

Gliridae (Rodentia, Mammalia) from the late Miocene fissure filling Rinascita 1 (Gargano, prov. Foggia, Italy)

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RESUMEN

MARTÍN-SUÁREZ, E. & FREUDENTHAL, M. Gliridae (Rodentia, Mammalia) del Mioceno inferior de la fisura kárstica Rinascita 1 (Gargano, prov. Foggia, Italy).

Se describen dos especies nuevas del género endémico *Stertomys* (Mammalia, Rodentia, Gliridae) de la fisura kárstica Rinascita 1 en la paleo-isla de Gargano (prov. Foggia, Italia): *S. simplex* y *S. lyrifer*. Una tercera especie se clasifica como *S. aff. daamsi* Freudenthal & Martín-Suárez, 2006. La fauna contiene tres especies de *Stertomys* más, que están representadas por muy poco material. Hay además un glirido no endémico: *Dryomys apulus* Freudenthal & Martín-Suárez, 2006.

Se reconocen dos grupos de especies en el género *Stertomys*:

1) Especies grandes con dentición complicada: *S. laticrestatus* Daams & Freudenthal, 1985, *S. daunius* Freudenthal & Martín-Suárez, 2006, y *S. lyrifer* sp. nov.

2) Especies más pequeñas con dentición más sencilla: *S. daamsi* Freudenthal & Martín-Suárez, 2006, *S. simplex* sp. nov., y *S. aff. daamsi*.

Palabras clave: Gliridae, Mioceno, Italia, endemismo, insularidad.

ABSTRACT

MARTIN-SUAREZ, E. & M. FREUDENTHAL. Gliridae (Rodentia, Mammalia) from the late Miocene fissure filling Rinascita 1 (Gargano, prov. Foggia, Italy).

Two new species of the endemic genus *Stertomys* (Mammalia, Rodentia, Gliridae) are described from the Late Miocene fissure filling Rinascita 1 on the palaeo-island Gargano (prov. Foggia, Italy): *S. simplex* and *S. lyrifer*. A third species is classified as *S. aff. daamsi* Freudenthal & Martín-Suárez, 2006. The fauna contains poor remains of three more species of *Stertomys*, and a non-endemic glirid: *Dryomys apulus* Freudenthal & Martín-Suárez, 2006.

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Two groups of species are recognized within the genus *Stertomys*:

1) Large species with complicated dental pattern: *S. laticrestatus* Daams & Freudenthal, 1985, *S. daunius* Freudenthal & Martín-Suárez, 2006, and *S. lyrifer* sp. nov.

2) Smaller species with a simpler dental pattern: *S. daamsi* Freudenthal & Martín-Suárez, 2006, *S. simplex* sp. nov., and *S. aff. daamsi*.

Keywords: Gliridae, Miocene, Italy, endemism, insularity.

INTRODUCTION

The Gargano promontory in S. Italy (see map in Fig. 1) is a block of uplifted Mesozoic limestones that is part of the Adria plate. The area was an island or a group of islands, separated from the Italian mainland by the Apennine Foredeep, that supposedly got 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.

Freudenthal & Martín-Suárez (2006) described the glirid fauna recovered from the oldest of the Gargano fissure fillings, Biancone 1. This paper is dedicated to the glirids from the second oldest locality, Rinascita 1.

Technical data

The material was collected by Freudenthal in 1971, and is stored 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, connected to a computer through a Sony Magnescale measuring unit. The photos were made on the ESEM FEI Quanta 400 in environmental mode of the 'Centro Andaluz de Medio Ambiente' in Granada.



Fig. 1. Map of Italy, indicating the studied area.
Fig. 1. Mapa de Italia, indicando el área estudiada.

Measurements are given in 0.1 mm units. The nomenclature of parts of the cheek teeth is as defined by Freudenthal & Martín-Suárez (2006).

ABBREVIATIONS

- BIA1 Biancone 1
RIN1 Rinascita 1
RGM Code of the geological collections of the National Museum of Natural History, Leiden, the Netherlands

THE GLIRIDAE FROM RINASCITA 1

Genus *Stertomys* Daams & Freudenthal, 1985
Stertomys aff. *daamsi* Freudenthal & Martín-Suárez, 2006
Plate 1, Figs. 1-8

Locality

Rinascita 1

Material and measurements

See Table 1a and 1b.

Description

The dimensions of all elements are on average clearly smaller than those of *S. daamsi*, but morphologically there are only minor differences in the frequency distribution of character states. Therefore we did not create a new species for this material, and we will refrain from an exhaustive description, and only mention some differences.

A problem of this material is that *S. simplex* sp. nov. from the same locality partly overlaps its size range, and that only the upper molars of that species are really different from *S. aff. daamsi*. For the lower molars the separation has been made on the basis of size, and it is quite certain that a number of specimens are incorrectly classified; such errors are bound to influence the frequency of character states, and a complete listing of all frequencies is therefore not useful.

D_4 - The type population of *S. daamsi* from BIA1 has yielded 33 D_4 and 140 P_4 . The sum, 173, is fairly close to the frequency of other elements in the BIA1 population. In RIN1 56 P_4 of *S. aff. daamsi* have been found, and that makes one expect to find at least 10 specimens of D_4 . However, only a few D_4 of *S. lyrifer* sp. nov. have been found. We have no explanation for this discrepancy.

P_4 - The morphology of P_4 presents the same difficulties as the P_4 from Biancone 1. Most specimens can be classified in one of the morphotypes of *S. daamsi* (Freudenthal & Martín-Suárez, 2006, Fig. 3):

Four specimens have conserved the basic glirid pattern (morphotype A). The Z-shaped metalophid of morphotype B is present in five cases, and morphotype H (the most common one in BIA1) is found in two specimens. In *S. aff. daamsi* morphotype G is the most frequent (nine cases); it looks quite similar to morphotype I, but the backward crest is not longitudinal but oblique from the anterolingual border towards the axis of the tooth. It is difficult to understand the homology of this crest. Anyway, in the majority of the specimens the transverse structure of the anterior part of the P_4 has been replaced by a more or less longitudinal structure. An additional problem is, that we can't even be sure that all specimens are correctly classified as *S. aff. daamsi*. Some of them may belong to *S. simplex* sp. nov.

The hind part of the P_4 has a normal pattern: the mesolophid is complete, and connected to the entoconid. The posterotropid is small (7), of medium length (5), or long (18).

$M_{1,2,3}$ present no morphological differences whatsoever in comparison with *S. daamsi*.

D^4 - See the description of *S. simplex* sp. nov.

P^4 - Basically, the morphology is identical to that of the P^4 of *S. daamsi*. Maybe the precentroloph is somewhat less developed, and the presence of a midcentroloph (centrally placed, without a clear homology with either pre- or postcentroloph) is slightly more frequent.

$M^{1,2}$ - In comparison with *S. daamsi* the precentroloph is less frequently connected to the metaloph, and the postcentroloph is less frequently missing, and on average longer.

M^3 - The anteroloph is lingually connected to the protoloph in four cases, and there may be a complete endoloph. The precentroloph/prototrope is less frequently connected to the metaloph than in BIA1. The postcentroloph is on the average shorter. The centrolophs are more frequently interconnected.

The few differences observed are insignificant, and may well be accidental.

***Stertomys simplex* sp. nov.**

Plate 2, Figs. 1-16

Type-locality

Rinascita 1

Derivatio nominis

From latin *simplex* = simple, as a reference to the simple dental pattern of the upper molars.

Holotype

M¹ sin., RGM 535470

Diagnosis

Upper molars with simple dental pattern, often only one centroloph, resulting in a total of only five crests, contrasting with the general presence of seven crests in the lower molars.

Differential diagnosis

Similar in size to *S. daamsi*, larger than *S. aff. daamsi* from RIN1. Dental pattern of the upper molars simpler than in all the other known *Stertomys* species.

Material and measurements

See Table 1a and 1b.

*D*₄ - Like in the case of *S. aff. daamsi* no specimens have been found that might be attributed to *S. simplex*, quite a surprising circumstance.

*P*₄ - In the majority of the specimens the anterolophid presents one or two interruptions. The pattern of cusps and crests may correspond to one of the classified morphotypes, but the interruptions make it different. Morphotypes A, B, D, G', H, I, M, M', and O' are present in numbers varying from two to six; G', M', and O' differ from G, M, and O by interruptions in the anterolophid. There is one massive root that may be grooved labially and/or lingually, rarely split at its tip.

*M*₁ - The anterolophid is labially free. The anterotropid is small (5), of medium length (3), or long (17). The metalophid is free (5), low connected to the metaconid (1), or the connection is high (18). The centrolophid is of medium length (3) or long (21). The centrolophid-metaconid connection is absent (5), low (3), or high (15). The mesolophid is connected to the entoconid. The posterotropid is of medium length (1) or long (23). The anterior root is smooth or grooved, less frequently split. The posterior root is smooth.

*M*₂ -The anterolophid is labially free. The anterotropid is absent (2), small (3), of medium length (1), or long (11). The metalophid is free (3), low connected to the metaconid (3), or the connection is high (8). The centrolophid is of medium length (5) or long (12). The centrolophid-metaconid connection is absent (1), low (1), or high (13). The mesolophid is connected to the entoconid (14). The posterotropid is short (1) or long (13). There are two anterior roots, and a posterior one.

*M*₃ -The anterolophid is labially free (11) or labially connected (1). The anterotropid is of medium length (10) or long (4). The metalophid is free (1), low

connected to the metaconid (3), or the connection is high (6). The centrolophid is short (3) or of medium length (11). The centrolophid-metaconid connection is low (1) or high (14). The mesolophid is connected to the entoconid (15). The posterotropid is of medium length (3) or long (11). The roots are like in M_2 .

D^4 - The entire collection from Rinascita 1 contains four D^4 . One larger specimen belongs quite certainly to *S. lyrifer*. The other three may represent *S. aff. daamsi* or *S. simplex*, and *S. lyrifer* cannot be excluded either. The size of the specimens falls within the range of the D^4 of *S. daamsi*, and therefore it seems most probable that they belong to *S. simplex*, because *S. aff. daamsi* is smaller.

There is a half-long anteroloph; protoloph and metaloph are connected in a Y-pattern. There is a short centroloph, reduced to nothing more than a small cusp in the center of the tooth, in one specimen. The other specimen has a long postcentroloph, connected to the middle of the protoloph. The posteroloph is separated from the hypocone. There are three divergent roots.

P^4 -The anteroloph is long, split into two cusps in some specimens. The anterotrope is absent. In 10 specimens there is no centroloph; in five specimens there is a short centrally placed midcentroloph; in three specimens there is one centroloph (the precentroloph), which is either short, of medium length, or long; in four specimens there are two centrolophs, both of medium length and interconnected, and one specimen presents only a short postcentroloph. There is no prototrope, nor a metatrope. There is a posterotrope in one case. The endoloph is formed by the protocone alone. Anteroloph and posteroloph are lingually free. Three roots.

M^1 -There is a small concavity on the anterolingual wall in eight out of 23 specimens. The anteroloph is lingually free. The precentroloph is of medium length (1), long and straight (8), curved towards the metaloph (13), or connected to that crest (2). The precentroloph is detached from the paracone. Postcentroloph, prototrope, metatrope and posterotrope are absent. The posteroloph is lingually free, separated from the hypocone by a furrow, which is frequently deep and wide. Three roots.

M^2 - There is a small concavity on the anterolingual wall in five out of 21 specimens. The anteroloph is lingually free. The precentroloph is long and straight (9), curved towards the metaloph (14), or connected to that crest (1). The precentroloph is united with the paracone (1), low connected to the paracone (2), or detached from the paracone (21). The postcentroloph is absent (16), short (5), of medium length (2), or long (1); when present it is generally not connected to the metacone (7). The prototrope is absent (22) or short (2). The metatrope is absent. Only in one case the centrolophs are interconnected lingually. The posterotrope is absent. The posteroloph is lingually free, separated from the hypocone by a furrow, which is frequently deep and wide. Three roots.

M^3 - The anteroloph is lingually connected in one case only. The number of crests inside the trigone is one (5), two (7), or three (3). In most specimens a crest runs from the labial border linguad, curving backwards towards the metaloph, connected to that crest in only two cases. It is most logical to suppose that the mentioned crest is the pre-

centroloph, because of homology with M^{1,2}. However, in five specimens it is placed so far backwards that it appears to be the postcentroloph. The postcentroloph is separated from the hypocone in five specimens. The endoloph is formed by the protocone alone (4), anteriorly interrupted (6), or posteriorly interrupted (1). Three, rarely four, roots.

Stertomys lyrifer sp. nov.

Plate 3, Figs. 1-20

Type-locality

Rinascita 1

Derivatio nominis

From latin *lyra* = lyre and *ferre* = bear; because of the lyre-shaped connection between centrolophid and mesolophid in the majority of the lower molars.

Holotype

M₁ dext., RGM 535225

Diagnosis

Centrolophid and mesolophid frequently form a lyre-shaped loop at the labial border. Precentroloph not connected to the middle of the metaloph. Proto-loph and metaloph in most cases connected at the lingual border in M¹, and separated in M².

Differential diagnosis

Resembling *S. laticrestatus* and *S. daunius*, but considerably smaller. Larger than *S. daamsi*, and on average larger than *S. simplex*; dental pattern much more complicated than that of the latter two.

Material and measurements

See Table 1a and 1b.

*D*₄ - Two specimens show a morphology similar to that of *S. daunius* (Freudenthal & Martín-Suárez, 2006, Fig. 6), with a dominating crest from the hypoconid towards the foremost tip of the tooth. Labially of this crest there is a low platform, with an elongated cusp on the border. The mesolophid and a small posterotropid are easily recognized. In front of the mesolophid there are one or two cusps of uncertain homology. The third specimen is quite different: there is no mesolophid, and there are two

very oblique crests in the lingual half of the tooth that run from anterolingual to posterolabial. There are two very divergent roots, the anterior one is round, the posterior one oval, with the longest diameter transverse.

P_4 - The P_4 has a rounded outline. The most common morphology consists of between six and nine more or less parallel ridges: anterolophid, anterotropid, metalophid, centrolophid, mesolophid, posterotropid, and posterolophid, eventually with thin accessory crests in front of the centrolophid, and/or behind it. In the front part of the tooth this regular pattern may be broken up into a number of smaller cusps and crests that are often impossible to homologise. Lingually, the centrolophid is usually not connected to the metaconid; on the labial side it may be connected to the mesolophid, forming a continuous loop (6), or these two crests are separated (12). The mesolophid is firmly connected to the entoconid. The posterotropid is always long. There is one root, with a labial and a lingual groove. In one specimen there are no grooves, and in another one they are deep, and the tip of the root is split.

M_1 - The anterolophid is separated from the protoconid by a deep or shallow furrow in 13 out of 16 cases. Usually there are nine crests, due to the presence of three centrolophids; there may be a total of 11 crests, through the presence of a second anterotropid, a second posterotropid, and/or tiny extra crests in the centrolophid area. The main centrolophid is the middle one of the three, connected with the mesolophid in a lyre-shaped loop in 13 out of 20 specimens. The posterotropid is always long, lingually free, and in several cases labially connected to the hypoconid. Fourteen specimens have one anterior oval root; three have an anterior root, which is split at its tip, and in two cases there are two anterior roots.

M_2 - The anterolophid is nearly always separated from the protoconid by a deep or shallow furrow. There are nine crests, like in M_1 , without additional crests. The main centrolophid and the mesolophid form a lyre-shaped loop in 19 out of 24 specimens. The posterotropid is long, nearly always free at both ends. There are two specimens with only one anterior root, in two cases the anterior root is split at its tip, and in 23 cases there are two anterior roots.

M_3 - The anterolophid is nearly always separated from the protoconid by a deep or shallow furrow. There are nine crests (6), ten crests when there are two posterotropids (20 specimens), and in one case there are eleven crests because the posterotropid is triple. The main centrolophid is connected with the mesolophid in a lyre-shaped loop in 23 out of 29 specimens. The main posterotropid is frequently connected to the hypoconid, in several cases imitating the lyre-shaped loop of centrolophid/mesolophid. There are three round roots, two smaller ones in front, and a bigger, backwards sloping, root behind.

D^4 - Of the four D^4 found in RIN1, the largest one (RGM 535257) has protoloph and metaloph connected in Y-shape, a short anteroloph that, together with the protoloph, encircles an anterolabial valley, and a long postcentroloph; the posteroloph is lingually detached from the metaloph. The other three specimens are attributed to *S. aff. daamsi*, though they might belong to *S. simplex* or *S. lyrifer* as well.

*P*⁴ - The anteroloph is long (29). The number of crests varies between six and ten. In the case of six crests these are the four main crests plus a short, medium or long precentroloph, and a long postcentroloph; the precentroloph is shorter and frequently thinner than the postcentroloph. Additional crests are mainly the metatrope, which may be absent (12), short (7), of medium length (4), or long (2); and the posterotrope: absent (9), short (4), of medium length (4), or long (10); a short anterotrope and a short prototrope are present in one case each, and in three specimens an extra crest is present between the centrolophs. Usually protoloph and metaloph are connected, but in about 30% of the specimens there is a shallow furrow between them, and in one case they are separated. Most specimens have three divergent roots. In one case the anterior root and the lingual root are fused; in two cases then posterior root and the lingual root are fused, and in one case the anterior and posterior root are fused, forming a big labial root.

*M*¹ - The anteroloph is lingually free. There are between 8 and 12 crests. The anterotrope is absent (3), short (3), of medium length (5), or long (5). The precentroloph is oblique, and ends near the metaloph; it is firmly connected to the paracone (3), the connection is low (5), or it is detached from the paracone (8). The postcentroloph is of medium length (1) or long (15), always connected to the metacone by a high or low connection. The prototrope is long. The metatrope is absent (6), short (3), of medium length (2), or long (3). In nine out of 16 specimens there is a crest between the centrolophs, which may be short (1), of medium length (5), long (3). The centrolophs are not connected (9) or interconnected (7). The posterotrope is long. The posteroloph is separated from the hypocone by a shallow groove (9) or it is connected (8). Protoloph and metaloph form a continuous crest (8), they are slightly separated by a shallow furrow (2), or they are well separated (2). There is one flat, grooved lingual root (split at its tip in one case), and two smaller labial roots that have a circular section.

*M*² - The anteroloph is lingually free. There are between 9 and 11 crests. The anterotrope is absent (3), short (4), of medium length (3), or long (6). The precentroloph is long and straight (7), or curved, ending near the metaloph (10); it is well connected to the paracone (2), the connection is low (11), or it is detached from the paracone (3). The postcentroloph is of medium length (1) or long (16), high or low connected to the metacone (11), or free from the metacone (5). The prototrope is long. The metatrope is absent (4), short (1), of medium length (8), or long (4). In 13 out of 17 specimens there is a crest between the centrolophs, which may be short (2) or long (11). The centrolophs are not interconnected (14), or interconnected lingually (3). The posterotrope is long. The posteroloph is separated from the hypocone by a shallow groove (11) or it is connected (3). Protoloph and metaloph form a continuous crest (4), they are slightly separated by a shallow furrow (8), or they are well separated (2). The roots are like in *M*¹; in two specimens there is small accessory root in the center of the molar.

*M*³ - The anteroloph is lingually free (20), lingually low connected (2), or the connection is high (2). The number of crests varies between 10 and 11 (with one extreme case, where 13 crests are present), distributed as follows: the anterotrope is absent (13), short (13), of medium length (1), or long (1); the posterotrope is absent (1), short (1), of medium length (3), or long (22) and inside the trigone there are: two crests (1),

five crests (13), or more than five crests (9). So, the most common morphology is: four main crests, five inside the trigone, and a posterotrope, accounting to 10 crests; when an anterotrope is added the total number is 11. When there are more than 11 crests, the additional ones are usually insignificantly small. The five crests inside the trigone are fairly easily recognized as prototrope, precentroloph, postcentroloph, metatrope, and the crest between the centrolophs, as frequently present in M². The endoloph is formed by the protocone/hypocone alone (13), anteriorly interrupted (5), posteriorly interrupted (1), or complete (2). In three specimens there is a deep furrow between protocone and hypocone. There are three roots: a round one under the paracone, an oval lingual root, and a round posterior root. The latter two are fused in six out of 25 cases, producing a big, grooved posterolingual root.

Stertomys sp. 1

Locality

Rinascita 1

One very big M³ dext., 24.9 x 30.6, has a complex pattern with 14 crests, like the most complicated specimens of *S. daunius*. It is much larger than *S. lyrifer*, and smaller than *S. daunius* from Biancone 1. Apparently it is the only specimen of an unknown species.

Stertomys sp. 2

Locality

Rinascita 1

Measurements

See Table 1a and 1b.

The relatively simple morphology (seven crests) of the M₃ is like that of *S. simplex*, but it is larger, of the size of *S. lyrifer*. M¹ and M² are at the upper limit of the size distribution of *S. simplex*, but their morphology is too complex for that species; they might belong to *S. daamsi*, but the M₃ is too large.

Stertomys sp. 3

Locality

Rinascita 1

Measurements

See Table 1a and 1b.

A dozen specimens have the morphology of *S. aff. daamsi*, but they are so small that they probably represent yet another species of *Stertomy*s. It cannot be excluded, however, that they represent the lower size limit of that species.

Dryomys apulus Freudenthal & Martín Suárez, 2006

Locality

Rinascita 1

Material and measurements

	Length						Width					
	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
M ₂	1		12.00				1		10.60			
M ¹	1		9.70				1		12.40			
M ²	4	9.5	9.78	10.1	6.1	0.28	4	11.4	11.73	12.1	6.0	0.38

One M₂, one M¹, and four M² of *D. apulus* have been found in Rinascita 1. They are identical in size and morphology to the material from Biancone 1.

DISCUSSION

Two species of *Stertomy*s have been recognized in Biancone 1, and in Rinascita 1 five or six species are present. In that respect one might pose the question whether in BIA1 another species is present that cannot be distinguished from *S. daamsi*. Table 1a and 1b show that the value of the variability coefficient V' is not extremely high, except for D₄ and D⁴. Morphological variation of the molars is not large, and may even be called small, in comparison with populations of species of other glirid genera. So, there is no reason to suspect the presence of more than two species in BIA1.

The six species of *Stertomy*s known at present may be arranged in two groups:

1. The lyrifer-group: *S. laticrestatus*, *S. daunius*, and *S. lyrifer*, large species with an extremely complicated dental pattern, a lyre-shaped loop in the lower molars, and frequently a separation between protoloph and metaloph.

2. The daamsi-group: *S. daamsi*, *S. aff. daamsi*, and *S. simplex*, smaller species, with a less complex pattern, never a lyre-shaped loop, and protoloph and metaloph always interconnected.

We did consider the possibility that they represent two genera. However, we suppose they have a common ancestor: *Myomimus dehmi* or another Messinian *Myomimus* species (see Freudenthal & Martín-Suárez, 2006); creating yet another genus name would not help to clarify their common origin.

Of all the known species *S. simplex*, with only five crests in the upper molars, is morphologically least modified in comparison with mainland Gliridae. *S. daamsi* has a more complex pattern, six to seven crests in the upper molars, but it still is simple in comparison with the lyrifer-group.

The lyrifer-group is considerably more modified: larger size, larger number of crests, lyre-shaped connection between centrolophid and mesolophid very frequent, separation of paracone and metacone from the respective centrolophs always strong, protoloph and metaloph separated; in general in the upper molars the crests have acquired a more transverse position. On the other hand, the separation of posteroloph and hypocone is less than it is in *S. daamsi*, and the anterolophid may be labially connected to the protoconid.

In the daamsi-group the precentroloph is directed obliquely backward and it may be connected to the middle of the metaloph; in the lyrifer-group this connection has not been observed. It is not clear how this should be interpreted. It is possible that this connection did not exist in the ancestor, and that it is a new acquirement in *S. daamsi* that does not appear in the other group. However, it is also possible that the common ancestor of both groups developed this connection, and that it got lost posteriorly in the lyrifer-group, being incompatible with the large number of parallel crests.

Within the daamsi-group the oldest species, *S. daamsi*, is clearly larger than the younger *S. aff. daamsi*. *S. simplex* is of the same size as *S. daamsi*, but has a simpler dental pattern. *S. simplex* cannot be placed in one lineage with *S. daamsi*. If we admit a decrease in size, *S. aff. daamsi* may well be a descendant of *S. daamsi*, the more so since a species with the same morphology, and still much smaller, is found in the clearly younger locality of San Giovannino.

Within the lyrifer-group there is an evident increase in size from the oldest, *S. daunius*, to the youngest, *S. laticrestatus*, but the intermediate *S. lyrifer* is smaller than *S. daunius*. Taking the number of crests as parameter, *S. daunius* is the most advanced, and the lyre-shaped bend in the lower molars is best developed in *S. lyrifer*. Apparently these three species do not form one single lineage; they present different mixtures of advanced and conservative characters.

Apart from the three well-documented species from Rinascita 1, three more species are present that are very poorly represented, and that cannot be placed in any phylogenetic lineage either. The extreme species richness of RIN1 is difficult to explain. Possible causes are:

1. *Stertomys* underwent different developments on various islands; RIN1 represents a moment in which faunal interchange between neighbouring islands with similar faunas takes place.

2. The remains of the poorly represented species may be introduced by birds, preying on neighbouring islands.

3. The fissure filling RIN1 may be heterogeneous, due to the mixture of material from various ages. Such mixtures are known to occur in some Gargano fissures, especially in those that are bound to one of the important faults, and that we usually did not sample, not even when they were very rich. It must be admitted that some specimens from RIN1 show signs of rolling and polishing that seem to be the result of transport. On the other hand, the frequently well-preserved roots of the isolated specimens are not compatible with transport. The small size range of the two *Mikrotia* species from RIN1, and their almost monotonous morphology (see Freudenthal, 1976;

for the spelling *Mikrotia* instead of *Microtia*, see Freudenthal, 2006) certainly do not point towards a contaminated sample. An unexpectedly large number of species at this locality is not only found in the Gliridae, but also in the Cricetidae.

For a discussion on the age of the fauna, see Freudenthal & Martín-Suárez, 2006.

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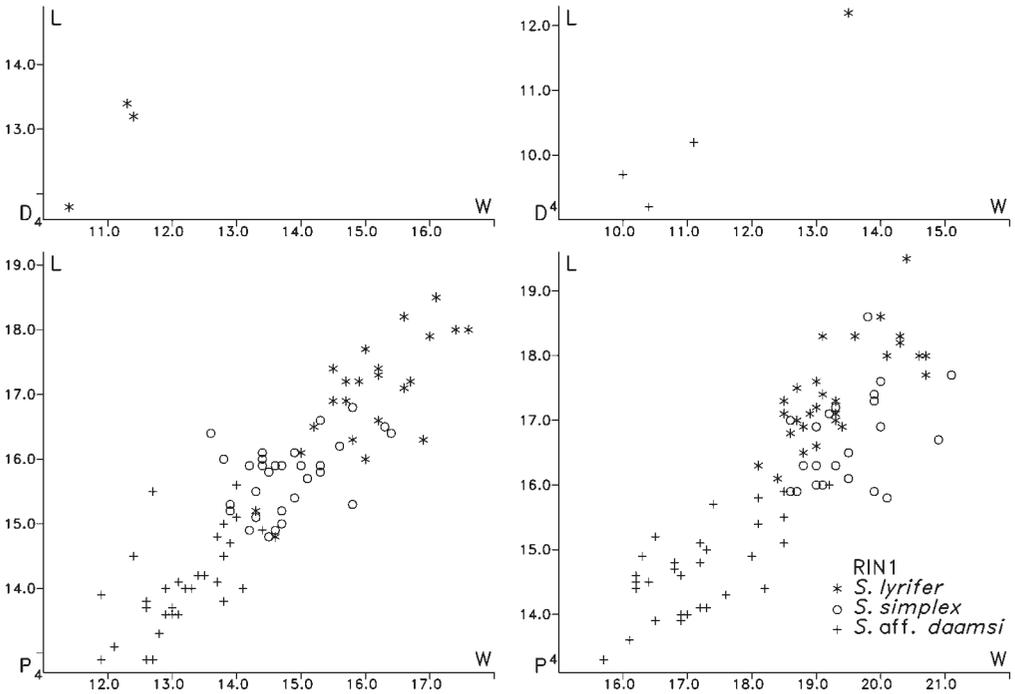


Fig. 2. Length/width diagrams of D4 and P4 of *Stertomys* from Rinascita 1.

Fig. 2. Diagramas longitud/anchura de los D4 y P4 de *Stertomys* de Rinascita 1.

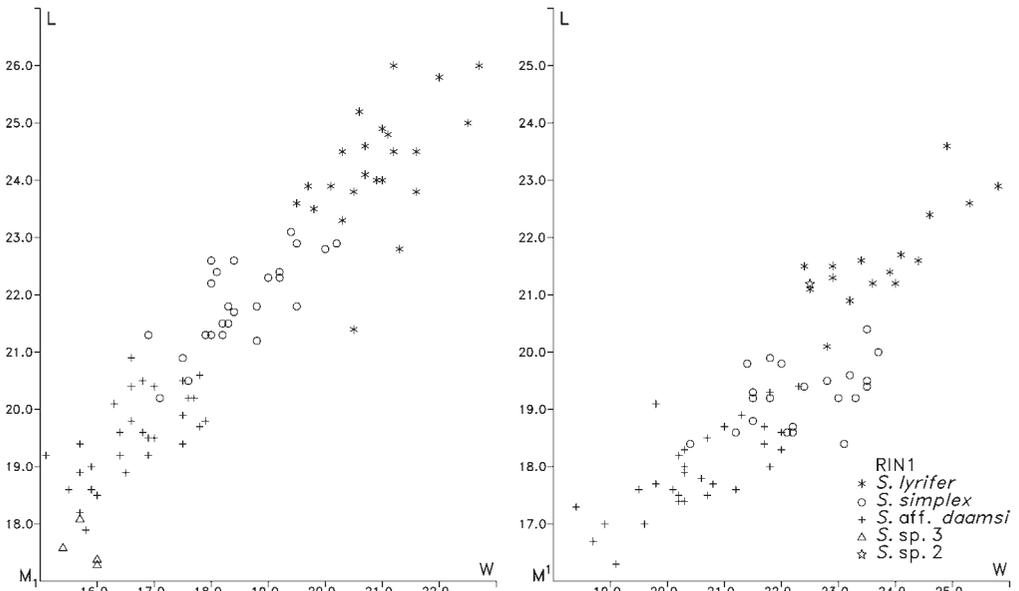


Fig. 3. Length/width diagrams of M₁ and M₁' of *Stertomys* from Rinascita 1.

Fig. 3. Diagramas longitud/anchura de los M₁ y M₁' de *Stertomys* de Rinascita 1.

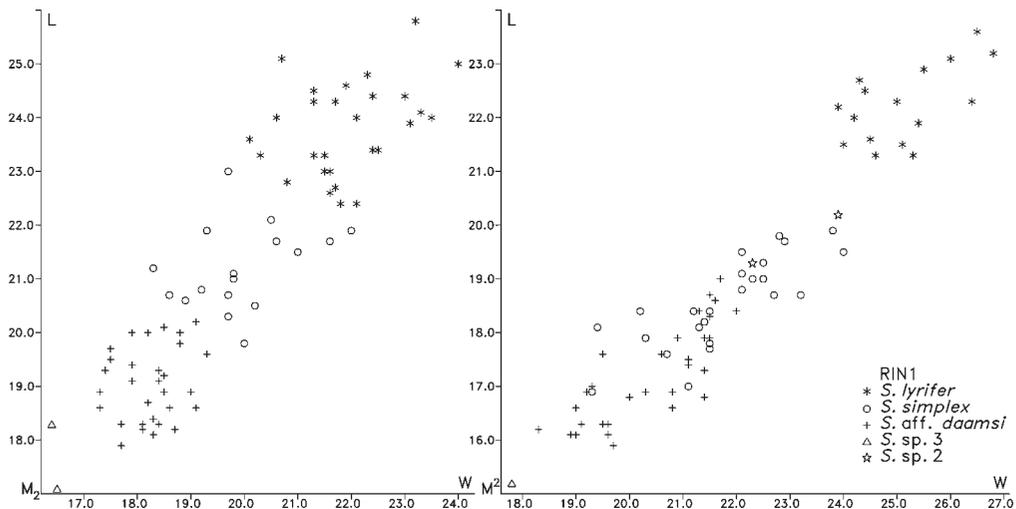


Fig. 4. Length/width diagrams of M_2 and M^2 of *Sertomys* from Rinascita 1.

Fig. 4. Diagramas longitud/anchura de los M_2 y M^2 de *Sertomys* de Rinascita 1.

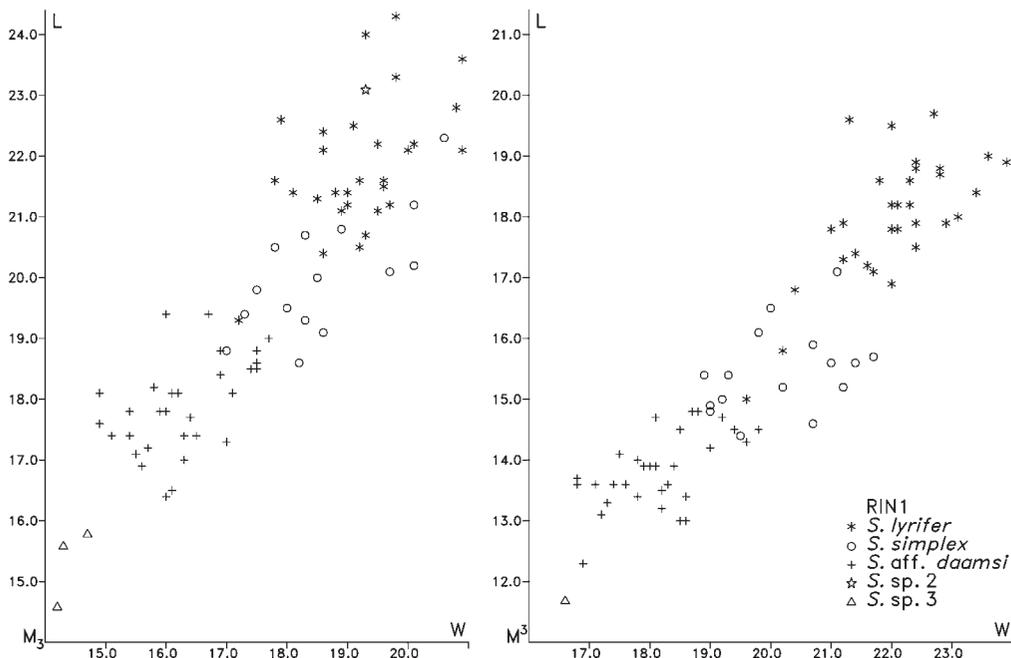


Fig. 5. Length/width diagrams of M_3 and M^3 of *Sertomys* from Rinascita 1.

Fig. 5. Diagramas longitud/anchura de los M_3 y M^3 de *Sertomys* de Rinascita 1.

	Length						Width					
	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
D₄												
<i>S. daunius</i>	4	16.0	17.20	19.1	17.7	1.36	4	13.6	14.28	15.1	10.5	0.64
<i>S. lyrifer</i>	3	11.8	12.80	13.4	12.7		3	10.4	11.03	11.4	9.2	
<i>S. daamsi</i>	32	8.0	9.85	11.7	37.6	1.06	32	7.6	9.10	10.7	33.9	0.84
P₄												
<i>S. laticrestatus</i>	2	28.6	30.65	32.7	13.4		2	27.5	28.75	30.0	8.7	
<i>S. daunius</i>	8	23.7	25.73	27.4	14.5	1.41	7	19.9	22.79	24.0	18.7	1.36
<i>S. lyrifer</i>	23	14.8	16.99	18.5	22.2	0.93	23	14.3	16.07	17.6	20.7	0.85
<i>S. simplex</i>	30	14.8	15.75	16.8	12.7	0.54	30	13.6	14.78	16.4	18.7	0.70
<i>S. daamsi</i>	50	14.9	16.15	17.8	17.7	0.69	50	13.1	14.84	16.6	23.6	0.76
<i>S. aff. daamsi</i>	30	12.9	14.07	15.6	18.9	0.72	30	11.9	13.16	14.4	19.0	0.67
M₁												
<i>S. laticrestatus</i>	6	38.2	41.12	43.3	12.5	1.84	5	32.0	34.66	37.1	14.8	1.82
<i>S. daunius</i>	8	33.3	35.80	38.5	14.5	1.66	6	29.0	31.48	32.7	12.0	1.34
<i>S. lyrifer</i>	23	21.4	24.26	26.0	19.4	1.04	23	19.5	20.90	22.7	15.2	0.82
<i>S. simplex</i>	25	20.2	21.86	23.1	13.4	0.77	25	16.9	18.50	20.2	17.8	0.85
<i>S. daamsi</i>	50	19.6	21.76	24.3	21.4	1.04	50	16.9	18.34	20.1	17.3	0.68
<i>S. aff. daamsi</i>	30	17.9	19.54	20.9	15.5	0.76	30	15.1	16.64	17.9	17.0	0.78
<i>S. sp. 3</i>	4	17.3	17.60	18.1	4.5	0.36	4	15.4	15.78	16.0	3.8	0.29
M₂												
<i>S. laticrestatus</i>	10	37.8	41.65	42.7	12.2	1.45	9	34.7	38.77	41.9	18.8	1.93
<i>S. daunius</i>	8	35.2	37.00	38.1	7.9	0.89	9	31.8	33.79	35.4	10.7	1.13
<i>S. lyrifer</i>	28	22.4	23.80	25.8	14.1	0.87	28	20.1	21.91	24.0	17.7	0.98
<i>S. simplex</i>	17	19.8	21.21	23.0	15.0	0.79	17	18.3	19.94	22.0	18.4	0.99
<i>S. daamsi</i>	50	18.9	20.80	23.6	22.1	0.91	50	18.0	19.60	21.6	18.2	0.79
<i>S. aff. daamsi</i>	30	17.9	19.04	20.2	12.1	0.68	30	17.3	18.25	19.3	10.9	0.56
<i>S. sp. 3</i>	2	17.1	17.70	18.3	6.8		2	16.4	16.45	16.5	0.6	
M₃												
<i>S. laticrestatus</i>	5	33.2	35.20	37.1	11.1	1.39	4	29.6	32.23	34.2	14.4	1.97
<i>S. daunius</i>	6	31.5	33.78	36.6	15.0	1.82	6	28.1	29.38	31.0	9.8	0.95
<i>S. lyrifer</i>	29	19.3	21.84	24.3	22.9	1.09	29	17.2	19.22	20.9	19.4	0.89
<i>S. simplex</i>	15	18.6	20.02	22.3	18.1	0.98	15	17.0	18.59	20.6	19.1	1.09
<i>S. daamsi</i>	50	17.1	19.38	21.3	21.9	1.02	50	15.2	17.18	19.3	23.8	0.86
<i>S. aff. daamsi</i>	30	16.4	17.89	19.4	16.8	0.78	30	14.9	16.27	17.7	17.2	0.81
<i>S. sp. 2</i>	3	14.6	15.33	15.8	7.9		3	14.2	14.40	14.7	3.5	
<i>S. sp. 3</i>	1		23.10				1		19.30			

Table 1a. Measurements of lower cheek teeth of various species of *Stertomys*. Species from Rinascita 1 in bold face. V' is the variability coefficient as defined by Freudenthal & Cuenca Bescós (1984).

Tabla 1a. Medidas de los dientes inferiores de las especies de *Stertomys*. Especies de Rinascita 1 en negrita. V' es el coeficiente de variabilidad definido por Freudenthal & Cuenca Bescós (1984).

	Length						Width					
	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
D ⁴												
<i>S. daunius</i>	2	17.3	17.85	18.4	6.2		2	18.5	19.20	19.9	7.3	
<i>S. lyrifer</i>	1		12.20				1		13.50			
<i>S. daamsi</i>	25	8.2	9.69	11.1	30.1	0.73	26	8.3	11.10	13.0	44.1	1.07
<i>S. aff. daamsi</i>	3	9.2	9.70	10.2	10.3		3	10.0	10.50	11.1	10.4	
P ⁴												
<i>S. laticrestatus</i>	4	30.2	30.48	30.9	2.3	0.31	4	30.0	30.93	31.7	5.5	0.70
<i>S. daunius</i>	4	26.5	27.13	27.8	4.8	0.62	4	29.0	29.93	31.5	8.3	1.09
<i>S. lyrifer</i>	28	16.1	17.45	19.5	19.1	0.77	29	18.1	19.33	20.7	13.4	0.76
<i>S. simplex</i>	22	15.8	16.70	18.6	16.3	0.74	22	18.6	19.51	21.1	12.6	0.69
<i>S. daamsi</i>	50	14.4	16.34	18.2	23.3	0.87	50	17.8	19.21	21.2	17.4	0.88
<i>S. aff. daamsi</i>	30	13.3	14.70	16.0	18.4	0.69	30	15.7	17.19	19.2	20.1	0.87
M ¹												
<i>S. laticrestatus</i>	7	29.9	37.73	39.3	27.2	3.46	7	30.8	39.34	42.3	31.5	3.90
<i>S. daunius</i>	9	32.0	33.52	35.3	9.8	0.97	9	33.3	35.19	36.8	10.0	1.05
<i>S. lyrifer</i>	16	20.1	21.66	23.6	16.0	0.85	16	22.4	23.79	25.8	14.1	1.01
<i>S. simplex</i>	23	18.4	19.26	20.4	10.3	0.54	22	20.4	22.34	23.7	15.0	0.92
<i>S. daamsi</i>	114	17.9	19.59	21.8	19.6	0.77	109	19.7	22.49	25.0	23.7	0.89
<i>S. aff. daamsi</i>	30	16.3	17.95	19.4	17.4	0.76	30	18.4	20.51	22.3	19.2	1.04
<i>S. sp. 2</i>	1		21.20				1		22.50			
M ²												
<i>S. laticrestatus</i>	8	38.8	39.71	41.8	7.4	1.30	8	39.2	41.98	43.6	10.6	1.51
<i>S. daunius</i>	8	31.2	33.28	35.6	13.2	1.41	8	34.3	36.84	38.1	10.5	1.13
<i>S. lyrifer</i>	17	21.3	22.21	23.6	10.2	0.71	16	23.9	25.12	26.8	11.4	0.93
<i>S. simplex</i>	24	16.9	18.56	19.9	16.3	0.84	24	19.2	21.76	24.0	22.2	1.24
<i>S. daamsi</i>	139	16.7	18.77	22.0	27.4	0.87	134	19.4	22.10	25.0	25.2	0.92
<i>S. aff. daamsi</i>	30	15.9	17.21	19.0	17.8	0.90	30	18.3	20.38	22.0	18.4	1.07
<i>S. sp. 2</i>	1		15.20				1		17.80			
<i>S. sp. 3</i>	2	19.3	19.75	20.2	4.6		2	22.3	23.10	23.9	6.9	
M ³												
<i>S. laticrestatus</i>	3	30.3	31.50	32.2	6.1		3	33.2	35.43	37.3	11.6	
<i>S. daunius</i>	10	26.4	27.66	29.8	12.1	1.18	10	31.5	32.71	34.6	9.4	0.96
<i>S. lyrifer</i>	31	15.0	18.01	19.7	27.1	1.04	31	19.6	22.03	23.9	19.8	0.96
<i>S. simplex</i>	16	14.4	15.46	17.1	17.1	0.70	16	18.9	20.17	21.7	13.8	0.96
<i>S. daamsi</i>	50	13.7	15.28	17.4	23.8	0.74	50	17.7	19.74	22.3	23.0	0.91
<i>S. aff. daamsi</i>	30	12.3	13.82	14.8	18.5	0.61	30	16.8	18.13	19.8	16.4	0.81
<i>S. sp. 1</i>	1		11.70				1		16.60			
<i>S. sp. 3</i>	1		24.90				1		30.60			

Table 1b. Measurements of upper cheek teeth of various species of *Stertomys*.Tabla 1b. Medidas de los dientes superiores de las especies de *Stertomys*.

Plate 1 / Lámina 1

Stertomys aff. *daamsi* Freudenthal & Martín Suárez, 2006.

Fig. 1. P₄ sin. RGM 514210.

Fig. 2. M₁ sin. RGM 514237.

Fig. 3. M₂ sin. RGM 514272.

Fig. 4. M₃ sin. RGM 535004.

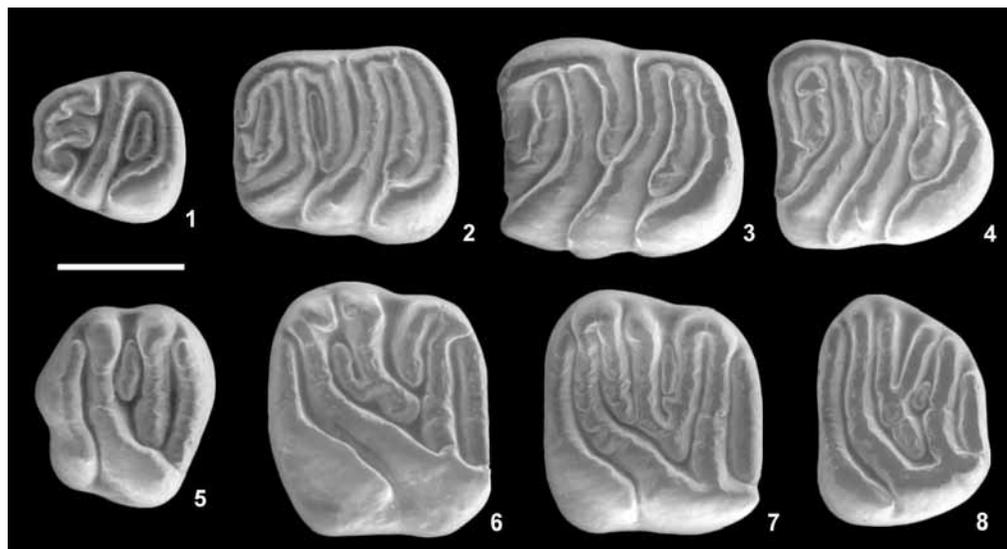
Fig. 5. P⁴ sin. RGM 535031.

Fig. 6. M¹ sin. RGM 535091.

Fig. 7. M² sin. RGM 535123.

Fig. 8. M³ sin. RGM 535061.

Scale represents 1mm / La escala representa 1 mm.



Stertomys simplex sp. nov.

Fig. 1. P₄ sin. RGM 535349.

Fig. 2. M₁ sin. RGM 535377.

Fig. 3. M₂ sin. RGM 535402.

Fig. 4. M₃ sin. RGM 535424.

Fig. 5. M₃ dext. RGM 535428.

Fig. 6. M₂ dext. RGM 535414.

Fig. 7. M₁ dext. RGM 535395.

Fig. 8. P₄ dext. RGM 535363.

Fig. 9. P⁴ sin. RGM 535445.

Fig. 10. M¹ sin. RGM 535470 Holotype.

Fig. 11. M² sin. RGM 535498.

Fig. 12. M³ sin. RGM 535455.

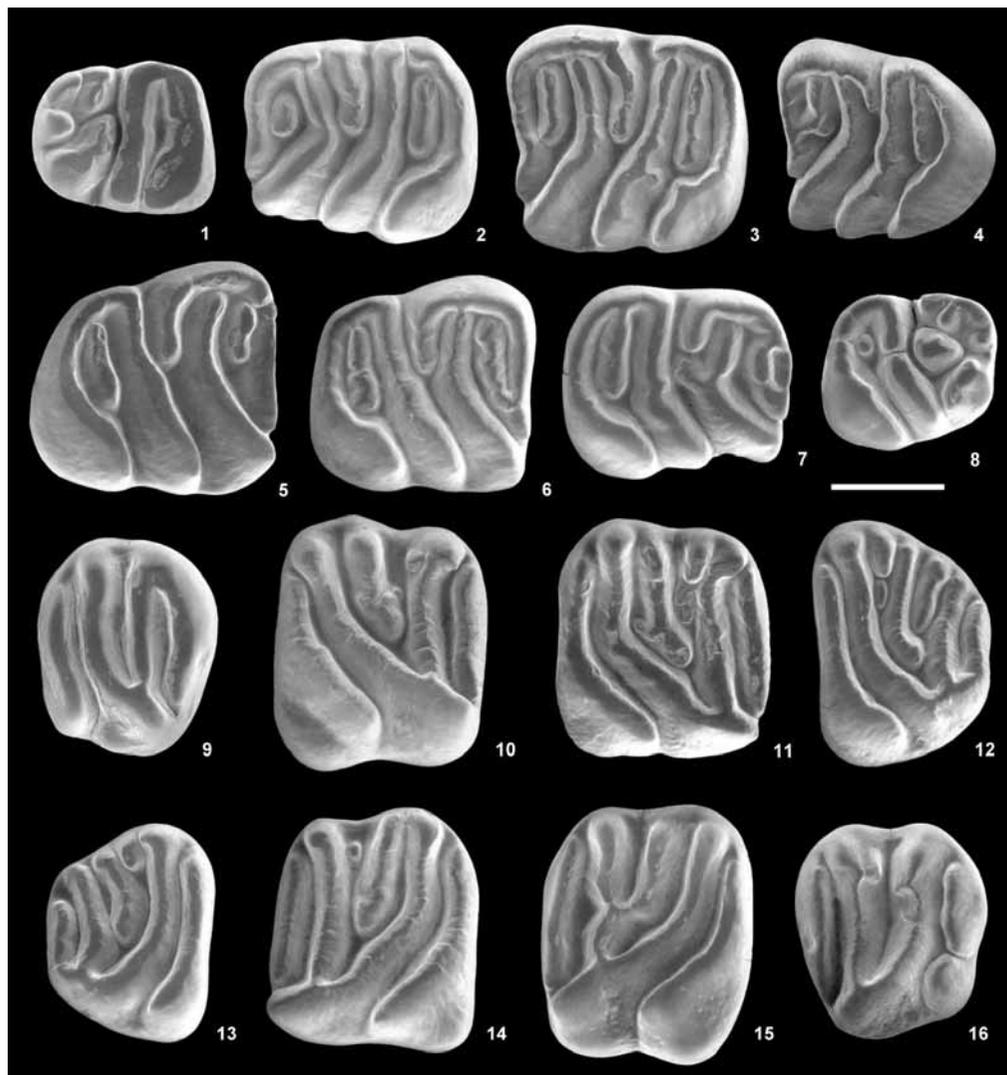
Fig. 13. M³ dext. RGM 535459.

Fig. 14. M² dext. RGM 535504.

Fig. 15. M¹ dext. RGM 535484.

Fig. 16. P⁴ dext. RGM 535447.

Scale represents 1mm / La escala representa 1 mm.



Sertomys lyrifer sp. nov.

- Fig. 1. P₄ sin. RGM 535153.
Fig. 2. M₁ sin. RGM 535210.
Fig. 3. M₂ sin. RGM 535229.
Fig. 4. M₃ sin. RGM 535176.
Fig. 5. M₃ dext. RGM 535196.
Fig. 6. M₂ dext. RGM 535255.
Fig. 7. M₁ dext. RGM 535225 Holotype.
Fig. 8. P₄ dext. RGM 535174.
Fig. 9. D₄ sin. RGM 535151.
Fig. 10. D₄ dext. RGM 535152.

- Fig. 12. D⁴ dext. RGM 535257.
Fig. 13. P⁴ sin. RGM 535258.
Fig. 14. M¹ sin. RGM 535320.
Fig. 15. M² sin. RGM 535330.
Fig. 16. M³ sin. RGM 535288.
Fig. 17. M³ dext. RGM 535300.
Fig. 18. M² dext. RGM 535340.
Fig. 19. M¹ dext. RGM 535322.
Fig. 20. P⁴ dext. RGM 535271.

Sertomys lyrifer sp. nov. or *Sertomys simplex* sp. nov.

- Fig. 11. D⁴ dext. RGM 535256.

Scale represents 1mm / La escala representa 1 mm.

