	6.7	0.27	
CHR5A	21	8.5	9.13	9.5	11.1	0.26	20	8.2	9.15	10.0	19.8	0.44	
AGT2D	110	8.0	8.91	9.7	19.2	0.37	109	7.8	8.89	10.2	26.7	0.46	
DEBRUG	2	9.2	9.25	9.3	1.1		2	9.0	9.05	9.1	1.1		
SOS2B	21	7.5	8.20	8.9	17.1	0.40	21	7.6	8.55	9.2	19.0	0.50	
SOS1	107	6.6	8.10	8.8	28.6		107	7.0	8.31	9.4	29.3		
ROBIAC	43	8.0	8.87	9.6	18.2	0.39	43	7.8	8.67	9.6	20.7	0.47	
M <sub>3</sub>													
OLA4	36	6.6	7.51	8.3	22.8	0.38	34	6.3	7.38	8.2	26.2	0.45	
FF3B	4	6.8	7.50	8.0	16.2	0.53	4	7.1	7.45	7.7	8.1	0.26	
UMB1B	1		8.60				1		8.10				
CHR6C	25	7.7	8.39	9.1	16.7	0.37	24	7.6	8.17	8.7	13.5	0.37	
AGT5A	10	7.7	8.47	9.1	16.7	0.40	10	8.0	8.61	9.6	18.2	0.49	
AGT6	24	7.6	8.46	9.3	20.1	0.43	25	7.4	8.34	9.2	21.7	0.45	
VRS15B	6	7.3	8.02	8.8	18.6	0.55	7	7.4	8.00	8.7	16.1	0.45	
CHR5B	8	7.5	8.31	9.1	19.3	0.46	7	7.7	8.30	9.5	20.9	0.61	
CHR5A	9	7.5	8.43	9.5	23.5	0.60	9	7.8	8.30	9.4	18.6	0.49	
AGT2D	23	7.2	8.39	9.3	25.5	0.47	24	7.4	8.15	9.0	19.5	0.41	
DEBRUG	3	8.2	8.53	9.0	9.3		3	7.7	8.17	8.5	9.9		
SOS2B	1		7.80				1		8.10				
SOS1	25	7.2	8.00	8.3	14.2		25	7.2	7.90	9.1	23.3		
ROBIAC	21	7.7	8.63	10.0	26.0	0.64	21	7.8	8.41	9.0	14.3	0.34	

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
P <sup>3</sup>												
ROBIAC	1		5.20				1		6.50			
D <sup>4</sup>												
OLA4	15	6.2	6.83	7.3	16.3	0.34	15	6.6	7.36	8.4	24.0	0.45
FF3B	4	6.7	7.25	8.2	20.1	0.66	4	7.4	7.63	7.8	5.3	0.17
UMB1B	2	7.9	8.00	8.1	2.5		3	8.0	8.33	8.5	6.1	
CHR6C	17	6.6	7.29	8.5	25.2	0.55	19	6.9	7.45	8.3	18.4	0.32
AGT5A	1		7.60				1		7.50			
AGT6	6	7.0	7.57	8.1	14.6	0.45	6	7.0	7.68	8.8	22.8	0.66
VRS15B	2	7.3	7.30	7.3	0.0		2	7.1	7.70	8.3	15.6	
CHR5B	3	7.1	7.23	7.4	4.1		3	6.8	7.53	8.2	18.7	
AGT2D	11	6.8	7.60	8.5	22.2	0.54	11	6.8	7.76	8.6	23.4	0.44
ROBIAC	5	6.1	6.88	7.2	16.5	0.45	5	8.0	8.24	8.6	7.2	0.25
P <sup>4</sup>												
OLA4	24	6.0	6.67	7.3	19.5	0.40	25	7.2	8.04	8.7	18.9	0.37
FF3B	5	6.0	6.42	7.2	18.2	0.49	5	7.9	8.26	9.2	15.2	0.57
UMB1B	2	7.9	8.30	8.7	9.6		2	8.8	9.20	9.6	8.7	
CHR6C	22	6.6	7.25	8.3	22.8	0.41	21	7.9	8.64	9.6	19.4	0.45
AGT5A	15	6.2	7.35	7.9	24.1	0.46	15	7.8	8.82	9.2	16.5	0.44
AGT6	15	6.8	7.33	8.3	19.9	0.44	15	7.7	8.65	9.5	20.9	0.47
VRS15B	6	6.4	6.95	7.4	14.5	0.41	6	7.4	8.18	8.6	15.0	0.46
CHR5B	8	6.6	7.09	7.6	14.1	0.39	8	8.5	9.21	9.6	12.2	0.36
CHR5A	13	6.8	7.34	8.0	16.2	0.37	13	8.3	9.27	10.3	21.5	0.63
AGT2D	39	6.6	7.27	8.2	21.6	0.39	35	7.9	8.94	10.0	23.5	0.50
DEBRUG	2	6.7	6.7	6.7			2	8.4	8.45	8.5	1.2	
SOS1	25	6.1	6.60	7.1	15.2		25	7.0	7.80	8.6	20.5	
ROBIAC	10	6.7	7.56	8.0	17.7	0.38	10	6.8	7.34	8.3	19.9	0.49
M <sup>1</sup>												
OLA4	26	6.8	7.54	8.0	16.2	0.32	26	8.5	9.09	9.9	15.2	0.37
FF3B	7	6.7	7.30	7.8	15.2	0.39	7	8.9	9.24	9.8	9.6	0.33
UMB1B	3	8.0	8.70	9.3	15.0		3	8.9	10.20	11.2	22.9	
CHR6C	32	7.4	8.06	8.6	15.0	0.33	33	8.9	9.63	10.4	15.5	0.36
AGT5A	9	7.7	8.48	9.4	19.9	0.54	8	9.1	9.66	10.4	13.3	0.38
AGT6	16	7.8	8.36	9.2	16.5	0.39	14	9.0	9.61	10.3	13.5	0.36
VRS15B	10	7.4	8.03	8.8	17.3	0.41	9	8.3	9.27	9.7	15.6	0.43
CHR5B	6	8.1	8.50	8.8	8.3	0.30	6	10.0	10.42	10.9	8.6	0.34
CHR5A	8	7.1	8.13	8.7	20.3	0.51	7	8.2	9.61	10.4	23.7	0.82
AGT2D	37	7.5	8.36	9.1	19.3	0.35	36	8.4	9.86	10.9	25.9	0.44
SOS2B	2	8.0	8.00	8.0	0.0		2	8.9	9.00	9.1	2.2	
SOS1	63	6.5	7.50	8.9	31.2		63	7.2	8.80	10.6	38.2	

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
M <sup>2</sup>												
OLA4	31	6.4	7.31	8.1	23.4	0.37	29	8.2	9.13	10.0	19.8	0.47
FF3B	12	6.8	7.33	7.9	15.0	0.41	10	8.3	9.19	10.4	22.5	0.57
UMB1B	3	8.5	8.83	9.0	5.7		3	9.7	10.40	10.9	11.7	
CHR6C	27	7.0	7.89	8.6	20.5	0.36	26	8.5	9.79	10.3	19.1	0.41
AGT5A	13	7.5	8.02	8.7	14.8	0.40	11	9.7	10.19	10.8	10.7	0.40
AGT6	17	7.3	8.09	8.6	16.4	0.37	15	9.7	10.09	10.6	8.9	0.30
VRS15B	5	7.9	8.00	8.1	2.5	0.10	5	9.2	9.68	10.1	9.3	0.35
CHR5B	5	7.8	8.20	8.3	6.2	0.22	2	10.3	10.55	10.8	4.7	
CHR5A	11	7.7	8.35	8.8	13.3	0.33	9	10.3	10.82	11.4	10.1	0.40
AGT2D	54	7.1	8.18	9.0	23.6	0.39	53	8.8	10.09	11.1	23.1	0.47
SOS2B	6	7.6	8.00	8.4	10.0	0.28	6	8.7	9.18	9.5	8.8	0.29
SOS1	34	6.6	7.40	8.5	25.2		34	8.2	8.70	10.5	24.6	
M <sup>1,2</sup>												
OLA4	57	6.4	7.41	8.1	23.4	0.37	55	8.2	9.11	10.0	19.8	0.42
FF3B	19	6.7	7.32	7.9	16.4	0.39	17	8.3	9.21	10.4	22.5	0.47
UMB1B	6	8.0	8.77	9.3	15.0	0.46	6	8.9	10.30	11.2	22.9	0.85
CHR6C	59	7.0	7.98	8.6	20.5	0.35	59	8.5	9.70	10.4	20.1	0.39
AGT5A	22	7.5	8.20	9.4	22.5	0.51	19	9.1	9.97	10.8	17.1	0.46
AGT6	33	7.3	8.22	9.2	23.0	0.40	29	9.0	9.86	10.6	16.3	0.40
VRS15B	15	7.4	8.02	8.8	17.3	0.33	14	8.3	9.41	10.1	19.6	0.44
CHR5B	11	7.8	8.36	8.8	12.0	0.30	8	10.0	10.45	10.9	8.6	0.33
CHR5A	19	7.1	8.25	8.8	21.4	0.41	16	8.2	10.29	11.4	32.7	0.86
AGT2D	91	7.1	8.25	9.1	24.7	0.38	89	8.4	10.00	11.1	27.7	0.47
DEBRUG	5	8.2	8.44	8.7	5.9	0.23	5	9.7	10.16	10.6	8.9	0.43
SOS2B	8	7.6	8.00	8.4	10.0	0.24	8	8.7	9.14	9.5	8.8	0.26
SOS1	97	6.5	7.46	8.9	31.2		97	7.2	8.76	10.6	38.2	
ROBIAC	27	7.8	8.44	9.1	15.4	0.33	27	8.7	9.43	10.2	15.9	0.38
M <sup>3</sup>												
OLA4	33	5.6	6.37	7.6	30.3	0.44	32	7.1	8.20	9.6	29.9	0.63
FF3B	2	6.1	6.20	6.3	3.2		2	7.5	7.60	7.7	2.6	
UMB1B	2	7.2	7.55	7.9	9.3		2	9.0	9.10	9.2	2.2	
CHR6C	18	6.0	6.59	7.2	18.2	0.34	18	7.8	8.33	9.1	15.4	0.32
AGT5A	13	6.4	7.10	7.9	21.0	0.46	11	7.7	8.73	9.5	20.9	0.51
AGT6	17	6.1	6.79	7.7	23.2	0.44	16	8.0	8.73	9.8	20.2	0.48
VRS15B	5	6.6	6.86	7.0	5.9	0.17	5	8.0	8.46	8.7	8.4	0.34
CHR5B	2	6.9	7.00	7.1	2.9		2	8.0	8.25	8.5	6.1	
CHR5A	11	7.0	7.46	8.1	14.6	0.35	11	8.1	8.80	9.5	15.9	0.40
AGT2D	25	6.3	7.07	7.8	21.3	0.34	25	7.9	8.74	9.5	18.4	0.38
DEBRUG	1		7.6				1		9.3			
SOS1	27	6.0	7.10	7.5	22.2		27	7.1	8.70	9.6	29.9	
ROBIAC	2	7.0	7.50	8.0	13.3		2	7.5	8.10	8.7	14.8	

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***Glamys priscus* from Aguatón 2D (AGT2D)**

Plate 2, Fig. 1-20

*Material and measurements*

see Table 11

*Description*

Some specimens of P<sup>4</sup> present a very weak anterior facet that may prove the existence, at least in some cases, of a P<sup>3</sup>. Consequently, some of the smallest P<sup>4</sup> described here, may be P<sup>3</sup>.

*D*<sub>4</sub> -The anterolophid is interrupted (2) or continuous (8). The anterotropid is absent. The metalophid is low connected to the metaconid (1) or high connected to that cusp (9). The centrolophid is absent. The mesostylid is absent. The mesoconid is absent (1), placed on the labial border (7), or more centrally (2). The mesolophid is absent (2), short (1), of medium length and interrupted (2), or of medium length (5). In one case the mesolophid forked, and connected to centrolophid and posterotropid. The posterotropid is absent (9) or of medium length (1).

*P*<sub>4</sub> -The shape is anteriorly blunt. The anterolophid is interrupted (22), but may be continuous (3). The anterotropid is absent. The metalophid is free (9), low connected to the metaconid (8), or high connected to that cusp (10). The centrolophid is absent (23), short (3), or of medium length (1). The mesostylid is absent (24) or present (2). The mesoconid is placed on the labial border (24) or more centrally (2). The mesolophid is short (3), directed towards the metaconid (3), directed towards the entoconid (19), or connected to the entoconid (2). The posterotropid is absent (23), very small (1), or small (3).

*M*<sub>1</sub> -The anterolophid is labially free (52). The anterotropid is absent. The metalophid is free (12), low connected to the metaconid (13), or high connected to that cusp (27). The centrolophid is absent (50), short (1), or of medium length (1). The mesostylid is absent (44) or present (7). The mesoconid is placed on the labial border (40) or more centrally (12). The mesolophid is short (1), of medium length (19), curved forward (1), directed towards the metaconid (8), directed towards the entoconid (22), or connected to the entoconid (1). It frequently shows complications in the center of the main valley: forked, a backward branch, or two backward branches, etc. The posterotropid is absent (37), very small (7), small (7), or long (1).

*M*<sub>2</sub> -The anterolophid is labially free (62). The anterotropid is absent (59). The metalophid is free (18), low connected to the metaconid (31), or high connected to that cusp (9). The centrolophid is absent (54) or of medium length (1). The mesostylid is absent (50) or present (4). The mesoconid is placed on the labial border (59) or more centrally (4). The mesolophid is of medium length (14), curved forward (2), directed towards the metaconid (4), connected to the metaconid (1), directed towards the entoconid (36), or connected to the entoconid (5); it shows the same complications as M<sub>1</sub>. The posterotropid is absent (42), very small (5), small (6), of medium length (4), or long (2).

$M_3$  –The degree of reduction of this element is variable: in some cases, it affects only the corner behind the entoconid, which is rounded, and labial and lingual border are almost parallel; but, in most cases, the lingual border is oblique with respect to the labial border, and the width over the entoconid is smaller than over the protoconid. The anterolophid is labially free (24). The anterotropid is absent (24). The metalophid is free (8), low connected to the metaconid (13), or high connected to that cusp (1). The centrolophid is absent (15), short (1), or of medium length (6). The centrolophid is low connected to the metaconid in one single case. The mesostylid is absent (13) or present (9). The mesoconid is placed on the labial border (23) or more centrally (1). The mesolophid is directed towards the metaconid (5), connected to the metaconid (1), directed towards the entoconid (12), or connected to the entoconid (5); complications like in  $M_1$  2 are very rare. The posterotropid is absent (16), very small (3), small (1), of medium length (2), or long (1).

$D^4$  -The anteroloph is short (3), of medium length (7), or long (2). The anterotrope is absent (11). The precentroloph is absent (2), short (5), of medium length (4), or long (1). The postcentroloph is absent (11) or long (1). Prototrope, metatrope and posterotrope are absent. The endoloph is formed by the protocone only (3), or protocone and hypocone are connected (9). The lingual border is smooth (12).

$P^4$  -The anteroloph is short (4), of medium length (6), or long (27). The anterotrope is absent (38). The precentroloph is absent (2), of medium length (2), or long (36). The midcentroloph is absent (37), short (1), or long (2). The postcentroloph is absent (37), short (2), or of medium length (1). The prototrope is absent (39) or of medium length (1). Metatrope and posterotrope are absent. The endoloph is formed by the protocone only (18), or protocone and hypocone are connected (20). The lingual border is smooth (38). Only in one case there are two centrolophs, a long precentroloph and a much shorter postcentroloph, connected to the precentroloph at its center. The shape of the specimen proves, that it is a *Glamys*, and not a *Bransatoglis*, the second frequent glirid in AGT2D.

$M^1$  – The anteroloph is lingually free (40). The anterotrope is absent (39). The precentroloph is absent (11) or long (27); when present it is connected to the paracone (22), free from the paracone (2), or connected to a mesostyl (2). The midcentroloph is absent (27) or long (10). The postcentroloph is absent (38) or long and connected to the metacone (1). The prototrope is absent (38), short (1), of medium length (1), or long (1). Metatrope and posterotrope are absent. The endoloph is formed by the protocone only (22), or protocone and hypocone are connected (17). The lingual border is smooth (37) or crenulated (1).

$M^2$  -The anteroloph is lingually free (53). The anterotrope is absent (52). The precentroloph is absent (20) or long (34); when present it is connected to the paracone (25), free from the paracone (3), placed centrally (2), or connected to a mesostyl (3). The midcentroloph is absent (35) or long (19). The postcentroloph is absent (52) or long (2); when present, it is connected to the metacone (1), or placed centrally (1). Prototrope, metatrope and posterotrope are absent. The endoloph is formed by the protocone only (32), or protocone and hypocone are connected (19). The lingual border is smooth (52) or crenulated (1). In one specimen there is a backward crest on the metaloph that reaches the posteroloph.

$M^3$  -The anteroloph is lingually free (5), lingually low connected (6), or lingually high connected (12). The anterotrope is absent (26). Crests inside the trigone: one crest (18), two crests (6), or three crests (1). The mesostyl is absent (23) or present (1). The posterotrope is absent (14), short (9), or of medium length (2). The endoloph is formed by the protocone only (3), anteriorly interrupted (8), posteriorly interrupted (2), or complete (10). The lingual border is smooth (23) or crenulated (1).

### ***Glamys priscus* from Villarrosano 15A (VRS15A)**

Twenty-nine specimens from this locality present the same size and morphology as found in AGT2D. The collection is too small to judge whether there are any statistical differences.

### ***Glamys priscus* from Villarrosano 15B (VRS15B)**

Of the same size as AGT2D (see Table 11). The metalophid of  $P_4$  is on the average better developed. There is more frequently a centrolophid in the lower molars. The seven available  $M_3$  all have a mesostylid, and six of them have a posterotropid. The precentroloph of  $M^{1,2}$  is practically always connected to the paracone.

Both  $D^4$  have a long centroloph, which is not frequent in AGT2D. It cannot be excluded that they belong to *Bransatoglis* instead of *Glamys*.

### ***Glamys priscus* from Aguatón 6 (AGT6)**

All measurements are within the range found in AGT2D (see Table 11), and mean values are identical. Morphologically there are a few differences, like a more frequent centrolophid and mesostylid, especially in  $M_3$ ; a better developed posterotropid in  $M_3$ ; and a longer anteroloph in  $D^4$ . The  $M_3$  is quite reduced postero-lingually, maybe even more than in AGT2D. Specimens with parallel lingual and labial border are hardly found.

### ***Glamys priscus* from Aguatón 5A (AGT5A)**

The size distribution is basically the same as in AGT2D (see Table 11), and there are only minor morphological differences. In  $P_4$  the metalophid is on the average better developed; there is never a centrolophid, nor a posterotropid. In  $M_1$  and  $M_2$  the metalophid is also better developed, to such an extent, that it always reaches the metaconid, whereas in AGT2D, it frequently stays free from that cusp. There is more frequently a centrolophid, a mesostylid and a posterotropid in  $M_2$  and  $M_3$ . Six out of ten  $M_3$  have an anterotropid, and three out of fifteen  $M^2$  have a prototrope (always absent in AGT2D).

***Glamys priscus* from Bco. del Chorrillo 6C (CHR6C)**

The size distribution is identical to that in AGT2D (see Table 11). In  $M_1$  and  $M_3$  the metalophid is less developed than in AGT2D. In  $M_2$  and  $M_3$  the mesostylid is more frequent. The posterotropid is somewhat better developed. In  $D^4$  the anteroloph and the precentroloph are longer. These are only minor differences, and this population is attributed to *G. priscus*.

***Glamys priscus* from Cerro de Mas 1A (CDM1A)**

This small collection (27 specimens) has measurements, that fall within the range for AGT2D. Like in AGT5A the metalophid is well developed in  $P_4$ ,  $M_1$  and  $M_2$ , less developed in  $M_3$ . A mesostylid is present in various  $M_3$ , and in the single available  $M_2$ . A prototrope has not been observed. In one  $M^2$  there is a short and very low post-centroloph, next to a long precentroloph. The collection is too small to permit a comparison on the basis of percentages. AGT5A seems to be the population that resembles the one from CDM1A most.

***Glamys priscus* from Bco. de Puch 3 (PUC3)**

The size of these specimens (2  $M_1$ , 1  $M_2$ , 2  $M^1$ , 1  $M^2$ ) falls with the limits for AGT2D, and the morphology coincides with that population, except for the  $M^2$ . That specimen has a long postcentroloph, a feature that occurs in AGT2D in only 2 out of 52 specimens. Maybe this specimen is not a *Glamys*. The  $M_1$  have an extremely simple pattern, with a mesolophid of medium length, and no further complications. The  $M_2$  is very simple too, with a somewhat longer mesolophid.

***Glamys priscus?* from Aguatón 5B (AGT5B)**

A  $P_4$  (7.6 x 6.9), an  $M_2$  (– x 7.9), a  $P^4$  (7.0 x 8.4), and an  $M^2$  (8.2 x 9.9) belong to *G. olallensis* or *G. priscus*. The  $P_4$  has a small mesostylid, a feature that is very rare in AGT2D, and not found in our material from OLA4A. The  $P^4$  has a well-developed precentroloph. The molars are badly preserved. These specimens probably represent *G. priscus*, though *G. olallensis* cannot be excluded.

***Glamys* nov. sp. 1 aff. *priscus***

Plate 3, Fig. 1-16

Six populations (CHR5A, CHR5B, TOR1A, VRS8B, VRS17A, and MTM4B) are characterized by the frequent absence of a connection between centroloph and paracone. Either the centroloph is a midcentroloph, or it is a precentroloph without

connection. The measurements coincide perfectly with those from AGT2D. Stratigraphically these six localities are quite close to each other. They all are situated in the lowest part of the limestone sequence, and not a single locality from that lowest part has delivered “normal” *G. priscus*.

The high frequency of not connected centrolophs in six stratigraphically equivalent localities makes it probable, that we are dealing with a species different from *G. priscus*. One of the localities (CHR5A) offers good possibilities to collect more material. Although the sediment is not rich (1 *Glamys* specimen per 100 kg of sediment), it may be possible in the near future to decide whether this material represents just a variation of *G. priscus*, or should be attributed to a new species.

#### *Bco. del Chorrillo 5A + 5B (CHR5A, CHR5B)*

The measurements are like in AGT2D (see Table 11). In the P<sub>4</sub> the metalophid is on the average higher than in AGT2D, and the mesolophid is frequently connected to the entoconid. In the molars, however, the degree of development is similar to AGT2D, or the situation is even reversed, so the mentioned difference is probably due to chance, and not important. In M<sub>3</sub> the mesostylid is more frequent, in the other elements the development is similar to that in AGT2D. The posterotropid is better developed. In M<sup>1,2</sup> there is frequently a midcentroloph, at the expense of the precentroloph. The height of the centroloph is like in AGT2D. The number of crests within the trigone of M<sup>3</sup> is larger. In AGT2D the majority of the specimens has one crest, in CHR5 the majority has two or three crests.

#### *Bco. de Torrubia 1A (TORIA)*

In the three available M<sup>1,2</sup> there is a midcentroloph instead of a precentroloph.

#### *Villarrosano 17A (VRS17A)*

Among eight M<sup>1,2</sup> only one specimen has the precentroloph connected to the paracone.

#### *Villarrosano 8B (VRS8B)*

The only available M<sup>2</sup> has a long midcentroloph. In two out of three M<sub>1</sub> the mesolophid is connected to the entoconid; in one of them the mesoconid is very much withdrawn from the labial border. In the single available M<sub>2</sub> and M<sub>3</sub> the mesolophid is connected to the entoconid too.

#### *Matamoros 4B (MTM4B)*

In the two M<sub>2</sub> where this feature can be observed, there is a centrolophid, and all 4 M<sub>3</sub> have a centrolophid too. In four out of seven M<sup>1</sup> and in three out of five M<sup>2</sup> there is a midcentroloph, instead of a precentroloph.

***Glamys* nov. sp. 2 aff. *priscus* from Fuente Umbría 1 (UMB1B)**

Plate 3, Fig. 17-22

This small collection contains the largest *G. priscus*-like specimens found (see Table 11). All specimens are larger than the mean for AGT2D, and some measurements are larger than the maximum for AGT2D. One of the referees of this paper suggested, that the poor material might represent only three individuals, which, by mere chance are large ones. That possibility exists in UMB1B, as proven by the fact that in 2002 we found 15 of the 16 elements of one individual of a *Theridomys*. However, it can be discarded for the *Glamys* material, which was recovered from six different samples of 2000 kg (one sample per year), taken from the same bed at several spots that are up to 50 m apart.

In the two P<sub>4</sub> the labial end of the mesolophid is connected to the protoconid. The mesolophid is directed obliquely backwards, and in one specimen it curves forward, towards a short and low centrolophid. In three M<sub>2</sub> a well-developed mesostylid is present, in one specimen it is absent, and in 2 badly preserved specimens a mesostylid may have been present too. In the well-preserved specimens the complications around the mesolophid are important. In the only available M<sub>3</sub> there is a short anterotropid; the mesolophid is bifurcated; the posterior branch is connected to the posterotropid, and the anterior one is directed towards the mesostylid.

The three D<sup>4</sup> have one or more cusps inside the trigone, but there are no real centrolophs. The length and the height of the precentroloph in the P<sup>4</sup> and in the molars are like in *G. priscus*.

The character states found do occur in the AGT2D population too, and the number of specimens available does not permit discrimination on a statistical basis. Nevertheless, the size of the specimens gives the impression, that this population may represent yet another species, or at least an advanced stage of *G. priscus*.

UMB1B is the youngest locality in the Sierra Palomera, just before the intra-Oligocene unconformity. Its age may be quite close to FF3B, a locality with *G. olallensis*. On the basis of both size and morphology, attribution of this material to the latter species can be excluded.

Which one of these two localities is the older one, and which one is younger, cannot be decided in the field. According to Vianey-Liaud (pers. comm.) FF3B contains a small form of *Theridomys calafensis* and UMB1B a large form of that species; the sequence would be FF3B – Calaf – UMB1B. This poses a problem with respect to the distribution of the *Glamys* species, since the small *G. olallensis* occurs in FF3B and OLA4A, whereas the supposedly intermediate locality UMB1B contains the largest “*priscus*”-like species known at present. The other *Glamys* species, that occurs in both FF3B and UMB1B (*G. umbriae* sp. nov., to be described hereafter) does not solve this problem, since it is identical in both localities. An argument for Calaf to be younger than FF3B is, that Calaf contains *Atavocricetodon*, absent in FF3B.

***Glamys* nov. sp. 2 aff. *priscus* from Aguatón 9 (AGT9)**

This locality has delivered only two specimens, a P<sub>4</sub> (8.0 X 7.6) and an M<sub>3</sub> (8.5 X 8.3). They resemble the material from Fuente Umbría by their size and morphology.

In the  $P_4$  the mesolophid is strongly oblique, and connected to the protoconid, there is a clear mesostylid. In  $M_3$  there is a long anterotropid, a clear mesostylid, and a posterotropid of medium length; the mesolophid is long and straight, connected to the entoconid.

### ***Glamys* aff. *priscus* from Sossís 2B**

*Measurements of Glamys aff. priscus from Sossís 2B after van Dam (1998) – see Table 11.*

Comparison with the measurements of *G. priscus* from la Débruge shows, that the material from Sossís 2B is considerably smaller than the type material of this species. A problem with the Sossís 2B population is the absence of  $D_4$ ,  $P_4$ , and  $M^3$ , that is, the lack of all the small elements. Apparently the smaller fractions from Sossís were not picked out, or picking was not reliable. It is clear, that any statistical analysis of such a biased material may lead to wrong conclusions. If the small specimens are lacking, it is possible, that the minima of the existing sample are larger than they would be in a reliable sample. Anyway, the available data show that all mean values, several minimum values, and all maximum values for Sossís are smaller than the corresponding values in the sample from AGT2D. Apparently we are dealing with a different species, smaller than *G. priscus*, and morphologically very similar. The description by van Dam (1998) is not detailed enough to judge whether there are morphological differences, and, moreover, it is a generalized description of material from six different localities near Pobla de Segur. This makes an evaluation almost impossible. The only thing, that can be said is, that the two “morphotypes” that constitute 100 % of the ten available  $M_1$  (van Dam, op. cit., table 13) are very rare, if present at all, in our material of *G. priscus* and *G. olallensis*, and the posterior position of the centroloph (van Dam, table 7) is unusual too.

*G. aff. priscus* from the localities near Pobla de Segur is of the same size as *G. olallensis*, but it is improbable, that it belongs to that species, in view of the stratigraphic position.

### ***Glamys olallensis* Freudenthal, 1996**

#### *Type-locality*

Olalla 4A (Teruel, Spain)

#### *Holotype*

$M_1$  dext., OLA4A 817, Dpto de Ciencias de Tierra, University of Zaragoza.

#### *Other localities*

Fuenferrada 3B (Teruel, Spain)

### *Original diagnosis*

Small size, smaller than *G. priscus* from La Débruge and the Isle of Wight (Bosma & de Bruijn, 1979) and *G. robiacensis* (see Hartenberger, 1971), larger than *Gliravus minor* (Bosma & de Bruijn, 1982). Morphology similar to *G. priscus*, but there is no trace of a posterior centroloph in the upper molars and the anteroloph is generally connected to the paracone. The anteroloph of P<sup>4</sup> is quite well developed. In the lower molars the mesoconid is often separated from the lingual border.

### *Emended diagnosis*

Smaller than *G. priscus*, larger than *G. minor*. Morphology similar to *G. priscus*, but there is no trace of a postcentroloph in the upper molars and the precentroloph is connected to the paracone in about half the specimens. The centroloph and the mesolophid are very low. In the lower molars the mesoconid is often separated from the lingual border. A mesostylid is very rare in M<sub>1</sub> and M<sub>2</sub>. M<sub>3</sub> is more reduced than in *G. priscus*, the entoconid of M<sub>3</sub> has frequently disappeared. A posterotropid is rare in M<sub>2</sub>, absent in the other molars.

### *Differential diagnosis*

*G. olallensis* differs from other *Glamys* species by its smaller size; it differs from *G. priscus* by its lower centroloph and mesolophid, more anterior position of the centroloph, and more reduced M<sub>3</sub>.

In the original description of *G. olallensis* D<sub>4</sub>, P<sub>4</sub> and M<sub>3</sub> were underrepresented, in comparison with M<sub>1</sub> and M<sub>2</sub>. By now, all the finer fractions (0.5 to 0.63 mm) have been picked out, and the representation of the various elements is more equilibrated. We give here a new table of measurements, and a revised description. Apparently, for size comparisons of *Glamys* material, it is essential, that all fractions be picked out. To solve the question whether this species had a P<sup>3</sup> or not, one should wash the samples on a finer screen than the 0.5 mm now in use. Picking out those fractions is an almost impossible amount of work.

*Material and measurements of Glamys olallensis from Olalla 4A* – see Table 11.

### *Description*

*D<sub>4</sub>* – The anterolophid is continuous. There are no extra crests. The metalophid is free (1), connected to the base of the metaconid (1), or high to the metaconid (4). The centrolophid is absent. The mesoconid is absent (3), or it lies on the labial border (3). The mesolophid is absent (4), short (1), or directed towards the entoconid (1).

*P<sub>4</sub>* – The anterolophid is interrupted. There are no extra crests. The metalophid ends free (3), it is connected to the base of the metaconid (3), or high to the metaconid (15). The centrolophid is absent. The mesoconid is absent (3), it lies on the labial border (17) or more centrally (3). The mesolophid is absent (4), short (6), curved forward (1), or directed towards the entoconid (11).

$M_1$  – The anterolophid is not connected to the protoconid. There are no extra crests. The metalophid is free (2), connected to the base of the metaconid (12), or high to the metaconid (9). The centrolophid is absent (23) or short (1); in the latter case it is high connected to the metaconid. There is a mesostylid in one specimen. The mesoconid lies on the labial border (8) or more centrally (16). The mesolophid is short (2) or of medium length (21).

$M_2$  – The anterolophid is not connected to the protoconid. There is no anterotrope. The metalophid is free (3), connected to the base of the metaconid (17), or high to the metaconid (9). The centrolophid is absent (21) or short (2). The mesostylid is absent. The mesoconid lies on the labial border (21) or more centrally (13). The mesolophid is short (1), of medium length (17), curved forward (2), or longer and directed towards the metaconid (7), or towards the entoconid (4); it is connected to the entoconid in one case, and long and straight, ending between entoconid and metaconid in one other case. There may be a small backward crest on the tip of the mesolophid. The posterotrope is absent (22), very small (3), small (4), or of medium length (1).

$M_3$  – The anterolophid is connected to the protoconid in one single specimen. There are no extra crests. The metalophid is free (17), connected to the base of the metaconid (10), or high to the metaconid (6). The centrolophid is absent (30), short (1), or of medium length (1). The mesostylid is absent (26) or present (5), and it forms a crest in two specimens. The mesoconid lies on the labial border (22) or more centrally (14). The mesolophid is curved forward (1), directed towards the metaconid (1), directed towards the entoconid (21), or connected to that cusp (11); in one case it reaches the labial border between metaconid and entoconid. The posterotrope is absent (35), or very small (1). Protoconid and hypoconid may be connected by an ectolophid.

$D^4$  – The labial border is round; the centroloph is very thick. The anteroloph is short (1), of medium length (10), or long (5). The anterotrope is absent. The precentroloph is absent (3), of medium length (3), or long (8). The postcentroloph is absent (13) or long (3). The centrolophs are connected when there are two centrolophs (2 cases). There are no extra crests. The endoloph is formed by the protocone alone (1), by protocone plus hypocone, and anteriorly interrupted (10), or complete (2). The lingual border is smooth.

$P^4$  – The labial border is straight. The anteroloph is of short (3), of medium length (8) or long (12), not connected to the protocone. There are no extra crests. The precentroloph is absent (6), of medium length (3), or long (16), placed centrally in one case (= midcentroloph). The postcentroloph is absent. The posteroloph is connected to the protocone (7), or separated from it (12). The lingual border is smooth.

$M^1$  – The anteroloph is lingually free (24), or low connected to the protocone (1). There are no extra crests. The precentroloph is absent (1) or long (27); it is connected to the paracone (10), free (4), placed centrally (8), or connected to a mesostyl (2). The postcentroloph is absent. The posteroloph is connected to the protocone (5), or not connected (19). The lingual border is smooth (24), or crenulated (1).

$M^2$  – The anteroloph is lingually free (28), or low connected (1). There are no extra crests. The precentroloph is absent (1), or long (29); it is connected to the paracone (14), free (6), or placed centrally (6); in three of the latter cases it forms a

mesostyl. The midcentroloph is absent (28), or of medium length (1). The postcentroloph is absent. The posteroloph is connected to the protocone in (8), or not connected (21). The lingual border is smooth (24), or crenulated (1).

$M^3$  – The anteroloph is lingually free (15), lingually low connected (5), or lingually high connected to the protocone (6). The anterotrope is absent. Inside the trigone there no crests (3), one crest (21), two crests (5), or three crests (1). The mesostyl is absent (20), or present (6). The posterotrope is absent. The endoloph is formed by the protocone only (12), anteriorly interrupted (3), posteriorly interrupted (5), or complete (5). The lingual border is smooth.

### ***Glamys olallensis* from Montalbán 1D (MLB1D)**

Only a few *Glamys* specimens have been recovered from this very rich locality, an  $M_2$  (8.6 x 9.2) and an  $M^3$  (7.4 x 9.1). These measurements lie within the range of *G. priscus*, and at the maximum of the range of *G. olallensis*.

In the  $M_2$  the anterolophid descends from the metaconid in a continuous slope, and it ends labially at the level of the lingual wall of the protoconid, far away from the corner of the tooth. The metalophid ends at the basis of the metaconid. The entoconid is elongated, and not separated from the posterolophid. The labial end of the mesolophid lies more lingually than the lingual wall of protoconid and hypoconid. The mesolophid is long and straight, directed towards the entoconid. There are no additional complications, neither in front of the mesolophid, nor behind it.

It is impossible to classify a single tooth with certainty. The fact that the anterolophid and the mesolophid end far away from the labial border, and the shape of the entoconid, point towards *G. olallensis*, but if a similar specimen were found in a much older locality, it would certainly be classified as *G. priscus*. Montalbán 1D is, together with Itardies, the youngest locality with *Glamys* known.

### ***Glamys olallensis* from Montalbán 10 (MLB10)**

One single  $M_1$  (8.8 (estimated) x 8.3), not very well preserved, is attributed to *G. olallensis*. Its size coincides with the maximum values for OLA4A, and lies within the distribution of *G. priscus*. Morphologically there is no argument in favor of one species or the other. Since MLB10 is stratigraphically very close to MLB1D, it is most probable that it contains the same *Glamys* species.

### ***Glamys olallensis* from Olalla 10 (OLA10)**

A single  $M_2$  (8.9 x 8.5) has a simple dental pattern, without any extra crests. The metalophid is connected to the base of the metaconid. The mesolophid is directed towards the entoconid; the entoconid is elongated. It is classified as *G. olallensis* on the basis of its simple dental pattern, and of the stratigraphic position of the locality.

### ***Glamys* aff. *olallensis* or aff. *priscus* from Hoogbutsel (HB)**

Vianey-Liaud (1994) described *Glamys priscus* from Hoogbutsel. In size this material agrees better with *G. priscus* than with *G. olallensis*. However, the very simple dental pattern, and the mesoconid that is withdrawn from the labial border, indicate that it may be related to the latter species.

### **The *Glamys devoogdi-fordi* group**

Bosma & de Bruijn (1979) published two new species of *Gliravus*, *G. devoogdi* and *G. fordi*, from the Late Eocene (Headonian) and Early Oligocene of the Isle of Wight (UK), and regarded these species as descendants of *Glamys priscus*.

Vianey-Liaud (1994) transferred these two species to the genus *Glamys*. In my opinion the relationship of these two species with *Glamys* is far from certain. On the other hand, a relationship with *Gliravus* or *Schizoglriravus* is even less probable, so, for the moment, I prefer to respect the decision by Vianey-Liaud. The same author mentioned *G. devoogdi* from Monac and Asprières (France), and described it from Hoogbutsel (Belgium).

Anadón et al. (1987) described *G. fordi* from various Lower Oligocene sites near Calaf (Barcelona, Spain), and Herb et al. (1984) described a large *G. aff. fordi* from the Synclinal du Charbon (Savoie, France).

Freudenthal (1997b) described *G. aff. fordi* from Fuenferrada 3B (Teruel, Spain), and Freudenthal (1997a) mentions it from Fuente Umbría (Teruel, Spain). New material with similar characteristics is now available from Fuente Umbría 1B and Chorri-llo 2D, two new localities in the Sierra Palomera (Teruel, Spain).

In the Sierra Palomera the largest specimens are those from CHR2D, of the size of the *G. fordi* material from Bouldnor Cliff. CHR2D is a small pocket of marly sediment, fairly rich in fossils, but unfortunately exhausted. It is located at less than 10 meters distance from CHR6C, but a correlation is impossible, since due to the local tectonics these localities are separated by one or more faults. Comparing the type of sediment with several local stratigraphic columns, one gets the impression, that CHR2D may be somewhat younger than CHR6C, but not very much. It is certainly older than the lignitiferous level that terminates the Eocene/L. Oligocene sedimentation. That level contains the locality UMB1B, characterized by *G. umbriae* sp. nov., which is intermediate in size between *G. devoogdi* from Headon Hill and *G. fordi* from Bouldnor Cliff. In terms of MP units these localities may be placed in MP20.

So, in our area the first representative of the *devoogdi-fordi* morphology is a large species, of the size of *G. fordi*, found in CHR2D. The next record is *G. umbriae* sp. nov. from UMB1B, followed by the same species from FF3B. In all these localities it coexists with a smaller *Glamys* species, attributed either to *G. priscus* or to *G. olallensis*.

### ***Glamys umbriae* sp. nov.**

Plate 4, Fig. 1-19

#### *Synonymy*

*Gliravus* aff. *fordi* from Fuenferrada 3B in Freudenthal (1997b)

*Type-locality*

Fuente Umbría 1B (Teruel, Spain)

*Holotype*

M<sub>1</sub> dext., UMB1B 9, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

*Derivatio nominis*

after the name of the type-locality

*Other localities*

Fuenferrada 3B (Teruel, Spain)

*Material and measurements*

see Table 12

*Diagnosis*

Lower molars with the almost constant presence of a well-developed anterotripid, which is a broad, vague crest descending from the metaconid into the anterosinusid. The central valley is full of complications, that make it difficult to decide what is the mesolophid, and what is the posterotripid. A mesostylid is hardly ever present. The anterolophid is frequently interrupted. Metalophid and posterolophid are the dominant crests. In M1 the anteroloph frequently continues backward as a series of crenulations on the lingual wall of the protocone.

Table 12. Measurements of the dentition of the *devoogdi-fordi-umbriae* group. HB = *G. devoogdi* from Hoogbutsel (measurements Vianey-Liaud, 1994); HB\* = *G. devoogdi* from Hoogbutsel (own measurements coll. RGM); CF = *G. fordi* from Calaf; FF3B = *G. umbriae* from Fuenferrada 3B; UMB1B = *G. umbriae* from Fuente Umbría 1B; CHR2D = *G. aff. fordi* from Chorrillo 2D; BOULDC = *G. fordi* from Bouldnor Cliff; HH = *G. devoogdi* from Headon Hill 6 and 7.

Tabla 12. Medidas de la dentición del grupo *devoogdi-fordi-umbriae*. HB = *G. devoogdi* de Hoogbutsel (datos de Vianey-Liaud, 1994); HB\* = *G. devoogdi* de Hoogbutsel (medidas propias, col. RGM); CF = *G. fordi* de Calaf; FF3B = *G. umbriae* de Fuenferrada 3B; UMB1B = *G. umbriae* de Fuente Umbría 1B; CHR2D = *G. aff. fordi* de Chorrillo 2D; BOULDC = *G. fordi* de Bouldnor Cliff; HH = *G. devoogdi* de Headon Hill 6 y 7.

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
D <sub>4</sub>												
HB	14	7.1	7.5	8.1	13.3	0.27	14	6.1	6.5	7.2	16.9	0.33
HB*	5	7.9	8.12	8.4	6.2	0.23	5	6.6	6.96	7.1	7.2	0.21
FF3B	2	8.1	8.40	8.7	7.1		2	6.9	7.20	7.5	8.3	
UMB1B	4	8.3	8.60	9.0	8.1	0.29	4	5.7	6.40	6.8	17.2	0.48
CHR2D	1		9.80				2	8.1	9.40	10.7	27.7	
BOULDC	2	8.6	9.0	9.3	7.8		3	7.1	7.8	8.2	14.1	
HH7	4	7.5	7.6	7.7	2.6		4	6.2	6.6	6.9	10.6	
HH6	4	7.4	7.8	8.0	7.7		4	6.9	7.1	7.4	7.0	
P <sub>4</sub>												
HB	23	8.0	8.8	9.7	19.3	0.41	23	7.6	8.2	9.1	18.3	0.42
HB*	3	7.7	8.13	8.8	13.5		3	7.1	7.77	8.5	18.0	
FF3B	1		10.00				1		8.80			
UMB1B	14	8.7	10.04	10.5	17.9	0.46	13	7.6	8.72	9.3	19.5	0.49
CHR2D	3	10.0	10.63	11.2	11.3		2	10.5	10.55	10.6	0.9	
BOULDC	3	10.3	10.6	10.8	4.7		2	10.3	10.4	10.5	1.9	
HH7	2	8.6	8.8	8.9	3.4		2	8.5	8.7	8.8	3.4	
M <sub>1</sub>												
HB*	8	9.4	10.00	10.4	10.0	0.35	8	9.4	10.01	10.9	15.0	0.50
UMB1B	12	10.1	10.81	11.7	14.8	0.41	13	9.3	10.35	10.9	15.5	0.48
CF6	1		11.6				1		10.4			
CHR2D	1		13.00				1		13.30			
BOULDC	10	10.4	11.5	12.8	20.9		12	10.9	11.8	13.0	17.8	
HH7	5	9.4	9.8	10.0	6.1		5	9.6	10.1	10.4	7.9	
M <sub>2</sub>												
HB*	12	9.4	9.89	10.4	10.1	0.36	13	9.6	10.45	11.2	15.3	0.47
FF3B	4	10.0	11.00	11.8	16.4	0.81	3	10.4	11.23	11.7	11.6	
UMB1B	11	10.5	10.94	11.3	7.3	0.22	14	9.8	10.68	11.1	12.2	0.35
CHR2D	1		10.80				2	11.1	11.15	11.2	0.9	
BOULDC	11	10.5	11.4	12.0	13.2		14	11.5	12.3	13.3	14.6	
HH7	4	9.0	9.3	9.9	9.7		4	9.4	10.0	10.4	10.0	
HH6	4	9.5	9.7	9.8	3.1		4	10.5	10.7	10.9	3.7	
M <sub>1,2</sub>												
HB	73	8.7	9.7	11.0	23.7	0.41	73	9.0	10.2	11.6	25.5	0.47
HB*	20	9.4	9.93	10.4	10.1	0.35	21	9.4	10.28	11.2	17.5	0.52
FF3B	4	10.0	11.00	11.8	16.4	0.81	3	10.4	11.23	11.7	11.6	
UMB1B	23	10.1	10.87	11.7	14.7	0.33	27	9.3	10.52	11.1	17.1	0.44
CHR2D	2	10.8	11.90	13.0	18.5		3	11.1	11.87	13.3	18.5	
BOULDC	21	10.4	11.4	12.8	21.1		26	10.9	12.1	13.3	19.8	
HH7	9	9.0	9.6	10.0	10.4		9	9.4	10.1	10.4	9.9	
HH6	4	9.5	9.7	9.8	3.1		4	10.5	10.7	10.9	3.7	
M <sub>3</sub>												
HB	26	8.4	9.2	10.3	20.7	0.53	26	8.0	9.0	10.1	23.3	0.52
HB*	3	9.1	9.37	9.9	8.5		4	8.7	9.13	9.7	11.0	0.43
FF3B	2	10.1	10.45	10.8	6.7		2	10.2	10.30	10.4	1.9	
UMB1B	18	9.6	10.20	10.9	12.7	0.42	19	8.5	9.27	10.1	17.3	0.38
BOULDC	4	10.2	10.8	11.1	8.3		4	10.6	10.9	11.3	6.4	
HH7	5	8.8	9.5	10.0	12.6		5	8.8	9.5	10.6	18.9	
HH6	2	8.9	9.0	9.2	3.3		2	8.8	9.0	9.1	3.3	

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
D <sup>4</sup>												
HB	7	7.3	7.7	8.1	10.4	0.27	7	8.2	8.6	9.1	10.5	0.34
HB*	4	7.9	8.18	8.5	7.3	0.25	6	8.2	8.67	8.9	8.1	0.25
UMB1B	1		9.10				1		9.50			
HH7	2	7.5	7.7	7.9	5.2		2	7.9	8.2	8.5	7.3	
HH6	6	7.4	7.7	8.3	11.7		5	8.2	8.6	9.0	9.3	
P <sup>4</sup>												
HB	16	7.1	8.0	8.5	17.5	0.39	16	9.1	9.9	10.6	15.2	0.35
HB*	4	8.0	8.30	8.6	7.2	0.26	4	9.9	10.03	10.2	3.0	0.15
FF3B	3	9.3	9.70	9.9	6.2		3	11.4	11.87	12.2	6.7	
UMB1B	15	8.8	9.71	10.3	15.4	0.36	15	10.2	11.53	12.2	17.4	0.54
CHR2D	3	10.2	10.73	11.6	13.0		4	11.6	12.65	13.7	16.6	0.93
CF7	1		9.6				1		11.3			
BOULDC	6	8.4	9.6	10.1	17.7		7	10.5	12.0	12.7	18.3	
HH7	5	7.7	8.0	8.6	11.3		5	9.6	9.9	10.1	5.1	
HH6	3	8.1	8.3	8.5	4.8		3	10.3	10.8	11.5	11.1	
M <sup>1</sup>												
HB*	7	9.0	9.51	9.9	9.5	0.33	8	11.7	11.98	12.6	7.5	0.32
FF3B	2	10.7	10.75	10.8	0.9		2	12.2	12.55	12.9	5.6	
UMB1B	15	9.3	10.24	10.9	15.6	0.39	14	10.7	12.34	13.0	18.6	0.69
CHR2D	-						1		14.20			
CF7	1		10.5				1		12.9			
CF6	1		10.7				1		12.1			
M <sup>2</sup>												
HB*	7	8.8	9.37	9.9	11.7	0.35	7	11.0	11.64	12.7	14.6	0.57
FF3B	2	10.6	10.75	10.9	2.8		2	12.8	13.25	6.8	8.4	
UMB1B	16	9.3	10.26	11.0	16.6	0.43	16	10.8	11.88	13.0	18.5	0.52
CF7	1		10.8						11.7			
M <sup>1,2</sup>												
HB	91	8.3	9.2	10.1	19.6	0.39	91	10.4	11.5	12.7	20.0	0.47
HB*	14	8.8	9.44	9.9	11.6	0.34	15	11.0	11.82	12.7	14.4	0.47
FF3B	4	10.6	10.75	10.9	2.8	0.13	4	12.2	12.90	13.7	11.6	0.62
UMB1B	31	9.3	10.25	11.0	16.6	0.41	30	10.7	12.10	13.0	19.0	0.64
CHR2D	-						1		14.20			
BOULDC	14	9.5	10.3	11.2	16.5		15	11.7	13.1	14.6	22.1	
HH7	9	8.3	9.1	9.8	16.5		7	10.8	11.4	12.0	10.5	
HH6	7	8.8	9.2	9.7	9.8		8	10.5	11.5	12.1	13.9	
M <sup>3</sup>												
HB	15	7.0	7.6	8.5	19.7	0.41	15	8.8	9.7	10.9	21.6	0.55
HB*	2	8.8	8.90	9.0	2.2		1		10.70			
FF3B	3	8.8	8.97	9.3	5.6		2	11.2	11.30	11.4	1.8	
UMB1B	11	8.1	8.58	9.5	16.3	0.42	11	9.2	10.27	12.0	27.3	0.74
CHR2D	5	9.2	10.06	10.6	13.9	0.52	4	11.9	12.20	12.8	7.4	0.41
BOULDC	1		8.9				1		11.4			
HH7	7	7.3	7.7	8.2	11.7		5	8.8	9.4	9.9	11.7	
HH6	5	7.3	7.7	8.1	10.4		4	8.7	9.3	9.6	9.7	

### *Differential diagnosis*

Intermediate in size between *G. devoogdi* and *G. fordi*, larger than *G. priscus* and *G. olallensis*. It differs from *G. devoogdi* from Headon Hill by the more irregular pattern of the lower molars, and by the centrolophs: in *G. devoogdi* there are one or two centrolophs; if there are two, the anterior one is the longest. In *G. umbriae* there are always two centrolophs, and the anterior one is the shortest, because it is “pushed forwards” by the postcentroloph. In P<sup>4</sup> both centrolophs are frequently connected to the proto-loph. The degree of complexity of the lower molars is comparable to *G. fordi*, but the teeth are smaller.

### *Material and measurements*

see Table 12.

### *Description*

*D*<sub>4</sub> – Anterotropid, mesostylid, and posterotropid may be present, making this element more complex than it usually is in *Glamys*, *Schizogliviravus* or *Gliravus*.

*P*<sub>4</sub> – The metaconid is very voluminous and occupies generally more than half the anterior border of the tooth. The labial part of the metalophid is generally very oblique. In the space between protoconid and hypoconid often two crests start in lingual or postero-lingual direction. The anterior one is interpreted as the mesolophid; it is often of medium length, and curves forward, to get in contact with the metalophid. The posterior one, the supposed posterotropid, is quite irregular and variable, with a labial end that is often united to the anterior wall of the hypoconid, and a lingual end, that may be forked, split up in several cusps, and in various cases curved forward, parallel to the mesolophid. A mesostylid is present in 8 out of 13 specimens.

*M*<sub>1</sub> – The anterolophid is frequently interrupted midway. The anterotropid is a broad, low crest, descending from the metaconid, of medium length or long. The metalophid and the posterolophid are the dominant crests. Anterotropid, mesolophid and posterotropid are much lower.

*M*<sub>2</sub> – The anterolophid is frequently interrupted midway. The anterotropid is a broad crest, descending from the metaconid, on the average slightly shorter than in *M*<sub>1</sub>. The metalophid and the posterolophid are the dominant crests. Anterotropid, mesolophid and posterotropid are much lower.

*M*<sub>3</sub> – The corner behind the entoconid is rounded, but the tooth is not very much reduced; labial and lingual border are parallel. The anterolophid is frequently interrupted midway. All crests are equally high. The anterotropid descends from the metaconid, and frequently curves forward, to get in contact with the anterolophid. A mesostylid is present in one case only. The entoconid is poorly marked as a cusp, or it is nothing but the antero-lingual end of the posterolophid. In a few cases there is not even an interruption in front of the entoconid, resulting in a continuous crest along the lingual and posterior border of the tooth. Also, the anterolophid may continue around the proto-

nid, and end in the sinusid, or continue into the mesolophid. Or, quite frequently, the labial end of the mesolophid bends forward, and gets in contact with the protoconid.

$D^4$  – There is a long and low precentroloph.

$P^4$  – There is no facet for  $P^3$ . There is often a connection, through the middle of the protosinus, between anteroloph and proto-loph. Frequently, both the precentroloph and the postcentroloph curve forward and are connected to the proto-loph.

$M^1$  – Frequently, the anteroloph continues lingually of the protocone as a series of crenulations. There are two centrolophs, of which the anterior one is generally better developed. The centrolophs are equally long, or the precentroloph is somewhat longer. Both centrolophs generally consist of a series of small cusps and crests, instead of being one continuous crest. The centrolophs are generally connected to each other lingually, and at their meeting point frequently form a trident; the precentroloph is always connected to the paracone, the postcentroloph less frequently to the metacone. There is a prototrope in about half the specimens. The endoloph is generally formed by protocone and hypocone, though in several cases the protocone and hypocone are separated.

$M^2$  – Similar to  $M^1$ . The prototrope is more frequent. The postcentroloph is less frequently connected to the metacone than in  $M^1$ .

$M^3$  – In many glirids it is difficult to assess the homologies of the crests inside the trigone of  $M^3$ , and the best way to describe them is simply count the number of crests within the trigone. This solution fails in this species, since the crests are broken up in small cusps and crests, and the count gives no relevant result. Furthermore the fragmentation process affects the metaloph too, so that it is often impossible to decide which part of the crown lies inside the trigone. In several cases the anteroloph continues backwards, lingually of the protocone.

#### *Comparison with G. priscus*

In order to decide what species of *Glamys* or *Schizogliviravus* might be an ancestor of *G. umbriae*, it is necessary to analyze the modifications, that distinguish this species from a “normal” glirid. In the following *G. umbriae* is compared with *G. priscus*.

#### *Enamel thickness*

The enamel is very thick, maybe twice as thick as it is in *G. priscus*.

#### *Lower dentition*

In all dental elements longitudinal structures may be introduced, e.g. the forward curve of the mesolophid ( $P_4$ ), posterotropid and anterotropid.

$D_4$  – In *G. priscus* the dental pattern of  $D_4$  is very simple, with only one structure in the central valley, which can be interpreted as the mesolophid, without much doubt.

In *G. umbriae* the pattern is more complex: there may be an anterotripid in the anterior valley, and there are two or three structures in the central valley. In one specimen there are two crests running from the labial border into the central valley; the anterior one is the mesolophid, and the posterior one is the posterotripid. Such a long labial extension of the posterotripid is not known in any other Paleogene glirid. A second specimen has a long mesolophid, starting from a voluminous mesoconid, and one crest behind it (the posterotripid), and another crest between mesolophid and metalophid. The degree of complexity of this specimen is quite comparable to an exceptionally complex specimen of P<sub>4</sub> of *G. priscus*. Several specimens present a mesostylid, a feature that is absent in the D<sub>4</sub> of *G. priscus*, and very rare in its P<sub>4</sub>.

P<sub>4</sub> – The metaconid is more voluminous than it is in *G. priscus*. There may be an anterotripid, in contrast with the P<sub>4</sub> of *G. priscus*. The metalophid is broad and massive. The most striking feature is the presence of two (or even three) mesoconids, with or without their respective crests, mesolophid and posterotripid. In a number of cases there is a longitudinal structure, which seems to be the lingual part of the mesolophid (and/or the posterotripid), bent forward, and connected to the metalophid. This shape of the mesolophid is very rarely found in the M<sub>1</sub> and M<sub>2</sub> of *G. priscus*. A mesostylid is quite frequently present, a feature that is very rare in the P<sub>4</sub> of *G. priscus*.

M<sub>1</sub>-M<sub>3</sub> – The anterolophid is somewhat variable in *G. priscus*: it descends from the metaconid in a continuous slope, or it first descends steeply, and at the middle of the anterior border of the tooth it becomes horizontal; in some specimens, at the inflexion point it shows a tendency to be interrupted. This feature is strongest in M<sub>1</sub>, and almost absent in M<sub>3</sub> (see Table 13). In *G. umbriae*, on the other hand, the tendency is opposite: the interruption is much more pronounced than in *G. priscus*, and both the depth of the interruption and its frequency increase from M<sub>1</sub> to M<sub>3</sub>.

Anterolophid	N	G. priscus AGT2D		N	G. umbriae UMB1B	
		continuous	interrupted		continuous	interrupted
M <sub>1</sub>	52	75.0	25.0	12	83.3	16.7
M <sub>2</sub>	55	81.8	18.2	15	60.0	40.0
M <sub>3</sub>	24	95.8	4.2	18	22.2	77.8

Table 13. Appearance of the anterolophid of M<sub>1</sub>-M<sub>3</sub> (in percentages).

Tabla 13. Aspecto del anterolófidio de M<sub>1</sub>-M<sub>3</sub> (en porcentajes).

### *Anterotripid*

Among 52 M<sub>1</sub> and 55 M<sub>2</sub> of *G. priscus* from AGT2D not a single specimen has an anterotripid, and in some other *G. priscus* populations from the Sierra Palomera it is present, though extremely rare. When present, it looks like the specimen from Montmartre, figured by Hartenberger, (1971, pl. 5, fig. 9). In *G. umbriae* it is constantly present, and morphologically different from the specimen from Montmartre: it is a broad extension of the metaconid that descends into the anterosinusid. It is well developed in M<sub>1</sub> and M<sub>2</sub>; its development in M<sub>3</sub> is somewhat different, because the

interruption of the anterolophid affects the anterotropid too. It may curve forward and get in contact with the anterolophid. In other cases the metalophid loses contact with the metaconid, bending forward to the anterolophid, and cutting off the anterotropid.

### *Mesostylid*

The crest descending from the metaconid towards the entoconid may show an individualized cusp behind the metaconid. In *G. umbriae* this mesostylid is frequent in P<sub>4</sub>, and rare in the molars. In *G. priscus*, on the other hand this feature is absent in P<sub>4</sub>, and progressively frequent in M<sub>1</sub> through M<sub>3</sub>.

### *Mesolophid/posterotropid*

In *G. priscus* the posterotropid is always subordinate to the mesolophid. In the M<sub>1</sub> and M<sub>2</sub> of *G. umbriae*, on the other hand, the posterotropid is frequently more important than the mesolophid. In M<sub>3</sub> this does not happen. In all three molars the posterotropid is always present, in *G. priscus* it is present in less than 30% of the specimens, and about equally frequent in all three molars.

### *Centrolophid*

The appearance of the centrolophid is very similar in *G. umbriae* and *G. priscus*: hardly ever present in M<sub>1</sub> and M<sub>2</sub>, fairly frequent in M<sub>3</sub>.

### *Entoconid*

In *G. priscus* the entoconid is a round, well-defined cusp, with steep anterior and posterior walls. In *G. umbriae* the entoconid is more elongated, and integrated in the posterolophid; this feature is most evident in M<sub>3</sub>. A curious fact is, that the entoconid begins to wear down at an earlier stage of wear than it does in *G. priscus*. This probably means, that mastication – and therefore food habits – in these two species was different.

P<sup>4</sup> – Both precentroloph and postcentroloph are long, and they frequently curve forward and are connected to the protoloph. As a result, the precentroloph is generally shorter than the postcentroloph. In *G. priscus* only one centroloph is present, nearly always the precentroloph; it is generally straight, directed to the middle of the protocone, but in some cases it bends forward, and it may be in contact with the middle of the protoloph. The frequent presence of a prototrope in *G. umbriae* is one of the things that contribute to the complexity of the dental pattern. The forward curve of the precentroloph, and some small crests in the protosinus are structures that give the dental pattern a somewhat more longitudinal aspect than usual in glirids. M<sup>1</sup> and M<sup>2</sup> don't show such longitudinal structures.

M<sup>1</sup> and M<sup>2</sup> – In comparison with *G. priscus* M<sup>1</sup> are not fundamentally different. Of course the double centroloph and the prototrope are additions that are not present in AGT2D. The continuation of the anteroloph around the protocone is a new feature too.

*G. umbriae* is probably not a descendant of *G. priscus*. Its  $M_3$  has not suffered the reduction it usually has in the latter species. In *G. umbriae* the importance of the mesostylid diminishes from  $P_4$  to  $M_3$ . In *G. priscus* the reversed tendency is observed, and the same reversal of tendencies is present in the interruption of the anterolophid. In *G. priscus* the anterotropid, when present, is an individualized crest, whereas in *G. umbriae* it is a spur that descends from the metaconid. It is not likely, that the latter case is derived from the former one.

### ***Glamys* aff. *umbriae* from Fuenferrada 3B (FF3B)**

This population was published by Freudenthal (1997b) as *G. aff. fordi*. The measurements are slightly smaller than those of *G. fordi* from Bouldnor Cliff, and on the average larger than those of *G. umbriae* from UMB1B.

Morphologically it is similar to *G. umbriae*, as far as can be judged from the small number of specimens available in FF3B. However, the anterotropid is clearly more developed in FF3B than in UMB1B: in UMB1B the anterotropid is a broad, but vague crest descending from the metaconid; in FF3B it may still be in contact with the metaconid, but it tends to become detached, break up in several crests or cusps, and it is considerably higher, and more conspicuous. In the upper molars the centrolophs are broken up, and have lost contact with paracone and metacone.

This population may be considered to be a more developed stage of *G. umbriae*. It might as well be called *G. aff. fordi*, but the degree of development of the anterotropid is less in *G. fordi* from Bouldnor Cliff, and in that population the centrolophs are still in contact with paracone and metacone.

By its measurements, and by the shape of the anterotropid, this population is intermediate between *G. umbriae* and *G. fordi*. As far as the centrolophs are concerned, *G. fordi* has the intermediate position, and the population from FF3B is the most evolved.

### ***Glamys* aff. *fordi* from Chorrillo 2D**

A small collection of badly preserved material proves the existence of yet another species with similar characteristics of complexity. The crests are thin, and their tops constitute sharp cutting edges. Protoconid and hypoconid are just the labial end of metalophid and posterolophid, respectively, and not marked as cusps. The metalophid is not particularly dominant, the posterolophid may even be higher than the metalophid. There may be a long and thin anterotropid in the bottom of the first valley, and there is a long centrolophid.

The kind of complications of the dental pattern is fully comparable with *G. devoogdi*, *G. fordi* and *G. umbriae*: many little crests and cusps, especially in the lower molars, duplication of the mesoconid, and a tendency to form longitudinal connections.

If neither *G. devoogdi* nor *G. fordi* were known, one would never think of relating this material with *Glamys* or *Schizoglivrus*. The general aspect of the crests would induce one to search a relationship with *Bransatoglis* instead of *Glamys*, but, knowing the mentioned species, the similarity of the complications of the dental

pattern is an argument to consider these species related. Also, the shape of P<sup>4</sup> is not typical of *Bransatoglis*; it is more or less intermediate between the symmetrical, oval P<sup>4</sup> of *Bransatoglis* and the asymmetrical, triangular shape of the P<sup>4</sup> of *Glamys*.

In my opinion, however, this population may well be derived from *Bransatoglis*, and not from *Glamys*, and the complications of the dental pattern may be a result of parallelism. Apparently two different lineages acquire the same details of complication on a fundamentally different basic pattern. The potential of *Bransatoglis* to develop this kind of morphology is demonstrated by some of the latest representatives of the genus (e.g. *B. mayri*, Rabeder, 1984).

### *Glamys robiacensis* Hartenberger, 1965

Hartenberger (1971) described this species from Robiac Nord. Analysis of the measurements made it clear, that some errors occur in that paper: fig. 7 is the plot of the upper molars (and not the lower molars as stated), and fig. 8 gives the lower molars (and not the upper ones). In fig. 7 the symbols for P<sup>4</sup> and D<sup>4</sup> are interchanged, the open asterisks are D<sup>4</sup> and the solid asterisks are P<sup>4</sup>. The distribution of M<sup>1,2</sup> in fig. 7 does not coincide with the data in the measurements table. Probably, for the M<sup>1,2</sup> the horizontal axis is 0.8 where it says 0.7 and 0.9 where it says 0.8. Such a change would place the points for M<sup>1,2</sup> on a diagonal line with respect to the other elements, which is to be expected.

Hartenberger (1971) says, that *G. robiacensis* is smaller than *G. priscus* from La Débruge, but that is probably not correct. The small population from La Débruge is not sufficient to know the size range of that species, but it is clear that all measurements for La Débruge fall within the ranges obtained for AGT2D. The same goes for *G. robiacensis*. The size distributions for Robiac Nord and AGT2D are identical, and these two species can only be distinguished by morphology.

Hartenberger supposes *G. robiacensis* to be the ancestor of *G. priscus*, and Vianey-Liaud (1994) places it in *Glamys*, probably on the basis of this supposed relationship.

According to Hartenberger, in *G. robiacensis* the metalophid of M<sub>1</sub> is on the average less developed than that of M<sub>2</sub>. In the populations of *G. priscus* from the Sierra Palomera, no such rule can be observed (see Table 5). On the contrary, in *G. priscus* the metalophid is progressively less developed from M<sub>1</sub> to M<sub>3</sub>, opposite to the observation by Hartenberger for *G. robiacensis*.

In *G. robiacensis* a crest descends from the entoconid towards the mesolophid, without reaching that crest. In our *G. priscus* material the labial face of the entoconid is always round, without a descending crest. The mesolophid may be so long that it reaches the entoconid, but there is never a crest from the entoconid in labial direction. Such a crest does occur, however, in some *Bransatoglis* species, and in *Schizoglivravus itardiensis*.

The centroloph in *G. robiacensis* is anterior or posterior. In *G. priscus* postcentrolophs are extremely rare, but there seems to be a tendency for the precentroloph to shift backwards, and occupy a central position, losing contact with the paracone. This condition is in conflict with the supposed ancestor-descendent relationship of *G. robiacensis* and *G. priscus*. The generic position of this species is not certain; it is certainly not a

*Gliravus*, it may well be a *Glamys*, but *Schizoglriravus* cannot be discarded, and it seems to be a good candidate for the ancestorship of *Schizoglriravus* and/or *Bransatoglis*.

Agustí & Arcas (1997) described *G. aff. robiacensis* from Sossís 1. The figured specimens plead strongly in favor of an attribution to *Glamys*, but this material presents a problem. The measurements (here given in Table 11) show extremely high values for the variability coefficient  $V^2$ . Values of up to 38.2 prove that it is not a homogeneous population, even if one takes into account that the numbers of specimens are high. Van Dam (1998) described the new species *G. hispanicus* from Sossís 2, intermediate in size between his *G. priscus* and his *G. meridionalis*. Apparently the larger specimens classified as *G. aff. robiacensis* by Agustí & Arcas belong to *G. hispanicus*, and maybe the separation between *G. minor* and *G. aff. robiacensis* is not correct either. On the other hand, one must not forget, that the site Sossís is not the same as Sossís 2 of van Dam.

### ***Glamys* or *Schizoglriravus* sp. from Cerro de Mas 3A (CDM3A)**

This locality has delivered a dozen glirid teeth, three of which are classified as *Bransatoglis*. The remainder looks very much like *Glamys*, but there is doubt about their classification, and even about their specific homogeneity. Especially an  $M_1$  dext. (CDM3A 35, 10.8 x 10.5) and a  $P^4$  dext. (CDM3A 20, 8.2 x 9.8) might represent a different species.

The  $M_1$  has a reduced antero-lingual corner, the anterior half of the lingual border is strongly oblique, and the anterior border is much shorter than the posterior border. The metaconid is situated on the anterior border, displaced labially with respect to the entoconid; the backward crest from the metaconid is oblique, and forms a weakly individualized mesostylid. The labial end of the anterolophid is in contact with the protoconid. The metalophid is directed towards the posterior end of the mesostylid, and completely straight. The center of the tooth is damaged, but one gets the impression that the labial end of the mesolophid was in contact with the hypoconid. The size of the specimen is well above the upper limit of *G. priscus*. The  $P^4$  has two centrolophs that are connected to each other close to the lingual border, and form a Y-pattern. These features are highly unusual in *Glamys*, and seem to point to *Schizoglriravus*. In size these specimens coincide with *S. montisalbani* nov. sp., but their morphology is not typical of that species either. We are probably dealing with an unknown species of *Schizoglriravus*.

The remainder of the specimens can be classified as *Glamys* sp. However, one  $M_2$  dext. (CDM3A 36, 8.8 x 9.5) shows a valley on the posterior wall of the hypoconid that is unknown in glirids in general; in this case I think it is nothing but an aberrant case.

### **Evolutionary relationships**

*G. priscus* and *G. olallensis* probably have a common ancestor, but *G. priscus* is certainly not the ancestor of *G. olallensis*. *G. priscus* is larger than *G. olallensis*, but in this case size is only an additional argument. The true reason for placing these two

species in different lineages is their morphology: *G. olallensis* is much less modernized: lower and shorter mesolophids, lower centrolophs, centroloph-paracone connection more persistent, mesostylid very rare in  $M_1$  and  $M_2$ , posterotropid very rare. All this results in a simple dental pattern, that one would expect in an ancestor of *G. priscus*, not in its descendent. On the other hand *G. olallensis* is more advanced in some features, like the reduction of  $M_3$ .

*Glamys* nov. sp. 1 aff. *priscus* differs from *G. priscus* mainly by the position of the centroloph. If the localities where this species is found were scattered throughout the stratigraphic sequence, one would ascribe this feature to the normal intraspecific variation, but the six localities in question are all stratigraphically equivalent, and located in the lowermost part of the carbonate sequence. *G. priscus* is found in older and in younger levels, but does not occur in the range between MTM4B and CHR5B. Unless, and that is impossible to prove, the two species occur together in that level, and the poor material available in fact belongs to two species. I will assume that is not the case, and that the material from the earlier mentioned six localities is homogeneous, and represents a species different from *G. priscus*. *Glamys* nov. sp. 1 might well be a descendent of *G. priscus*, but then it is difficult to explain that *G. priscus* returns in younger levels. The most plausible explanation is that we are dealing with two different lineages, that mutually exclude each other, due to different environmental preferences, and either one or the other is present, as a result of a change in biotope. The appearance of *Glamys* nov. sp. 1 coincides with a radical change of sedimentation in the Palomera basin: the previously prevalent clastic flood plain sedimentation yields to a lake deposit of limestones with intercalated marls. The disappearance of *Glamys* nov. sp. 1 does not coincide with a change of sedimentation. The carbonate sequence simply continues.

Towards the top of the carbonate sequence thinly laminated limestones become frequent, and on top of the carbonates follows a clayey level with lignites, which I interpret as a phase of drying-up of the lake. In this level yet another species of *Glamys* appears, *G. nov. sp. 2* from UMB1B. In my opinion this is another reaction to changed environmental conditions. A descent of this species from *G. priscus* can't be proven nor denied, and whether *G. priscus* returns after this phase is unknown, because the sedimentation in the Sierra Palomera sub-basin is interrupted, and not resumed until in the upper part of the Upper Oligocene.

Bosma & de Bruijn (1979) observed a wavering pattern of size distributions throughout the stratigraphic sequence on the Isle of Wight. In particular they mention the remarkably small size of the material from Lacey's Farm Quarry, combined with a relatively complicated dental pattern. Maybe in that case too, there are two alternating lineages of *Glamys*, impossible to distinguish on the basis of the available material.

In the area of Montalbán sedimentation starts somewhere in the Lower Oligocene, with the locality FF3B, where *G. priscus* has been replaced by *G. olallensis*, and OLA4A. The few specimens from younger localities (MLB1D, MLB10) probably represent that species too.

*G. priscus* probably does not occur after the "Grande Coupure", and such citations should be revised. In Table 14 an interrogation point marks the presence of *G. aff. priscus* in Hoogbutsel, to indicate that this occurrence is not logical in view of the stratigraphic distribution of that species. In a previous paragraph I called it *G. aff. olallensis*, but the specimens have the size of *G. priscus*.

		<i>G. robiacensis</i>	<i>G. minor</i>	<i>G. priscus</i>	<i>G. aff. priscus</i>	<i>G. olallensis</i>	<i>G. aff. ford</i>	<i>G. umbriae</i>	<i>G. devoogdi</i>	<i>G. fordi</i>
MP23	MLB1D					x				
MP21	0LA4A HB Calaf 6,7 BOULDC				?	x			x	x x
MP20	FF3B UMB1B CHR2D CHR6C AGT5A AGT6			x x x	sp.2	x	x	aff. x		
MP19	CHR5A+B AGT2D Mormont HH6, 7			x x	sp.1				x	
MP18	Lacey's Farm La Débruge HH2, 3, 4		x	x x x						
MP17	Sossís				x					
MP16	Robiac	x								

Table 14. Stratigraphic distribution of *Glamys* species.Tabla 14. Distribución estratigráfica de las especies de *Glamys*.

The above considerations lead to the conclusion, that the small *Glamys* species represent at least three, and maybe four, different lineages. This explains why there is hardly any correlation between stratigraphical position and morphology. Their relationships are unknown, but a common ancestor is almost certain. One of the candidates as an ancestor is *Glamys robiacensis*, as supposed by Hartenberger (1971) and Vianey-Liaud (1994). But it is quite possible, that one of the mentioned lineages is derived from *Glamys minor*.

The larger *Glamys* species, *G. devoogdi*, *G. fordi*, *G. umbriae*, and *G. aff. ford*, with their peculiar complicated dental pattern, certainly do not form a single evolutionary lineage. They are best interpreted as local end-of-lineage forms, that develop independently in various areas, possibly due to the prevailing climatic conditions of the Early Oligocene, that lead to the "Grande Coupure". If that is true,

the form from Calaf is probably not *G. fordi*, but a form derived from one of the lineages existing in Spain. In the case of *G. aff. fordi* from CHR2D it is even possible, that some lineage of *Bransatoglis* underwent morphological changes similar to what happened in *Glamys*. The Eocene/Oligocene transition is generally thought to be a period of strong climatic changes, and the faunal break known as the “Grande Coupure” is probably related to these changes. Is it possible that under the influence of the changing climate various groups of glirids developed similar features independently ?

Each one of the previously mentioned lineages of small *Glamys* may have given rise to a dental pattern as found in the *devoogdi-fordi* group, and trying to establish lineages within this group seems to be premature. Furthermore, the stratigraphic distribution of *G. devoogdi* (Table 14) indicates, that the species found in Hoogbutsel is probably not the same as the one from Headon Hill 6 and 7.

One of the few cases, where one might draw a lineage, is *G. umbriae* (UMB1B) – *G. aff. umbriae* (FF3B). Nothing is opposed to the FF3B population being an advanced stage of the UMB1B population. If we want to extend this lineage to *G. fordi* from Bouldnor Cliff some incongruities arise. *G. aff. umbriae* (FF3B) and *G. fordi* are perfectly equivalent in degree of complexity, but they probably represent two different local evolutions.

## Paleoecology

Collinson & Hooker (2000) described gnaw marks on Eocene *Stratiotes* seeds, and attributed them to *Glamys*. Remarkably, in many of our fossil mammal localities *Stratiotes* seeds are abundant. Dr J. van den Burgh of Utrecht University (pers. comm.) came to the conclusion that the seeds in our material are void, and that may be the reason, that we did not find any gnaw marks. We do find many bone fragments with paired parallel scratches, which might be the traces of rodent incisors.

The important thing is that there seems to be a link between *Glamys* and the aquatic plant *Stratiotes*. Collinson & Hooker supposed the animals foraged on the lake margin, swam out to get the seeds, or even dived to the bottom. Apparently *Glamys* (or at least some species of the genus) was a good swimmer, and the coincidence with *Stratiotes* is an indication that it was highly adapted to an aquatic way of life.

Post mortem transportation is an important factor in the accumulation of fossil mammals, and the fact that most localities are extremely poor in fossils may be due to the fact that there was little transportation, which is confirmed by the complete lack of remains of macromammals. The animals lived practically in situ, and if that is true one must consider the possibility, that the representatives of the dominant group in our material, the Theridomorpha, had aquatic habits too.

The faunal diversity of our fossil localities is extremely low. In most localities only two or three species are found. This may be due to the fauna impoverishment prior to the “Grande Coupure”, but it is also possible that, due to the lack of transportation, the remains of non-aquatic species never reached the lake area where our localities are situated.

## ACKNOWLEDGEMENTS

This paper is the result of many years of work, during which my employer, the National Museum of Natural History (Naturalis) at Leiden, the Netherlands, permitted me to spend half the year in Spain. This facility has greatly contributed to the results, and I am very grateful for it. During these long periods of absence from the Museum my colleague and friend, Dr C.F. Winkler Prins, was always available to solve problems, that might have been difficult for me to solve at such a long distance; thank you, Cor.

During many years Dr I. Canudo from Zaragoza helped me to overcome the administrative barriers, and obtain the required permissions for the fieldwork.

I thank the Confederación Hidrográfica del Júcar for the permission to wash the samples in the river Turia near Chelva, and Dr J.I. Lacomba and Dr F. Ruiz from Valencia, for helping me to get that permission.

I am most grateful to the co-director of the project, Dr. E. Martín, and to the many students of the University of Granada, who participated in the fieldwork.

Dr M. Hugueney and Dr L. van den Hoek Ostende read the manuscript critically, and made suggestions that improved the text considerably. I am most grateful for their effort.

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## Appendix – morphology tables

### Abbreviations in this appendix

ant. = anterior; centrol. = centrolophid; conn. = connected; ecd = entoconid;  
lab. = labially; ling. = lingually; mcd = metaconid; part. = partially; pc = protocone;  
post. = posterior

D <sub>4</sub>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anterolophid	10		1		0		1		0		6		5	
interrupted	2	20.0	0	0.0	0	0.0	1	100.0	0	0.0	2	33.3	0	0.0
continuous	8	80.0	1	100.0	0	0.0	0	0.0	0	0.0	4	66.7	5	100.0
anterotropid	10		1		0		1		0		6		6	
absent	10	100.0	1	100.0	0	0.0	1	100.0	0	0.0	6	100.0	6	100.0
metalophid	10		1		0		1		1		6		6	
free	0	0.0	0	0.0	0	0.0	0	0.0	1	100.0	2	33.3	1	16.7
to mcd base	1	10.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	16.7
to mcd high	9	90.0	1	100.0	0	0.0	1	100.0	0	0.0	4	66.7	4	66.7
centrolophid	10		1		0		1		1		6		6	
absent	10	100.0	1	100.0	0	0.0	1	100.0	1	100.0	6	100.0	6	100.0
mesostylid	10		1		0		1		1		6		6	
absent	10	100.0	1	100.0	0	0.0	1	100.0	1	100.0	6	100.0	6	100.0
mesoconid	10		1		0		1		1		6		6	
absent	1	10.0	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0	3	50.0
labial border	7	70.0	1	100.0	0	0.0	0	0.0	1	100.0	6	100.0	3	50.0
centrally	2	20.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
mesolophid	10		1		0		1		1		6		6	
absent	2	20.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	4	66.7
short	1	10.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	16.7
medium+interrupt.	2	20.0	0	0.0	0	0.0	0	0.0	0	0.0	1	16.7	0	0.0
medium	5	50.0	1	100.0	0	0.0	0	0.0	1	100.0	5	83.3	0	0.0
free to mcd	0	0.0	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0	0	0.0
free to ecd	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	16.7
posterotropid	10		1		0		1		1		6		6	
absent	9	90.0	1	100.0	0	0.0	1	100.0	1	100.0	5	83.3	6	100.0
small	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	16.7	0	0.0
medium	1	10.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0

Table 15. Comparison of the morphology of D<sub>4</sub> of *G. (aff.) priscus* and *G. olallensis*.

Tabla 15. Comparación de la morfología del D<sub>4</sub> de *G. (aff.) priscus* y *G. olallensis*.

P <sub>4</sub>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
shape	25		18		9		16		18		29		22	
blunt	25	100.0	18	100.0	9	100.0	16	100.0	18	100.0	29	100.0	22	100.0
anterolophid	25		19		8		16		16		25		22	
interrupted	22	88.0	19	100.0	8	100.0	15	93.8	16	100.0	24	96.0	22	100.0
continuous	3	12.0	0	0.0	0	0.0	1	6.3	0	0.0	1	4.0	0	0.0
anterotropic	25		19		7		12		15		26		20	
absent	25	100.0	19	100.0	7	100.0	12	100.0	15	100.0	26	100.0	20	100.0
metalophid	27		19		7		15		16		29		21	
free	9	33.3	2	10.5	2	28.6	2	13.3	3	18.8	8	27.6	3	14.3
to mcd base	8	29.6	2	10.5	0	0.0	2	13.3	2	12.5	8	27.6	3	14.3
to mcd high	10	37.0	15	78.9	5	71.4	11	73.3	11	68.8	13	44.8	15	71.4
centrolophid	27		18		9		16		16		29		23	
absent	23	85.2	17	94.4	7	77.8	11	68.8	16	100.0	18	62.1	23	100.0
short	3	11.1	0	0.0	0	0.0	3	18.8	0	0.0	5	17.2	0	0.0
medium	1	3.7	1	5.6	1	11.1	0	0.0	0	0.0	3	10.3	0	0.0
long	0	0.0	0	0.0	1	11.1	2	12.5	0	0.0	3	10.3	0	0.0
centrold.-mcd	27		18		9		16		16		29		23	
not connected	27	100.0	18	100.0	9	100.0	16	100.0	16	100.0	25	86.2	23	100.0
low connected	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	4	13.8	0	0.0
mesostylid	26		18		9		15		16		29		23	
absent	24	92.3	16	88.9	7	77.8	13	86.7	14	87.5	25	86.2	23	100.0
present	2	7.7	2	11.1	2	22.2	2	13.3	2	12.5	4	13.8	0	0.0
mesoconid	26		19		9		16		18		29		23	
absent	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	3	13.0
labial border	24	92.3	18	94.7	9	100.0	14	87.5	17	94.4	22	75.9	17	73.9
centrally	2	7.7	1	5.3	0	0.0	2	12.5	1	5.6	7	24.1	3	13.0
mesolophid	27		19		9		16		17		29		23	
absent	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	4	17.4
short	3	11.1	1	5.3	1	11.1	1	6.3	0	0.0	6	20.7	6	26.1
curved forward	0	0.0	0	0.0	0	0.0	0	0.0	1	5.9	1	3.4	1	4.3
free to mcd	3	11.1	0	0.0	1	11.1	1	6.3	0	0.0	2	6.9	1	4.3
free to ecd	19	70.4	9	47.4	7	77.8	9	56.3	15	88.2	19	65.5	11	47.8
conn. to ecd	2	7.4	9	47.4	0	0.0	5	31.3	1	5.9	1	3.4	0	0.0
posterotropic	27		19		9		16		16		29		23	
absent	23	85.2	18	94.7	8	88.9	12	75.0	16	100.0	25	86.2	23	100.0
very small	1	3.7	0	0.0	0	0.0	2	12.5	0	0.0	0	0.0	0	0.0
small	3	11.1	0	0.0	0	0.0	2	12.5	0	0.0	2	6.9	0	0.0
medium	0	0.0	1	5.3	0	0.0	0	0.0	0	0.0	2	6.9	0	0.0
long	0	0.0	0	0.0	1	11.1	0	0.0	0	0.0	0	0.0	0	0.0

Table 16. Comparison of the morphology of P<sub>4</sub> of *G. (aff.) priscus* and *G. olallensis*.Tabla 16. Comparación de la morfología del P<sub>4</sub> de *G. (aff.) priscus* y *G. olallensis*.

M <sub>1</sub>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anterolophid lab.free	52		17		15		14		11		37		23	
	52	100.0	17	100.0	15	100.0	14	100.0	11	100.0	37	100.0	23	100.0
anterotropid absent	52		18		15		13		11		36		24	
	52	100.0	18	100.0	14	93.3	11	84.6	10	90.9	34	94.4	24	100.0
very small	0	0.0	0	0.0	1	6.7	1	7.7	0	0.0	0	0.0	0	0.0
small	0	0.0	0	0.0	0	0.0	0	0.0	1	9.1	2	5.6	0	0.0
medium	0	0.0	0	0.0	0	0.0	1	7.7	0	0.0	0	0.0	0	0.0
metalophid free	52		18		15		14		11		36		23	
	12	23.1	1	5.6	0	0.0	2	14.3	0	0.0	7	19.4	2	8.7
to mcd base	13	25.0	14	77.8	7	46.7	7	50.0	3	27.3	22	61.1	12	52.2
to mcd high	27	51.9	3	16.7	8	53.3	5	35.7	8	72.7	7	19.4	9	39.1
centrolophid absent	52		18		15		13		11		36		24	
	50	96.2	12	66.7	10	66.7	8	61.5	7	63.6	27	75.0	23	95.8
short	1	1.9	1	5.6	2	13.3	3	23.1	0	0.0	4	11.1	1	4.2
medium	1	1.9	3	16.7	3	20.0	2	15.4	4	36.4	4	11.1	0	0.0
long	0	0.0	2	11.1	0	0.0	0	0.0	0	0.0	1	2.8	0	0.0
centrold.-mcd not connected	52		18		15		13		11		36		25	
	52	100.0	18	100.0	14	93.3	13	100.0	7	63.6	34	94.4	24	96.0
low connected	0	0.0	0	0.0	1	6.7	0	0.0	4	36.4	1	2.8	0	0.0
high connected	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.8	1	4.0
mesostylid absent	51		17		14		13		11		36		25	
	44	86.3	15	88.2	12	85.7	7	53.8	8	72.7	26	72.2	24	96.0
present	7	13.7	2	11.8	2	14.3	6	46.2	3	27.3	10	27.8	1	4.0
mesoconid labial border centrally	52		17		15		13		11		38		24	
	40	76.9	14	82.4	11	73.3	8	61.5	7	63.6	32	84.2	8	33.3
	12	23.1	3	17.6	4	26.7	5	38.5	4	36.4	6	15.8	16	66.7
mesolophid short	52		18		15		13		11		38		23	
	1	1.9	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	8.7
medium	19	36.5	8	44.4	5	33.3	4	30.8	3	27.3	8	21.1	21	91.3
curved forward	1	1.9	1	5.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
free to mcd	8	15.4	2	11.1	2	13.3	2	15.4	1	9.1	9	23.7	0	0.0
conn. to mcd	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.6	0	0.0
free to ecd	22	42.3	6	33.3	7	46.7	7	53.8	7	63.6	19	50.0	0	0.0
conn. to ecd	1	1.9	1	5.6	1	6.7	0	0.0	0	0.0	0	0.0	0	0.0
ling. border	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.6	0	0.0
posterotropid absent	52		18		14		13		11		38		23	
	37	71.2	10	55.6	11	78.6	10	76.9	9	81.8	19	50.0	23	100.0
very small	7	13.5	0	0.0	0	0.0	1	7.7	1	9.1	1	2.6	0	0.0
small	7	13.5	3	16.7	2	14.3	0	0.0	0	0.0	9	23.7	0	0.0
medium	0	0.0	5	27.8	1	7.1	2	15.4	1	9.1	9	23.7	0	0.0
long	1	1.9	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0

Table 17. Comparison of the morphology of M<sub>1</sub> of *G. (aff.) priscus* and *G. olallensis*.Tabla 17. Comparación de la morfología del M<sub>1</sub> de *G. (aff.) priscus* y *G. olallensis*.

M <sub>2</sub>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anterolophid	62		9		9		18		18		29		34	
lab. free	62	100.0	9	100.0	9	100.0	18	100.0	18	100.0	29	100.0	34	100.0
anterotropid	59		9		10		19		14		27		29	
absent	59	100.0	9	100.0	9	90.0	17	89.5	13	92.9	24	88.9	29	100.0
very small	0	0.0	0	0.0	0	0.0	2	10.5	0	0.0	3	11.1	0	0.0
small	0	0.0	0	0.0	1	10.0	0	0.0	1	7.1	0	0.0	0	0.0
metalophid	58		9		8		19		16		25		29	
free	18	31.0	5	55.6	1	12.5	0	0.0	0	0.0	8	32.0	3	10.3
to mcd base	31	53.4	2	22.2	5	62.5	15	78.9	11	68.8	13	52.0	17	58.6
to mcd high	9	15.5	2	22.2	2	25.0	4	21.1	5	31.3	4	16.0	9	31.0
centrolophid	55		8		8		19		15		26		23	
absent	54	98.2	8	100.0	2	25.0	9	47.4	8	53.3	12	46.2	21	91.3
short	0	0.0	0	0.0	2	25.0	7	36.8	3	20.0	6	23.1	1	4.3
medium	1	1.8	0	0.0	4	50.0	3	15.8	3	20.0	6	23.1	1	4.3
long	0	0.0	0	0.0	0	0.0	0	0.0	1	6.7	2	7.7	0	0.0
centrold.-mcd	54		8		7		19		15		25		32	
not connected	54	100.0	8	100.0	7	100.0	19	100.0	15	100.0	22	88.0	31	96.9
low connected	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	3	12.0	1	3.1
mesostylid	54		8		7		18		14		25		32	
absent	50	92.6	7	87.5	5	71.4	14	77.8	7	50.0	13	52.0	31	96.9
present	4	7.4	1	12.5	2	28.6	4	22.2	7	50.0	11	44.0	1	3.1
crest	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	4.0	0	0.0
mesoconid	63		9		8		20		18		29		34	
labial border	59	93.7	9	100.0	7	87.5	14	70.0	16	88.9	23	79.3	21	61.8
centrally	4	6.3	0	0.0	1	12.5	6	30.0	2	11.1	6	20.7	13	38.2
mesolophid	62		9		9		21		18		27		33	
short	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.0
medium	14	22.6	0	0.0	0	0.0	3	14.3	3	16.7	1	3.7	17	51.5
curved forward	2	3.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	6.1
free to mcd	4	6.5	2	22.2	2	22.2	2	9.5	1	5.6	2	7.4	7	21.2
conn. to mcd	1	1.6	0	0.0	0	0.0	1	4.8	0	0.0	1	3.7	0	0.0
free to ecd	36	58.1	6	66.7	6	66.7	13	61.9	12	66.7	21	77.8	4	12.1
conn. to ecd	5	8.1	1	11.1	1	11.1	2	9.5	2	11.1	2	7.4	1	3.0
long+straight	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.0
posterotropid	59		8		9		20		17		28		30	
absent	42	71.2	6	75.0	6	66.7	12	60.0	8	47.1	16	57.1	22	73.3
very small	5	8.5	0	0.0	1	11.1	3	15.0	2	11.8	5	17.9	3	10.0
small	6	10.2	0	0.0	1	11.1	3	15.0	4	23.5	4	14.3	4	13.3
medium	4	6.8	2	25.0	1	11.1	2	10.0	2	11.8	3	10.7	1	3.3
long	2	3.4	0	0.0	0	0.0	0	0.0	1	5.9	0	0.0	0	0.0

Table 18. Comparison of the morphology of M<sub>2</sub> of *G. (aff.) priscus* and *G. olallensis*.Tabla 18. Comparación de la morfología del M<sub>2</sub> de *G. (aff.) priscus* y *G. olallensis*.

M <sub>3</sub>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anterolophid	24		16		7		25		10		26		36	
lab. free	24	100.0	16	100.0	7	100.0	25	100.0	10	100.0	26	100.0	35	97.2
lab. connected	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.8
anterotropid	24		16		7		24		10		26		35	
absent	24	100.0	13	81.3	3	42.9	5	20.8	4	40.0	21	80.8	35	100.0
very small	0	0.0	1	6.3	0	0.0	2	8.3	0	0.0	3	11.5	0	0.0
small	0	0.0	0	0.0	2	28.6	7	29.2	2	20.0	0	0.0	0	0.0
medium	0	0.0	2	12.5	1	14.3	7	29.2	4	40.0	1	3.8	0	0.0
long	0	0.0	0	0.0	1	14.3	3	12.5	0	0.0	1	3.8	0	0.0
metalophid	22		16		7		24		10		23		33	
free	8	36.4	12	75.0	5	71.4	11	45.8	2	20.0	19	82.6	17	51.5
to mcd base	13	59.1	3	18.8	2	28.6	13	54.2	7	70.0	3	13.0	10	30.3
to mcd high	1	4.5	1	6.3	0	0.0	0	0.0	1	10.0	1	4.3	6	18.2
centrolophid	22		17		7		22		10		23		32	
absent	15	68.2	12	70.6	2	28.6	9	40.9	4	40.0	10	43.5	30	93.8
short	1	4.5	0	0.0	1	14.3	3	13.6	2	20.0	4	17.4	1	3.1
medium	6	27.3	4	23.5	3	42.9	8	36.4	3	30.0	9	39.1	1	3.1
long	0	0.0	1	5.9	1	14.3	2	9.1	1	10.0	0	0.0	0	0.0
centrold.-mcd	24		17		7		23		10		23		33	
not connected	23	95.8	17	100.0	6	85.7	23	100.0	10	100.0	23	100.0	32	97.0
low connected	1	4.2	0	0.0	1	14.3	0	0.0	0	0.0	0	0.0	1	3.0
mesostylid	22		17		7		24		10		24		33	
absent	13	59.1	5	29.4	0	0.0	2	8.3	4	40.0	1	4.2	25	75.8
present	9	40.9	12	70.6	7	100.0	20	83.3	6	60.0	21	87.5	6	18.2
crest	0	0.0	0	0.0	0	0.0	2	8.3	0	0.0	2	8.3	2	6.1
mesoconid	24		17		7		25		10		26		36	
labial border	23	95.8	17	100.0	7	100.0	24	96.0	10	100.0	25	96.2	22	61.1
centrally	1	4.2	0	0.0	0	0.0	1	4.0	0	0.0	1	3.8	14	38.9
mesolophid	23		17		7		25		10		25		35	
curved forward	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.9
free to mcd	5	21.7	2	11.8	0	0.0	1	4.0	1	10.0	5	20.0	1	2.9
conn. to mcd	1	4.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
free to ecd	12	52.2	8	47.1	5	71.4	16	64.0	8	80.0	16	64.0	21	60.0
conn. to ecd	5	21.7	6	35.3	2	28.6	7	28.0	1	10.0	4	16.0	11	31.4
ling. border	0	0.0	1	5.9	0	0.0	1	4.0	0	0.0	0	0.0	1	2.9
posterotropid	23		17		7		23		10		25		36	
absent	16	69.6	7	41.2	1	14.3	3	13.0	4	40.0	12	48.0	35	97.2
very small	3	13.0	1	5.9	0	0.0	4	17.4	1	10.0	1	4.0	1	2.8
small	1	4.3	0	0.0	2	28.6	7	30.4	0	0.0	7	28.0	0	0.0
medium	2	8.7	9	52.9	4	57.1	8	34.8	4	40.0	5	20.0	0	0.0
long	1	4.3	0	0.0	0	0.0	1	4.3	1	10.0	0	0.0	0	0.0

Table 19. Comparison of the morphology of M<sub>3</sub> of *G. (aff.) priscus* and *G. olallensis*.Tabla 19. Comparación de la morfología del M<sub>3</sub> de *G. (aff.) priscus* y *G. olallensis*.

D <sup>4</sup>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anteroloph	12		3		2		6		1		19		16	
short	3	25.0	1	33.3	0	0.0	0	0.0	0	0.0	0	0.0	1	6.3
medium	7	58.3	1	33.3	0	0.0	2	33.3	1	100.0	1	5.3	10	62.5
long	2	16.7	1	33.3	2	100.0	4	66.7	0	0.0	18	94.7	5	31.3
anterotrope	11		3		2		6		1		19		13	
absent	11	100.0	2	66.7	1	50.0	6	100.0	1	100.0	19	100.0	13	100.0
short	0	0.0	1	33.3	1	50.0	0	0.0	0	0.0	0	0.0	0	0.0
precentroloph	12		3		2		6		1		19		14	
absent	2	16.7	2	66.7	0	0.0	1	16.7	0	0.0	6	31.6	3	21.4
short	5	41.7	1	33.3	0	0.0	1	16.7	0	0.0	2	10.5	0	0.0
medium	4	33.3	0	0.0	0	0.0	0	0.0	0	0.0	3	15.8	3	21.4
long	1	8.3	0	0.0	2	100.0	4	66.7	1	100.0	8	42.1	8	57.1
postcentroloph	12		3		2		6		1		19		16	
absent	11	91.7	3	100.0	2	100.0	6	100.0	1	100.0	19	100.0	13	81.3
long	1	8.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	3	18.8
prototrope	12		3		2		6		1		19		16	
absent	12	100.0	3	100.0	2	100.0	6	100.0	1	100.0	19	100.0	16	100.0
metatrope	12		3		2		6		1		19		16	
absent	12	100.0	3	100.0	2	100.0	6	100.0	1	100.0	19	100.0	16	100.0
centrolophs	12		3		2		6		1		19		16	
free	12	100.0	3	100.0	2	100.0	6	100.0	1	100.0	19	100.0	14	87.5
connected	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	12.5
posterotrope	12		3		2		6		1		19		16	
absent	12	100.0	3	100.0	2	100.0	6	100.0	1	100.0	19	100.0	16	100.0
endoloph	12		3		2		6		1		19		13	
protocone	3	25.0	1	33.3	0	0.0	4	66.7	0	0.0	8	42.1	1	7.7
ant. interrupt.	9	75.0	2	66.7	0	0.0	2	33.3	1	100.0	9	47.4	10	76.9
post. interrupt.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	10.5	0	0.0
complete	0	0.0	0	0.0	2	100.0	0	0.0	0	0.0	0	0.0	2	15.4
lingual border	12		3		2		6		1		19		14	
smooth	12	100.0	3	100.0	2	100.0	6	100.0	1	100.0	19	100.0	14	100.0

Table 20. Comparison of the morphology of D<sup>4</sup> of *G. (aff.) priscus* and *G. olallensis*.Tabla 20. Comparación de la morfología del D<sup>4</sup> de *G. (aff.) priscus* y *G. olallensis*.

P <sup>4</sup>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anteroloph	37		20		6		16		15		22		23	
absent	0	0.0	0	0.0	0	0.0	0	0.0	2	13.3	0	0.0	0	0.0
short	4	10.8	0	0.0	3	50.0	2	12.5	1	6.7	2	9.1	3	13.0
medium	6	16.2	1	5.0	1	16.7	3	18.8	2	13.3	5	22.7	8	34.8
long	27	73.0	19	95.0	2	33.3	11	68.8	10	66.7	15	68.2	12	52.2
anterotrope	38		20		6		15		15		22		19	
absent	38	100.0	20	100.0	6	100.0	15	100.0	15	100.0	22	100.0	19	100.0
precentroloph	40		21		6		15		15		22		25	
absent	2	5.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	6	24.0
short	0	0.0	1	4.8	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
medium	2	5.0	0	0.0	1	16.7	0	0.0	0	0.0	0	0.0	3	12.0
long	36	90.0	20	95.2	5	83.3	15	100.0	15	100.0	22	100.0	16	64.0
midcentroloph	40		22		6		14		15		22		27	
absent	37	92.5	22	100.0	6	100.0	14	100.0	15	100.0	22	100.0	26	96.3
short	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
long	2	5.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.7
postcentroloph	40		21		6		14		15		22		25	
absent	37	92.5	21	100.0	6	100.0	14	100.0	14	93.3	22	100.0	25	100.0
short	2	5.0	0	0.0	0	0.0	0	0.0	1	6.7	0	0.0	0	0.0
medium	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
prototrope	40		21		6		14		15		22		26	
absent	39	97.5	20	95.2	6	100.0	13	92.9	15	100.0	22	100.0	26	100.0
medium	1	2.5	0	0.0	0	0.0	1	7.1	0	0.0	0	0.0	0	0.0
long	0	0.0	1	4.8	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
metatrope	40		21		6		14		15		22		26	
absent	40	100.0	21	100.0	6	100.0	14	100.0	15	100.0	22	100.0	26	100.0
centrolophs	40		21		6		14		15		22		26	
free	39	97.5	21	100.0	6	100.0	14	100.0	15	100.0	22	100.0	26	100.0
connected	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
posterotrope	40		21		6		14		15		21		26	
absent	40	100.0	21	100.0	6	100.0	14	100.0	15	100.0	21	100.0	26	100.0
endoloph	38		21		5		14		15		21		19	
protocone	18	47.4	16	76.2	1	20.0	6	42.9	5	33.3	19	90.5	12	63.2
ant. interrupt.	20	52.6	5	23.8	4	80.0	8	57.1	10	66.7	2	9.5	7	36.8
lingual border	38		21		5		13		14		20		23	
smooth	38	100.0	21	100.0	5	100.0	13	100.0	14	100.0	20	100.0	23	100.0

Table 21. Comparison of the morphology of P<sup>4</sup> of *G. (aff.) priscus* and *G. olallensis*.Tabla 21. Comparación de la morfología del P<sup>4</sup> de *G. (aff.) priscus* y *G. olallensis*.

M <sup>1</sup>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anteroloph	40		15		10		20		9		34		25	
lingual free	40	100.0	15	100.0	10	100.0	20	100.0	9	100.0	33	97.1	24	96.0
ling. low conn.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.9	1	4.0
anterotrope	39		14		10		18		8		33		23	
absent	39	100.0	14	100.0	10	100.0	18	100.0	8	100.0	33	100.0	23	100.0
precentroloph	38		13		10		17		10		34		28	
absent	11	28.9	8	61.5	1	10.0	4	23.5	1	10.0	5	14.7	1	3.6
long	27	71.1	5	38.5	9	90.0	13	76.5	9	90.0	29	85.3	27	96.4
precentroloph	37		13		10		15		9		33		25	
absent	11	29.7	8	61.5	1	10.0	4	26.7	1	11.1	6	18.2	1	4.0
pac	22	59.5	3	23.1	9	90.0	10	66.7	5	55.6	20	60.6	10	40.0
free	2	5.4	1	7.7	0	0.0	1	6.7	2	22.2	6	18.2	4	16.0
central	0	0.0	1	7.7	0	0.0	0	0.0	1	11.1	1	3.0	8	32.0
mesostyl	2	5.4	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	8.0
midcentroloph	37		13		10		17		10		33		28	
absent	27	73.0	5	38.5	9	90.0	13	76.5	9	90.0	29	87.9	28	100.0
long	10	27.0	8	61.5	1	10.0	4	23.5	1	10.0	4	12.1	0	0.0
postcentroloph	39		15		10		17		10		35		27	
absent	38	97.4	13	86.7	10	100.0	16	94.1	10	100.0	34	97.1	27	100.0
long	1	2.6	2	13.3	0	0.0	1	5.9	0	0.0	1	2.9	0	0.0
postcentroloph	39		14		10		17		10		35		27	
absent	38	97.4	13	92.9	10	100.0	16	94.1	10	100.0	34	97.1	27	100.0
metacone	1	2.6	1	7.1	0	0.0	1	5.9	0	0.0	1	2.9	0	0.0
prototrope	40		14		10		16		10		34		25	
absent	37	92.5	14	100.0	9	90.0	16	100.0	10	100.0	34	100.0	25	100.0
short	1	2.5	0	0.0	1	10.0	0	0.0	0	0.0	0	0.0	0	0.0
medium	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
long	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
metatrope	39		15		10		17		10		35		25	
absent	39	100.0	15	100.0	10	100.0	17	100.0	10	100.0	35	100.0	25	100.0
posterotrope	39		15		10		19		11		35		26	
absent	39	100.0	15	100.0	10	100.0	19	100.0	11	100.0	35	100.0	26	100.0
endoloph	39		15		10		20		10		33		24	
protocone	22	56.4	14	93.3	7	70.0	11	55.0	4	40.0	21	63.6	19	79.2
ant. interrupt.	17	43.6	1	6.7	3	30.0	9	45.0	6	60.0	12	36.4	5	20.8
lingual border	38		14		10		20		8		34		25	
smooth	37	97.4	14	100.0	10	100.0	19	95.0	6	75.0	32	94.1	24	96.0
crenulated	1	2.6	0	0.0	0	0.0	1	5.0	2	25.0	2	5.9	1	4.0

Table 22. Comparison of the morphology of M<sup>1</sup> of *G. (aff.) priscus* and *G. olallensis*.Tabla 22. Comparación de la morfología del M<sup>1</sup> de *G. (aff.) priscus* y *G. olallensis*.

M <sup>2</sup>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anteroloph	53		12		5		18		13		28		29	
lingual free	53	100.0	12	100.0	5	100.0	18	100.0	13	100.0	27	96.4	28	96.6
ling. low conn.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.6	1	3.4
anterotrope	52		15		5		16		13		27		28	
absent	52	100.0	15	100.0	5	100.0	16	100.0	13	100.0	27	100.0	28	100.0
precentroloph	54		14		5		17		13		27		30	
absent	20	37.0	5	35.7	0	0.0	4	23.5	1	7.7	0	0.0	1	3.3
long	34	63.0	9	64.3	5	100.0	13	76.5	12	92.3	27	100.0	29	96.7
precentroloph	54		13		4		16		13		27		27	
absent	21	38.9	5	38.5	0	0.0	4	25.0	1	7.7	0	0.0	1	3.7
pac	25	46.3	3	23.1	2	50.0	7	43.8	5	38.5	17	63.0	14	51.9
free	3	5.6	3	23.1	2	50.0	2	12.5	4	30.8	5	18.5	6	22.2
central	2	3.7	2	15.4	0	0.0	2	12.5	3	23.1	3	11.1	3	11.1
mesostyl	3	5.6	0	0.0	0	0.0	1	6.3	0	0.0	2	7.4	3	11.1
midcentroloph	54		9		1		17		13		28		30	
absent	35	64.8	2	22.2	0	0.0	13	76.5	11	84.6	27	96.4	29	96.7
short	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.6	0	0.0
medium	0	0.0	0	0.0	0	0.0	0	0.0	1	7.7	0	0.0	1	3.3
long	19	35.2	7	77.8	1	100.0	4	23.5	1	7.7	0	0.0	0	0.0
postcentroloph	54		13		4		16		13		28		30	
absent	52	96.3	13	100.0	4	100.0	16	100.0	13	100.0	27	96.4	30	100.0
long	2	3.7	0	0.0	0	0.0	0	0.0	0	0.0	1	3.6	0	0.0
postcentroloph	54		13		4		16		13		28		30	
absent	52	96.3	13	100.0	4	100.0	16	100.0	13	100.0	27	96.4	30	100.0
metacone	1	1.9	0	0.0	0	0.0	0	0.0	0	0.0	1	3.6	0	0.0
central	1	1.9	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
prototrope	55		16		5		16		15		27		30	
absent	55	100.0	14	87.5	5	100.0	14	87.5	12	80.0	26	96.3	30	100.0
short	0	0.0	2	12.5	0	0.0	2	12.5	3	20.0	1	3.7	0	0.0
metatrope	56		16		5		17		13		27		30	
absent	56	100.0	16	100.0	5	100.0	17	100.0	13	100.0	27	100.0	30	100.0
posterotrope	56		16		5		19		14		27		30	
absent	56	100.0	16	100.0	5	100.0	19	100.0	13	92.9	27	100.0	30	100.0
short	0	0.0	0	0.0	0	0.0	0	0.0	1	7.1	0	0.0	0	0.0
endoloph	51		11		5		18		14		28		29	
protocone	32	62.7	6	54.5	5	100.0	8	44.4	6	42.9	23	82.1	21	72.4
ant. interrupt.	19	37.3	5	45.5	0	0.0	10	55.6	8	57.1	5	17.9	8	27.6
lingual border	53		11		5		19		14		28		28	
smooth	52	98.1	11	100.0	5	100.0	19	100.0	14	100.0	26	92.9	28	100.0
crenulated	1	1.9	0	0.0	0	0.0	0	0.0	0	0.0	2	7.1	0	0.0

Table 23. Comparison of the morphology of M<sup>2</sup> of *G. (aff.) priscus* and *G. olallensis*.Tabla 23. Comparación de la morfología del M<sup>2</sup> de *G. (aff.) priscus* y *G. olallensis*.

M <sup>3</sup>	AGT2D		CHR5A+B		VRS15B		AGT6		AGT5A		CHR6C		OLA4A	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
anteroloph	23		13		5		15		12		17		26	
lingual free	5	21.7	8	61.5	5	100.0	9	60.0	2	16.7	10	58.8	15	57.7
ling. low conn.	6	26.1	1	7.7	0	0.0	4	26.7	6	50.0	7	41.2	5	19.2
ling. high conn.	12	52.2	4	30.8	0	0.0	2	13.3	4	33.3	0	0.0	6	23.1
anterotrope	26		13		5		16		12		18		27	
absent	26	100.0	13	100.0	5	100.0	16	100.0	12	100.0	18	100.0	27	100.0
precentroloph	0		5		0		0		0		0		0	
absent	0	0.0	5	100.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
trigone crests	25		13		5		16		14		18		30	
absent	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	3	10.0
one crest	18	72.0	5	38.5	5	100.0	10	62.5	10	71.4	12	66.7	21	70.0
two crests	6	24.0	5	38.5	0	0.0	6	37.5	3	21.4	6	33.3	5	16.7
three crests	1	4.0	3	23.1	0	0.0	0	0.0	1	7.1	0	0.0	1	3.3
mesostyl	24		9		5		15		10		4		26	
absent	23	95.8	9	100.0	5	100.0	15	100.0	10	100.0	4	100.0	20	76.9
present	1	4.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	6	23.1
posterotrope	25		13		5		15		12		18		28	
absent	14	56.0	10	76.9	2	40.0	14	93.3	10	83.3	18	100.0	28	100.0
short	9	36.0	2	15.4	3	60.0	1	6.7	1	8.3	0	0.0	0	0.0
medium	2	8.0	0	0.0	0	0.0	0	0.0	1	8.3	0	0.0	0	0.0
long	0	0.0	1	7.7	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
endoloph	23		13		5		15		12		16		25	
protocone	3	13.0	3	23.1	2	40.0	5	33.3	1	8.3	5	31.3	12	48.0
ant. interrupt.	8	34.8	4	30.8	3	60.0	4	26.7	4	33.3	3	18.8	3	12.0
post. interrupt.	2	8.7	1	7.7	0	0.0	1	6.7	1	8.3	3	18.8	5	20.0
complete	10	43.5	4	30.8	0	0.0	5	33.3	6	50.0	5	31.3	5	20.0
part. around pc	0	0.0	1	7.7	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
lingual border	24		13		5		15		12		17		24	
smooth	23	95.8	13	100.0	5	100.0	15	100.0	12	100.0	17	100.0	24	100.0
crenulated	1	4.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0

Table 24. Comparison of the morphology of M<sup>3</sup> of *G. (aff.) priscus* and *G. olallensis*.Tabla 24. Comparación de la morfología del M<sup>3</sup> de *G. (aff.) priscus* y *G. olallensis*.

- Fig. 1. D<sub>4</sub> sin., MLB1D 1006  
Fig. 2. D<sub>4</sub> dext., MLB1D 1009  
Fig. 3. P<sub>4</sub> sin., MLB1D 1018  
Fig. 4. P<sub>4</sub> dext., MLB1D 1040  
Fig. 5. M<sub>1</sub> sin., MLB1D 1050, Holotype  
Fig. 6. M<sub>1</sub> dext., MLB1D 1075  
Fig. 7. M<sub>2</sub> sin., MLB1D 1086  
Fig. 8. M<sub>2</sub> dext., MLB1D 1126  
Fig. 9. M<sub>3</sub> sin., MLB1D 1148  
Fig. 10. M<sub>3</sub> dext., MLB1D 1182  
Fig. 11. D<sup>4</sup> sin., MLB1D 1193  
Fig. 12. D<sup>4</sup> dext., MLB1D 1202  
Fig. 13. P<sup>4</sup> sin., MLB1D 1212  
Fig. 14. P<sup>4</sup> dext., MLB1D 1233  
Fig. 15. M<sup>1</sup> sin., MLB1D 1257  
Fig. 16. M<sup>1</sup> dext., MLB1D 1293  
Fig. 17. M<sup>2</sup> sin., MLB1D 1306  
Fig. 18. M<sup>2</sup> dext., MLB1D 1329  
Fig. 19. M<sup>3</sup> sin., MLB1D 1346  
Fig. 20. M<sup>3</sup> dext., MLB1D 1376

Scale represents 1 mm / Escala representa 1 mm

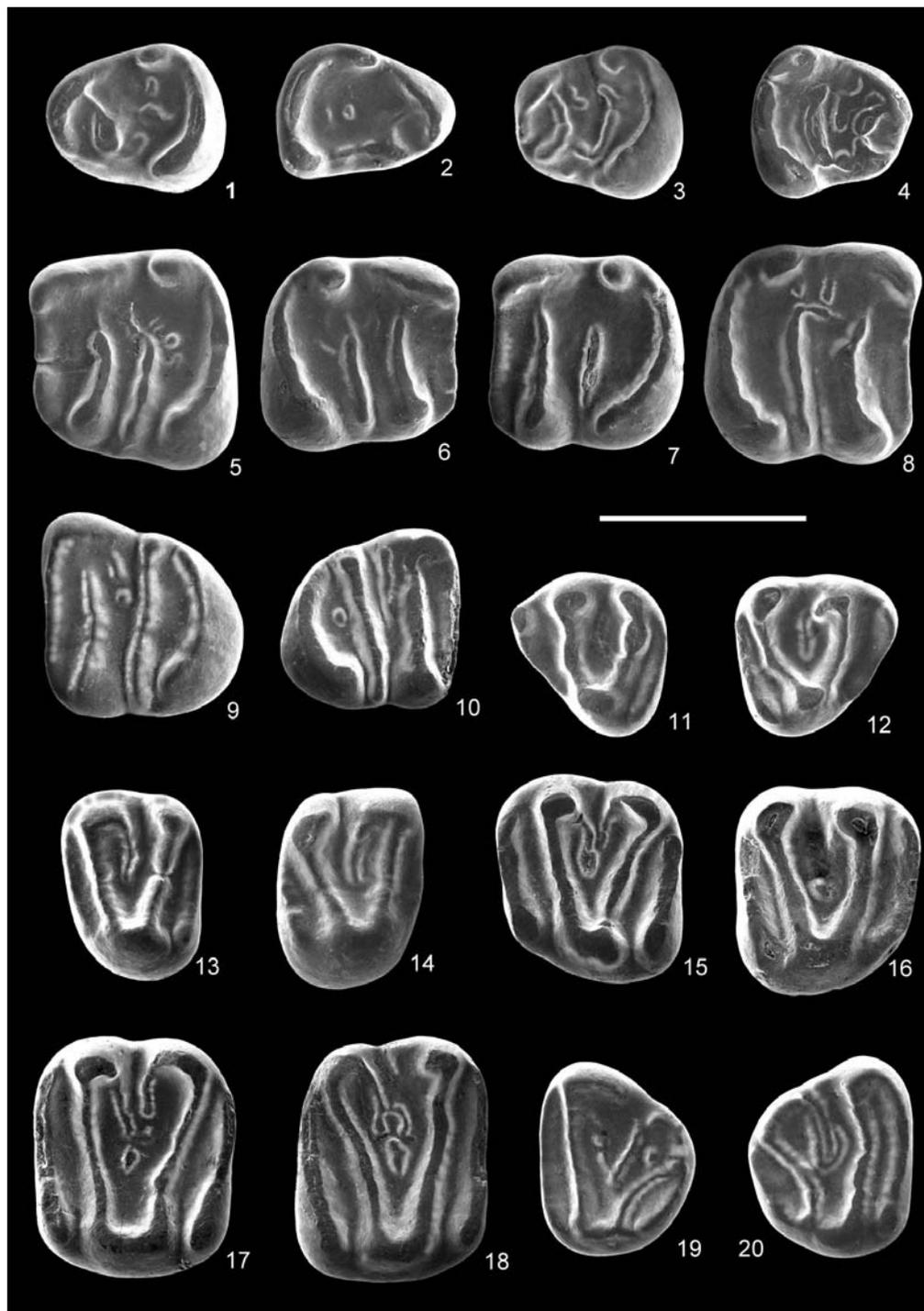
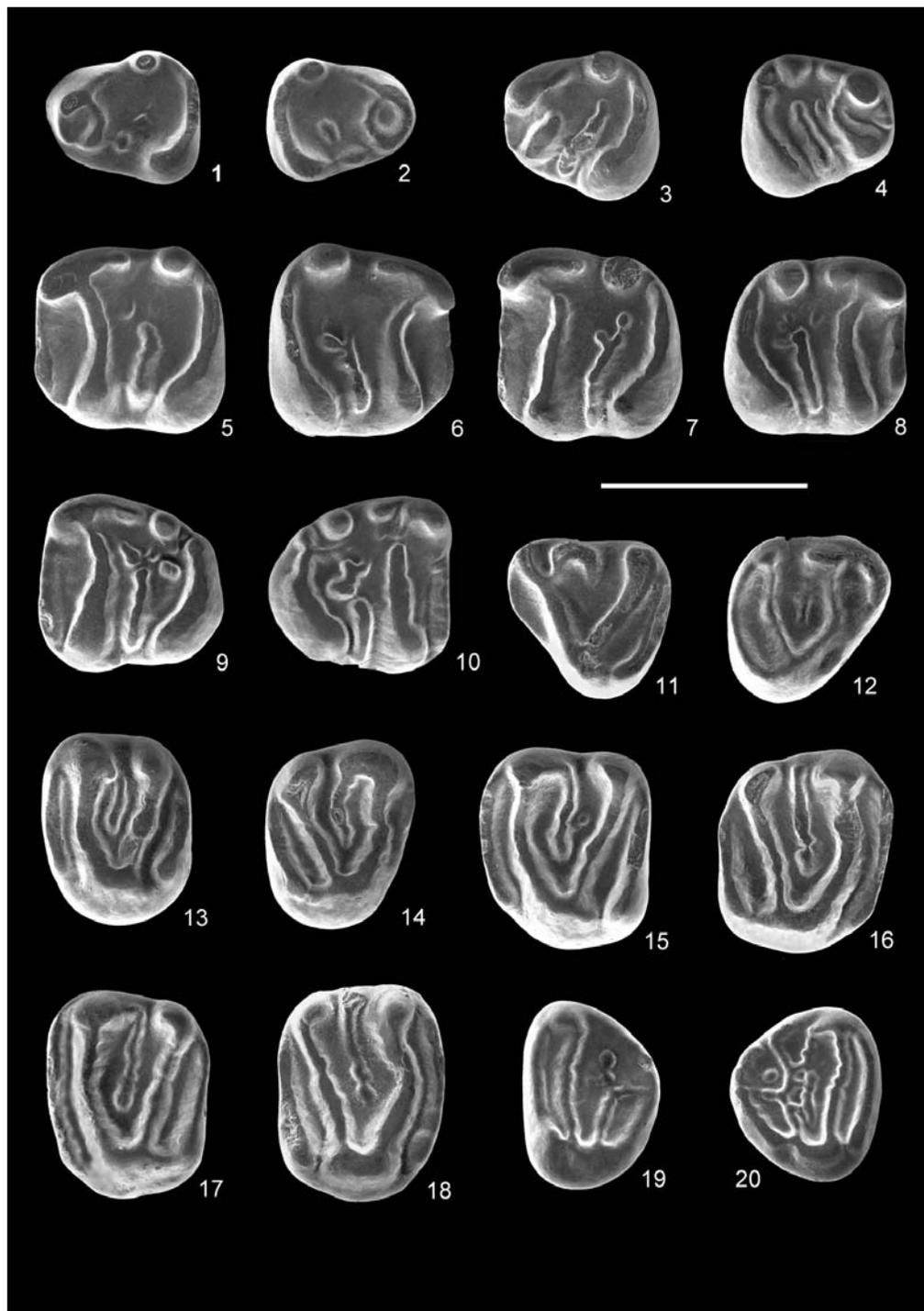


Plate 2 / Lámina 2  
*Glamys priscus* from Aguatón 2D

- Fig. 1. D<sub>4</sub> sin., AGT2D 286
- Fig. 2. D<sub>4</sub> dext., AGT2D 287
- Fig. 3. P<sub>4</sub> sin., AGT2D 383
- Fig. 4. P<sub>4</sub> dext., AGT2D 742
- Fig. 5. M<sub>1</sub> sin., AGT2D 295
- Fig. 6. M<sub>1</sub> dext., AGT2D 143
- Fig. 7. M<sub>2</sub> sin., AGT2D 147
- Fig. 8. M<sub>2</sub> dext., AGT2D 408
- Fig. 9. M<sub>3</sub> sin., AGT2D 591
- Fig. 10. M<sub>3</sub> dext., AGT2D 770
- Fig. 11. D<sup>4</sup> sin., AGT2D 415
- Fig. 12. D<sup>4</sup> dext., AGT2D 305
- Fig. 13. P<sup>4</sup> sin., AGT2D 417
- Fig. 14. P<sup>4</sup> dext., AGT2D 421
- Fig. 15. M<sup>1</sup> sin., AGT2D 607
- Fig. 16. M<sup>1</sup> dext., AGT2D 610
- Fig. 17. M<sup>2</sup> sin., AGT2D 612
- Fig. 18. M<sup>2</sup> dext., AGT2D 78
- Fig. 19. M<sup>3</sup> sin., AGT2D 614
- Fig. 20. M<sup>3</sup> dext., AGT2D 328

Scale represents 1 mm / Escala representa 1 mm



## Plate 3 / Lámina 3

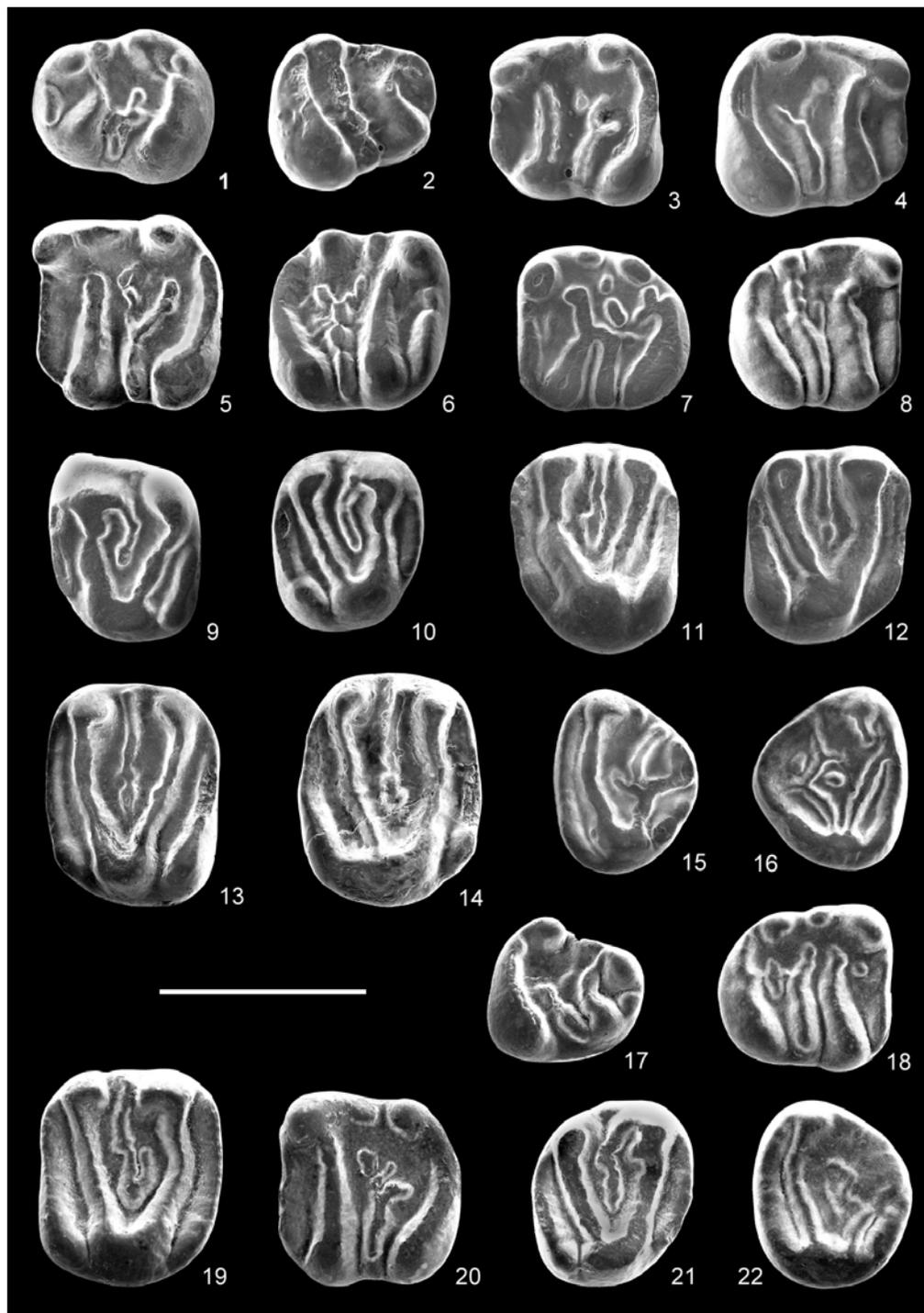
*Glamys* nov. sp. 1 aff. *priscus* from Bco. del Chorrillo 5A

- Fig. 1. P<sub>4</sub> sin., CHR5A 478
- Fig. 2. P<sub>4</sub> dext., CHR5A 189
- Fig. 3. M<sub>1</sub> sin., CHR5A 190
- Fig. 4. M<sub>1</sub> dext., CHR5A 385
- Fig. 5. M<sub>2</sub> sin., CHR5A 593
- Fig. 6. M<sub>2</sub> dext., CHR5A 387
- Fig. 7. M<sub>3</sub> sin., CHR5A 598
- Fig. 8. M<sub>3</sub> dext., CHR5A 483
- Fig. 9. P<sup>4</sup> sin., CHR5A 110
- Fig. 10. P<sup>4</sup> dext., CHR5A 114
- Fig. 11. M<sup>1</sup> sin., CHR5A 487
- Fig. 12. M<sup>1</sup> dext., CHR5A 392
- Fig. 13. M<sup>2</sup> sin., CHR5A 296
- Fig. 14. M<sup>2</sup> dext., CHR5A 297
- Fig. 15. M<sup>3</sup> sin., CHR5A 196
- Fig. 16. M<sup>3</sup> dext., CHR5A 396

*Glamys* nov. sp. 2 aff. *priscus* from Fuente Umbría 1

- Fig. 17. P<sub>4</sub> dext., UMB1B 137
- Fig. 18. M<sub>3</sub> dext., UMB1B 190
- Fig. 19. M<sup>2</sup> dext., UMB1B 69
- Fig. 20. M<sub>2</sub> sin., UMB1B 115
- Fig. 21. P<sup>4</sup> dext., UMB1B 18
- Fig. 22. M<sup>3</sup> sin., UMB1B 138

Scale represents 1 mm / Escala representa 1 mm



- Fig. 1. D<sub>4</sub> sin., UMB1B 163  
Fig. 2. D<sub>4</sub> dext., UMB1B 136  
Fig. 3. P<sub>4</sub> sin., UMB1B 165  
Fig. 4. P<sub>4</sub> dext., UMB1B 75  
Fig. 5. M<sub>1</sub> sin., UMB1B 168  
Fig. 6. M<sub>1</sub> dext., UMB1B 9, Holotype  
Fig. 7. M<sub>2</sub> sin., UMB1B 35  
Fig. 8. M<sub>2</sub> dext., UMB1B 79  
Fig. 9. M<sub>3</sub> sin., UMB1B 40  
Fig. 10. M<sub>3</sub> dext., UMB1B 127  
Fig. 11. D<sup>4</sup> sin., UMB1B 108  
Fig. 12. P<sup>4</sup> sin., UMB1B 46  
Fig. 13. P<sup>4</sup> dext., UMB1B 48  
Fig. 14. M<sup>1</sup> sin., UMB1B 129  
Fig. 15. M<sup>1</sup> dext., UMB1B 95  
Fig. 16. M<sup>2</sup> sin., UMB1B 13  
Fig. 17. M<sup>2</sup> dext., UMB1B 4  
Fig. 18. M<sup>3</sup> sin., UMB1B 187  
Fig. 19. M<sup>3</sup> dext., UMB1B 100

Scale represents 1 mm / Escala representa 1 mm

