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GLIRIDAE (RODENTIA, MAMMALIA) FROM THE LATE MIOCENE FISSURE FILLING BIANCONE 1 (GARGANO, PROVINCE OF FOGGIA, ITALY)

Matthijs Freudenthal and Elvira Martín-Suárez

ABSTRACT

Two new species of the endemic genus *Stertomys* (Mammalia, Rodentia, Gliridae) are described from the Late Miocene fissure filling Biancone 1 on the palaeo-island Gargano (Province of Foggia, Italy): *S. daamsi* and *S. daunius*. A third new species, *Dryomys apulus*, presents no endemic features at the generic level and is assigned to the extant genus *Dryomys.* The new taxa suggest that faunal immigration to Gargano occurred in one event, and that the Biancone deposit is, at most, Late Miocene in age. Additionally, an analysis of all fossil Myomiminae argues that *Stertomys* belongs to that subfamily, and that it may be derived from *Myomimus dehmi* or *Miodyromys aegercii*.

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Key words: Gliridae; Miocene; Italy; endemism; insularity; new species

INTRODUCTION

The Gargano Promontory in SE Italy (see map in Figure 1) is a block of uplifted Mesozoic limestones, forming part of the Adria Plate. The area was an island or a group of islands, separated from the Italian mainland by the Apennine Foredeep, which may have been populated during the low sea-level phase of the Messinian. Hundreds of karst fissure fillings in the limestones have yielded vertebrate faunas with typical endemic characteristics like gigantism in small mammals. Studies have been carried out on the endemic murids and cricetids (Freudenthal 1972, 1976, 1985), lagomorphs (Mazza 1987a, 1987b, 1987c), insectivores (Freudenthal 1972, Butler 1980), artiodactyls (Leinders 1984), otters (Willemsen 1983), and birds (Ballmann 1973, 1976).

The Gliridae form another important element of the fauna, but have hardly been studied. The only publication on this group so far is by Daams

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http://palaeo-electronica.org/paleo/2006_2/fissure/index.html

Figure 1. Map of Italy, indicating the studied area.

and Freudenthal 1985, who described the gigantic glirid genus *Stertomys* from San Giovannino, one of the youngest fissure fillings of the Late Miocene localities of Gargano. In this paper the Gliridae from the oldest locality, Biancone 1, are described, the taxonomy of *Stertomys* is revised and an attempt is made to solve the question of its origin.

Besides *Stertomys* a second glirid genus, *Dryomys*, is present in Biancone 1, represented by one species that by size and morphology lies within the known range of the genus.

Technical data. The material was collected by Freudenthal in 1970 and is deposited in the collections of the National Museum of Natural History, Leiden, the Netherlands. Measurements were taken with a Wild M8 stereomicroscope, equipped with a mechanical stage with electronic sensors, and connected to a computer through a Sony Magnescale measuring unit. The photos were made on the ESEM FEI Quanta 400 in environmental mode at the 'Centro Andaluz de Medio Ambiente' in Granada (Spain).

Measurements are given in 0.1 mm units. The nomenclature of parts of the cheek teeth is as defined by Freudenthal 2004 (see Figure 2).

Abbreviations

BIA1. Biancone 1

RGM. Code of the geological collections of the National Museum of Natural History, Leiden, the Netherlands

V' is the variability coefficient as defined by Freudenthal and Cuenca Bescós 1984.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family GLIRIDAE Thomas, 1897
Genus *STERTOMYS* Daams and Freudenthal, 1985

Daams and Freudenthal 1985 created the genus *Stertomys*, based on the type species *S. laticrestatus*, and placed it in the subfamily Glirinae because of the slightly concave occlusal surface and the low ridges of the molars of the type species. The dental pattern was thought mostly to resemble that of *Glis*.

However, the crests in the upper molars of *Glis glis* are more or less transverse, and the four main crests are equidistant on lingual and labial border. In *Stertomys laticrestatus* the lingual end of the protoloph is placed backward, close to the metaloph, and the protoloph is oblique. If protoloph and metaloph were united, it would almost certainly have been classified as a member of the Myomiminae.

The study of the Gliridae from Biancone 1 has led to the recognition of two new species of *Stertomys.* In one of these the protoloph is united to the metaloph, in the other one the protoloph is directed far backward, and separated from the metaloph by

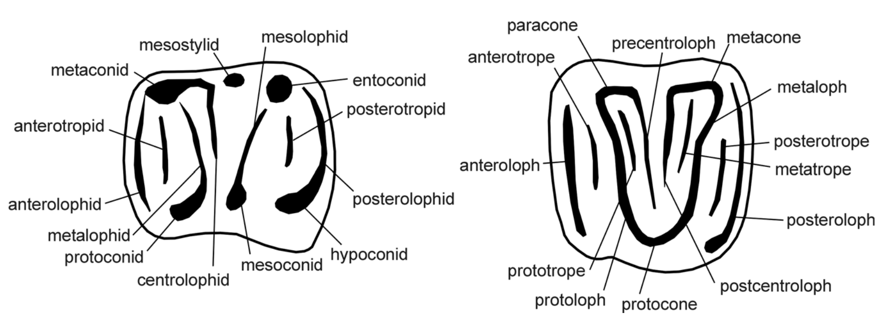

Figure 2. Nomenclature of parts of the cheek teeth, adapted after Freudenthal 2004. When there is only one centroloph, and its homology can't be decided, it is called midcentroloph. The figures are drawn as left-hand molars with the anterior side facing to the left.'

a narrow furrow. They both have a disposition of the crests typical for the Myomiminae, and many details of the dental pattern are similar to that of *S. laticrestatus*. Therefore *Stertomys* is considered to belong to the Myomiminae, and not to the Glirinae. *S. laticrestatus* is the youngest representative of the genus and has undergone important modifications of the typical dental pattern of Myomiminae; the Biancone material, however, makes its origin clear.

New diagnosis of *Stertomys*: Myomiminae of medium to very large size with slightly to moderately concave molars. D_4 relatively small. In the lower molars the anterolophid and protoconid are generally separated by a furrow. In the upper molars the lingual end of the protoloph lies far backward, either connected to the metaloph or detached from it. The precentroloph is frequently detached from the paracone. The precentroloph is longer than the postcentroloph, and directed far backward, often in contact with the middle of the metaloph. The number of ridges varies between five and twelve in the upper molars and between seven and twelve in the lower ones.

Stertomys daamsi sp. nov.
Figure 3.1-17

Type locality: Biancone 1

Derivatio nominis: Dedicated to our friend and colleague, the late Dr. R. Daams

Holotype: Maxilla dext. with P^4 - M^3, RGM 455905

Age: Late or post-Messinian

Diagnosis: Small *Stertomys* with a moderately complex dental pattern. Centrolophid and mesolophid not connected labially. Centrolophid frequently connected to the middle of the metalophid. Precentroloph separated from the paracone, and frequently connected to the middle of the metaloph. Postcentroloph generally separated from the metacone. Protoloph and metaloph firmly connected posterolingually, and separated from the posteroloph.

Differential diagnosis: Smallest *Stertomys* known so far. Dental pattern simpler than in *S. laticrestatus* and *S. daunius* sp. nov.

Material: RGM 386851 - 386992, RGM 455774 - 455918, RGM 455982 - 455994, RGM 513043 - 513100, RGM 513830 - 514129.

Measurements: See Table 1.

D_4–The occlusal pattern of this element is so different from a normal glirid tooth that a description using the standard terminology is impossible. Variability is very great, so all the specimens have been drawn schematically (see Figure 4). Many specimens are characterized by an oblique crest, from posterolabial to anterolingual, which likely connects hypoconid, protoconid, and anterolophid; if that is correct, it means that the protoconid lies somewhere in the middle of the tooth, far away from the labial border. Scatter plots of length and width measurements of D_4 are shown in Figure 5.

P_4–The variability and peculiar shape of the anterior part of P_4 of many specimens make a description difficult. Therefore, in Figure 6 the dental pattern of a number of specimens is represented in a schematical way. Scatter plots of length and width measurements of P_4 are shown in Figure 5.

Morphotype A (RGM 513830) is a common pattern in the P_4 of many Gliridae: an interrupted anterolophid, a metalophid, and a centrolophid are easily recognized (four cases). This may be the original pattern, from which the other morphotypes are derived.

In morphotype B (RGM 513833) the protoconid is elongated and oblique, from posterolabial to anterolingual; the metalophid runs longitudinally backward and then turns toward the labial border in a transverse orientation. This gives the protoconid/metalophid complex a Z-shape (10 cases).

In morphotype C through G the previous patterns are broken up into isolated cusps; they all do have a centrolophid. D and E are represented by two specimens each. C, F, and G are single cases.

The remainder of the specimens has no centrolophid, or one cannot distinguish between metalophid and centrolophid. Morphotype H (RGM 513832) has a continuous anterolophid and a funnel behind it, which seems to be formed by the Z-shaped metalophid of morphotype B (14 cases).

In morphotype I (RGM 513839) this funnel is open posteriorly (six cases). The morphotypes B, H, and I (together 30 cases) share the presence of a longitudinal crest running from the foremost tip of the tooth backward. This replacement of a transverse pattern by a longitudinal pattern seems to be the basic character of the P_4 and reflects to some extent the pattern of D_4. The remaining morphotypes, all single cases, seem to be modifications of morphotype H or A.

The above enumeration is certainly not exhaustive. From a total of 140 P_4 50 specimens have been studied. Among the remaining 90 specimens different configurations are probably present.

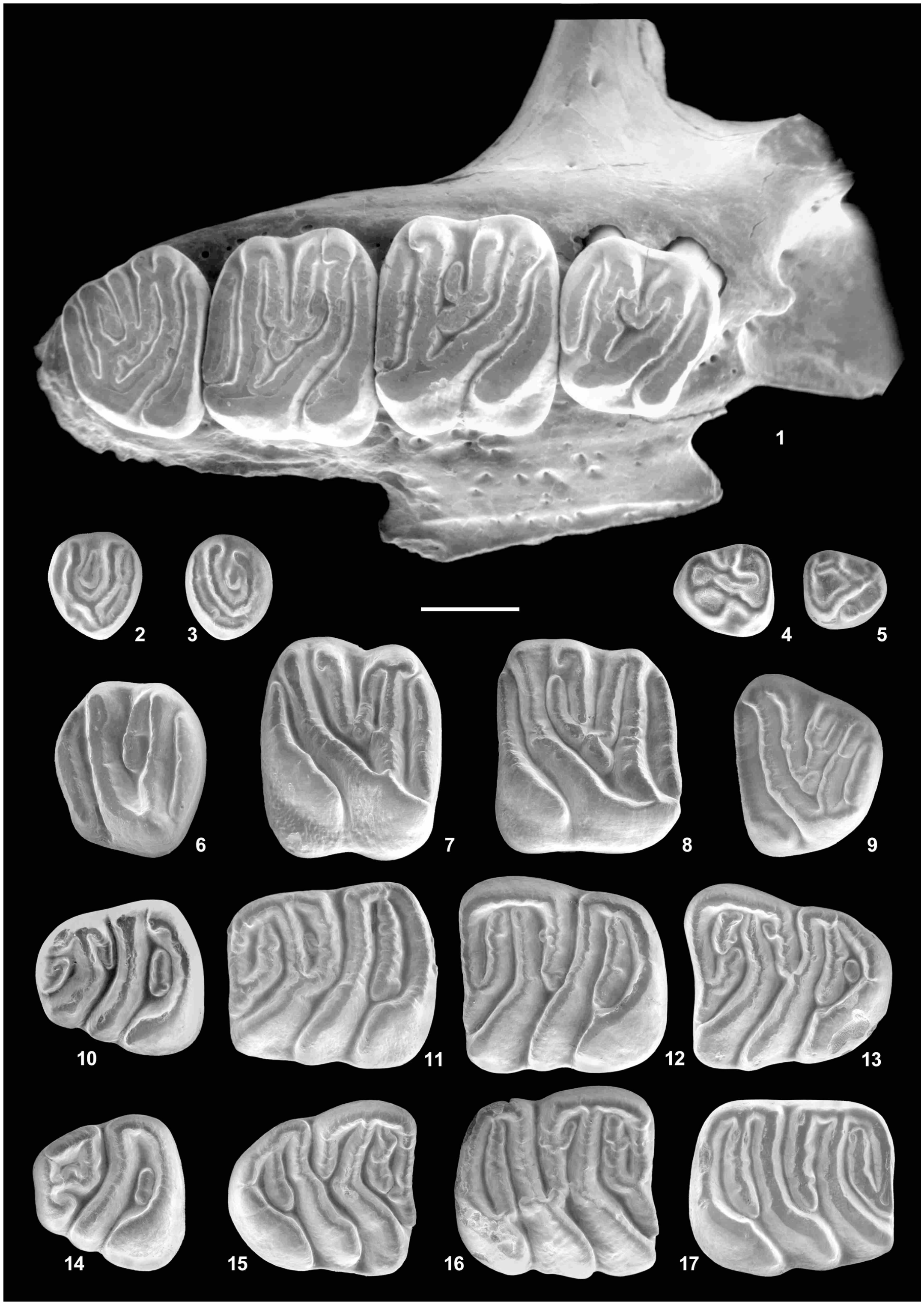

Figure 3. *Stertomys daamsi.* 1. Maxilla dext. with P^4 - M^3 RGM 455905 Holotype, 2. D^4 sin. RGM 513076, 3. D^4 dext. RGM 513088, 4. D_4 sin. RGM 513043, 5. D_4 dext. RGM 513065, 6. P^4 sin. RGM 514043, 7. M^1 sin. RGM 455811, 8. M^2 sin. RGM 386882, 9. M^3 sin. RGM 514083, 10. P_4 sin. RGM 513832, 11. M_1 sin. RGM 513882, 12. M_2 sin. RGM 513932, 13. M_3 sin. RGM 513985, 14. P_4 sin. RGM 513830, 15. M_3 dext. RGM 514012, 16. M_2 dext. RGM 513956, 17. M_1 dext. RGM 513912. Scale is 1 mm.

Table 1. Measurements of the cheek teeth of various species of *Stertomys*. V' is the variability coefficient as defined by Freudenthal and Cuenca Bescós (1984).

	Length						Width					
	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
D_4												
S. daunius	4	16.0	17.20	19.1	17.7	1.36	4	13.6	14.28	15.1	10.5	0.64
S. daamsi	32	8.0	9.85	11.7	37.6	1.06	32	7.6	9.10	10.7	33.9	0.84
P_4												
S. laticrestatus	2	28.6	30.65	32.7	13.4		2	27.5	28.75	30.0	8.7	
S. daunius	8	23.7	25.73	27.4	14.5	1.41	7	19.9	22.79	24.0	18.7	1.36
S. daamsi	50	14.9	16.15	17.8	17.7	0.69	50	13.1	14.84	16.6	23.6	0.76
M_1												
S. laticrestatus	6	38.2	41.12	43.3	12.5	1.84	5	32.0	34.66	37.1	14.8	1.82
S. daunius	8	33.3	35.80	38.5	14.5	1.66	6	29.0	31.48	32.7	12.0	1.34
S. daamsi	50	19.6	21.76	24.3	21.4	1.04	50	16.9	18.34	20.1	17.3	0.68
M_2												
S. laticrestatus	10	37.8	41.65	42.7	12.2	1.45	9	34.7	38.77	41.9	18.8	1.93
S. daunius	8	35.2	37.00	38.1	7.9	0.89	9	31.8	33.79	35.4	10.7	1.13
S. daamsi	50	18.9	20.80	23.6	22.1	0.91	50	18.0	19.60	21.6	18.2	0.79
M_3												
S. laticrestatus	5	33.2	35.20	37.1	11.1	1.39	4	29.6	32.23	34.2	14.4	1.97
S. daunius	6	31.5	33.78	36.6	15.0	1.82	6	28.1	29.38	31.0	9.8	0.95
S. daamsi	50	17.1	19.38	21.3	21.9	1.02	50	15.2	17.18	19.3	23.8	0.86
D^4												
S. daunius	2	17.3	17.85	18.4	6.2		2	18.5	19.20	19.9	7.3	
S. daamsi	25	8.2	9.69	11.1	30.1	0.73	26	8.3	11.10	13.0	44.1	1.07
P^4												
S. laticrestatus	4	30.2	30.48	30.9	2.3	0.31	4	30.0	30.93	31.7	5.5	0.70
S. daunius	4	26.5	27.13	27.8	4.8	0.62	4	29.0	29.93	31.5	8.3	1.09
S. daamsi	50	14.4	16.34	18.2	23.3	0.87	50	17.8	19.21	21.2	17.4	0.88
M^1												
S. laticrestatus	7	29.9	37.73	39.3	27.2	3.46	7	30.8	39.34	42.3	31.5	3.90
S. daunius	9	32.0	33.52	35.3	9.8	0.97	9	33.3	35.19	36.8	10.0	1.05
S. daamsi	114	17.9	19.59	21.8	19.6	0.77	109	19.7	22.49	25.0	23.7	0.89
M^2												
S. laticrestatus	8	38.8	39.71	41.8	7.4	1.30	8	39.2	41.98	43.6	10.6	1.51
S. daunius	8	31.2	33.28	35.6	13.2	1.41	8	34.3	36.84	38.1	10.5	1.13
S. daamsi	139	16.7	18.77	22.0	27.4	0.87	134	19.4	22.10	25.0	25.2	0.92
M^3												
S. laticrestatus	3	30.3	31.50	32.2	6.1		3	33.2	35.43	37.3	11.6	
S. daunius	10	26.4	27.66	29.8	12.1	1.18	10	31.5	32.71	34.6	9.4	0.96
S. daamsi	50	13.7	15.28	17.4	23.8	0.74	50	17.7	19.74	22.3	23.0	0.91

The posterior part of the P_4 does not show modifications with respect to a normal glirid P_4: The mesolophid is complete, and connected to the entoconid. The posterotropid is very small (2), small (7), of medium length (7), or long (34). P_4 has one root, normally grooved, rarely split.

M_1–The anterolophid is labially free (49) or labially connected (1). The anterotropid is absent (1), of medium length (2), or long (47), nearly always obliquely connected to the labial tip of the anterolophid. In a few cases there is a small extra crest in front of the anterotropid. The metalophid is free (6), low connected to the metaconid (1), or the connection is high (42). The centrolophid is absent (1), of medium length (5), or long (44). In 29 cases the labial end of the centrolophid is connected with the metalophid, in two cases to the mesolophid, and in

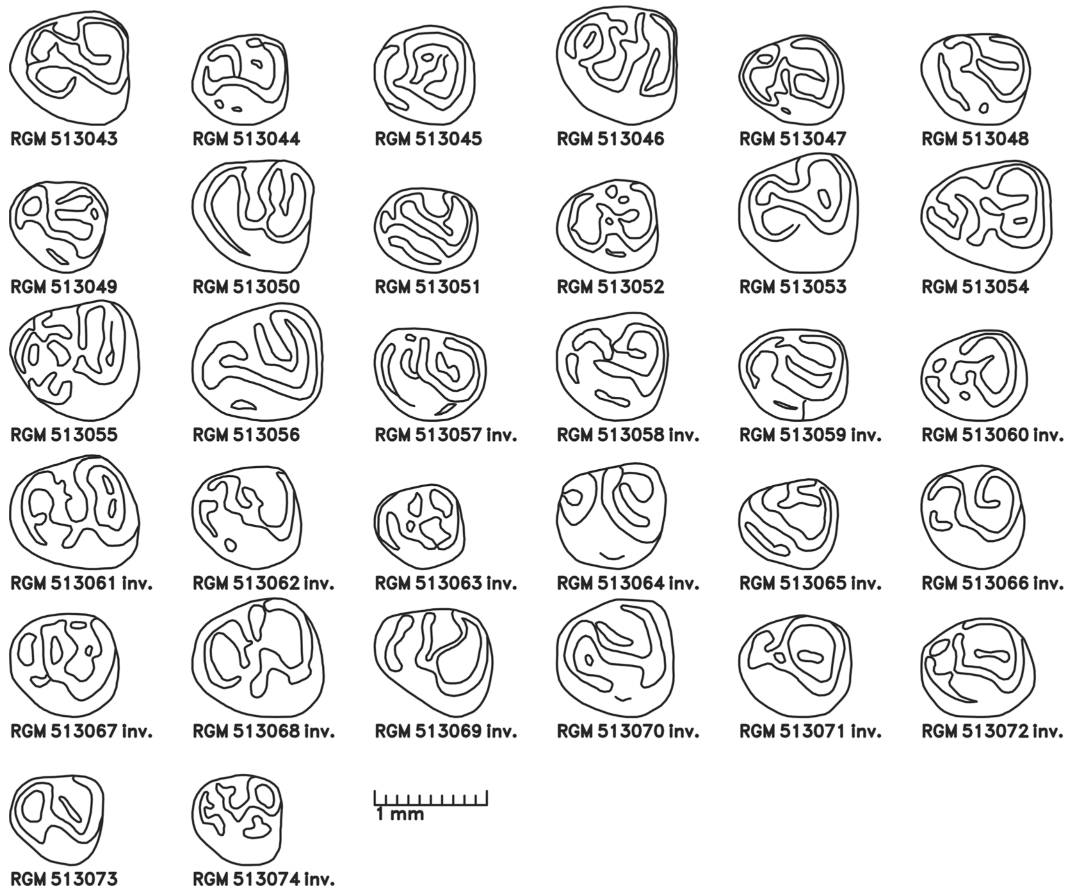

Figure 4. *Stertomys daamsi*: Deciduous lower premolars (D_4), all figured as left-hand specimens.

two cases to both these crests. The centrolophid-metaconid connection is absent (6) or high (43). The mesoconid is placed on the labial border. The mesolophid is connected to the entoconid. The posterotropid is long. There are two roots, the posterior one flat, the anterior one grooved, or -less frequently- split. Scatter plots of length and width measurements of M_1 are shown in Figure 7.

M_2–The anterolophid is labially free. The anterotropid is of medium length (1) or long (49), obliquely connected to the labial tip of the anterolophid, or—rarely—perpendicular to the middle of that crest. The metalophid is free from the metaconid (1), low connected (7), or the connection is high (41). The centrolophid is of medium length (23) or long (27). It is labially connected to the metalophid (13), to the mesolophid (7), or to both (4). The centrolophid-metaconid connection is absent (four specimens; the lingual end of the centrolophid forms a cusp), low connected (4), or the connection is high (41). There may be an extra crest between centrolophid and metalophid (5). The mesoconid is placed on the labial border. The mesolophid is connected to the entoconid. The posterotropid is long, frequently connected to hypoconid and/or entoconid. There are three roots, two anterior and one posterior. Scatter plots of length and width measurements of M_2 are shown in Figure 8.

M_3–The anterolophid is labially free (45) or connected (5) to the protoconid. The anterotropid is small (1), of medium length (7), or long (42), and it is labially connected to the anterolophid, either obliquely or longitudinally. The metalophid is free (2) from the metaconid, low connected to the metaconid (5), or the connection is high (43). The centrolophid is short (6) or of medium length (44). The centrolophid is detached from the metaconid in two cases; it is labially connected to the metalophid in six cases, labially connected to the mesolophid in seven cases. The mesoconid is placed on the labial border. The mesolophid is connected to the entoconid in all cases except one. The posterotropid is long, nearly always connected to the entoconid, frequently connected to the hypoconid, labially connected to the mesolophid in one case only. There is a small extra crest in front of the

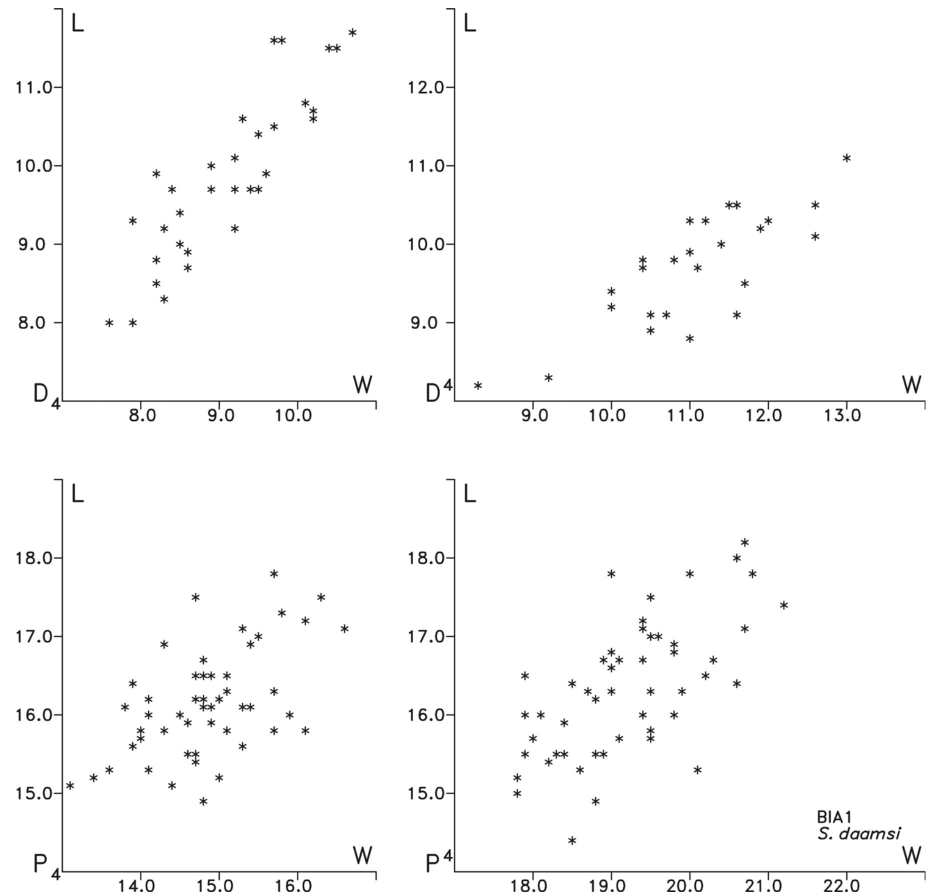

Figure 5. Plot of length versus width for deciduous and permanent lower and upper premolars of *Stertomys daamsi:* D_4, D^4 (upper row), P_4, P^4 (lower row).

anterotropid in one case, in front of the posterotropid (2), behind the posterotropid (4), and there is an axial connection between posterotropid and posterolophid in two cases. There are three roots, like in M_2. Scatter plots of length and width measurements of M_3 are shown in Figure 9.

Figure 6. *Stertomys daamsi:* Permanent lower premolars (P_4), all figured as left-hand specimens.

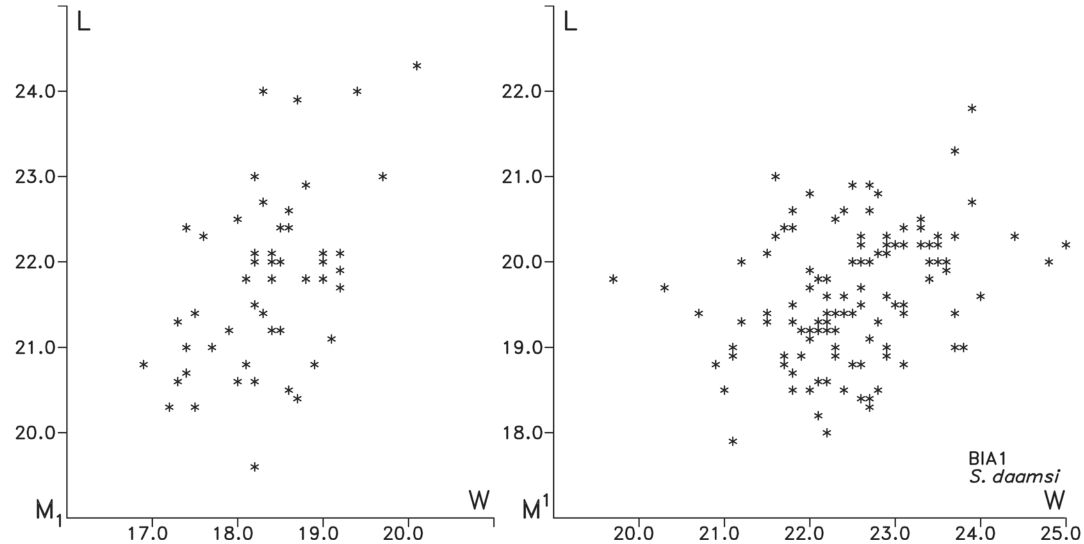

Figure 7. Plot of length versus width for M_1 and M^1 of *Stertomys daamsi.*

D^4–Like in D_4 variability is very great, and description quite difficult. All 26 specimens have been drawn schematically (see Figure 10). Most specimens have an anteroloph, generally small or of medium length; it may, however, continue along the lingual border and meet the posteroloph. Protoloph and metaloph are connected in a V- or Y-pattern. There is one centroloph, labially free, and lingually connected to the protoloph in many cases, though frequently reduced to nothing more than a small cusp in the center of the tooth. Scatter plots of length and width measurements of D^4 are shown in Figure 5.

P^4 -The anteroloph is long. The anterotrope is absent. The precentroloph is absent (25), short (2), of medium length (10), or long (13). The postcentroloph is absent (33), of medium length (5), or long (12). In 14 specimens only one centroloph is present, which is placed in a central position. It cannot be homologized with either pre- or postcentroloph, and is called midcentroloph; it is short (10) or of medium length (4). The prototrope and

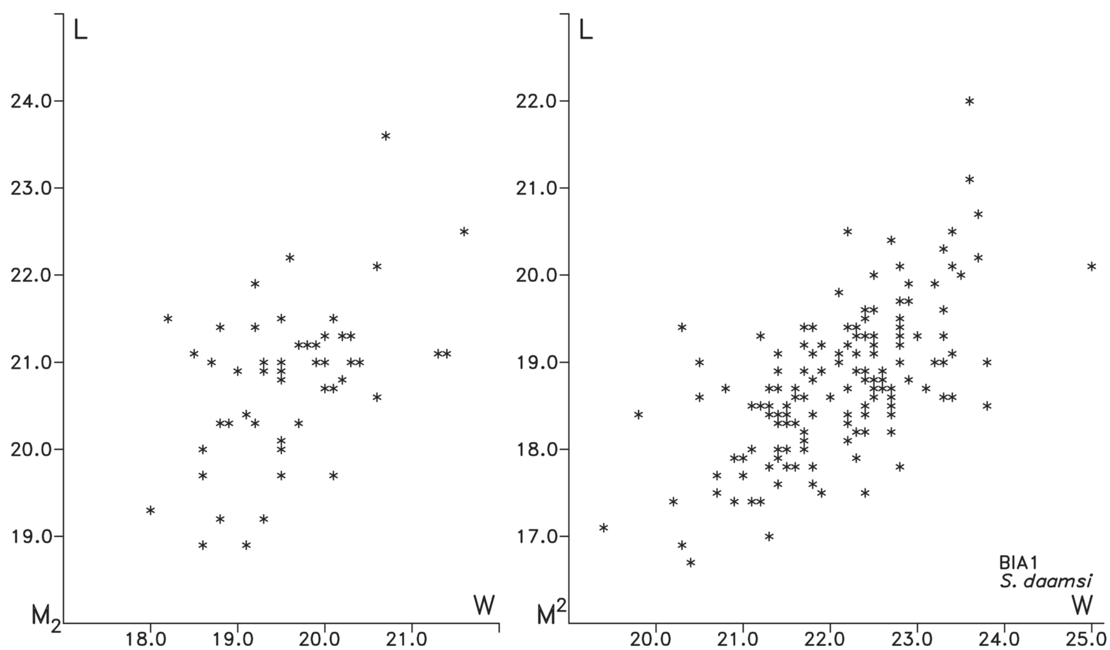

Figure 8. Plot of length versus width for M_2 and M^2 of *Stertomys daamsi.*

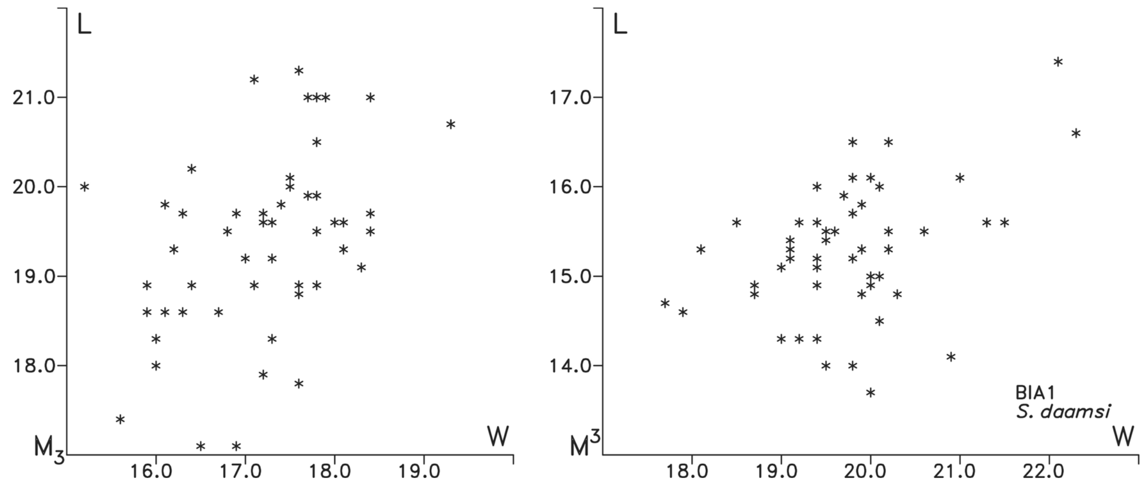

Figure 9. Plot of length versus width for M_3 and M^3 of *Stertomys daamsi.*

metatrope are absent. The centrolophs are not connected (45) or interconnected (5). The posterotrope is absent. The posteroloph is lingually free. Scatter plots of length and width measurements of P^4 are shown in Figure 5.

M^1–In about half the specimens there is a small concavity on the anterolingual wall of the tooth, which may develop a cusp. The anteroloph is lingually free (114). The precentroloph ends near the metaloph (76) or is connected to it (38). The pre-

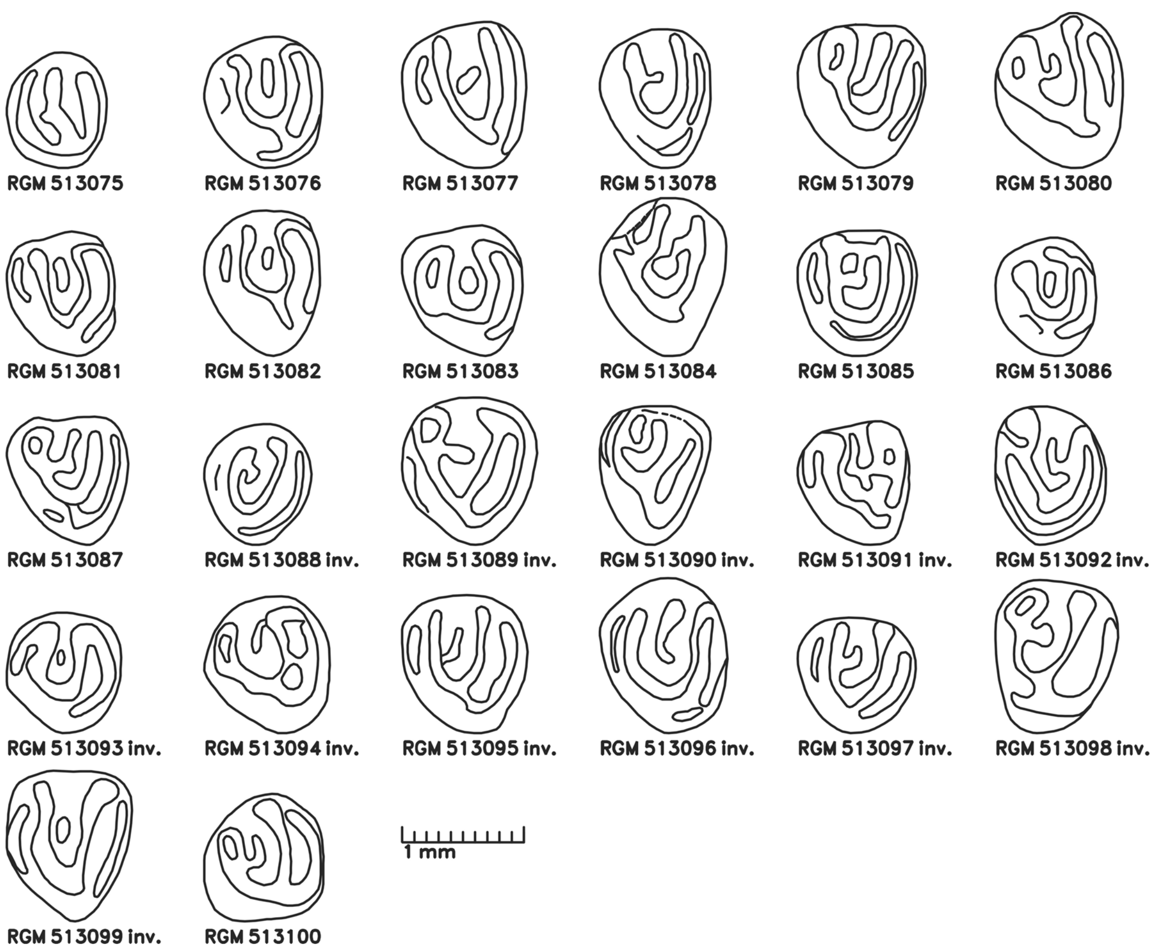

Figure 10. *Stertomys daamsi:* deciduous upper premolars (D^4), all figured as left-hand specimens.

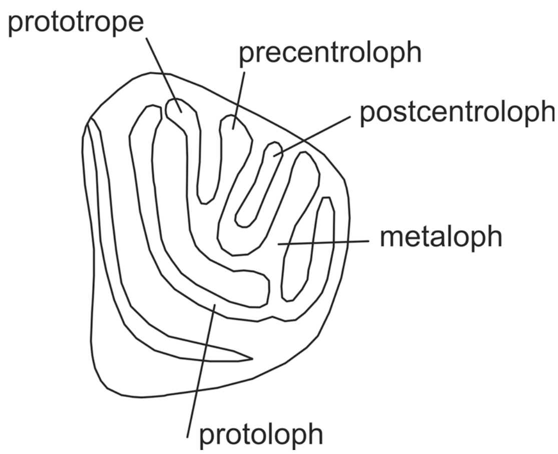

Figure 11. Interpretation of some elements of the occlusal surface of M^3 of *Stertomys* based on M^3 sin, RGM 514084, of *S. daamsi.*

low connected (6), or detached from it (111). The postcentroloph is absent (36), short (21), or of medium length (57). When present, the postcentroloph is connected to the metacone (24) or free from the metacone (52). The prototrope is absent (76), short (17), of medium length (17), or long (4). The metatrope is absent (113) or short (1). The centrolophs are not connected (52), interconnected lingually (2), or interconnected midway (60). The posterotrope is absent (110), short (3), or of medium length (1). Lingually the protoloph reaches far backward, and it is firmly connected to the metaloph; there rarely is a longitudinal component in this connection. The posteroloph is lingually free (110) or lingually connected (2); when free the separation may be deep, but frequently it is superficial. Scatter plots of length and width measurements of M^1 are shown in Figure 7.

M^2–In 11 out of 140 specimens there is a small concavity on the anterolingual wall of the tooth. The anteroloph is lingually free (141). The precentroloph is long and not directed to the metaloph (6), it ends near the metaloph (84), or it is connected to the metaloph (50). The precentroloph is connected to the paracone (3), low connected (16), or free from the paracone (119). The postcentroloph is absent (2), short (8), of medium length (72), or long (57). The postcentroloph is connected to the metacone (62) or not (70). The prototrope is absent (18), short (19), of medium length (37), or long (66). The metatrope is absent (131), short (3), of medium length (5), or long (1). The centrolophs are not connected (62), interconnected lingually (36), interconnected midway (40), or there are two connections (1). The posterotrope is absent (140) or short (1). Lingually the protoloph is firmly connected to the metaloph, but, in comparison with M^1, the labial end of this crest is frequently more longitudinal, because it reaches the labial border in a more anterior position. The posteroloph is lingually free (123) or lingually connected (2); when free the division may be deep, but frequently it is superficial. In a few cases there is a small extra crest between the centrolophs, or between protoloph and precentroloph. Normally the precentroloph is the second dominant diagonal crest after the protoloph, but in some cases the prototrope takes over this role. Scatter plots of length and width measurements of M^2 are shown in Figure 8.

M^3–The anteroloph is lingually free; it frequently reaches far backward along the lingual molar border. The anterotrope is absent. Inside the trigone there are two crests (11), three crests (36), four crests (2), or five crests (1).

In the case of two crests these are interpreted as a long precentroloph and a much shorter postcentroloph; only in one case the postcentroloph is the longer one.

When there are three crests these seem to be the prototrope and the two centrolophs. In most of these the prototrope is the main crest, which has taken over the role of the precentroloph (see Figure 11). The latter crest is placed far backward, and the main interruption in the labial wall of the tooth lies in front of the precentroloph. It joins the prototrope in the middle of the tooth, and then curves obliquely backward. The specimens with four or five crests inside the trigone are variations of this pattern, with an additional crest of little importance.

The precentroloph/prototrope ends near the metaloph (18), or is connected to it (27). The postcentroloph is of medium length (24) or long (26). In three cases it is curved backward and connected to the metaloph. The centrolophs are not connected (34) or interconnected (16). The posterotrope is absent. The posteroloph is lingually connected (29) or lingually free (17).

M^3 has three roots (plus sometimes a small extra central root); the lingual root may possess a furrow, and the lingual root and posterior root may be fused. In a few cases the anterolabial root shows a tendency to split. Scatter plots of length and width measurements of M^3 are shown in Figure 9.

Distinction of M^1 and M^2: Daams 1981 manages to distinguish M^1 and M^2 of *Myomimus* by their shape: M^1 is narrower anteriorly, and M^2 is wider

Table 2. Number of specimens of *S. daamsi.*

	D_4	P_4	M_1	M_2	M_3	D^4	P^4	M^1	M^2	M^3
mounted	33	50	50	50	50	24	50	114	141	50
on jaw			6	7	7		20	23	8	
not mounted		90	156	113	92		70			106
broken/ worn								26	30	
total	33	140	212	170	149	24	140	163	179	156

anteriorly. In *S. daamsi* this does not apply, though the posterolingual corner is generally more rounded in M^2 than in M^1. We have seven maxillae in which M^1 and M^2 are present and 15 maxillae in which M^1 only is present; these specimens permit an attempt to distinguish these elements:

1. M^1 appears to be longer and narrower than M^2, but there certainly is an overlap. In many cases M^1 has a trapezoid shape, being longer lingually than labially, whereas M^2 has a more regular, rectangular shape.
2. In M^1 the protoloph appears to be more oblique, and fairly straight, whereas in M^2 the protoloph is less oblique; moreover, the protoloph of M^2 shows an angle, and the labial part of that crest is -almost- transverse.
3. The lingual end of the protoloph of M^1 reaches the molar border very far backward, already fused with the metaloph, whereas in M^2 it frequently reaches the border before getting in contact with the metaloph.
4. In M^1 the paracone forms part of the anterior border, and the anteroloph reaches the paracone lingually of the anterolabial corner of the tooth; in M^2, on the other hand, the anteroloph occupies the entire anterior border, and the paracone lies slightly more backward.
5. The lingual roots of M^1 may be slightly divergent, due to the oblique position of the anterior one.
6. The precentroloph tends toward—or reaches—the metaloph more lingually in M^2 than in M^1.

None of these features is 100% decisive, but combining them appears to give a fairly reliable result. It cannot be denied, however, that a wrong decision may have been taken in a number of cases.

In order to check the separation of M^1 and M^2 all isolated specimens of these elements were mounted and measured, except for broken and much-worn ones. Table 2 gives the total number of specimens of each element, and shows a fairly well equilibrated distribution.

In many glirid species there is a statistical size difference between M^1 and M^2. In classifying these two elements, size was not taken into account, because that might have led to a circular reasoning. Table 1 shows there is no appreciable size difference.

M^1 and M^2 have three roots. The lingual root may be grooved. The difference between M^1 and M^2 is not significant (see Table 3), and furthermore the depth of the groove may depend on the age of the animal: apparently in young individuals with recently formed roots (roots with thin walls and wide canal) the groove is on the average less pronounced. In both M^1 and M^2 the anterolabial root is somewhat stronger than the posterolabial one. The degree of development of an accessory root in the center of the molar shows a difference, but not suf-

Table 3. Roots of M^1 and M^2.

	M^1	M^2		M^1	M^2		M^1	M^2
lingual root	N=82	N=90	acc. root	N=86	N=95	labial roots	N=56	N=45
not grooved	46 %	34 %	absent	57 %	42 %	parallel	5 %	94 %
shallow groove	52 %	56 %	small	30 %	27 %	divergent	95 %	6 %
deep groove	1 %	10 %	medium		19 %			
			big	13 %	12 %			

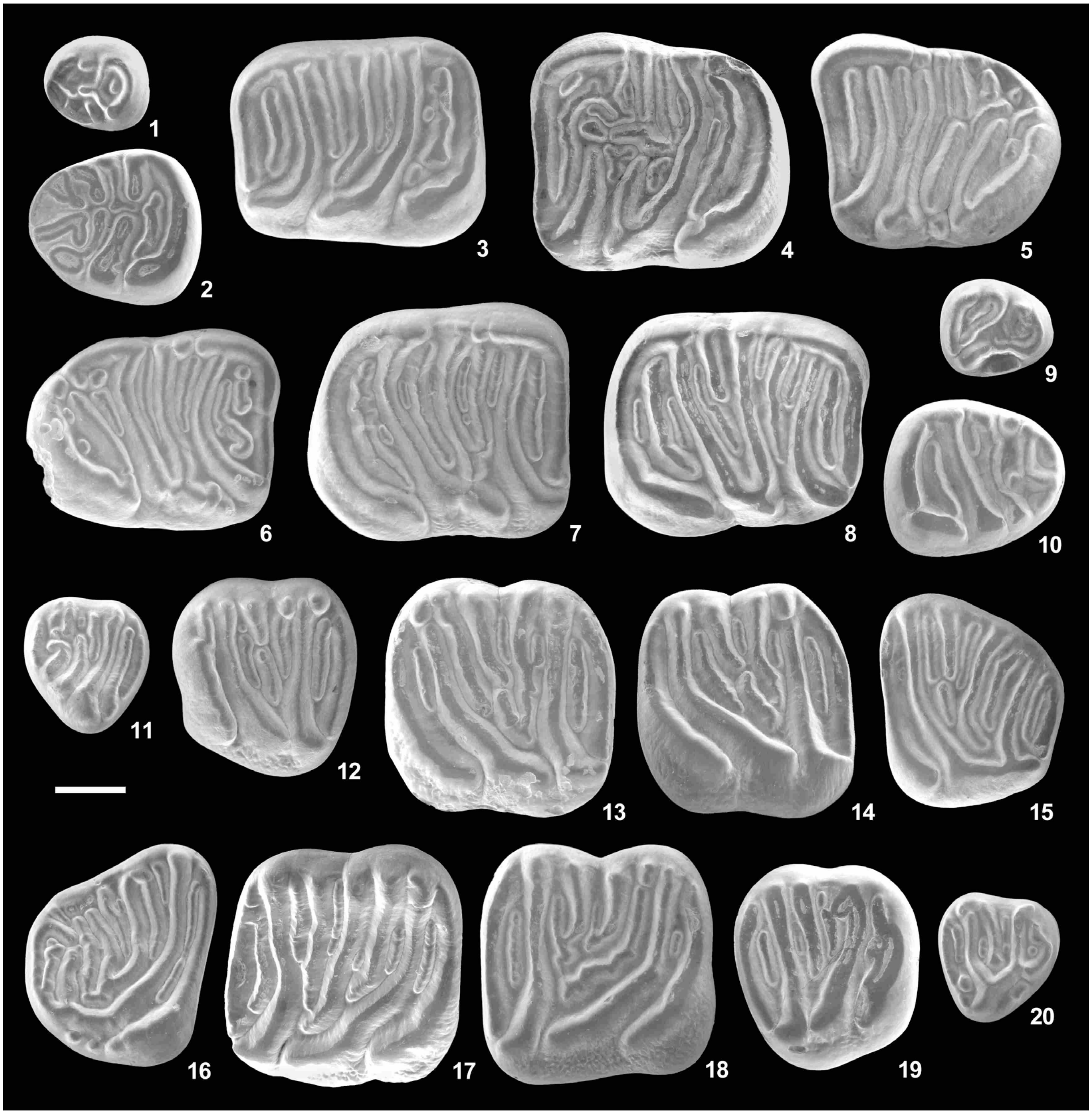

Figure 12. *Stertomys daunius*.1. D_4 sin. RGM 514130, 2. P_4 sin. RGM 514136 , 3. M_1 sin. RGM 514143, 4. M_2 sin. RGM 514149, 5. M_3 sin. RGM 514157 , 6. M_3 dext. RGM 514160, 7. M_2 dext. RGM 514154, 8. M_1 dext. RGM 514145, 9. D_4 dext. RGM 514133, 10. P_4 dext. RGM 514139, 11. D^4 sin. RGM 514162, 12. P^4 sin. RGM 514165, 13. M^1 sin. RGM 514174, 14. M^2 sin. RGM 514180 Holotype, 15. M^3 sin. RGM 514188, 16. M^3 dext. RGM 514193, 17. M^2 dext. RGM 514184, 18. M^1 dext. RGM 514177, 19. P^4 sin. inv. RGM 514168, 20. D^4 dext. RGM 514163, Scale is 1 mm.

ficient to serve as a criterion for distinguishing these two elements.

Stertomys daunius sp. nov.
Figure 12.1-20

Type locality: Biancone 1

Derivatio nominis: Daunii is a tribe that lived in Northern Apulia in Roman times.

Holotype: M^2 sin., RGM 514180

Age: Late or post-Messinian

Diagnosis: Medium-sized *Stertomys* with a very complicated dental pattern. Lower molars with two

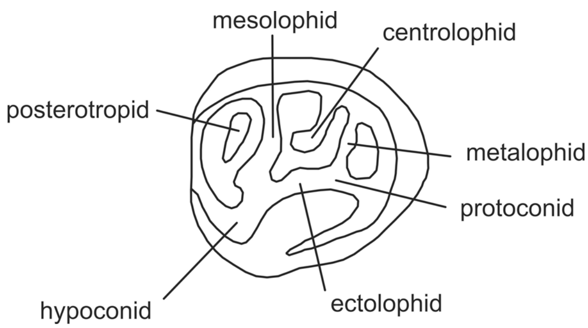

Figure 13. Interpretation of the occlusal elements of D_4 in *Stertomys,* based on a right D_4, RGM 514131 of *S. daunius.*

to four centrolophids, the main one of which may be connected labially to the mesolophid in a lyre-shape. Precentroloph not connected to the middle of the metaloph. Protoloph and metaloph separated at the lingual border in $M^{1,2}$ and in most M^3.

Differential diagnosis: Dental pattern like in *S. laticrestatus*, more complicated than in *S. daamsi*; larger than *S. daamsi* and smaller than *S. laticrestatus.*

Material: RGM 514130 - 514198

Measurements: See Table 1.

D_4–(see Figure 13) The interpretation of the dental pattern is difficult. It is dominated by an oblique longitudinal ridge from hypoconid to anterolophid which is supposed to be the ectolophid. This ridge is supposed to enclose the protoconid, which lies somewhere in the center of the tooth. Labial to this ridge there is a low platform, bordered by a cingulum ridge. Apart from anterolophid and posterolophid, lingually of the ectolophid three to four ridges may be seen, interpreted as metalophid, centrolophid, mesolophid, and posterotropid. Scatter plots of length and width measurements of D_4 are shown in Figure 14.

P_4–The anterior wall is rounded, not blunt. The anterolophid is interrupted (5) or continuous (2). The anterotropid is present in six out of seven specimens, beginning at the labial part of the anter-

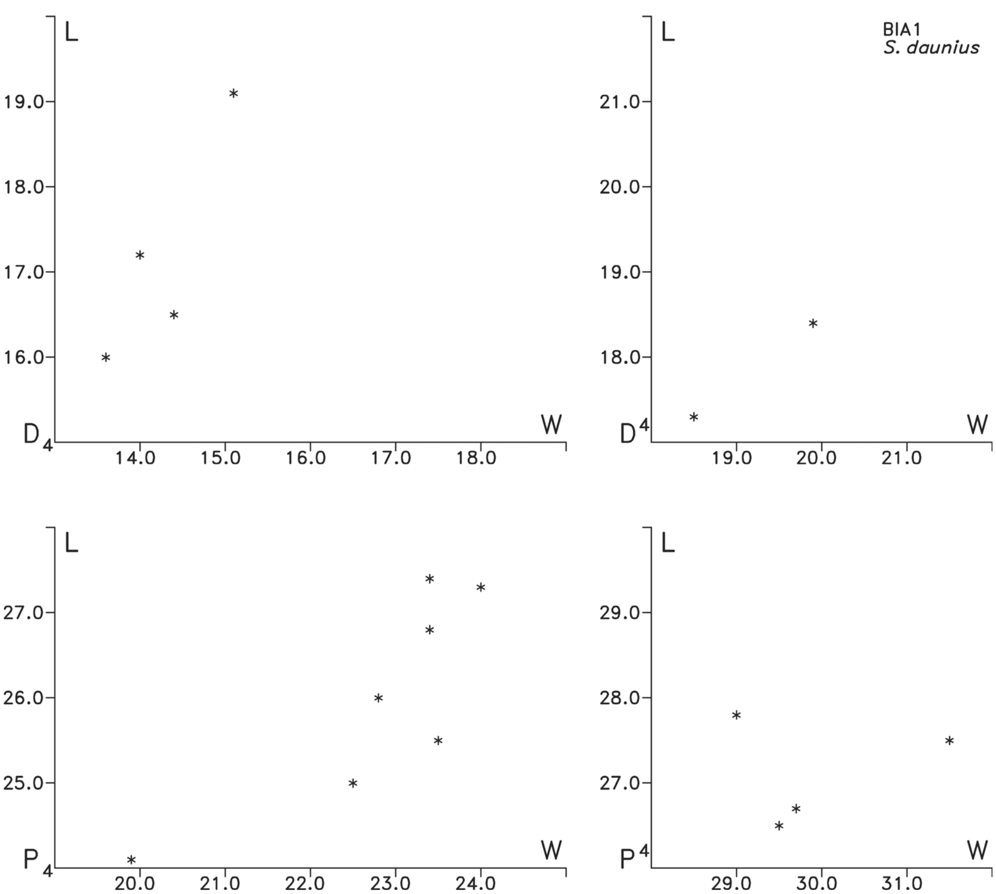

Figure 14. Plot of length versus width for deciduous and permanent lower and upper premolars of *Stertomys daunius:* D_4, D^4 (upper row), P_4, P^4 (lower row).

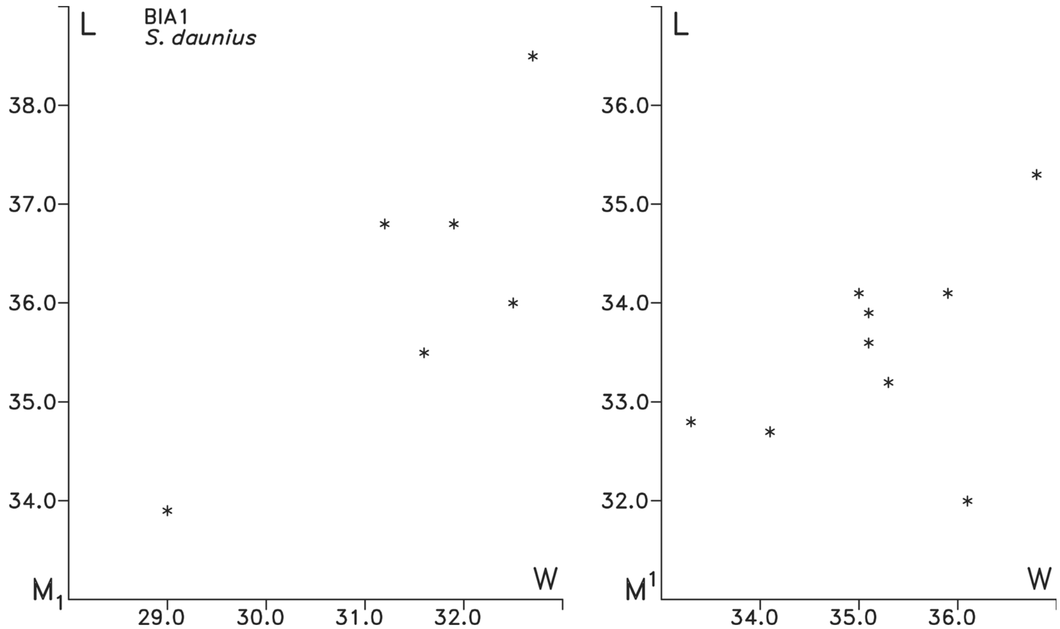

Figure 15. Plot of length versus width for M_1 and M^1 of *Stertomys daunius*.

olophid, and running longitudinally backward, or transversely linguad. The metalophid is connected to the metaconid, either complete, or broken up into several cusps. The centrolophid is long, labially connected to the protoconid or to the metalophid, or ending free on the labial border. Its lingual end is inflated and forms a cusp on the lingual border. Between centrolophid and metalophid there may be an accessory crest, or yet another cusp on the lingual border of the tooth. The mesolophid is complete (5), or interrupted midway (2), and there may be an extra crest between mesolophid and centrolophid. The posterotropid is long, connected to the hypoconid in three cases. P_4 has one grooved root. Scatter plots of length and width measurements of P_4 are shown in Figure 14.

M_1–The number of crests varies between 9 and 13: anterolophid, prototropid, from two to four centrolophids, mesolophid, posterotropid, and posterolophid, which are all more or less of the same height. Additionally there may be low and thin extra crests between metalophid and centrolophid, between mesolophid and posterotropid, between centrolophid and mesolophid, and between posterotropid and posterolophid. The anterolophid is separated from the protoconid by a furrow on the anterior border of the tooth. In three out of seven specimens the main centrolophid and the mesolophid form a lyre-shaped bend on the labial border. In three cases the centrolophid ends against the mesolophid, and in one case it reaches the labial border independent of the mesolophid. There are two roots: one deeply grooved anterior root, and a flat posterior one. Scatter plots of length and width measurements of M_1 are shown in Figure 15.

M_2–The number of crests varies between 10 and 12: anterolophid, prototropid, three centrolophids, mesolophid, posterotropid, and posterolophid, which are all more or less of the same height. Additionally there may be low and thin extra crests between prototropid and metalophid, between metalophid and centrolophid, in between the centrolophids, between mesolophid and posterotropid, and between centrolophid and mesolophid. The anterolophid is separated from the protoconid by a furrow on the anterior border of the tooth. In five out of eight specimens the main centrolophid and the mesolophid form a lyre-shaped bend on the labial border and in the other cases the centrolophid ends against the mesolophid, without reaching the labial molar border. There are three roots, two anterior and one posterior.

In one specimen (RGM 514149, Figure 12.4) the regular, parallel pattern of the crests is broken up by an irregular longitudinal crest through the center of the molar from prototropid to mesolophid. There are three roots. Scatter plots of length and width measurements of M_2 are shown in Figure 16.

M_3–There are between nine and eleven crests, with the same orientation as in M_1 and M_2. The main centrolophid reaches the molar border independent of the mesolophid in two cases, it forms a

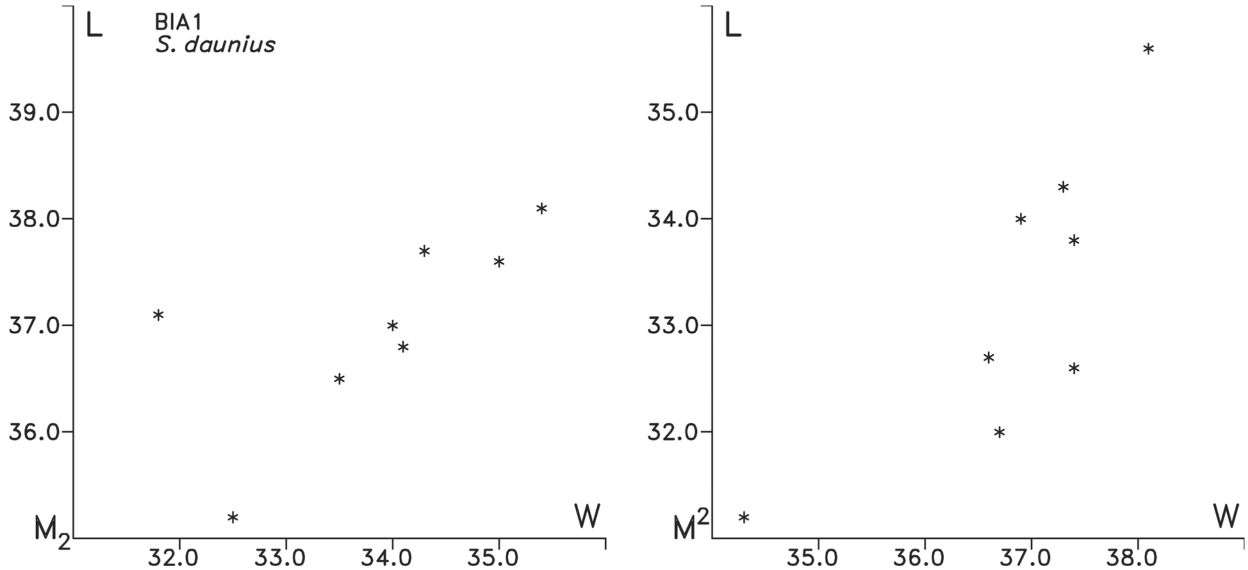

Figure 16. Plot of length versus width for M_2 and M^2 of *Stertomys daunius.*

lyre-shaped bend with the mesolophid in three cases, and in one specimen it ends before reaching the mesolophid. The posterior part of the molar, behind the mesolophid may present an irregular pattern of broken-up crests. There are three roots, two anterior and one posterior. Scatter plots of length and width measurements of M_3 are shown in Figure 17.

D^4–One specimen is a fairly normal glirid tooth with anteroloph, protoloph, two centrolophs, metaloph, posterotrope, and posteroloph. To these a small anterotrope and metatrope are added. The precentroloph is small and isolated, and the postcentroloph is long, curved forward, and connected to the middle of the protoloph. In the second specimen the longitudinal connections are lost, and of the protoloph only two remnants of the anterior part are present. In this specimen the precentroloph is longer than the postcentroloph and slightly curved forward. Scatter plots of length and width measurements of D^4 are shown in Figure 14.

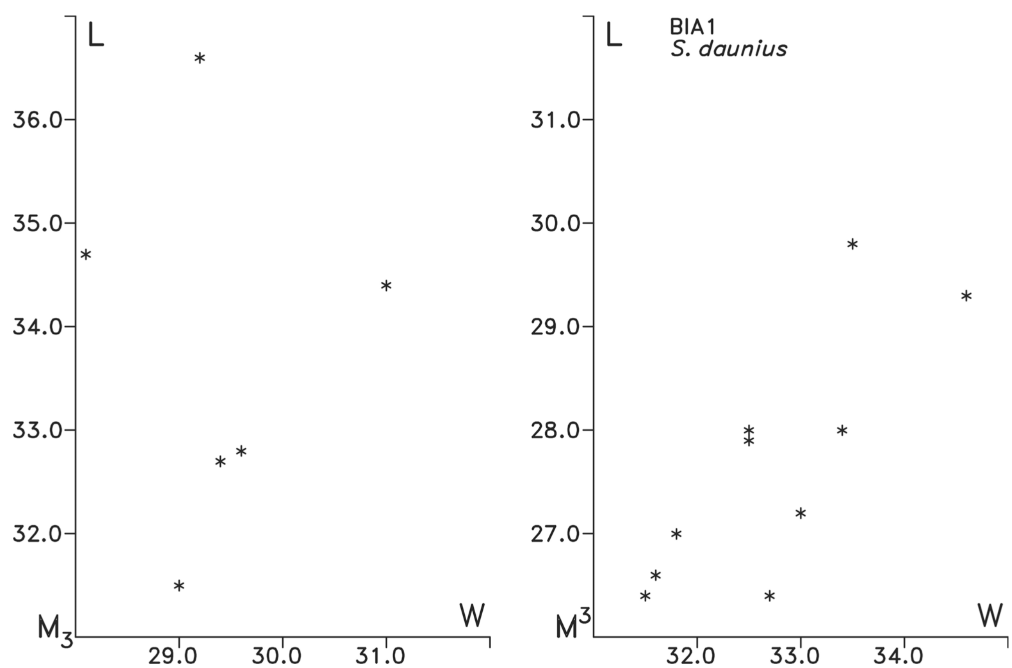

Figure 17. Plot of length versus width for M_3 and M^3 of *Stertomys daunius.*

P^4–Protocone and metaloph may be separated or connected, but they are not fused into one cusp. There are two centrolophs, postcentroloph longer than precentroloph, not connected lingually, accompanied by a prototrope or a metatrope. There may be an anterotrope, and all specimens have a long posterotrope. The posteroloph is lingually free, or attached to the hypocone. P^4 has three roots, the lingual root and the anterior root may be fused. Scatter plots of length and width measurements of P^4 are shown in Figure 14.

M^1–The number of crests varies between 10 and 15. The principal crests, all about the same height are: anteroloph, protoloph, prototrope, precentroloph, postcentroloph, metaloph, and posteroloph; in each valley between these crests an additional thin and low crest may be present. Of these, the posterotrope is the longest, and anterotrope and posterotrope are always present. Only the lingual half of the protoloph is strongly oblique, the other crests are transverse to slightly oblique. The centrolophs are detached from paracone and metacone, respectively. Most crests are inflated at their labial end, so that up to seven cusps may be present on the labial border of the tooth. Scatter plots of length and width measurements of M^1 are shown in Figure 15.

In the simplest specimen (RGM 514169) there is a long prototrope, a very long precentroloph that turns backward lingually, towards the metaloph, and a long postcentroloph that touches the tip of the precentroloph.

In the most complex specimen (RGM 514172) one is inclined to think that there are two precentrolophs, the first one long, and the second one shorter, and two very long postcentrolophs that are lingually connected in a U-shape. But in fact one can't know in which position the surplus of crests has been added. In some specimens the prototrope is the crest that takes over the role of the precentroloph and almost reaches the metaloph. But none of these crests is connected to the metaloph. Protocone and metaloph are separated, though in several cases this separation is very superficial. The posteroloph is lingually free or connected to the hypocone. There are three roots.

M^2–The number of crests varies between 10 and 13. The dental pattern is like in M^1. The precentroloph seems to be straighter and not so clearly directed toward the metaloph. However, the separation of M^1 and M^2 is not absolutely certain. There are three roots. Scatter plots of length and width measurements of M^2 are shown in Figure 16.

M^3–There are 11 to 14 crests. In the simplest case one might still make an attempt to name them, but in the most complex specimen such an attempt fails, the more so, since all crests are almost of the same height. Protocone and metaloph are separated (6) or connected (3). Posteroloph and hypocone are separated in six out of eight specimens. M^3 has three roots. Scatter plots of length and width measurements of M^3 are shown in Figure 17.

Origin and Evolution of *Stertomys*: Daams and Freudenthal 1985 placed *Stertomys* in the subfamily Glirinae, but the oblique orientation of the crests in the upper molars proves that it belongs to the Myomiminae. Daams and de Bruijn 1995 thought *S. laticrestatus* to have descended from *Glis* "because in both genera the protoloph and metaloph end separately at the lingual border." However, this separation may be superficial in *S. laticrestatus*, and almost non-existent in *S. daunius*, a species which is closely related to *S. laticrestatus* in all respects, and which may well be its ancestor. Apparently, *Stertomys* is derived from an ancestor with a connected protoloph/metaloph.

The known species of *Stertomys* represent two different groups:

1. *S. daunius* and *S. laticrestatus* form a group of large species, strongly modified in comparison with mainland Gliridae, with an extremely complicated dental pattern, a lyre-shaped loop in the lower molars, and frequently a separation between protoloph and metaloph. In general, in the upper molars the crests tend to acquire a transverse position. Paracone and metacone are fully separated from the centrolophs. The separation of posteroloph and hypocone is less than it is in *S. daamsi*, and the anterolophid may be labially connected to the protoconid. Another species of this group will be described in a forthcoming publication on the glirids from Rinascita 1.
2. *S. daamsi* belongs to a group of smaller species, which is less modified: a less complex pattern, never a lyre-shaped loop, separation of paracone and metacone from the respective centrolophs not fully developed, anterotrope and posterotrope rarely present, and protoloph and metaloph always interconnected.

This group contains the dominant glirid in practically all Gargano fissure fillings.

For some characters it is not possible to say whether they are advanced or not: the separation of posteroloph and hypocone, and the separation of anterolophid and protoconid, which are practically 100% realized in *S. daamsi*. They probably are advanced features, because they do not appear in the oldest Myomiminae.

In *S. daamsi* the precentroloph is directed obliquely backward and may be connected to the middle of the metaloph; in *S. daunius* this connection has not been observed. It is not clear how this should be interpreted. Possibly, this connection existed in the common ancestor and got lost in the more advanced species; it might be incompatible with the large number of parallel crests in *S. daunius*. However, it is also possible that it did not exist in the ancestor, and that it is a new acquisition in *S. daamsi* that does not appear in the other group.

We did consider the possibility that these groups represent two genera. However, their basic dental patterns are identical, and the differences are later acquisitions; creating yet another genus name would not help to clarify their common origin. Furthermore, only a small part of the rich Gargano collection has been studied so far, and other localities may yield species that might not fit in the characterization of these two groups. Whether in the end a new genus name for group 2 is useful will have to be decided in the future when the study of the Gargano glirids, especially those from San Giovannino, will be complete.

The ancestry of *Stertomys*: In order to find a possible ancestor of *Stertomys*, it is compared with all known genera of Myomiminae:

Myomimus Ognev, 1924 has a simple dental pattern with only five crests in the upper molars and four crests in the lower ones, according to the original description. However, a sketch of the holotype of *M. personatus*, provided to us by Dr. G. Storch (Frankfurt), reveals six to seven crests in the upper molars. Other species of *Myomimus,* like *M. roachi* and *M. qafzensis*, have a simpler pattern.

The oldest species (*M. dehmi*) has six, and occasionally seven, crests. The centroloph is not connected to the metaloph. The posteroloph is lingually connected to the metaloph. *M. dehmi* (de Bruijn 1966a) is indeed one of the possible candidates for the ancestry of *Stertomys*. However, its attribution to *Myomimus* has never been justified. It was originally known from Pedregueras 2C (MN9, Spain), and has been recorded from Lefkon (MN10, Greece, Daxner-Höck 1995), and El Arquillo (MN13, Spain, Azanza et al. 1989). A related species, *M. maritsensis*, is known from Monasteri and Maramena (MN13, Greece) (de Bruijn 1989, Daxner-Höck 1995).

In *Miodyromys* Kretzoi, 1943 the protoloph and metaloph reach the lingual border separately and are connected by an endoloph, of which the posterior end continues into the posteroloph. M^1 and M^2 have six main ridges. The precentroloph is directed toward the middle of the metaloph, but not connected to it. The type species, *M. hamadryas* (Forsyth Major 1899), has more crests than one would expect for an ancestor of *Stertomys*. However, *M. aegercii* (Baudelot 1972) may be considered a possibility, the more so, since paracone and precentroloph may be separated labially.

Dryomimus Kretzoi, 1959 has an endoloph as in *Miodyromys* and a simpler dental pattern. It is known from the Pliocene only, younger than *Stertomys*, and not considered further.

Prodryomys Mayr, 1979. Lower molars with seven crests. The M^2 of *P. satus* shows two centrolophs, interconnected in the middle of the tooth or more labially, forming an almost symmetrical Y-pattern. The M^1 is more asymmetrical. There may be a complete endoloph, which would mean that *Prodryomys* is probably a Dryomyinae and not a Myomiminae.

Pseudodryomys de Bruijn, 1966a has a simple dental pattern with four to six crests. The precentroloph is connected to the postcentroloph when both are present, and may be in contact with the middle of the metaloph. The precentroloph is not detached from the paracone. The posteroloph is lingually connected to the metaloph. The type species, *P. ibericus* de Bruijn, 1966a is much too old to be the direct ancestor of *Stertomys*, but a more remote relationship cannot be ruled out.

Peridyromys Stehlin and Schaub, 1951 has shorter centrolophs, the posteroloph is lingually connected, and the precentroloph is connected to the paracone. The postcentroloph is connected to the metacone. As far as the origin of *Stertomys* is concerned, it is in the same position as *Pseudodryomys ibericus*.

Daams and de Bruijn 1995 mentioned the possible synonymy of *Miodyromys*, *Prodryomys*, *Pseudodryomys*, and *Peridyromys.* With the exception of *Prodryomys*, which may well be a Dryomyinae, this possibility should certainly be considered, the more so, since no good diagnoses and differential diagnoses of these genera exist. de Bruijn et al. 2003 put *Peridyromys* in synonymy with *Myomimus*; a more profound investigation should clarify this case.

Vasseuromys Baudelot and de Bonis, 1966 is characterized by a longitudinal prolongation of the labial cusps that form a nearly continuous ecto-

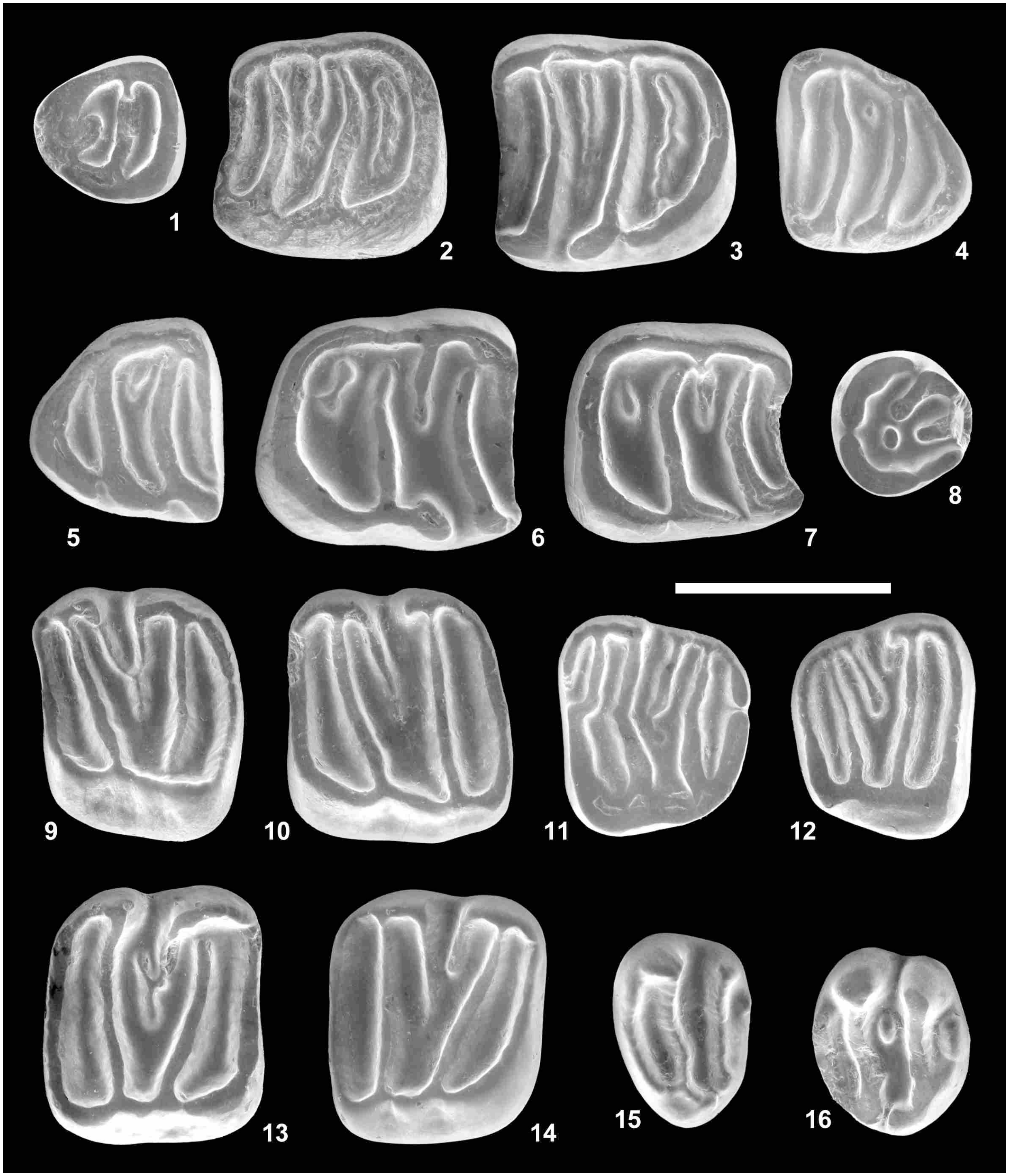

Figure 18. *Dryomys apulus.* 1. P_4 sin. RGM 455919, 2. M_1 sin. RGM 455921, 3. M_2 sin. RGM 455927, 4. M_3 sin. RGM 455939, 5. M_3 dext. RGM 455944, 6. M_2 dext. RGM 455931, 7. M_1 dext. RGM 455924 Holotype, 8. P_4 dext. RGM 455920, 9. M^1 sin. RGM 455956, 10. M^2 sin. RGM 455963, 11. M^3 sin. RGM 455977, 12. M^3 dext. RGM 455978, 13. M^2 dext. RGM 455971, 14. M^1 dext. RGM 455957, 15. P^4 dext. RGM 455948, 16. D^4 dext. RGM 455946. Scale is 1 mm.

Table 4. Measurements of *Dryomys apulus* sp. nov.

	Length						Width					
	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
P_4	2	6.5	6.65	6.8	4.5		2	6.6	6.65	6.7	1.5	
M_1	5	9.8	10.48	10.9	10.6	0.42	5	9.3	9.84	10.4	11.2	0.50
M_2	9	10.3	11.04	12.2	16.9	0.61	9	10.4	10.96	11.7	11.8	0.42
M_3	10	8.4	9.08	10.2	19.4	0.51	10	8.7	9.37	10.3	16.8	0.52
D^4	2	6.7	6.95	7.2	7.2		2	8.2	8.65	9.1	10.4	
P^4	3	6.4	6.47	6.5	1.6		3	8.7	8.90	9.2	5.6	
M^1	13	9.0	9.58	10.3	13.5	0.35	13	11.0	11.74	12.2	10.3	0.35
M^2	11	8.9	9.93	10.9	20.2	0.56	9	11.2	11.94	13.0	14.9	0.60
M^3	7	7.7	8.17	8.6	11.0	0.36	6	10.0	10.38	10.9	8.6	0.34

lophid in the lower molars. The two centrolophs may be of about equal length, and the postcentroloph may even be the longer one of the two. The precentroloph is connected to the paracone or infrequently separated. The posteroloph is lingually connected to the metaloph. There may be up to 12 crests in both the upper and lower molars, much too complicated for a potential ancestor of *Stertomys*.

Praearmantomys de Bruijn, 1966b and *Armantomys* de Bruijn, 1966b have much more hypsodont molars, and a simpler dental pattern.

Nievella Daams, 1976 also is too hypsodont. There are two isolated centrolophs and a prototrope. The posteroloph is separated from the hypocone by a shallow furrow.

Tempestia Van de Weerd, 1976 has more hypsodont molars with a simpler dental pattern. There is only one—isolated—centroloph.

Altomiramys Díaz and López, 1979 has only the anterior centroloph, which joins the anteroloph in an arch-shaped ridge. Its lingual end is connected to the middle of the metaloph. The lingual end of the posteroloph is connected to the metaloph.

Ramys García Moreno and López Martínez, 1986 has already developed more extra ridges than *S. daamsi*, and there may be a complete endoloph.

Carbomys Mein and Adrover, 1982 and *Margaritamys* Mein and Adrover, 1982. These endemic glirids from the Isle of Majorca show some details that remind one of *Stertomys*: anterolophid detached from the protoconid, centrolophid connected to the middle of the metalophid, posteroloph detached from the hypocone, precentroloph detached from the paracone. But the longest centroloph, and the one that connects to the middle of the metaloph, is the postcentroloph. Furthermore, the D_4 of *Margaritamys* has no similarity with that of *Stertomys*. Moreover, their size is not compatible with a potential ancestor of *Stertomys*, and the similarities may well be due to parallelism. However, some kind of relationship, through the Majorca - Sardinia - Corsica - Calabria island arch cannot be excluded.

In summary, we may say that *Myomimus dehmi* (Late Miocene, MN9-MN13, Spain, MN11, Austria), *M. maritsensis* (MN13, Greece), and *Miodyromys aegercii* (Middle Miocene, MN6, France and Germany) are among the best candidates for the ancestry of *Stertomys.* In the latter case the time gap between the age of *M. aegercii* and the supposed Messinian age of the migration into Gargano is quite large. It is not impossible that there exists a relationship with the endemic glirids of Majorca.

Dryomys apulus sp. nov.
Figure 18.1-16

Type locality: Biancone 1

Derivatio nominis: Latin "apulus," "from Apulia," the region in Southern Italy, that Gargano belongs to.

Holotype: M_1 dext., RGM 455924

Age: Late or post-Messinian

Diagnosis: Small glirid, of the size of *D. nitedula* (Pallas 1778), with a tendency to form continuous ectolophids and endolophids in the lower molars. The P_4 is relatively small. The anterior wall of M_1 is concave, with a forwardly protruding labial corner. There is a complete endoloph in the upper molars.

Differential diagnosis: P_4 relatively smaller than in *D. nitedula* (Pallas 1778), and lower molars narrower; dental pattern somewhat less complex.

Material: RGM 455919 - 455981

Measurements: (see Table 4).

P_4–The shape is oval, almost circular. In one specimen a complete circular crest forms the border of the occlusal surface; there is a broad, incomplete metalophid, from the anterolophid obliquely backward, and a mesolophid that is interrupted in the center of the tooth. In the other one, the bordering crest is almost complete; there are two longitudinal crests from the anterolophid backward, which may constitute the metalophid, and a cusp in the center of the tooth, which may be a remnant of the mesolophid. One root.

M_1–Anterior border moderately to strongly concave, with a protruding, often hook-shaped labial corner. Four complete crests: anterolophid, metalophid, mesolophid, and posterolophid. The anterotropid is absent; the centrolophid is of medium length (2) or long (3). The posterotropid is short (2), of medium length (2), or long (1), placed lingually. There is a continuous, high endolophid on the molar border. The anterolophid is labially connected to the protoconid; the posterolophid is labially connected to the mesolophid, and the mesolophid extends forward along the labial border, leading to the formation of an almost complete ectolophid. Two or three roots.

M_2–The anterior border is less concave than in M_1, the hook-shaped anterolabial corner is less pronounced. The main crests are like in M_1. There is no anterotropid; the centrolophid is of medium length (7) or long (1). The posterotropid is short (1), of medium length (5), or long (2), placed lingually. There is a continuous, high endolophid on the molar border. The anterolophid is labially connected to the protoconid; the posterolophid is labially low connected to the mesolophid (3), or the connection is high (6). The mesolophid extends forward along the labial border, leading to the formation of an almost complete ectolophid. Two or three roots.

M_3–Triangular shape, with a pronounced angle at the level of the entoconid. There are four crests. Additionally there is an anterotropid in one specimen, and a short centrolophid in five cases out of ten. There is a complete endolophid in all cases, and the ectolophid is complete in two specimens. Three roots.

D^4–Oval shape. There is a small anteroloph, almost symmetrical protoloph and metaloph, and an arch-shaped posteroloph. In one of the two specimens there is a tiny cusp-like centroloph in the center of the tooth. In the less-worn specimen there is a furrow in the lingual border, separating protoloph and metaloph.

P^4–One specimen has the morphology of D^4, but it is triangular, shorter, and broader; it might be a D^4. A second one is bean-shaped. The anterior part is damaged. Protoloph and metaloph meet in the center of the tooth in a Y-shape. Finally, a third one has the oval shape and the morphology of D^4, but a long anteroloph; it is not sure whether it is D^4 or P^4. There is one root that ends in three separate tips.

M^1–The endoloph is complete. The protoloph is oblique and the metaloph is transverse. The precentroloph is absent (2), short (3), of medium length (5), or long (3), the postcentroloph is of medium length (9), or long (4). The centrolophs are not interconnected (6), interconnected lingually (4), or interconnected in Y-shape (3); in the latter situation the precentroloph is considered to be long; in reality it may be a shorter precentroloph, connected midway to a longer postcentroloph; the postcentroloph is on average longer than the precentroloph. The posteroloph is connected at both ends. Possibly some of the supposed M^1 are M^2. Three roots.

M^2–The endoloph is complete. The protoloph is oblique, and the metaloph is transverse. The precentroloph is of medium length (4), or long (7), the postcentroloph is absent (1), short (1), of medium length (5), or long (4). The centrolophs are not connected (4), interconnected lingually (3), or interconnected in Y-shape (4); the postcentroloph is on the average shorter than the precentroloph. The posteroloph is connected at both ends. Three roots.

M^3–Anteroloph, endoloph, and posteroloph form a continuous crest. There is one crest inside the trigone, which is of medium length (4), or long (3), accompanied by a short second crest in two cases. Three roots.

The origin of *Dryomys apulus*: The attribution of this species to *Dryomys* is only tentative, and one might consider *Eliomys* Wagner, 1840 as well. In fact there exist no diagnoses that permit to distinguish clearly between these two genera. The pointed shape of P_4 may distinguish *Eliomys* from *Dryomys*, which has a rounded or trapezoidal P_4. The dental pattern of *D. apulus* resembles more that of extant *D. nitedula* than that of *E. quercinus* (Linnaeus, 1766). Especially the continuous endolophid in the lower molars may occur in *D. nitedula*, and probably not in *Eliomys.*

According to Daams and de Bruijn 1995 the oldest occurrence in Europe of *Dryomys* may be that of *Dryomys* sp. from the Late Miocene (MN11) of Dorn-Dürkheim (Franzen and Storch 1975), but it is essentially restricted to the Pleistocene and Holocene.

Eliomys is known from several species, e.g., *E. truci* Mein and Michaux, 1970 from the Late Miocene-Pliocene, MN13-14, of France and Spain, and *E. assimilis* Mayr, 1979 and *E. reductus* Mayr, 1979 from the Late Miocene of Germany. It is not clear why they are attributed to *Eliomys*, and not to *Dryomys*, and one of these species might be the ancestor of *D. apulus*.

AGE OF THE FAUNA

The Gargano faunal complex is likely the result of one single migration wave, which took place during the low sea-level phase of the Messinian, and migration events suggested by differences among some of the Gargano localities can be referred to faunal exchange between neighbouring islands rather than to multiple migrations from the mainland (Freudenthal 1976).

De Giuli et al. 1987 said that Gargano was populated in two migration waves, one during the Early Miocene (ochotonids, erinaceids, glirids, cervoids), and one during the Messinian (*Apodemus*, *Cricetus*, *Microtia*, *Eliomys*) respectively.

In support of their hypothesis, de Giuli et al. 1987 said that Butler 1980 suggested an Early Miocene age for the immigration of *Deinogalerix*. In fact, however, Butler 1980 carefully avoided such a suggestion, and only said *Deinogalerix* most likely was an immigrant entering Gargano from the East, across the Adriatic. Similarly, Leinders 1984 did not state that *Amphimoschus* is the ancestor of *Hoplitomeryx*.

For the ochotonids, de Giuli et al. 1987 noted that *Prolagus oeningensis* is not recorded later than the Vallesian, which is quite different from suggesting an Early Miocene migration. Furthermore, according to López Martínez and Thaler 1975, *P. oeningensis - P. michauxi* form an evolutionary lineage, and *P. apricenicus* may be derived from that lineage, which is documented in El Arquillo (MN13, Spain) and Maramena (MN13, Greece); possibly related forms have been reported from Monte Castellaro, Capo di Fiume and Brisighella (MN13, Italy).

The Gargano glirids do not support the hypothesis of an Early Miocene immigration. Possible ancestors like *Myomimus dehmi* and *M. maritsensis* were reported from Messinian (MN13) deposits in Spain and Greece (Azanza et al. 1989, de Bruijn 1989, Daxner-Höck 1995).

Not only do *Prolagus and Myomimus* occur in El Arquillo and Maramena, but these localities have also yielded material of species related to the other micromammals of Gargano that were supposed to represent the second migration wave. Thus, potential ancestors of all the micromammals of Gargano belong to the normal Messinian mainland fauna, and may have reached Gargano simultaneously, during the Messinian sea-level lowstand. For the larger mammals (*Deinogalerix* and *Hoplitomeryx*) potential ancestors are not known, neither in Messinian, nor in older deposits. Concluding an Early Miocene migration on the basis of lack of evidence is not justified.

Rook et al. 2000 also said that the Gargano faunas were the result of various immigration phases because of the presence of the endemic genus *Hoplitomeryx* Leinders, 1984 in Lower Tortonian calcarenites of Scontrone (Abruzzi), deposited before the arrival of Muridae in Europe. However, the dating of the Scontrone mammal bed seems to be unreliable, and the only thing one can say is that they are not older than Early Tortonian.

Thus, there is no conclusive evidence that supports the hypothesis of various migration waves, all the available data are in good accord with the hypothesis of one single migration.

The presence in Biancone 1 of two species of *Stertomys*, both much bigger than their supposed common ancestor on the mainland, demonstrates that there must be an undocumented time span between the moment of immigration from the mainland, and the age of that locality. Unfortunately the amount of time is unknown, but certainly the area was submerged during the Pliocene, because the fissure fillings are covered by a Pliocene calcarenite. The best current estimate is that the faunas are of Late Miocene age, though an Early Pliocene age cannot be ruled out.

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