Cricetidae (Rodentia) from the Neogene of Gargano (Prov. of Foggia, Italy)

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Hattomys, a new genus of Cricetidae, is described and three new species *H. beetsi, H. nazarii* and *H. gargantua* are attributed to it. *Hattomys* are very large cricetids, and the evolution of the genus is characterized by a considerable increase in size, and an increasing predominance of ridges over cusps. The supposedly oldest Gargano localities yielded, apart from the lineage *H. beetsi-nazarii-gargantua*, some scarce material of three other hamster species: a *Megacricetodon*, a *Cricetulodon* and a *Cricetus*. Comparison with the Spanish sequences of rodent faunas shows that the Gargano faunas probably are of late Turolian age, equivalent of the Messinian.

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Introduction

Three families of rodents are represented in the Neogene Gargano fissure faunas. Among these the Muridae are by far the most frequent, but Gliridae and Cricetidae are also found in considerable quantities and number of species. Gliridae are present throughout the entire biostratigraphic range of Gargano faunas as constructed by Freudenthal (1976). Cricetidae, on the other hand, are lacking in the youngest localities. As a matter of fact the extinction of the Gargano cricetids seems to be linked to a phase of diversification of the murids. In the oldest localities two or three species of cricetids may occur; these soon disappear, and then only one species per locality persists, until the level of Chiro 2 - Chiro 10, where they reach their maximum size, and then suddenly disappear. The material studied was collected by a team of the Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands, with additional financial support by the Nederlandse Organisatie voor Zuiver-Wetenschappelijk Onderzoek (Z.W.O) and the Consiglio Nazionale delle Ricerche (C.N.R.). The material is kept in the Rijksmuseum van Geologie en Mineralogie under registration numbers RGM 258 181-258 800 and 263 231-263 931.

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For a history of the research on the Gargano faunas the reader is referred to Daams & Freudenthal, 1985.

METHODS

At first I tried to measure the material with the Ortholux microscope with measuring equipment as described by Freudenthal (1966). It turned out, however, that many of the specimens are so large that orientation under this mocroscope presented serious difficulties. I then decided to use a Wild M5 binocular with ocular micrometer. Though this is a less accurate measuring method, I think the procentual error is probably not much larger, in view of the large size of the teeth. The smaller specimens (belonging to the genera *Cricetulodon, Cricetus* and *Megacricetodon*) presented no problems and were measured on the Ortholux. Measurements are given in tenths of millimetres.

The orientation of the specimens for measurement is as described by Freudenthal (1966). Due to its peculiar form the M^1 of *Hattomys* caused some difficulties and produced irrealistic values for its width. Therefore the width of M^1 has been measured perpendicularly to a tangent to the lingual border, between this tangent and the paracone or metacone, or simply over hypocone and metacone.

For the description of the teeth the terminology proposed by Mein & Freudenthal (1971) has been used. However, the anterior parts of M^1 and M_1 of *Hattomys* are so complex, that the description became a rather complicated affair. For this reason I decided to introduce a new term: preloph(id). Normally in cricetids, protoconid, metaconid and anterolophulid meet at a point between the anteroconid and the first pair of main cusps. In *Hattomys*, however, there is not one single anterolophulid, but there are two or three (or even four) crests pointing backwards from the anteroconid. The anterolophulids, protoconid and the protolophulid may meet in one point, but in many cases there is a transversal crest, halfway between the anteroconid and the first pair of main cusps, on which the anterolophulids, the protoconid and the protolophulid insert. This crest is

called 'prelophid', and it is considered to be long when it stretches over about 25% of the width of the molar measured over protosinusid and anterosinusid. The preloph is a similar structure in the upper molars.

Descriptions

Family Cricetidae
Subfamily Cricetinae

Genus *Hattomys* gen. nov.

Type species — *Hattomys gargantua* sp. nov.
Deriatio nominis — This genus is named after bishop Hatto of Mainz, who was possibly one of the greatest hamsters ever. According to the legend he amassed huge amounts of wheat in his warehouses and refused to give any to the hungry people. Finally he admitted the starvelings in his warehouse, closed the door behind them and set fire to the building. The mice were driven out of the building and entered the bishops castle where they ate everything. The bishop fled to an island in the Rhine, but the mice came after him and ate him too. Equally, the genus *Hattomys* became extinct when giant mice invaded the island Gargano. (Reference: H. Hoitz, Rheinwanderbuch, W. Stollfuss, Bonn, 120 pp.).

Diagnosis — Large to very large cricetids (first upper molar up to 6 mm long, tooth row up to 15 mm). Infraorbital foramen triangular, wider above than below, palate ending between the M^3, foramen incisivum ending before the M^1. Jugal arch placed high on the brain case. Anteroconid of M_1 generally split, anterolophulid of M_1 double. Mesolophid of M_3 generally present, often long. Anterocone of M^1 split, anterolophule of M^1 double. Mesolophs long. Third molars not very much reduced. Labial walls of labial cusps often provided with a flange along the border of the molars. M^1 has three or four roots, M^2 has four roots, M^3 has three or four roots. The higher number of roots is linked to larger size.

Differential diagnosis — Morphologically *Hattomys* has much in common with *Cricetulodon*. It differs from *Cricetulodon* by its larger size, the complexity of the anterior part of the M_1, the less reduced third molars, and the morphology of the mesolophids and anterior hypolophulids.

The smallest *Hattomys* are of about the same size as *Cricetus*. *Hattomys* differs from this genus by the complexity of the anterior part of M_1, the tendency to form longitudinal connections in metaconid, entoconid and paracone, the frequent presence of ectomesolophids and entomesolophs, the transversal position of the mesolophs, and the shorter palate.

Hattomys beetsi sp. nov.
Fig. 1; Pl. 1, figs 1-16.

Derivatio nominis— In honour of Dr C. Beets, former director of the RGM, who participated in the discovery of the Neogene Gargano faunas.
Holotype — Mandibula dext. with M_1-M_3, RGM 263 775, Pl. 1, fig. 1.
Type locality — Biancone 1, Gargano, Prov. of Foggia, Italy.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	25	29.6	31.2	34.1	1.04	25	17.4	19.1	21.3	0.79
M_2	26	24.3	25.6	26.9	0.76	26	19.0	20.3	22.1	0.79
M_3	26	23.8	26.1	27.6	1.01	26	19.0	20.4	21.6	0.78
M^1	25	31.1	33.4	35.5	1.32	25	20.0	22.1	24.1	0.98
M^2	25	23.5	25.7	28.8	1.32	25	20.2	21.8	23.6	0.78
M^3	25	21.4	23.8	25.9	0.96	25	19.7	20.7	22.9	0.77

Diagnosis — So far the smallest representative of the genus (see Figs. 7-14). The anteroconid and anterolophulid of M_1 present rather complex structures. Mesolophids are generally absent in M_1 and long in M_3. Traces of double anterior hypolophulids are not uncommonly present in the lower molars. Anterocone of M^1 deeply split. Labial border of M^1 almost straight, outer walls of labial cusps of upper molars hardly or not flanged, cusps hardly or not carved in. The mesolophs of the upper molars are generally long, often in contact with the metacone, so that the mesoloph is an anterior metalophule; there never is a mesoloph plus an anterior metalophule. Entomesolophs are absent in M^1 and may be present in M^2 and M^3.

Description

M_1 — Anteroconid generally split into a smaller lingual cusp, and a larger labial one. In about 30 % of the specimens this labial cusp is subdivided again, so that the anterolophid may consist of three or — in one case — even four cusps. The connection between the anterolophid and the first pair of main cusps is rather complex, generally consisting of three ridges. The central ridge is longitudinal, connecting the foremost point of the protoconid with the lingual edge of the labial anteroconid cusp; it may be

Plate 1

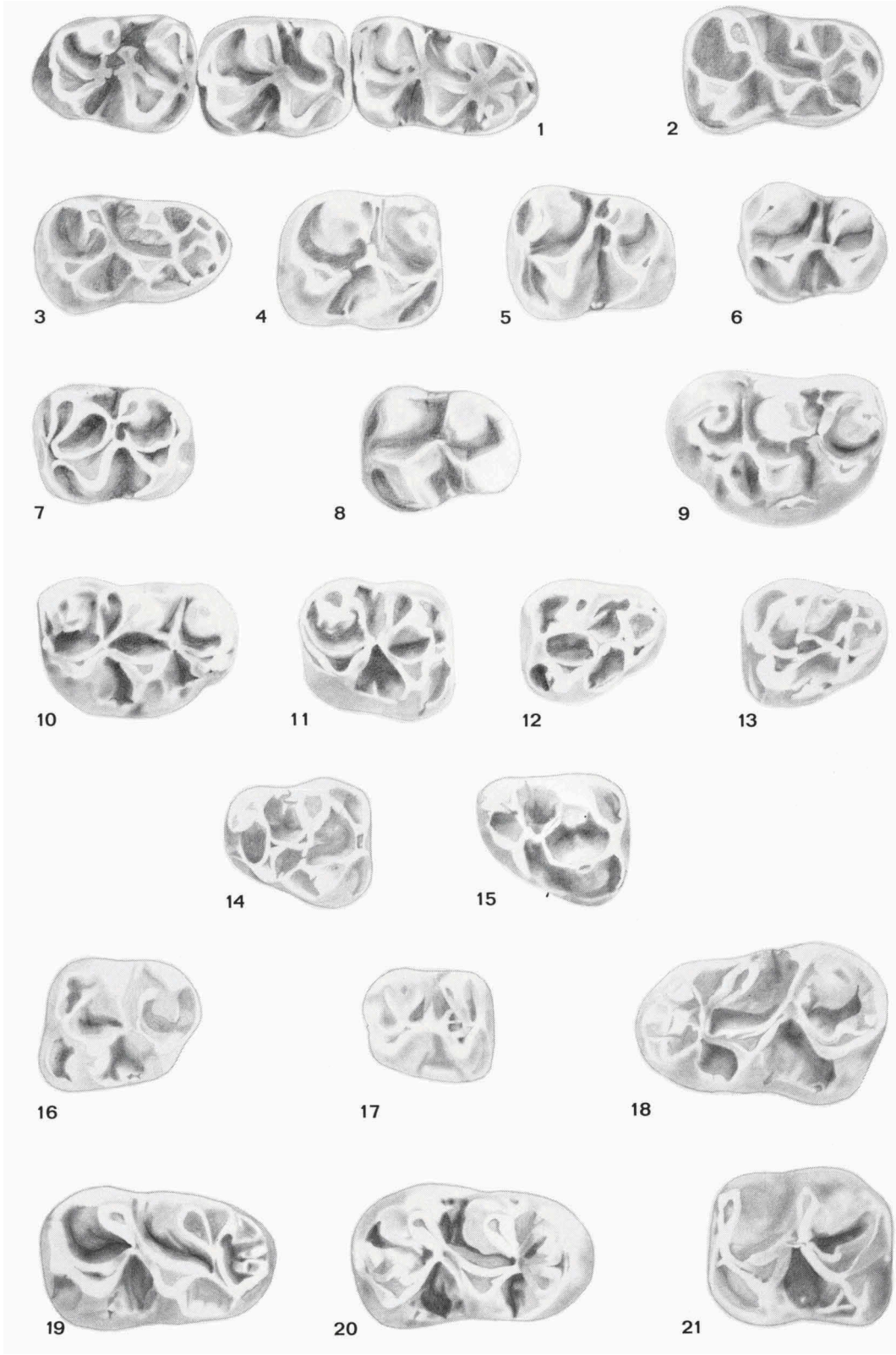
Fig. 17 × 15, all others × 10.

Hattomys beetsi sp. nov. from Biancone:
1. M_1-M_3 dext., RGM 263 775, holotype.
2. M_1 dext., RGM 263 789.
3. M_1 dext., RGM 263 799.
4. M_2 dext., RGM 263 812.
5. M_3 sin., RGM 263 825.
6. M_3 sin., RGM 263 829.
7. M_3 sin., RGM 263 831.
8. M_3 sin., RGM 263 832.
9. M^1 sin., RGM 263 851.
10. M^1 dext., RGM 263 871.
11. M^2 dext., RGM 263 887.
12. M^3 sin., RGM 263 898.
13. M^3 sin., RGM 263 905.
14. M^3 dext., RGM 263 909.
15. M^3 dext., RGM 263 915.
16. M^2 sin., RGM 263 882.

Megacricetodon sp. from Biancone:
17. M^2 dext., RGM 263 922.

Hattomys nazarii sp. nov. from Nazario 2 B:
18. M_1 sin., RGM 263 574, holotype.
19. M_1 dext., RGM 263 586.
20. M_1 dext., RGM 263 591.
21. M_2 sin., RGM 263 599.

Plate 1



considered as the anterolophulid. The labial connection originates from the anterolophulid and runs obliquely or transversely toward the labial end of the anteroconid; it may be interpreted as the labial spur of the anterolophulid. The third connection runs longitudinally or obliquely toward the lingual cusp of the anteroconid, originating either from the anterolophulid or from the foremost point of the metaconid. The metaconid points obliquely forward, but in most specimens the metalophulid is not a smooth continuation of this oblique direction: the foremost points of protoconid and metaconid are connected by a transversal ridge, the prelophid, from which the three forward connections originate. This transversal connection may also be absent, causing the mesosinusid to continue forward towards the anteroconid. As a matter of fact any of the mentioned ridges and connections may be partial, interrupted, or absent, causing a very high degree of morphological variability in the front part of M_1. The mesolophid is always absent, and a weak to very weak ectomesolophid may be present (4 specimens). The hypolophulid is anterior, a posterior hypolophulid never exists, but in about seven specimens there is a second connection (though very weak) between entoconid and hypoconid, shortly behind the hypolophulid, and in seven other specimens such a second connection is indicated by a bulge of the internal walls of hypoconid and/or entoconid. These phenomena never lie farther backward than the middle of the hypoconid, and are always weaker than the hypolophulid. It seems possible that these phenomena represent remnants of an ancient hypolophulid, and that the dominating connection has developed from the mesolophid. The posterolophid is rather broad and well connected to the posterior edge of the entoconid encircling a large posterosinusid.

M_2 — A trace of the lingual anterolophid may be present, but there is no anterosinusid. The mesolophid is absent in 20 specimens, very short in 4, and long and thin in 1 specimen. Traces of a second hypolophulid, like in M_1, are present in 4 out of 26 specimens, and in one case a longitudinal posterior hypolophulid is present. Ectomesolophids are present in 17 out of 25 specimens, but they are rarely well-developed. The posterolophid is broad and strongly fused with the postero-internal corner of the entoconid.

M_3 — The lingual anterolophid is slightly better developed than it is in M_2, so that a — very small — anterosinusid is frequently present. The posterior part of the tooth is quite variable: generally the mesolophid is long, or at least well-developed, and its end may be in contact with the metaconid. In 19 specimens the entoconid is directed forward, meeting the mesolophid halfway the mesosinusid. In 5 out of these 19 specimens this is the only connection of the entoconid, in 8 specimens there is a second connection towards the foremost point of the hypoconid, in 5 there is a second connection towards the middle of the hypoconid, and in the 19th specimen the ectolophid is interrupted between hypoconid and protoconid, resulting in a very long sinusid which reaches the entoconid-mesolophid-connection. In 3 specimens there is a mesolophid and a normal anterior hypolophulid, in 2 specimens there is only a normal anterior hypolophulid. In the latter situation it can simply not be decided whether this connection is the mesolophid, or whether the mesolophid actually is missing. In 11 out of 26 specimens a very weak ectomesolophid is present.

M^1 — The anterocone is divided into two more or less equal cusps. The anterolophule is forked; one longitudinal connection reaches the lingual anterocone-cusp; the other one is generally oblique and well connected to the labial cusp; it may, however, be transversal and skim the posterior slope of this cusp. The posterior protolophule is connected to the entoloph, or to the mesoloph, or — rarely — there is a connection to each of these ridges. Apart from the posterior protolophule an anterior connection exists in half the number of specimens, but it is generally weak, or even interrupted. The

mesoloph is medium or long, often reaching the border of the molar, skimming the anterior wall of the metacone, or sending a small longitudinal spur backwards towards the metacone. Only in one case it presents itself as an anterior metalophule. Apart from the solid connection with the end of the posteroloph the metacone has a second, not very well developed connection with the middle of the posteroloph, which is the posterior metalophule. There is no entomesoloph. The labial border of the tooth is straight, or slightly concave.

M^2 — The protolophule is symmetrically double in most specimens; in one case the posterior protolophule is absent, in another case it is forked near the entoloph. The mesoloph is medium or long, connected to the metacone. Generally there is a posterior metalophule, connected to the middle of the posteroloph. In 8 out of 25 specimens there is a very weak entomesoloph. There are four roots.

M^3 — The protolophule is double, and in one case the posterior protolophule is forked near the entoloph. For an M^3 the entoloph is rather long. Hypocone and metacone are smaller than the anterior cusps, but still well-developed. They are connected anteriorly by a crest that may be the original mesoloph, and that still may have a free end reaching the border of the molar. In 3 specimens an entomesoloph is present. The posterior branch of the protocone may be interrupted or low. In some cases the width of the posterior part of the tooth is hardly smaller than the anterior width.

Locality — Rinascita 1.

Material and measurements

M_1 30.0 × 17.8
M_2 29.7 × 23.0, 27.5 × 21.3, 27.9 × 21.3, 27.9 × 23.8, 29.2 × 24.2
M_3 31.7 × 23.7, 30.2 × 22.1, — × 17.0
M^1 37.9 × 24.9, 38.0 × 24.7, 36.6 × 26.0
M^2 27.2 × 22.9
M^3 23.4 × 21.6.

Description

M_1 — The anteroconid is split in a large labial and a small lingual cusp. The lingual anterolophulid is longitudinal, the labial one is transverse, the prelophid is long. There is no free mesolophid.

M_2 — The lingual anterolophid is present and may be long. The mesolophid is absent, long, or there is a prolonged mesostylid, which may be a remnant of the lingual part of the mesolophid. One specimen has a second anterior hypolophulid, enclosing a funnel behind the main connection. One specimen has an ectomesolophid.

M_3 — The mesolophid is long, with a spur branching off towards the metaconid. In one specimen the entoconid is connected longitudinally to the mesolophid, and there is a second transversal connection to the middle of the hypoconid. Both specimens have an ectomesolophid.

M^1 — The anterocone is split; the anterolophule is double; 2 specimens have a preloph. There is a long spur in the anterosinus. The anterior protolophule is oblique (2), or double, forming a funnel with the preloph (1). The posterior protolophule is connected obliquely to the entoloph. The mesoloph is long. There is no metalophule. The entomesoloph is present or absent.

M^2 — The anterior protolophule is double and encloses a funnel, the posterior one is oblique towards the entoloph. The mesoloph is medium and forms a typical anterior hypolophule in one specimen. The posterior metalophule is present. There is no entomesoloph.

Locality — Trefossi 1.

Description — A single M^1 sin., measuring 35.6 × 23.5, is attributed to *H. beetsi*. It has a well-divided anterocone, two anterolophules and a long spur in the anterosinus; the anterior protolophule has almost disappeared, the mesoloph is long and bent towards the metacone; there is no metalophule.

Locality — Chiro 19.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	2	33.3	35.0	36.7	2.40	1	—	23.3	—	—
M_2	6	25.0	27.0	28.8	1.37	5	20.8	22.5	24.2	1.33
M_3	7	27.5	29.2	31.3	1.29	8	20.4	22.3	24.2	1.10
M^1	1	—	35.0	—	—	1	—	23.3	—	—
M^2	3	27.1	27.4	27.9	0.46	3	22.1	23.1	24.2	1.06
M^3	2	24.2	24.6	25.0	0.57	2	21.7	21.9	22.1	0.28

This material agrees completely with *H. beetsi* from Biancone 1. In size it is intermediate between the material from Biancone and the population from Chiro 3 A, which is attributed to *H. nazarii*. The scarcity of the material renders it impossible to make a specific identification with certainty.

Hattomys nazarii sp. nov.
Fig. 2; Pl. 1, figs. 18-21; Pl. 2, figs. 1-12.

Derivatio nominis — The species is named after the type locality.
Holotype — M_1 sin., RGM 263 574, Pl. 1 , fig. 18.
Type locality — Nazario 2 B.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	21	35.0	38.7	41.2	1.40	20	22.1	23.8	25.0	0.90
M_2	40	30.0	32.0	33.7	1.03	40	22.9	25.7	28.3	1.32
M_3	29	31.2	33.8	35.8	1.44	28	22.5	26.1	28.3	1.32
M^1	23	39.6	42.0	45.4	1.57	23	25.0	27.1	28.7	0.92
M^2	24	30.8	33.0	35.0	1.41	24	25.4	27.5	29.6	1.07
M^3	21	29.2	31.3	33.3	1.14	21	23.7	26.1	28.3	1.15

Diagnosis — *Hattomys* of intermediate size between *H. beetsi* and *H. gargantua*. Anteroconid generally split into two or three cusps, with two or three backward connections. Free mesolophid generally absent in M_1, long in M_3. Traces of double hypolophulids rarely present in the lower molars. Ectomesolophids may be present. Anterocone of M^1 deeply split, labial border of M^1 concave. Mesolophs of the upper molars often long, generally in contact with the metacone. Entomesolophs may be present in M^1, M^2 and M^3, but are least developed in M^1.

Description

M_1 — The anterolophid is a half circle, without subdivision (1), bearing two cusps (7), three cusps (5), or four cusps (1). The subdivision takes place from behind. In 1 specimen there are two backward connections, in 14 there are three, and in 1 specimen there are four connections. The number of connecting crests is not related to the number of cusps. When there are three connections one is axial and longitudinal, one is oblique and labial, and one is oblique or transverse and lingual. The specimen with four crests is basically one with three connections, in which the lingual one is forked. Anyone of the crests may be more or less interrupted. In most cases these double or triple anterolophulids meet in a prelophid (see the chapter Methods). The prelophid is less well-developed than it is in *H. gargantua*. The metaconid points obliquely forward, or longitudinally towards the prelophid. The anterior branch of the protoconid is always longitudinal and meets the labial end of the prelophid. In a few cases there is a second connection between protoconid and metaconid, a little farther backward, thus creating a small funnel. The mesolophid is absent in 15 specimens, but in 4 of these a prolonged mesostylid might be interpreted as the lingual part of the mesolophid; in 2 specimens the mesolophid is short and directed obliquely toward the metaconid, in 2 specimens it is long. In a few specimens a bulge on the lingual wall of the hypoconid might be a remnant of a second hypolophulid. The main hypolophulid is directed obliquely forward; it may have originated from the mesolophid. There is no ectomesolophid.

M_2 — In about half the number of specimens a very small remainder of the lingual anterolophid is present, but there never is an anterosinusid. The mesolophid is long in 8 specimens, short and oblique toward the metaconid in 3, and absent in 26. Of these 26 specimens 4 present a prolonged mesostylid that could be a remnant of the lingual part of the mesolophid; in 1 of the 26 there is a thin second hypolophulid behind the main one, and in several specimens the lingual wall of the hypoconid is bulged. Three specimens have an ectomesolophid.

M_3 — The lingual anterolophid is slightly better developed than it is in M_2; there even may be a very small anterosinusid. The mesolophid is long; its labial part is generally fused with the anterior hypolophulid. In 8 out of 24 specimens a second connection is present between the entoconid and the anterior branch of the hypoconid, and in 2 more specimens such a connection is indicated; 2 of these 10 specimens even show a third connection, somewhat more backward. An ectomesolophid is present in 12 out of 26 specimens; it is often well-developed. The posterior part of the molar is only slightly narrower than the anterior part.

M^1 — The anterocone is divided into two more or less equal cusps. There are two anterolophules. Generally the protocone, the anterior protolophule and the two anterolophules meet in one point, but there may be a preloph. In 3 specimens there is no anterior protolophule. The posterior protolophule is connected to the entoloph. Small extra crests may be present in the anterosinus. Only in one case the paracone is connected longitudinally to the labial anterolophule. The mesoloph is long, bending towards the metacone at its labial end. There is no anterior metalophule. A posterior metalophule is present in 8 out of 22 specimens. One specimen out of 24 has an entomesoloph. The labial border of the molar is concave.

M^2 — In 20 specimens the protolophule is symmetrically double, in 3 specimens the anterior connection is absent. In 3 of the specimens with the double connection a third — longitudinal — connection exists between the metacone and the anteroloph. Like in M^1 the mesoloph is long and bent, and there is no anterior metalophule connecting metacone and hypocone directly. In 12 out of 22 specimens there is a posterior metalophule. Seventeen out of 24 specimens have an entomesoloph. There are four roots.

M^3 — In 12 specimens the protolophule is symmetrically double, in 1 specimen there is no anterior connection, in 1 specimen there is a longitudinal connection toward the anteroloph, instead of the normal protolophule, and in 3 there is an anterior protolophule plus a longitudinally forward connection. The posterior cusps are well-developed, though smaller than the anterior ones. The lingual part of the mesoloph appears to be fused with the anterior metalophule (or it simply constitutes this connection). Halfway the metalophule a spur may split off which should be the free labial end of the mesoloph. There are generally three roots, but a tiny fourth root may exist under the sinus: this fourth root is a derivate of the protocone root, which may be deeply grooved.

Locality — Fina D.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	10	35.8	36.8	38.3	0.83	11	21.7	23.0	24.2	0.77
M_2	8	29.2	29.8	30.8	0.57	8	24.2	25.0	26.2	0.83
M_3	11	28.3	30.8	32.1	1.31	11	23.3	24.5	25.8	0.79
M^1	17	36.7	39.7	42.5	1.60	17	24.2	25.3	26.7	0.85
M^2	16	29.2	31.0	33.7	1.31	17	23.3	25.3	26.7	0.91
M^3	8	28.3	29.5	30.8	0.92	8	23.7	24.8	25.8	0.66

M_1 — The anteroconid is a simple curved ridge with indications of two or three cusps (4), it is split in two (3), or in three cusps (2). The anterolophulid is double (2), or triple (9). The prelophid is absent, short, or long. In about half the number of specimens there is a direct connection between protoconid and metaconid shortly behind the

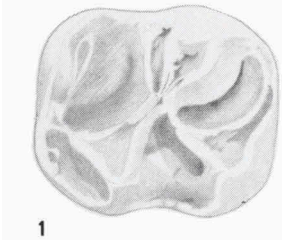
Plate 2

All figures × 10.

Hattomys nazarii from Nazario 2 B:
1. M_2 sin., RGM 263 602.
2. M_2 sin., RGM 263 604.
3. M_3 dext., RGM 263 647.
4. M_3 sin., RGM 263 634.
5. M_3 sin., RGM 263 635.
6. M^1 sin., RGM 263 659.
7. M^1 sin., RGM 263 661.
8. M^1 dext., RGM 263 674.
9. M^2 dext., RGM 263 688.
10. M^2 dext., RGM 263 689.
11. M^3 sin., RGM 263 707.
12. M^3 sin., RGM 263 708.

Hattomys gargantua sp. nov. from Pizzicoli 11:
13. M_1 sin., RGM 258 731.
14. M_1 sin., RGM 258 733.
15. M_2 sin., RGM 258 756.
16. M_2 sin., RGM 258 764.
17. M_3 sin., RGM 258 783.

Plate 2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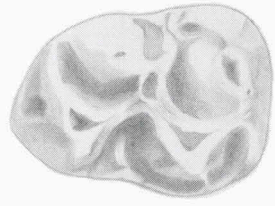
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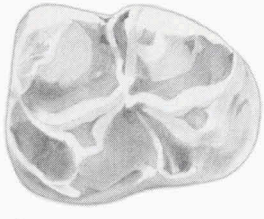
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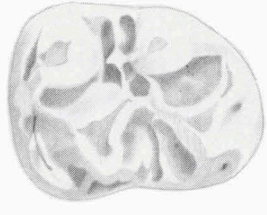
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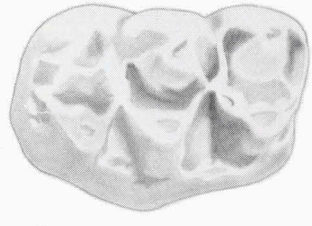
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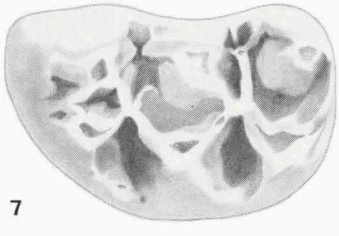
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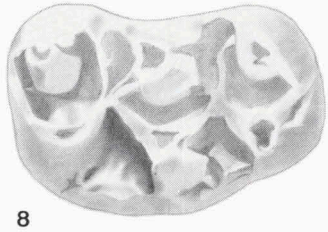
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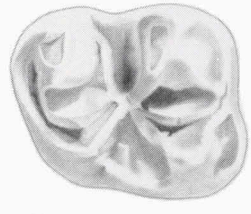
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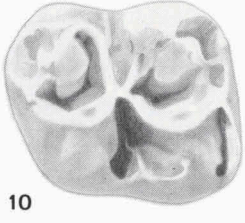
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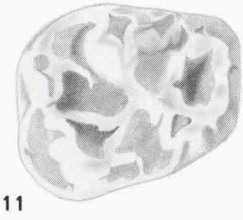
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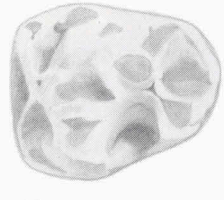
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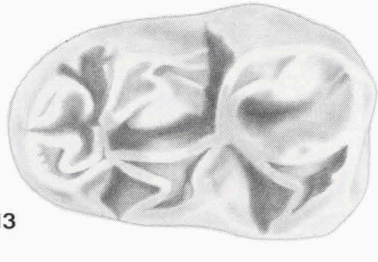
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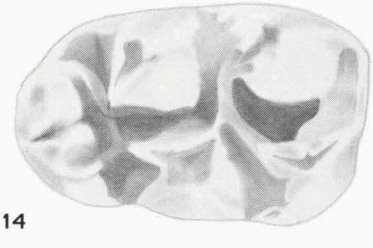
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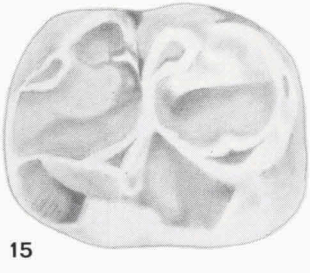
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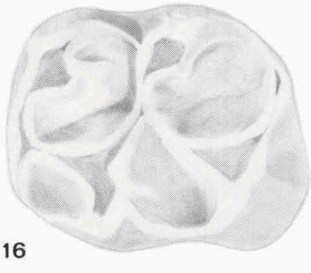
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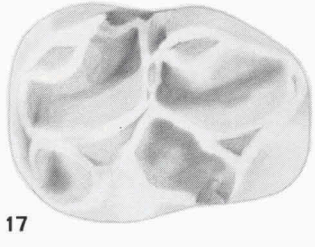

17

prelophid, so that a small funnel is formed. There is no free mesolophid. The lingual wall of the hypoconid may be bulged.

M_2 — Three out of 7 specimens have a small lingual anterolophid. One specimen has a long, poorly developed, mesolophid.

M_3 — The lingual anterolophid is relatively well-developed. The mesolophid is short or long. Six out of 7 specimens have an ectomesolophid.

M^1 — The anterocone is deeply split. The preloph is absent (11), or short (4). Ten specimens have a transversal spur in the anterosinus. A normal anterior protolophule is present (12), or absent (3); in two specimens the protolophule and the anterolophules together form a small funnel. The protolophule is generally oblique towards the anterior branch of the protocone, but in 2 specimens it is longitudinal, towards the labial anterolophule. The posterior protolophule is oblique, connected to the entoloph. The mesoloph is long; it bends backwards to the metacone before reaching the border of the molar. In some cases there is a connection between the lingual part of the mesoloph and the metacone, that looks like a normal anterior metalophule. The posterior metalophule is present (6), or absent (8). Three specimens have a weak entomesoloph.

M^2 — Both the anterior and posterior protolophule are present, and symmetrically oblique. In one specimen there is a third, longitudinal connection, towards the middle of the labial anteroloph. The mesoloph is as in M^1. The posterior metalophule is present (11), or absent (4). Twelve specimens have an entomesoloph.

M^3 — Both protolophules are present, and in two specimens a third forward connection towards the labial anteroloph exists. The labial part of the mesoloph branches off from the anterior metalophule in 7 specimens; it is absent in 3. The entomesoloph is present (7), or absent (4).

Locality — Cantatore 3 A.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	5	34.2	36.3	38.3	1.58	5	20.8	22.1	23.3	0.93
M_2	5	27.1	29.4	31.3	1.84	5	21.7	23.2	24.2	1.09
M_3	1	—	31.3	—	—	1	—	24.6	—	—
M^1	2	37.5	37.5	37.5	0.0	2	23.3	23.8	24.2	0.64
M^2	2	28.3	29.2	30.0	1.20	2	24.2	24.2	24.2	0.0
M^3	3	25.0	26.3	27.5	1.25	3	22.1	22.7	23.8	0.98

In size and morphology this material agrees with *H. nazarii* from Fina D.

Locality — Chiro 7 A.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	6	36.3	38.1	40.0	1.27	6	22.9	24.1	25.4	0.90
M_2	7	29.2	30.5	31.7	1.03	7	22.9	24.7	26.3	1.02
M_3	8	30.8	33.0	34.2	1.15	8	23.8	25.6	27.1	0.96
M^1	5	39.2	41.0	43.3	1.79	6	24.2	25.8	28.3	1.48
M^2	4	30.8	33.1	35.0	1.87	4	25.8	26.8	27.5	0.73
M^3	1	—	30.0	—	—	1	—	25.0	—	—

M_1 — The anteroconid is split into two cusps. The anterolophulid is triple, the prelophid is short or long. Prelophid and metalophulid enclose a funnel in 2 specimens. There is no separate mesolophid, nor an ectomesolophid.

M_2 — It has no mesolophid or ectomesolophid in 5 specimens, 1 specimen has both these features.

M_3 — The mesolophid is long, branching off from the hypolophulid (6), or separately attached to the ectolophid (2). In 2 specimens the anterior hypolophulid is double. An ectomesolophid is present (1), or absent (7).

M^1 — The preloph is absent. There is a spur in the anterosinus. The anterior protolophule is oblique (4), or absent (1). The posterior protolophule is oblique (4), longitudinal (1), or both connections exist (1). The mesoloph is long and bent towards the metacone. The posterior metalophule is present or absent. One specimen has a very weak axial crest from the posteroloph towards the base of the metacone. The entomesoloph is absent.

M^2 — The anterior protolophule is oblique (3), or longitudinal (1), the posterior one is oblique. The posterior metalophule is absent or present. Three specimens have an entomesoloph.

M^3 — The mesoloph branches off, halfway the metalophule, and sends a spur to the paracone. There is an entomesoloph.

Locality — Nazario 2 A.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	12	38.7	40.7	43.3	1.54	11	24.2	25.2	25.8	0.65
M_2	26	30.4	32.5	34.6	1.25	26	24.2	26.4	29.2	1.15
M_3	15	32.1	35.1	36.7	1.54	15	25.0	26.7	28.7	1.14
M^1	25	40.0	42.8	45.8	1.62	25	25.8	27.4	29.2	1.07
M^2	24	30.8	32.7	35.0	1.08	25	25.8	27.3	29.6	0.96
M^3	11	29.2	31.1	32.5	0.97	10	25.4	26.2	26.7	0.45

Description

M_1 — The anteroconid is simple (1), split into two (8), or split into three (3). The anterolophulid is triple (11), or double (1). The prelophid is long, short, or absent. In 4 specimens the prelophid and a somewhat more backward metalophulid enclose a small funnel. The mesolophid is short and oblique (3), long (1), or absent (8). The lingual wall of the hypoconid is frequently bulged, in one specimen there is a very weak trace of a central hypolophulid. One specimen has an ectomesolophid.

M_2 — Eight specimens out of 26 have a trace of a lingual anterolophid. The mesolophid is short (4), long (6), or absent (14). Behind the anterior hypolophulid a second connection exists in 2 specimens. One specimen has an ectomesolophid.

M_3 — The mesolophid is long. A second anterior hypolophulid is indicated in 2 specimens. An ectomesolophid is present (7), or absent (8).

M^1 — The preloph is absent (13), short (6), or long (4). Three specimens have a small funnel behind the preloph. In 17 specimens out of 25 a spur is found in the anterosinus. The anterior protolophule is absent in 6 specimens; in the others it is generally oblique. The posterior protolophule is oblique. The mesoloph is long. In one specimen an axial crest runs from the entoloph forward, through the valley between protocone and paracone. A similar crest in the valley between hypocone and metacone

exists in 2 specimens; in 1 it forms an anterior metalophule. Only one other specimen has a — normal — anterior metalophule. The posterior metalophule is present (11), or absent (11). There is an entomesoloph in 7 specimens.

M^2 — The anterior protolophule is generally oblique, directed to the anterocone, but in several specimens it has a more longitudinal direction, and in three specimens it is forked, forming an oblique and a longitudinal connection; the enclosed funnel is very small. The mesoloph is long. The posterior metalophule is present (12), or absent (9). A crest from posteroloph to mesoloph occurs, as described in Chiro 10 C. The entomesoloph is present (19), or absent (6).

M^3 — In one specimen the anterior protolophule is double. A free mesoloph branches off from the anterior metalophule in 8 specimens. Seven have an entomesoloph.

Locality — Nazario 4.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	14	37.5	42.2	45.0	2.42	14	24.2	27.1	29.2	1.32
M_2	16	32.5	34.6	37.5	1.49	16	25.8	28.1	30.0	1.44
M_3	16	32.5	36.9	40.0	1.85	16	25.8	28.8	33.3	1.76
M^1	10	41.7	45.9	48.3	1.99	10	27.9	29.6	30.8	0.94
M^2	6	35.0	35.9	37.5	1.14	6	28.3	29.4	30.4	0.79
M^3	6	31.7	33.0	35.0	1.12	6	27.1	28.3	29.2	0.70

Description

M_1 — The anteroconid is slightly split (4), split into two cusps (10), or even three cusps (1). In 1 specimen there are two anterolophulids, in 11 there are three, and in 3 specimens there are four crests: the labial and lingual one are complete, the two central ones are interrupted or complete. The prelophid is absent (1), short (5), or long (9). In 1 specimen, shortly behind the prelophid, there is a second connection between protoconid and metaconid. The mesolophid as a separate crest exists in 1 specimen only; it forms a posterior protolophulid in that case. A mesostylid is sometimes present and may be a remnant of a long mesolophid. The lingual wall of the hypoconid is bulged in some specimens, a trace of a second hypolophulid, shortly behind the main one, is present in 1. An ectomesolophid is present in 2 out of 14 specimens.

M_2 — The mesolophid is absent (5), short (1), medium (3), or long (5); only in 1 specimen the long mesolophid is completely free from the hypolophulid; in the others its

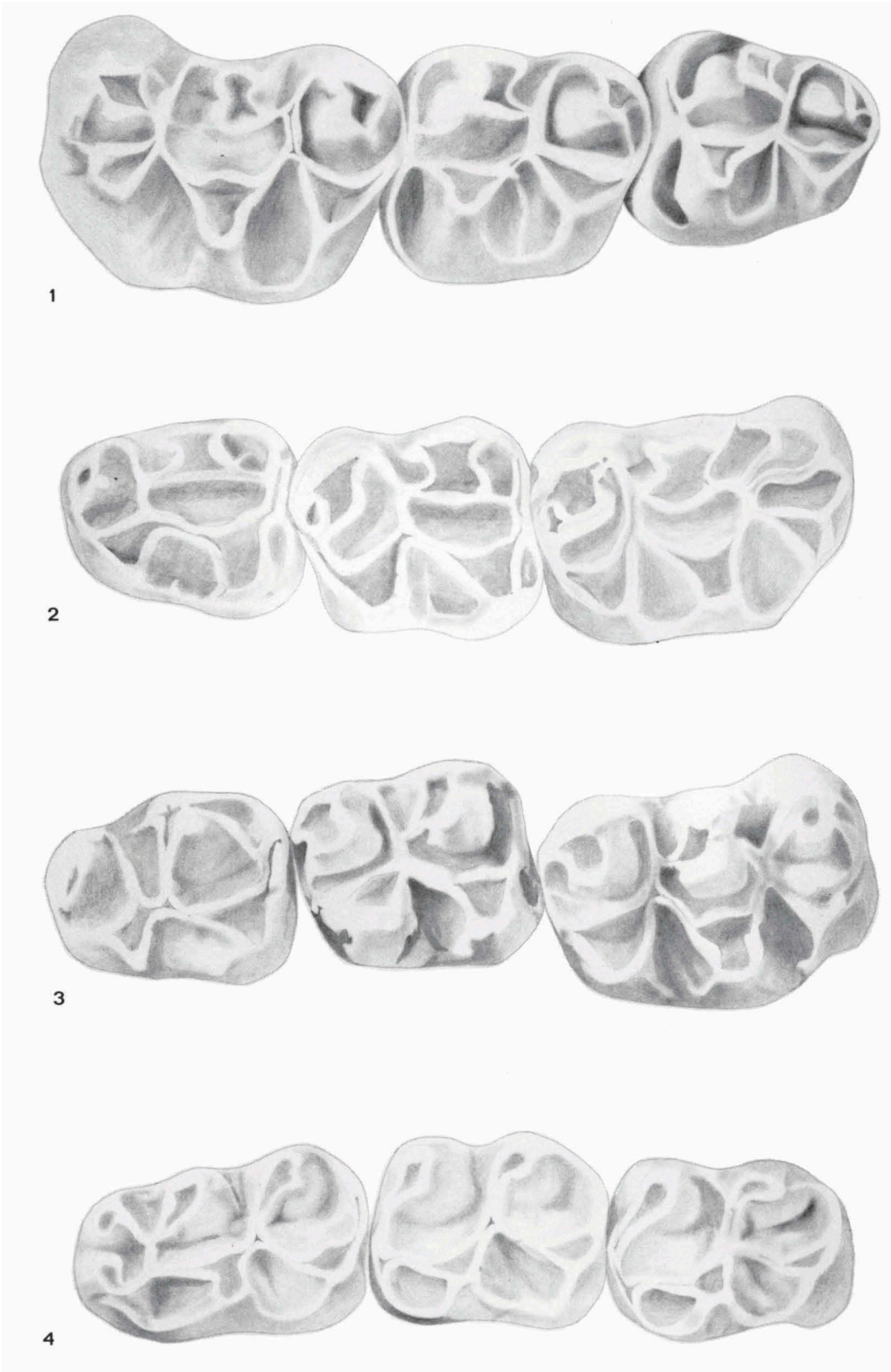
Plate 3

All figures × 10.

Hattomys gargantua sp. nov. from Pizzicoli 11:
1. M^1-M^3 sin., RGM 263-234.
2. M^1-M^3 dext., RGM 263 235.

Hattomys gargantua nov. sp. from Chiro 2 N:
3. M^1-M^3 dext., RGM 263 555, holotype.
4. M_1-M_3 sin., RGM 263 558.

Plate 3



labial part is fused. One specimen has a second hypolophulid shortly behind the main one. An ectomesolophid is present in 1 out of 15 specimens.

M_3 — The mesolophid is long; generally its labial part is fused with the hypolophulid, but in one case its entire length is free, and the hypolophulid lies farther backwards. In 2 other specimens there is a weak second hypolophulid behind the main one. In 1 specimen the metaconid is directed longitudinally backwards towards the middle of the mesolophid.

M^1 — The anterocone is deeply split. Though the position of the crests in the anterior part of the tooth comes very close to the forming of a preloph, a typical preloph does not exist. In 3 specimens the two anterolophules, the protocone and the protolophule meet in a cross. In 7 specimens the two anterolophules are fused in the form of an arch; slightly backwards the protolophule is fused to the protocone. A short to very short longitudinal axial crest unites these two structures. The labial anterolophule may send a spur into the anterosinus (3), or a similar spur may branch off from the protolophule. Two specimens have a long spur in the protosinus. The anterior protolophule is oblique (9), or absent (1). The posterior protolophule is oblique, connected to the entoloph. The mesoloph is long and bent towards the metacone. In 5 specimens the mesoloph is forked, half-way its length; one branch fuses with the anterolabial corner of the metacone, the other one ends freely at the border of the molar. In only 1 specimen an anterior metalophule connects the anterolingual corner of the metacone longitudinally with the mesoloph. In the other specimens the anterior metalophule is absent. The posterior metalophule is present in 1 specimen out of 10. In another specimen there exists a crest that is described in more detail in the material from Chiro 10 C: it runs from the posteroloph longitudinally forward to the basis of the metacone. An entomesoloph is present in 1 specimen only.

M^2 — Both anterior and posterior protolophule are present and symmetrically oblique. The mesoloph is long; in 1 specimen an anterior metalophule is in contact with the mesoloph; the posterior metalophule is present (4), or absent (2). All 6 specimens have an entomesoloph.

M^3 — The anterior protolophule is longitudinal, oblique, or forked, the posterior one is transversal. The labial part of the mesoloph forms a free spur in 4 specimens, it reaches the metacone in 1, and in another one there is no free spur. One specimen has an entomesoloph.

Hattomys transition *nazarii-gargantua*
Figs. 3, 4; Pl. 4, figs. 3-4.

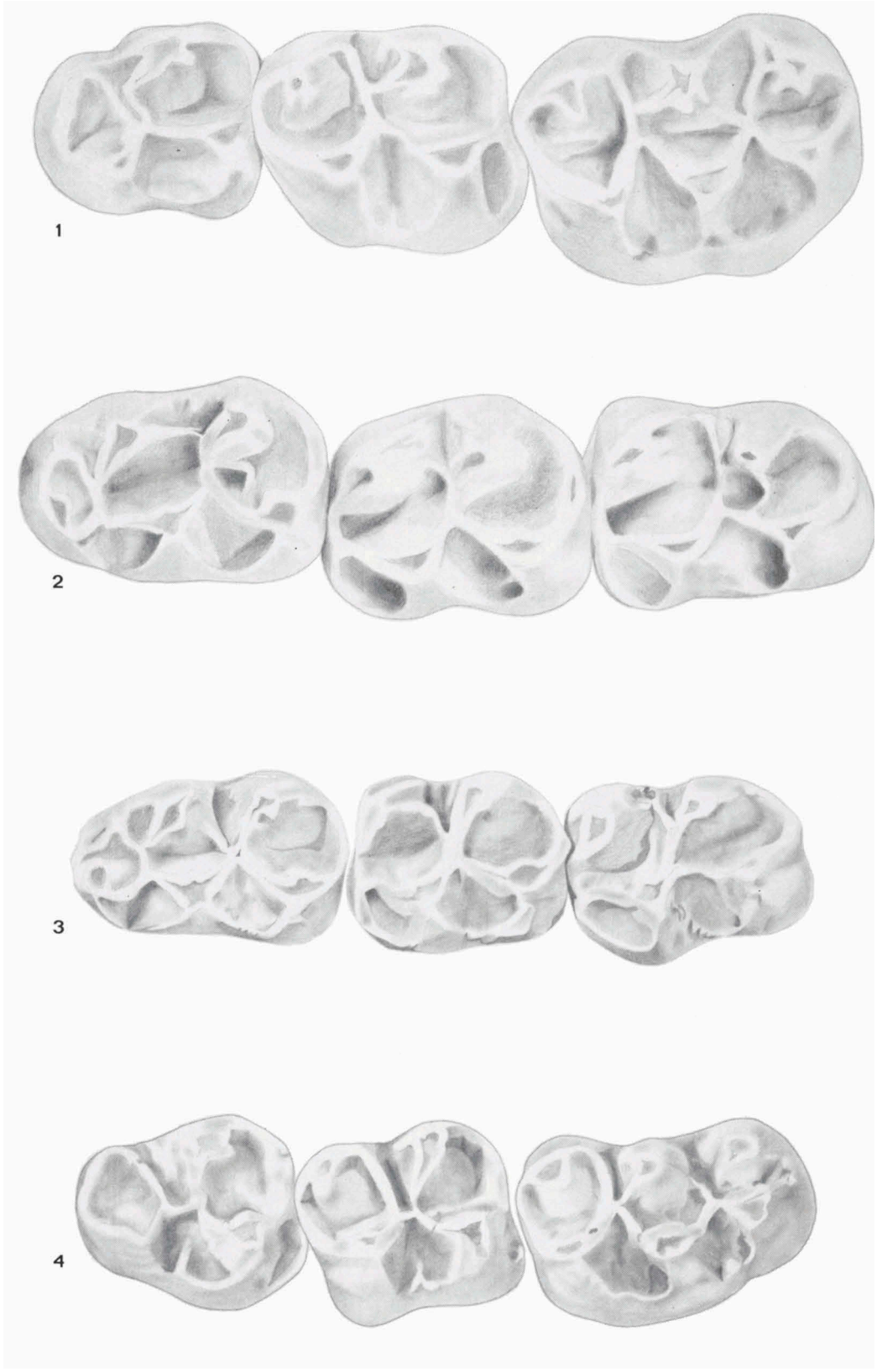
Plate 4

All figures × 10.

Hattomys gargantua sp. nov. from Chiro 2 S:
1. M^1-M^3 dext., RGM 263 513.
2. M_1-M_3 sin., RGM 263 520.

Hattomys nazarii-gargantua from Chiro 27:
3. M_1-M_3 sin., RGM 258 436.
4. M^1-M^3 dext., RGM 258 476.

Plate 4



The localities of Chiro 27, Chiro 5 A, and Chiro 29 have yielded good collections of *Hattomys*. In size and in morphology this material appears to represent the transition of *H. nazarii* to *H. gargantua*. Since we are dealing with chronospecies a sharp line between *nazarii* and *gargantua*, or between any of these species and a transitional form, cannot be drawn. The identification has to be arbitrary.

Locality — Chiro 27.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	16	42.1	44.2	47.5	1.60	18	25.8	28.0	30.0	1.12
M_2	16	35.0	37.5	39.2	1.36	16	27.5	29.9	31.7	1.25
M_3	16	37.5	40.2	42.5	1.29	15	27.5	30.4	35.0	1.84
M^1	16	46.7	50.1	52.5	1.53	15	30.8	32.4	35.0	1.22
M^2	12	35.8	38.3	40.0	1.46	14	30.0	31.7	32.5	0.80
M^3	12	33.3	36.0	40.0	1.92	13	27.5	29.9	31.7	1.22

Description

M_1 — The anteroconid is split into two cusps. There are generally two or three crests pointing backwards from the anteroconid, but the majority of the specimens have two crests. In most cases these crests unite in a prelophid, which may be equally developed as in *H. gargantua*, but in several cases it is shorter, and in about 4 specimens it doesn't exist at all. Consequently the metaconid is either longitudinally, or obliquely directed forwards. A short mesolophid serving as a posterior protolophulid is present in 2 specimens; in the other ones no separate mesolophid is visible. There is no ectomesolophid, nor is there a second hypolophulid. Flanges on the outer walls of the labial cusps are well-developed.

M_2 — A — much reduced — lingual anterolophid is present in 1 specimen only, in the other ones it has completely vanished. A short or medium mesolophid is present in about half the number of specimens and in some others the free lingual part of the mesolophid branches off from the anterior hypolophulid. There is no ectomesolophid.

M_3 — The mesolophid is long and nearly always reaches the border of the molar. Its labial part is fused with the hypolophulid. In 2 specimens there is a second hypolophulid, shortly behind the main one. An ectomesolophid is present in 2 out of 10 specimens.

M^1 — The anterocone is deeply split. In 13 specimens the anterolophules, the protolophule and the protocone meet in a cross, in 4 specimens there is a short preloph. The posterior protolophule is longitudinal towards the mesoloph (5), or oblique towards the entoloph (10). The mesoloph is long and bends towards the metacone. In one specimen a backward spur from the mesoloph touches the anterior wall of the metacone. In only 2 specimens a normal anterior metalophule is present. A posterior metalophule is present in 5 out of 14 specimens. An entomesoloph is well-developed (2), weak (3), or absent (12).

M^2 — The anterior protolophule is longitudinal (4), oblique (6), or absent (4). The posterior protolophule is oblique, connected to the entoloph (13), or to the mesoloph (1). The mesoloph is long and bent, like in M^1. There is an anterior metalophule in 1 out of 15 specimens. The posterior metalophule is present in half the number of specimens. An entomesoloph is well-developed (6), poorly developed (7), or absent (1).

M^3 — The anterior protolophule is longitudinal (9), oblique (1), or absent (3). An entomesoloph is present in 3 specimens out of 11.

Locality — Chiro 5 A (Figs. 3, 4).

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	29	43.3	46.4	50.0	1.61	30	27.5	29.7	31.7	1.20
M_2	30	35.8	39.1	41.7	1.31	30	28.3	31.6	33.3	1.20
M_3	31	36.7	41.0	44.6	1.60	31	27.9	31.0	32.5	1.10
M^1	34	47.5	51.0	54.2	1.96	33	31.7	34.1	39.2	1.58
M^2	31	35.8	39.3	41.7	1.37	31	31.7	33.0	34.6	0.83
M^3	23	33.8	36.3	40.0	1.42	23	28.7	30.7	32.5	1.02

Description

M_1 — The anteroconid is split into two cusps, rarely simple. The anterolophulid is single (2), double (21), or triple (4). The prelophid is absent (1), short (19), or long (7). The mesolophid as a separate crest is short (1), long (1), and absent in all others. There is no ectomesolophid.

M_2 — The mesolophid is generally short, oblique and connected to the metaconid (17), absent (5), or long (5). An ectomesolophid is hardly ever present.

M_3 — The mesolophid is long, often forked. The entoconid is generally longitudinally forward. Five specimens have a central funnel, enclosed by mesolophid and hypolophulid. Seven specimens have an ectomesolophid.

M^1 — The preloph is absent (9), short (23), or long (2). A few specimens have a spur in the anterosinus. The anterior protolophule is longitudinal (18), or oblique (15). The posterior one is longitudinal (33), or oblique (2). The posterior metalophule is present in a few specimens only. In 2 specimens there is an axial crest from the posteroloph along the base of the metacone toward the mesoloph, forming an anterior metalophule; in three more specimens the posterior part of such a crest is present. Ten specimens have an entomesoloph.

M^2 — The anterior protolophule is absent (8), oblique (4), or longitudinal (18). The posterior one is longitudinal (23), oblique (6), or double (1). The posterior metalophule is present (18), or absent (10). One specimen has an axial crest from posteroloph to mesoloph. The entomesoloph is nearly always present.

M^3 — The anterior protolophule is absent (7), oblique (2), or longitudinal (12). The posterior protolophule is transversal to oblique (18), longitudinal (2), or oblique plus longitudinal (2). In 4 specimens a labial tip of the mesoloph branches off from the metalophule. Three specimens have an entomesoloph.

Locality — Chiro 29.

Description

M_1 — The anteroconid is split into two cusps, the anterolophulid is single (1), double (6), or triple (2); the prelophid is generally long. There is no free mesolophid. In 1 specimen there is a longitudinal connection between metaconid and hypolophulid.

M_2 — The mesolophid is visible in 5 specimens, branching off somewhere from the hypolophulid.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	11	45.0	46.6	49.2	1.05	11	28.3	30.0	32.5	1.10
M_2	11	36.7	38.5	40.0	1.04	11	29.6	31.4	34.2	1.21
M_3	11	39.2	40.3	41.7	0.87	11	28.3	31.0	32.5	1.12
M^1	13	50.0	52.4	54.2	1.27	14	30.8	33.9	35.4	1.13
M^2	14	36.7	39.1	41.7	1.32	14	31.7	32.9	34.6	0.73
M^3	13	33.3	36.3	38.3	1.60	13	30.0	31.1	32.5	0.82

M_3 — The mesolophid is long. The entoconid points longitudinally forward, and is attached to the middle of the mesolophid; the mesolophid may bend towards the metaconid, or send a longitudinal spur toward this cusp. In other specimens the mesolophid does not touch the metaconid (apart from the 'cingulum' along the molar border). In 1 specimen ectolophid, mesolophid and hypolophulid form a funnel in the centre of the molar. One specimen has an ectomesolophid.

M^1 — The preloph is generally short. Two specimens have a spur in the anterosinus. The anterior protolophule is oblique (4), longitudinal (8), or double (1). The posterior protolophule is directed longitudinally backwards, towards the middle of the mesoloph. The mesoloph is long, labially bent towards the metacone. There is no anterior metalophule. The posterior metalophule is present (5), or absent (5). In a few specimens there is a trace of an axial crest from the posteroloph to the base of the metacone, as described in Chiro 10 C. The entomesoloph is present (4), or absent (8).

M^2 — The anterior protolophule is absent (6), or longitudinal (7); the posterior one is longitudinal towards the mesoloph (10), oblique towards the entoloph (2), or absent (1). The anterior metalophule is absent, the posterior one present (5), or absent (5). One specimen has a trace of an axial crest along the base of the metacone. The entomesoloph is present (10), or absent (4).

M^3 — The anterior protolophule is longitudinal (7), or absent (4). There is no free mesoloph. The entomesoloph is poorly developed, present (3), or absent (9).

Hattomys gargantua sp. nov.
Figs. 5, 6; Pl. 2, figs. 13-17; Pl. 3, figs. 1-4; Pl. 4, figs. 1-2; Pl. 5, figs. 10-11.

Derivatio nominis — The species is named after Rabelais' giant Gargantua.
Holotype — Cranium with maxilla dext., RGM 263 555, Pl. 3, fig. 3; Pl. 5, figs. 10-11.
Type locality — Chiro 2 N, Gargano (Prov. of Foggia, Italy).

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	11	46.7	50.6	54.2	2.58	11	30.0	32.0	33.7	1.37
M_2	21	39.2	42.0	44.2	1.45	20	31.2	33.5	35.4	1.29
M_3	18	41.2	44.2	49.2	2.29	18	30.4	33.6	35.8	1.78
M^1	15	52.1	55.8	59.2	1.94	16	34.2	37.9	40.0	1.72
M^2	11	38.7	41.5	45.4	1.91	11	34.6	35.8	37.5	0.95
M^3	11	35.8	38.7	41.2	1.76	12	31.2	32.8	34.6	0.91

Diagnosis — *Hattomys* of very large size. Anteroconid of M_1 split, anterolophulid double, prelophid well-developed. A separate mesolophid is rarely present in M_1, frequent and well-developed in M_3. Anterocone of M^1 displaced labially, so that the labial border of the tooth is very concave in occlusal view. Preloph well-developed. Mesoloph and entomesoloph of upper molars well-developed. Labial walls of labial cusps of the (upper and lower) molars often flanged.

Note — *H. gargantua* is known from quite a number of fissures in the Gargano area, and among these Chiro 2 N is certainly not the one that yielded the richest material. Nevertheless Chiro 2 N was chosen as type locality since it produced a fairly complete skull, and several incomplete ones. In the following description Chiro 2 N and Chiro 2 S are treated as one locality, because no differences were found and these two samples were collected at two different spots of the same fissure that are only 10 m apart.

Description

M_1 — Anteroconid deeply split in 9 specimens, slightly subdivided in 1, and simple in another one. The two cusps of the anteroconid are more or less of the same size. The prelophid is generally long. The protoconid and the anterior metalophulid are fused to the labial and lingual ends of the prelophid, respectively. The same goes for the two anterolophulids. The labial anterolophulid is longitudinal, the lingual one is oblique. In 2 specimens the labial anterolophulid is double, so that a total of three anterolophulids is present. The labial cusps of M_1 (and of the other lower molars too) are provided with a broad plate along the border of the molar. This feature is most developed in the protoconid of M_1, which consequently has a carved-in aspect, with concave anterior and posterior walls. In 2 specimens a long thin mesolophid is present. In 2 other specimens a low longitudinal connection between the posterior wall of the metaconid and the hypolophulid represents the mesolophid; in the other 7 specimens there is no separate mesolophid. It is probably hidden in the anterior hypolophulid. Only 1 specimen shows a second hypolophulid, a low crest connecting the entoconid with the middle of the hypoconid. There is no ectomesolophid.

M_2 — The lingual anterolophid has disappeared. A free mesolophid is present in 3 specimens only; in 14 specimens there are an anterior hypolophulid and a posterior metalophulid, which have their labial parts in common. This common crest is the labial part of the mesolophid, the lingual part of the mesolophid forms the rest of the posterior metalophulid, which may meet the centre of the posterior wall of the metaconid, or its lingual end. In 5 specimens the posterior metalophulid is absent. A long, low ectomesolophid is present in 1 specimen.

M_3 — A lingual anterolophid is rarely present. The mesolophid is long and serves as an anterior hypolophulid. In 2 specimens the lingual part of the mesolophid serves as a posterior metalophulid as in M_2. In 13 specimens the mesolophid is transversal, the entoconid points longitudinally forward to meet the mesolophid. In 5 of these 13 specimens there is a second hypolophulid, from the entoconid towards the anterior end of the hypoconid. Four specimens have an ectomesolophid. All four cusps are well-developed, there is little reduction in the posterior part of the molar.

M^1 — Anterocone deeply split into two more or less equal cusps. From each of these cusps a crest runs backwards towards the preloph. Protocone and anterior protolophule are connected to the ends of the preloph. The mesoloph is long and bends towards the metacone at its labial end. A posterior spur of the paracone points longitudinally backwards and reaches the middle of the mesoloph. A well-developed entomeso-

loph is present in 3 out of 16 specimens, in 2 specimens it is weak. The posteroloph is well fused with the metacone; besides, a posterior metalophule towards the middle of the posteroloph exists in 6 specimens. The labial border of the molar is concave, the external walls of the labial cusps (and to a lesser extent those of the lingual cusps too) are provided with vertical flanges. There are four roots, the anterior one is very broad.

M^2 — In its homologous parts M^2 is generally identical to M^1. The anterior protolophule is often absent (6) and if present it tends to have a rather labial position, directed longitudinally towards the anteroloph. The entomesoloph is less well-developed, but more frequent (10 out of 12 specimens). The posterior metalophule is present in 4 out of 11 specimens. The flanges on the labial cusps are present but less conspicuous. There are four roots.

M^3 — The anterior part of M^3 is identical to M^2. The posterior part is narrower, but the cusps remain well-developed. The posterior protolophule is connected to the mesoloph in 6 specimens, to the entoloph in 7. In 1 specimen the mesoloph connection plus a trace of the entoloph connection are present. Mesoloph and posteroloph close the valley between hypocone and metacone. An entomesoloph, not much developed, is present in 7 out of 14 specimens. There are three or four roots, the fourth root being long and thin, placed under the anterolingual corner of the hypocone.

Locality — Pizzicoli 11.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	25	45.0	48.4	51.7	1.81	25	27.9	30.5	34.2	1.31
M_2	28	37.9	41.0	43.7	1.48	28	30.0	32.5	35.0	1.33
M_3	21	39.6	43.1	46.7	1.70	21	30.0	32.5	35.4	1.51
M^1	30	51.7	55.1	59.2	1.82	29	35.0	37.7	41.7	1.78
M^2	28	38.3	42.1	45.8	1.91	28	33.3	35.7	38.3	1.22
M^3	20	35.0	38.4	42.1	1.99	20	30.0	32.7	35.4	1.50

Plate 5

Figs. 1-9 × 15, figs. 10 and 11 natural size.

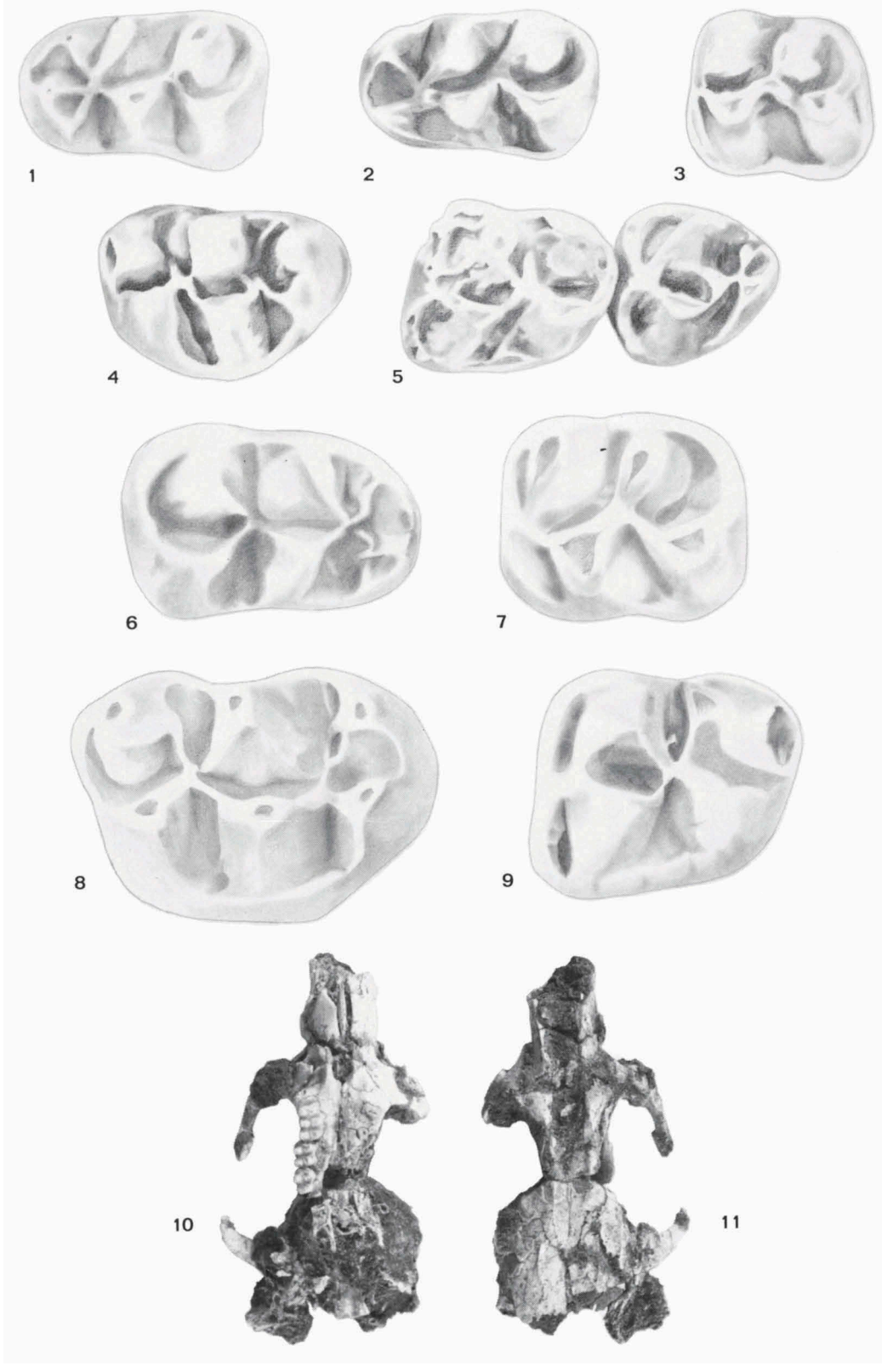
Cricetulodon sp. from Biancone 1:
1. M_1 sin., RGM 263 924.

Cricetulodon sp. from Rinascita 1:
2. M_1 sin., RGM 263 492.
3. M_2 sin., RGM 263 495.
4. M^1 dext., RGM 263 497.
5. M^2-M^3 sin., RGM 263 498.

Cricetus sp. from Rinascita 1:
6. M_1 dext., RGM 263 491.
7. M_2 sin., RGM 263 516.
8. M^1 dext., RGM 263 518.
9. M^2 sin., RGM 263 519.

Hattomys gargantua sp. nov. from Chiro 2 N:
10. dorsal view of holotype skull.
11. ventral view of holotype skull.

Plate 5



Description

M_1 — The anteroconid is simple (1), slightly split (4), or clearly split (19); the anterolophulid is double (19), or triple (5). The prelophid is always present, in most cases long to very long. The mesolophid is absent (13), or the lingual end of a long mesolophid is visible (8). In 3 specimens — without mesolophid — there is a transversal connection between the metaconid and the entoconid. There is no ectomesolophid. The flanges on the labial cusps may be very conspicuous.

M_2 — The lingual anterolophid has disappeared. The mesolophid is generally medium or long, its labial part fused with the hypolophulid, its lingual part free and fused to the metaconid. The lingual wall of the hypoconid may be bulged. The entoconid is generally directed obliquely forward. There is no ectomesolophid.

M_3 — The mesolophid is as in M_2. The entoconid is more longitudinal. Apart from the anterior metalophulid, 1 specimen has an oblique posterior one. Behind the hypolophulid a second connection may be present (1), or at least indicated (1). There is no ectomesolophid.

M^1 — The anterocone is deeply split. The preloph is absent (7), short (17), long (5), or very long (1). In 18 specimens there is a spur in the anterosinus. The anterior protolophule is absent (4), oblique (7), longitudinal (18), or oblique plus longitudinal (1); the posterior protolophule is always longitudinal. The mesoloph is long and bent towards the metacone labially. The anterior metalophule is present in 1 specimen; a second specimen has an anterior metalophule formed by a low crest from posteroloph to mesosinus along the base of the metacone; in several other specimens this crest is incompletely developed. An entomesoloph is present in 7 specimens.

M^2 — The anterior protolophule is absent (3), oblique (4), or longitudinal (21). The posterior one is longitudinal. The anterior metalophule is present in 1 specimen only; the posterior one is present (24), or absent (4). The entomesoloph is present (23), or absent (6).

M^3 — The anterior protolophule is absent (4), oblique (3), or longitudinal (10). The posterior one is longitudinal (13), oblique (1), oblique plus longitudinal (2), or it begins longitudinally and then bends at a sharp angle to the entoloph (3). The mesoloph is long. An axial crest through the posterior sinus is more or less well indicated in 6 specimens. An entomesoloph is present in 9 specimens.

Locality — Pepo 1 A.

Material and measurements

M_1	48.3 × 30.8, 45.8 × 28.3
M_2	39.2 × 31.7, 40.8 × 31.7
M_3	40.0 × 33.7, 44.2 × 32.9
M^2	40.8 × 34.2, 42.1 × 36.2
M^3	37.5 × 32.9, 37.5 × 32.5.

This material fully agrees with *H. gargantua*.

Locality — Chiro 10 C.

During the collecting of this material it was noted that the fissure of Chiro 10 C was in a fault plane. For this reason it was considered possible that the sample might contain material of various ages, the more so since part of the matrix was red, and another part was yellow. After washing the material, it was divided into specimens that still had red matrix attached, and others that showed traces of yellow matrix. Analysis has shown that

there is no significant difference between these two groups. On the other hand, one M^1 from the yellow matrix is considerably smaller than all others, and evidently represents another species, or at least a much smaller population than the one to which most of the material from Chiro 10 C belongs. In size it agrees with the populations from Chiro 5 A, Chiro 27, and Nazario 4. It is treated as *Hattomys* sp., as the identification of a single specimen is impossible.

Material and measurements from Chiro 10 C red

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	14	43.3	48.2	51.7	2.31	13	27.1	30.7	33.3	1.91
M_2	15	36.7	40.6	43.3	1.82	16	29.2	32.4	34.6	1.47
M_3	12	38.3	42.6	46.7	2.60	12	30.0	32.9	35.0	1.54
M^1	22	51.7	55.7	58.7	1.78	22	35.4	37.8	40.8	1.42
M^2	16	37.9	41.9	44.2	1.82	16	35.0	36.2	37.9	1.05
M^3	11	38.3	39.2	41.2	0.95	11	32.1	32.8	33.7	0.48

Material and measurements from Chiro 10 C yellow

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	25	46.2	49.3	52.9	1.70	25	29.2	31.6	35.0	1.43
M_2	31	37.5	41.2	43.3	1.31	30	30.8	32.6	35.8	1.38
M_3	31	40.0	43.2	45.8	1.59	31	28.7	32.6	35.4	1.35
M^1	30	53.3	56.7	60.4	1.77	30	35.8	39.0	41.7	1.71
M^2	22	40.4	43.2	46.7	1.42	22	34.2	36.5	39.2	1.40
M^3	18	35.8	39.2	42.1	1.67	19	31.7	33.4	35.8	1.26

Measurements of Chiro 10 C red and Chiro 10 C yellow combined

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	39	43.3	48.9	52.9	1.99	38	27.1	31.3	35.0	1.63
M_2	46	36.7	41.0	43.3	1.50	46	29.2	32.5	35.8	1.40
M_3	43	38.3	43.0	46.7	1.91	43	28.7	32.7	35.4	1.40
M^1	52	51.7	56.3	60.4	1.83	52	35.4	38.5	41.7	1.67
M^2	38	37.9	42.6	46.7	1.71	38	34.2	36.4	39.2	1.26
M^3	29	35.8	39.2	42.1	1.42	30	31.7	33.2	35.8	1.08

Measurements of *Hattomys* sp. from Chiro 10 C yellow: M^1 48.7 × 31.7.

Description (Chiro 10 C yellow)

M_1 — The anteroconid is slightly split (2), or deeply split (19); there are always two anterolophulids, the prelophid is absent in one specimen only, in the others it is short or long. The mesolophid is absent in 9 specimens, short and oblique towards the metaconid in 3, long in 2. In 2 specimens the mesolophid is medium or long, but only its lingual part is visible; in 5 specimens a longitudinal connection between metaconid and entoconid, half-way the mesosinusid, represents a part of the mesolophid. There is no ectomesolophid.

M_2 — There is no lingual anterolophid. The mesolophid is absent (5), short (1), medium (11), or long (11). The labial part of the mesolophid is generally not visible, the lingual part joins the metaconid. There is no ectomesolophid.

M_3 — The mesolophid is long (26), or absent (3); only its lingual part is visible. In 2 of the specimens with mesolophid it is forked lingually: one branch reaches the border of the molar, the other one joins the posterior wall of the metaconid. The entoconid generally points longitudinally forward. Six out of 30 specimens have an ectomesolophid. In 2 specimens there is a trace of a second hypolophulid between the entoconid and the anterior corner of the hypoconid.

M^1 — The anterocone is deeply split. The labial anterolophule is absent in 1 specimen. The preloph is absent (7), short (18), or long (5); in 11 specimens the preloph is prolonged labially into the anterosinus. The anterior protolophule is longitudinal (14), oblique (9), or both connections exist (6). In 1 specimen the oblique connection is formed by a low crest running along the basis of the paracone, that also forms a posterior protolophule. The longitudinal posterior protolophule exists in all specimens, and besides it an oblique one is more or less well developed in 3. The mesoloph is long. In 5 out of 27 specimens a crest runs from the posteroloph to the mesoloph, along the basis of the metacone, in 7 specimens the posterior part of such a crest is present. Nine out of 32 specimens have a normal posterior metalophule, descending from the metacone. About half the number of specimens have an entomesoloph.

M^2 — The anterior protolophule is oblique or close to the anterocone (7), longitudinal (8), or absent (5). The posterior metalophule is present in half the number of specimens. The crest along the base of the metacone, as described in M^1, is present in 2 specimens. An entomesoloph is present in 16 out of 22 specimens.

M^3 — The posterior protolophule is longitudinal (10), oblique toward the entoloph (4), or both connections are more or less developed (3). In 4 specimens there is a well developed crest from the posteroloph to the mesoloph through the middle of the valley. About half the number of specimens have an entomesoloph.

Description (Chiro 10 C red)

M_1 — The anteroconid is hardly split (2), or deeply split (11); the anterolophulid is double (9), or triple (4). The prelophid is short, or long, and in one specimen a second transversal crest connects protoconid and metaconid, shortly behind the prelophid. The mesolophid is absent (6), short (1), medium (2), or long (3); in 1 specimen the mesolophid presents itself as a longitudinal connection between metaconid and entoconid. There is no ectomesolophid.

M_2 — There is no lingual anterolophid. The mesolophid is absent (2), medium (4), or long (9), and in 1 specimen a longitudinal connection between metaconid and entoconid represents the mesolophid. Only 1 specimen has an ectomesolophid.

M_3 — The mesolophid is always long, in one case it is forked lingually. Three out of 13 specimens have an ectomesolophid. In 3 specimens there is a trace of a second anterior hypolophulid.

M^1 — The anterocone is deeply split. The preloph is generally short, less frequently long, rarely absent. In 1 specimen there is no labial anterolophule. In about half the number of specimens the preloph is prolonged labially into the anterosinus and may reach the border of the molar. The anterior protolophule is absent (1), oblique (4), longitudinal (13), or a longitudinal plus an oblique connection exist (4). The posterior protolophule is directed longitudinally backwards, towards the middle of the mesoloph; in 1 specimen there is also an oblique posterior protolophule, connected to the entoloph.

The mesoloph is long. There is no anterior metalophule, except in 2 specimens where a low longitudinal crest runs from the posteroloph to the mesoloph, along the labial basis of the metacone. In about half the number of specimens a trace of the posterior part of such a crest is present. A normal posterior metalophule, descending from the metacone is always absent. Six out of 20 specimens have an entomesoloph.

M^2 — The anterior protolophule is longitudinal (5), oblique or at least directed towards the anterocone (10), or absent (1). The posterior protolophule is longitudinal towards the middle of the mesoloph. The mesoloph is long. A trace of an anterior metalophule in the form of a longitudinal crest exists in 1 specimen. The M^1 of the same maxilla is one of the 2 specimens that have a similar crest fully developed. In about half the number of specimens a posterior metalophule is present. An entomesoloph is absent (2), or present (14), generally well-developed.

M^3 — The posterior protolophule runs longitudinally backward towards the mesoloph (4), or obliquely towards the lingual part of the mesoloph (2). In one specimen it is first longitudinal, and then bends at a 90° angle towards the entoloph. Two out of 9 specimens have an entomesoloph.

Locality — Chiro 12.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	12	44.1	49.1	51.2	1.98	12	28.4	30.1	31.0	0.78
M_2	13	38.3	41.4	43.6	1.44	13	29.5	32.5	34.5	1.28
M_3	11	40.7	43.7	46.5	1.58	11	30.4	32.2	34.4	1.35
M^1	16	51.7	54.9	58.3	2.20	16	35.0	38.3	40.8	1.79
M^2	22	39.2	42.4	45.0	1.87	22	32.5	35.8	38.3	1.35
M^3	11	37.5	40.0	43.3	1.67	11	30.4	32.8	35.8	1.69

Description

M_1 — The anteroconid is deeply split (6), hardly split into two cusps (4), or into three cusps (1), or a simple curved ridge (1). The anterolophulid is single (1), double (9), or triple (2). The prelophid is generally long. In 2 specimens the short mesolophid serves as a posterior metalophulid, in 2 specimens the free end of the mesolophid reaches the border of the molar; in the other specimens no separate mesolophid is visible. There is no ectomesolophid. The flanges on the labial cusps are extremely well marked in several specimens.

M_2 — Generally a short or medium mesolophid serves as a posterior metalophulid. There is no ectomesolophid. The flanges on the labial cusps are well-developed.

M_3 — The mesolophid is long, and its lingual end bends towards the metaconid; in 1 specimen it is forked. Two specimens have an ectomesolophid.

M^1 — The anterocone is deeply split, the anterolophules meet in a long or short preloph, or — less frequently — they form a cross with the protocone and the protolophule. Most specimens have a transversal spur in the anterosinus. The anterior protolophule is either longitudinal towards this spur, or longitudinal towards the end of the preloph. Generally the mesoloph is long, as it normally is in *H. gargantua*, but in several cases it is shorter. A posterior metalophule is present in 6 out of 16 specimens, in 2 of these cases it is very weak. In 2 other cases it is not a normal metalophule descending from the

metacone, but a more or less longitudinal low crest, skimming the base of the metacone, and running from the posteroloph towards the mesoloph. In addition to this feature one of these specimens shows two small backward spurs on the posterior wall of the metacone. An entomesoloph is present in 5 specimens. The flanges on the labial cusps are well-developed.

M^2 — The anterior protolophule is longitudinal (14), oblique (1), or absent (6). Mesoloph and posterior protolophule are normal for *H. gargantua*. The posterior metalophule is present in 9 out of 20 specimens. An entomesoloph is present in 18 out of 21 specimens.

M^3 — The anterior protolophule is longitudinal (9), or absent (2). A weak entomesoloph is present in 2 specimens only.

Locality — Chiro 10 B.

Material and measurements

	length					width				
	n	min.	mean	max.	sigma	n	min.	mean	max.	sigma
M_1	5	46.7	50.3	54.2	3.25	5	30.0	31.5	33.7	1.39
M_2	8	40.8	42.0	44.6	1.23	8	31.2	33.1	35.0	1.21
M_3	11	40.4	42.7	44.2	1.18	11	32.1	33.1	35.4	1.04
M^1	14	52.5	55.5	59.2	1.98	14	35.0	37.9	41.2	1.65
M^2	17	39.2	41.8	44.6	1.56	16	33.7	35.8	38.7	1.37
M^3	11	36.7	38.2	41.2	1.26	11	31.7	32.9	35.4	1.25

M_1 — Anteroconid split (4), or simple (1); anterolophulid double (3), or triple (2). Labial cusps flanged. There is no mesolophid, but in 3 specimens there is a low longitudinal connection between the posterior wall of the metaconid and the hypolophulid.

M_2 — There always is a connection between the hypolophulid and the posterior wall of the metaconid, which is interpreted as the lingual part of the mesolophid. One specimen has a trace of a second hypolophulid on the anterior branch of the hypoconid, and a similar structure on the anterior branch of the protoconid. It is the only specimen with an ectomesolophid. The flanges on the labial cusps are well-developed.

M_3 — The lingual part of the mesolophid reaches the border of the molar, and then bends towards the metaconid, or it is split into a free spur and one that reaches the metaconid. The labial part of the mesolophid forms the hypolophulid. The entoconid is not oblique, but points longitudinally forward. One specimen has a thin second hypolophulid shortly behind the main connection, on the anterior branch of the hypoconid. In 1 specimen there is a short ectomesolophid. The labial cusps are flanged.

M^1 — The anterocone is split. The anterolophules may end backwards in a short or long preloph, but in several cases the anterolophules, the protocone and the protolophule form a more or less regular cross. The protolophule is either longitudinal, or oblique. In 6 out of 11 specimens there is a transversal crest in the anterosinus, which reaches the border of the molar. The posterior protolophule is directed longitudinally backwards towards the middle of the mesoloph. The mesoloph is long, bending towards the metacone at the border of the molar, or somewhat more lingually, but never in contact with the anterolingual corner of the metacone. The posterior metalophule is present in 10 out of 12 specimens. An entomesoloph is present in 3 out of 12 specimens.

M^2 — The anterior protolophule is longitudinally connected to the anteroloph (7), obliquely to the anterocone (6), or absent (2); the posterior protolophule is always longitudinal, toward the middle of the mesoloph. The mesoloph is as in M^1. The posterior metalophule is present in 15 out of 16 specimens. An entomesoloph is always present, in 14 out of 16 specimens it is strongly developed.

M^3 — The anterior protolophule is longitudinal (8), oblique (1), or absent (1). The entomesoloph is present in 6 out of 11 specimens, but only in one case it is well-developed.

Other localities

Apart from the mentioned localities *H. gargantua*, or the transitional form *H. nazarii-gargantua*, has been found in Chiro 5 B, Chiro 6, Chiro 9, Chiro 10 A, Chiro 10 C, Chiro 14 A, Chiro 14 B, Chiro 30, Chiro 30 A, Chiro 30 B, Fina H, Monte Granata 1, and Trefossi 2 A.

Hattomys sp.

Locality — Rinascita 1.

Description — A single M^2, 38.4 × 32.2, from Rinascita 1 is much too large for *H. beetsi* from the same locality. Morphologically and by its size it might belong to *H. nazarii-gargantua* but the flanges on the labial cusps are better developed than they normally are in that species.

OTHER CRICETID GENERA

The oldest localities, Biancone 1, Rinascita 1 and Trefossi 1, yielded some specimens of cricetids, much smaller than the coexistent species of *Hattomys*. In Rinascita 1 even two species of such a small cricetid may be recognized.

This material shows resemblances with *Cricetulodon, Kowalskia, Cricetus,* and *Hattomys*. First of all it must be noted that the difference between *Kowalskia* and *Cricetulodon* is not clear at all. *K. polonica* Fahlbusch, 1969 is characterized by a divided lingual root in M^1 and M^2 (Fahlbusch, 1969). *K. fahlbuschi* Bachmayer & Wilson, 1970 has the same feature in M^2, but in M^1 it is less developed. *Cricetulodon* is generally supposed to have three roots only. De Bruijn (1976) practically uses the number of roots in M^2 as the only distinguishing character between *Kowalskia* and *Cricetulodon*; the other features he mentions (protolophule, metalophule, anterolophulid, mesolophs, and mesolophids) usually are so variable that they can't serve for the distinction of two genera. Since Agusti (1981) showed that four-rooted M^2 occur in the topotype collection of *C. sabadelliensis* Hartenberger, 1966, there remains not a single character separating these two genera. Each species referred to either *Kowalskia* or *Cricetulodon* has its own characteristic combination of features, but there exists no clear-cut division into two groups of species:

In most populations M^2 is four-rooted, in *C. sabadelliensis* this feature is rare, in *C. hartenbergeri* (Freudenthal, 1967) it seems to be absent.

M_3 is a relatively well-developed element, in comparison with Miocene cricetids like *Democricetodon* and *Megacricetodon*, but generally M_3 is slightly smaller than M_2 (length

ratio M_2/M_3 1.00 to 1.04). In *K. fahlbuschi* from Kohfidisch M_3 is less reduced (length ratio 0.96) and in *K. fahlbuschi* from Crevillente 1 M_3 is considerably reduced (length ratio 1.11).
In the populations attributed to *Kowalskia* the anterolophulid of M_1 is often double, in *Cricetulodon* it is generally simple but the double crests, as found in *K. fahlbuschi* from Crevillente, may easily be derived from the simple crest found in *C. hartenbergeri*.
Mesolophids and mesolophs are long in *K. polonica*, short or medium, sometimes absent, in *K. fahlbuschi* and in *Cricetulodon*. Furthermore, the description of *Hattomys* has shown that the mesolophid may be hidden in the anterior hypolophulid. If this situation exists in *Kowalskia-Cricetulodon* it is quite possible that a species with long mesolophids like *K. polonica* Fahlbusch, 1969 is closely related to a species with no apparent mesolophid at all.

Since no sharp distinction exists between *Cricetulodon* Hartenberger, 1966 and *Kowalskia* Fahlbusch, 1969 these two names must be considered synonyms, *Cricetulodon* having priority.

Genus *Cricetulodon* Hartenberger, 1966

Cricetulodon sp.
Pl. 5, figs. 2-5.

Locality — Biancone 1, Gargano.

Material and measurements
M_1 20.6 × 13.1
M^1 20.3 × 12.8.

Description — The anteroconid of M_1 is divided into two cusps, the anterolophulid is triple, there is no mesolophid. The anterocone of M^1 is split, there are two anterolophules and a preloph; the anterior protolophule is double: oblique towards the protocone, and longitudinal towards the preloph. Preloph and protolophules enclose a small funnel. The mesoloph is of medium length. The lingual root of M^1 is simple. The M^1 seems to be small in relation with the M_1. Supposing that this material belongs to one single species, the M^1 should represent the lower variation limit and the M_1 should be at the upper limit of the variation.

Locality — Rinascita 1, Gargano.

Material and measurements
M_1 19.4 x 12.7, 19.6 x 11.8
M_2 15.6 × 13.3, 16.3 × 13.3
M^1 20.6 × 13.7, 19.4 × 13.7, 18.8 × 13.3
M^2 17.1 × 14.1
M^3 10.9 × 9.8, 13.6 × 13.1.

Description

M_1 — The anteroconid is a curved ridge, hardly or well divided into two cusps. There are two anterolophulids. Ectolophid and hypolophulid form a continuous oblique ridge in 1 specimen. The connection of the hypoconid to this ridge is very low. There is no mesolophid.

M_2 — A lingual anterolophid is present, the labial anterolophid is broad and massive, but leaves the protosinusid open labially. There is a small mesoconid and no mesolophid.

M^1 — The anterocone is split from behind, the anterior wall is a smooth curved ridge. The anterolophule is double in one specimen, single in the other. Of the double anterolophule one branch is longitudinal, the other — labial — one is oblique. In the other specimen the longitudinal anterolophule is accompanied by a small labial spur and an anterior protolophule. Both specimens have a short mesoloph. The posterior metalophule is present in one specimen and absent in the other. There are three roots.

M^2 — The protolophule is symmetrically double. The mesoloph is of medium length, and remains more or less free from the metacone. There is a posterior metalophule. The lingual root is divided into two.

M^3 — The anterior part of M^3 is like M^2. In the posterior part hypocone and metacone are small but recognizable. Crests from the paracone, hypocone and metacone join in a small cusp in the centre of the molar.

Note — Like in Biancone this material from Rinascita also shows a discrepancy in the size of M^1 and M_1; normally M^1 should be larger than M_1. If they belong to the same species they should represent the upper and lower limits of the fields of variation, respectively.

Locality — Trefossi 1, Gargano.

Material and measurements
M_1 20.9 × 12.8, 18.9 × 12.4.

Description — The anterolophid is a simple curved ridge, wihout cusps; there are two anterolophulids; the mesolophid is absent. In the second specimen the anterolophid is slightly split into two cusps and there is a prelophid.

Genus *Cricetus* Leske, 1779

Cricetus sp.
Pl. 5, figs. 6-9.

Locality — Rinascita 1, Gargano.

Material and measurements
M_1 24.8 × 16.4, 24.2 × 15.3, 23.0 × 14.7
M_2 20.9 × 17.0
M^1 30.6 × 20.1
M^2 22.2 × 19.7, 22.0 × 18.6.

Description

M_1 — The anteroconid is a curved ridge, sligthly split into two cusps from behind. In one specimen there are three anterolophulids, in the second one the central anterolophulid is missing, in the third one the central and the labial anterolophulids are very weak. There is no mesolophid.

M_2 — There is a small lingual anterolophid and a small anterosinusid. The protosinusid is closed labially. There is no mesolophid. The posterosinusid is very wide.

M_3 — This is only a fragment; the anterior part is identical to M_2.

M^1 — The anterocone is well split from behind. There is a lingual longitudinal anterolophule, an oblique labial one, and a spur in the anterosinus. The mesoloph is of medium length and directed towards the metacone. There is no posterior metalophule.

M^2 — The protolophule is symmetrically double; the mesoloph is long and bends towards the metacone. The posterior metalophule is present.

Subfamily Cricetodontinae
Genus *Megacricetodon* Fahlbusch, 1964

Megacricetodon sp.
Pl. 1, fig. 17

Locality — Biancone 1, Gargano.

Material and measurements
M^2 11.2 × 9.7.

Description — This is a typical *Megacricetodon*, with double protolophule, spur on the paracone, long mesoloph, and anterior hypolophule.

Discussion — *Megacricetodon* could be a good marker to decide the age of the Gargano faunas. Since it is represented by one specimen only, contamination with a sample from another area cannot be excluded. Specific determination is impossible.

Discussion

As may be seen from Figs. 7-14 the evolution of *Hattomyson* the Gargano island is primarily marked by a considerable increase in size. The mean length of M_1 increases from 31.6 in Biancone to 50.6 in Chiro 2, and similar increases are found in all other molars, and in the lengths of complete tooth rows. Morphologically the most important evolutionary features are:
The anteroconid of M_1 becomes more deeply split.
Reduction of the number of anterolophulids from three to two.
Progressive development of prelophids and prelophs.
Disappearance of the lingual anterolophid in M_2.
Disappearance of a second hypolophulid behind the main one (which is the mesolophid).
The forward connection of the entoconid of M_3 shifts from oblique to longitudinal.
The lingual part of the mesolophid tends to isolate itself from the hypolophulid.
Flanges develop on the labial walls of the labial cusps in both the upper and the lower molars. Cusps get a carved-in aspect. Crests tend to become dominating over the cusps.
The most-developed teeth remind one slightly of the teeth of *Melissiodon*.
The anterocone of M^1 is displaced in a labial direction. Consequently the labial border of the molar becomes increasingly concave.
Progressive development of entomesolophs.
The posterior protolophule of M^1 and M^2 shifts from an oblique to a longitudinal position.

The anterior protolophule of M^2 tends to shift from oblique to a more longitudinal position.
The M^1 and M^3 tend to develop 4 roots, through the splitting of the lingual root.

All these evolutionary tendencies are based on the sequence of the localities construed by Freudenthal (1976) on the basis of the murid genus *Microtia*. Basically I have tried to construct a theoretical sequence of the localities, using *Hattomys* in the same way as I did with *Microtia*. However, the molars of *Hattomys* are much more complex than those of *Microtia*, and therefore a quantification of the morphology was not possible. The main argument used to construct a — chronological — sequence of the *Hattomys* localities is the size. The resulting sequence is quite satisfactory, since it agrees quite well with the above mentioned morphological evolution of *Hattomys*, and it fits in with the sequence deduced from the size and the morphology of *Microtia*.

In the locality of Chiro 10 C (yellow) a single M^1 is much smaller than the rest of the material. In size it agrees with *H. nazarii*, or with the transitional form *nazarii-gargantua*. If this occurrence is not caused by contamination it is hard to explain.

The most problematic of all localities mentioned in this paper is Rinascita 1. This locality contains a species supposed to be close to *Cricetulodon*, another one attributed to *Cricetus*, and two species of *Hattomys*. The largest *Hattomys* is much too large for the stratigraphic level attributed to Rinascita 1. It has the size of *H. nazarii-gargantua*, but morphologically it seems to be more developed. Contamination with material from another locality is therefore not probable. The smaller *Hattomys* species from Rinascita 1 also presents some problems. It has been attributed to *H. beetsi* on the basis of the size of M_1, M^2 and M^3. On the other hand M^1, M_2 and M_3 fall within the size range of *H. nazarii*. This could mean that this locality even contains one cricetid species more, but the scarcity of the material does not permit to solve this problem.

Comparison of Rinascita with the Crevillente faunas described by de Bruijn et al. (1975) from southern Spain led to some striking results. In Crevillente occurs a *Cricetulodon fahlbuschi* that might be considered as a parallel of *Cricetulodon* sp. from Rinascita 1. The M_1 of both localities are of about the same size, M^3 are reduced as they are in *Democricetodon*, and mesolophs remain more or less free from the metacone. In Crevillente the M_1 has a mesolophid, whereas the M_1 from Rinascita lack this crest. It seems, however, that the mesolophid has not actually disappeared, but that it forms the anterior hypolophulid, or at least is fused with this crest.

The second small species from Rinascita, referred to *Cricetus* sp., may well be compared with *Cricetus* cf. *kormosi* Schaub, 1930 from Crevillente 6. In both populations the mesolophids are absent in M_1 and M_2, but they may be hidden in the anterior hypolophulid. The mesolophs are fairly long and their labial tips fuse with the metacone. Unfortunately, the M^3 from Rinascita is unknown; in Crevillente the M^3 is little reduced. *Cricetus* sp. from Rinascita 1 and *Cricetus* cf. *kormosi* from Crevillente 6 may be closely related.

The phylogenetic origin of *Hattomys* is not clear. There are evident resemblances with *Kowalskia-Cricetulodon*, e.g. the morphology of the anterior part of M_1, but on the other hand *Cricetulodon* cannot be the ancestor of *Hattomys* because its third molars are more reduced than they are in *Hattomys*. *Democricetodon*, the supposed ancestor of *Kowalskia-Cricetulodon* also has these reduced third molars, and unless a reversal of this reduction is supposed, the ancestor of *Hattomys* must be another, probably Upper Miocene, cricetid.

Basically the dental pattern of *Cricetus* cf. *kormosi* and of *Hattomys* are not too far apart. The mesolophs in *Hattomys* are considerably longer than they are in *kormosi*, but the way in which they fuse with the metacone is fundamentally the same. The M^3 of *Hattomys* are not very much reduced, as they are in *kormosi*.

Probably *Cricetulodon* sp. from Rinascita 1 and *Cricetulodon fahlbuschi* from Crevillente are quite close to a common ancestor. *Cricetus* sp. from Rinascita 1 and *Hattomys* may have a common ancestor that is derived from a species close to *C. kormosi*.

If this is true the age of the invasion of Gargano may be equal to, or somewhat older than, the age of the Crevillente faunas, i.e. Turolian. De Bruijn et al. (1975) correlate part of the Crevillente section with the Messinian. In fact the low sea-level of the Messinian presents a good condition for the fauna to have migrated from the continent to the Gargano island.

The correlation of the oldest Gargano faunas with the Turolian of Crevillente is confirmed by the presence of *Apodemus* cf. *primaevus* Hugueney & Mein, 1965 in Crevillente and a very similar *Apodemus* in the oldest Gargano fissures; furthermore the genus *Stephanomys*, considered to be the ancestor of the Gargano murid *Microtia*, is present in Crevillente and other localities of the same age. One of the Gargano Gliridae seems to be close to *Eliomys truci* Mein & Michaux, 1970, another component of the faunas of Crevillente.

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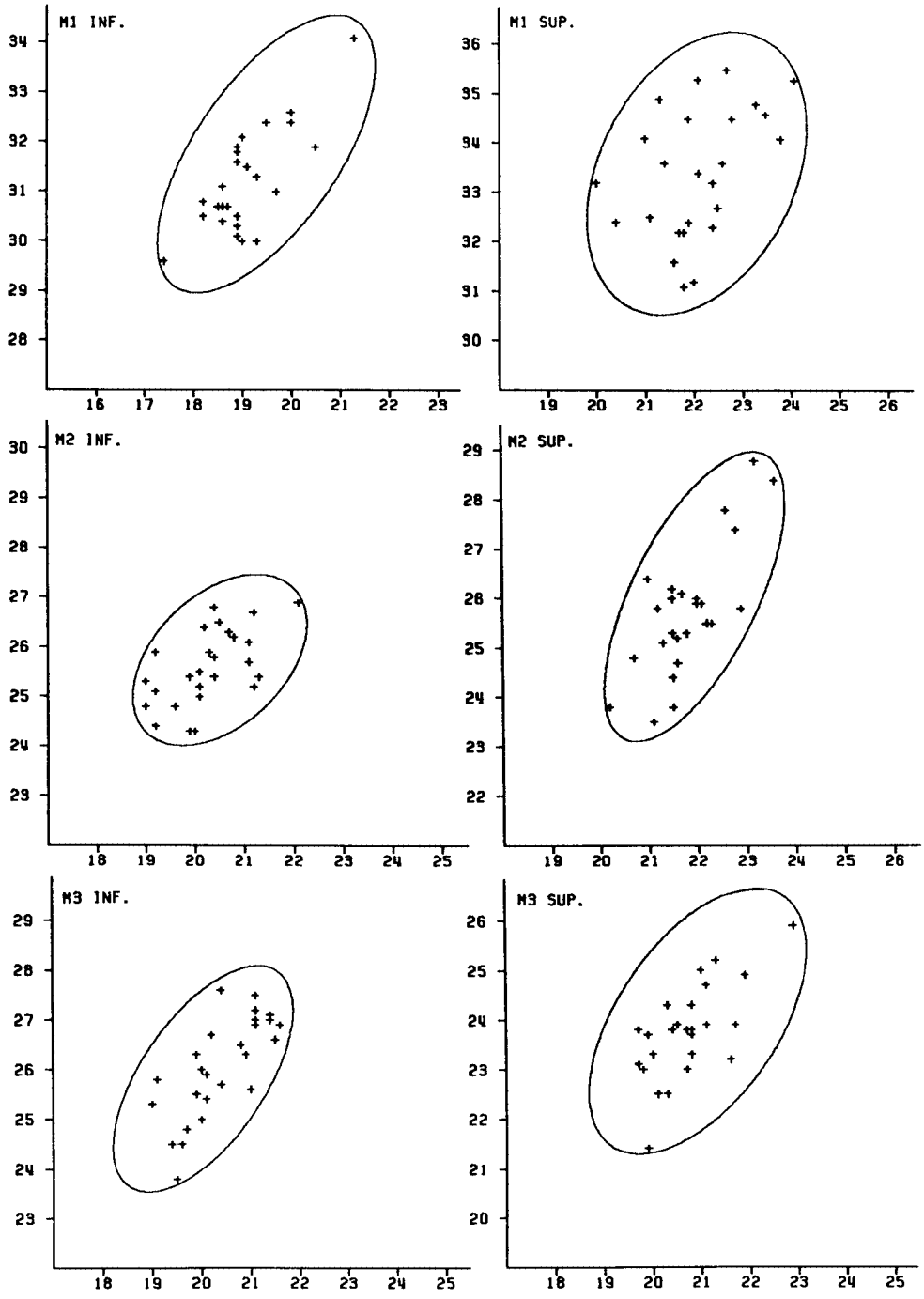

Fig. 1. Length-width diagrams of molars of *H. beetsi* from Biancone 1; length on the ordinate, width on the absciss.

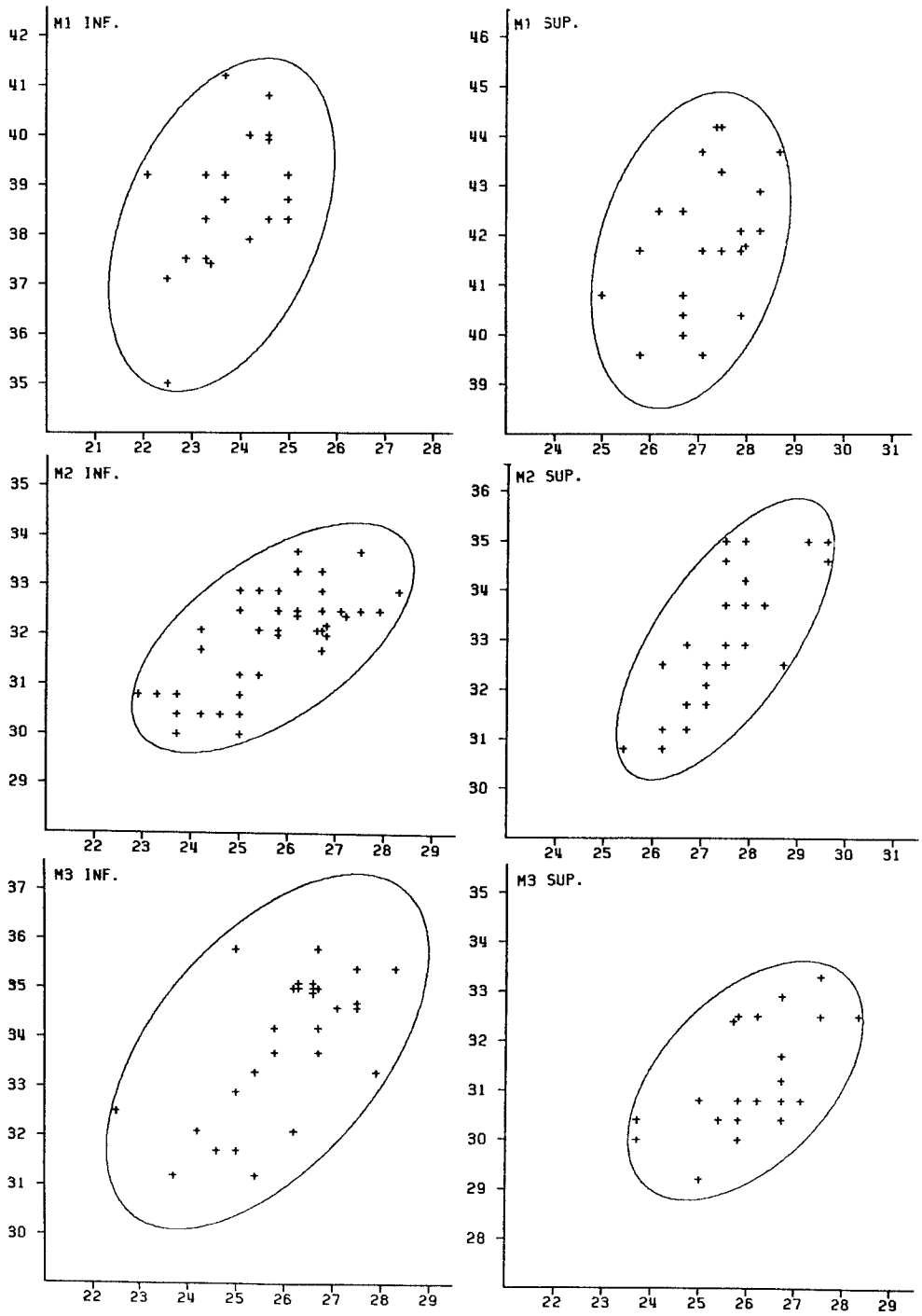

Fig. 2. Length-width diagrams of molars of *H. nazarii* from Nazario 2 B; length on the ordinate, width on the absciss.

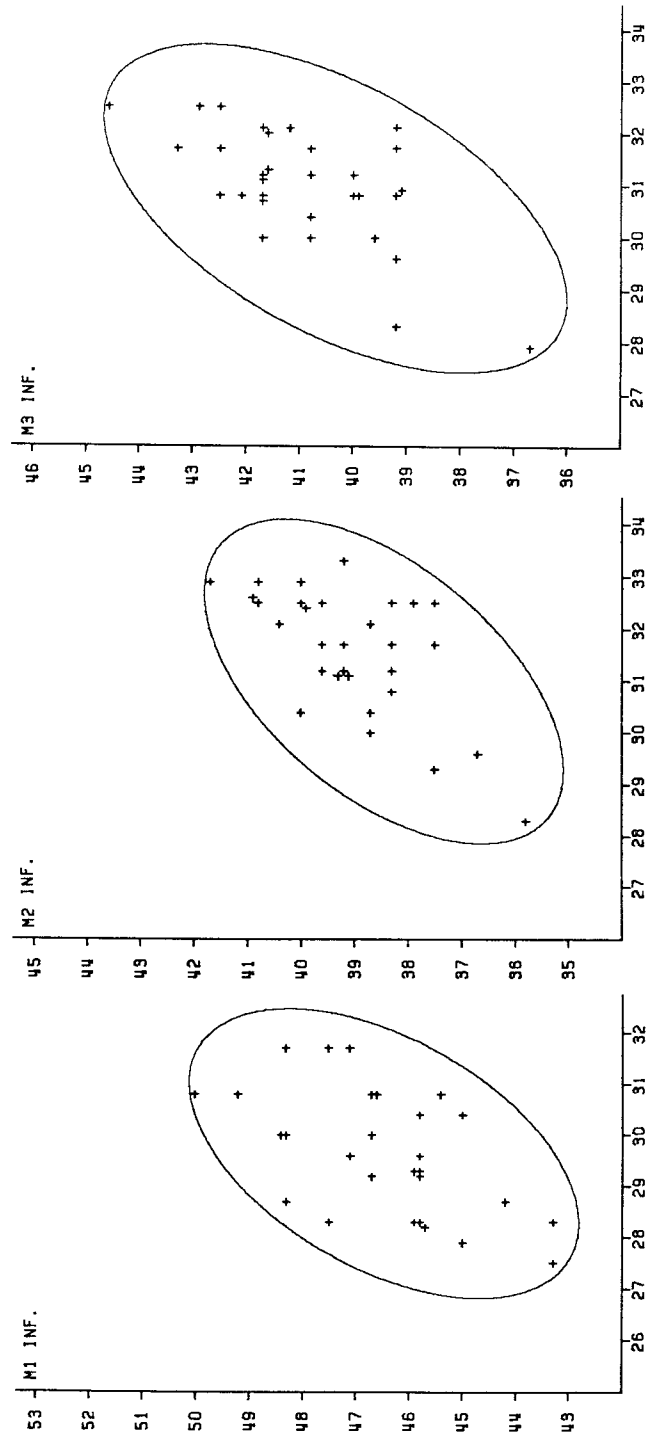

Fig. 3. Length-width diagrams of lower molars of *H. nazarii-gargantua* from Chiro 5 A; length on ordinate, width on absciss.

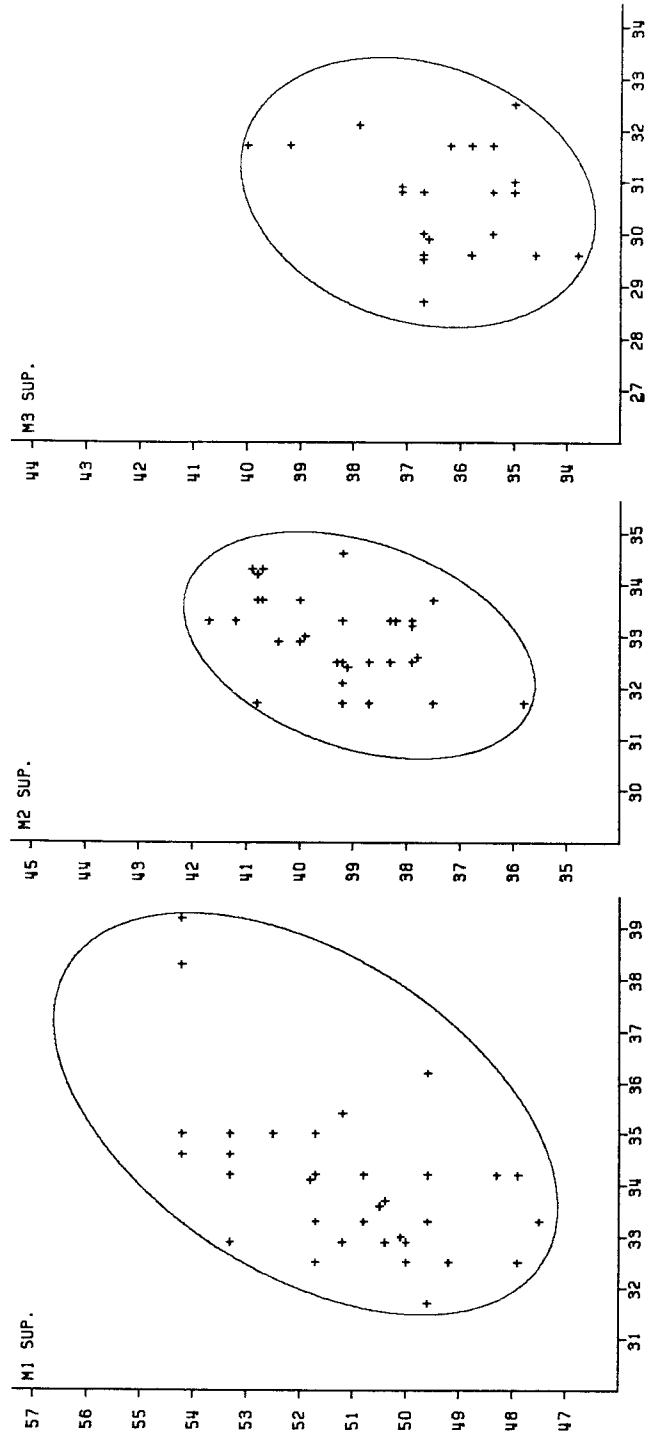

Fig. 4. Length-width diagram of upper molars of *H. nazarii-gargantua* from Chiro 5 A; length on ordinate, width on absciss.

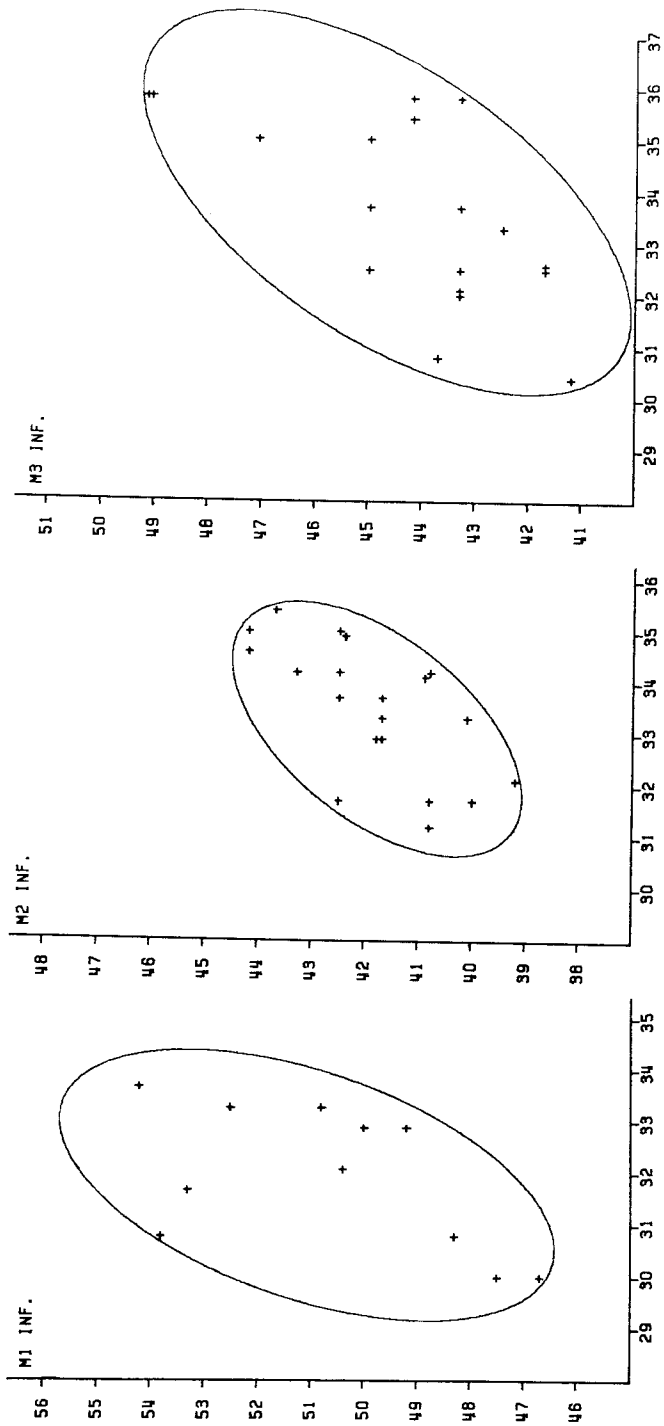

Fig. 5. Length-width diagrams of lower molars of *H. gargantua* from Chiro 2; length on ordinate, width on absciss.

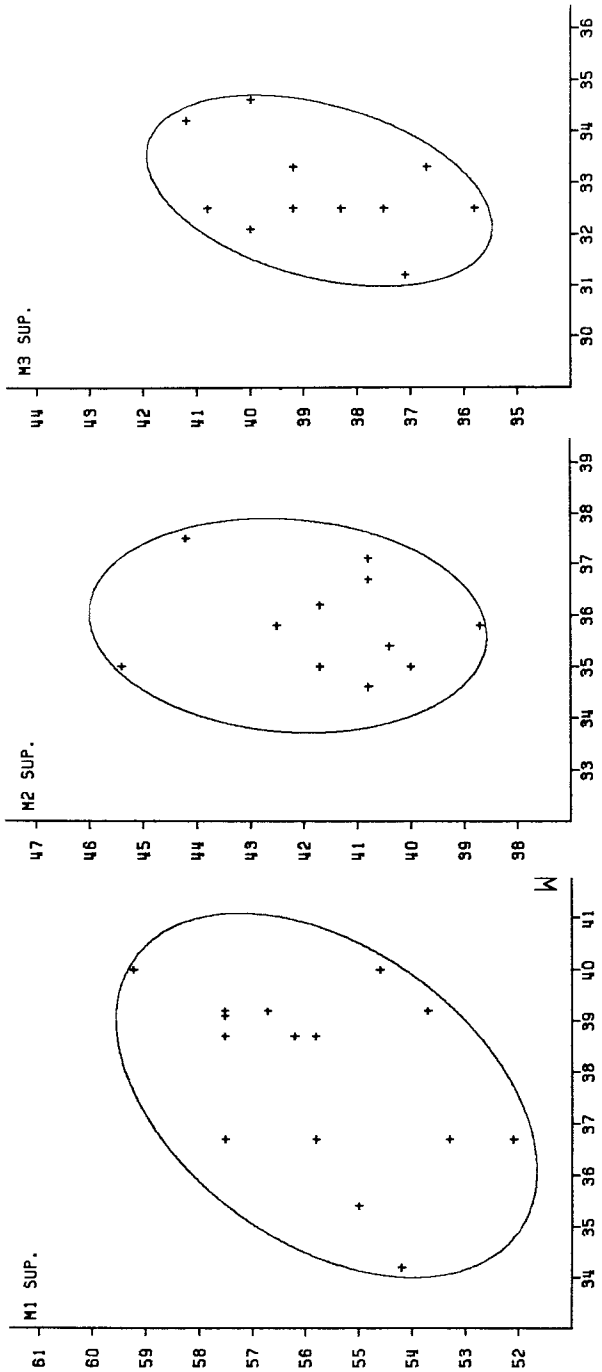

Fig. 6. Length-width diagrams of upper molars of *H. gargantua* from Chiro 2; length on ordinate, width on absciss.

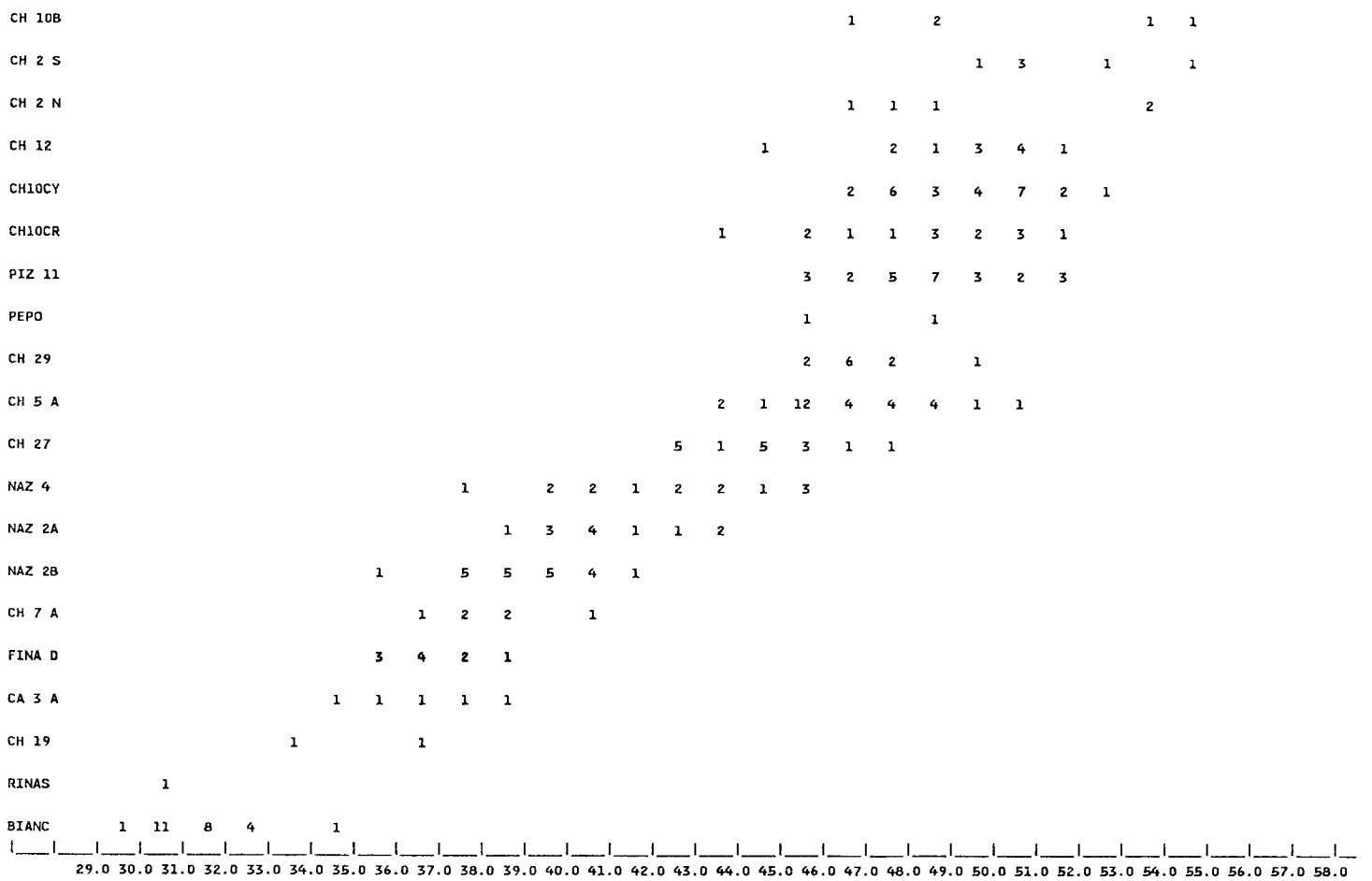

Fig. 7. Frequency distribution of the length of M_1 of *Hattomys*.

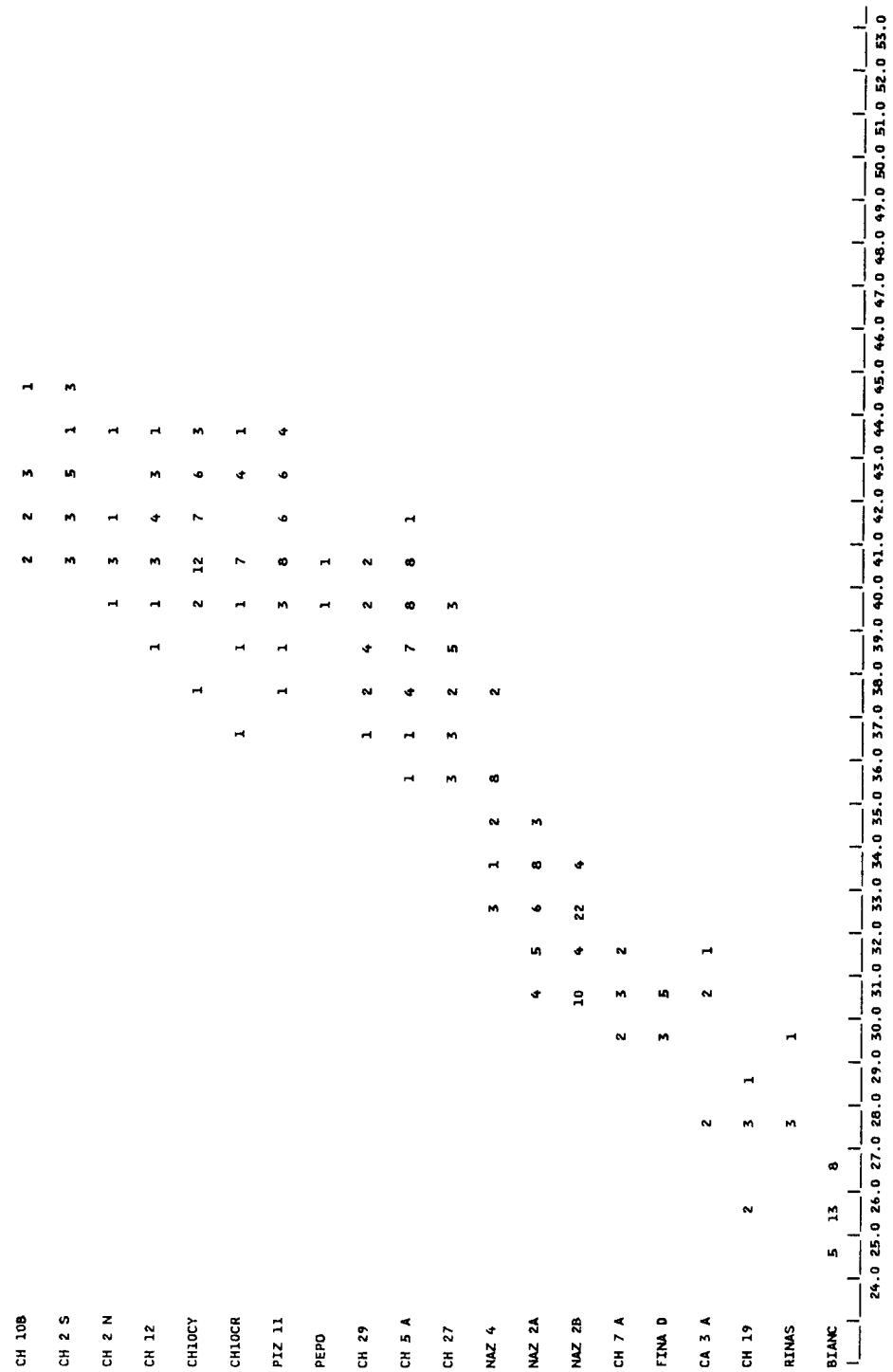

Fig. 8. Frequency distribution of the length of M_2 of *Hattomys*.

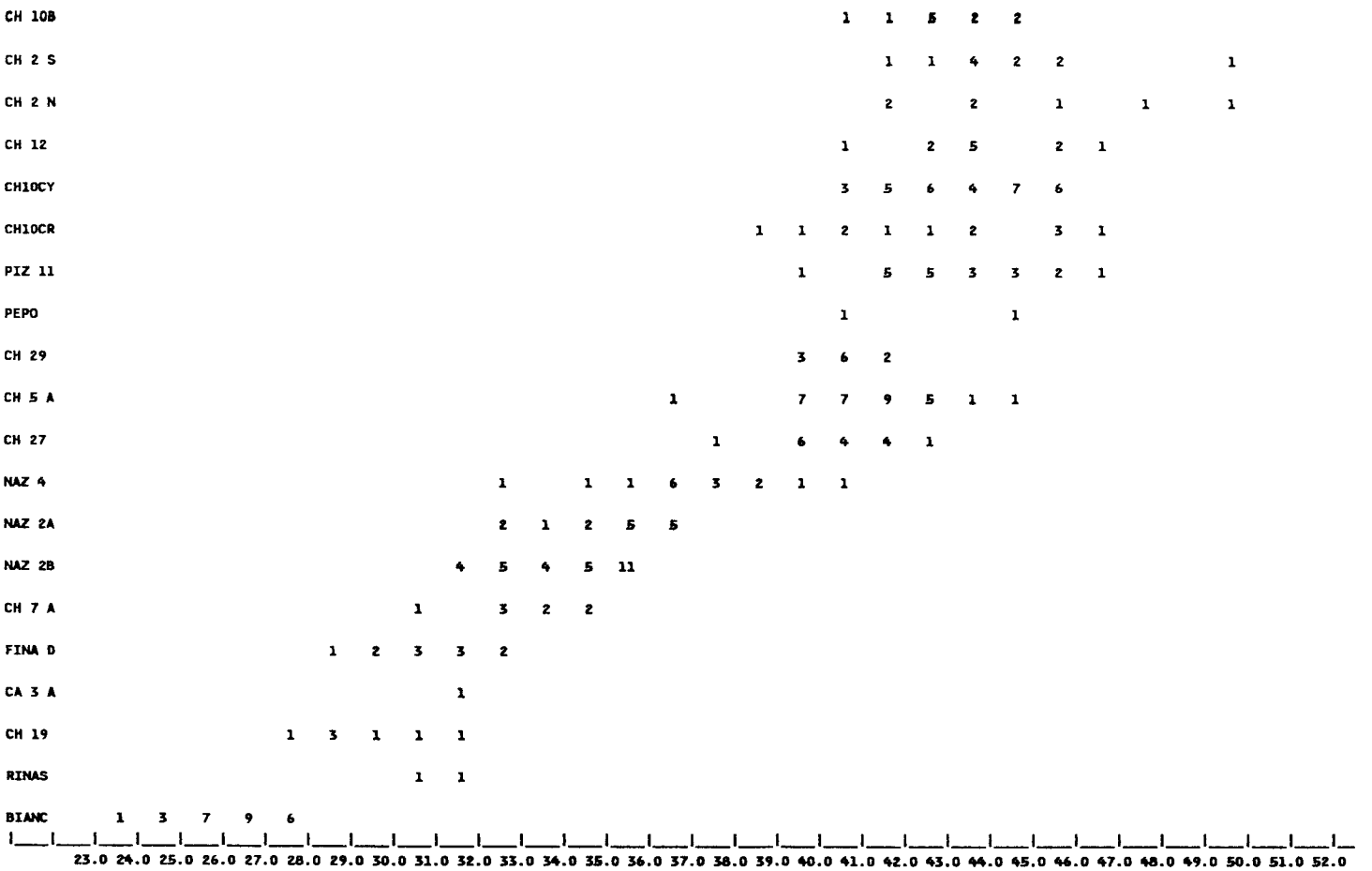

Fig. 9. Frequency distribution of the length of M_3 of *Hattomys*.

	31.0	32.0	33.0	34.0	35.0	36.0	37.0	38.0	39.0	40.0	41.0	42.0	43.0	44.0	45.0	46.0	47.0	48.0	49.0	50.0	51.0	52.0	53.0	54.0	55.0	56.0	57.0	58.0	59.0	60.0
CH 10B																						1	2	2	5	1	1	1	1	
CH 2 S																						1	1	1	2	2	2		1	
CH 2 N																							1	1	1		2			
CH 12																					3	1	1		5	3	2	1		
CH10CY																		1					2	3	5	5	10		4	1
CH10CR																					1		3	3	5	5	3	2		
PIZ 11																					1	2	4	9	6	3	3	1	1	
CH 29																				2	4	2	4	1						
CH 5 A																	3	2	5	8	7	1	4	4						
CH 27																1	1		3	8	1	2								
NAZ 4											1			1	3	2	1	2												
NAZ 2A										5	2	9	1	4	4															
NAZ 2B									2	5	5	5	3	2	1															
CH 7 A									1	2		1	1																	
FINA D						1	2	2	2	8		2																		
CA 3 A							2																							
CH 19					1																									
RINAS						1	1	1																						
BIANC	3	7	5	7	3																									

Fig. 10. Frequency distribution of the length of M^1 of *Hattomys*.

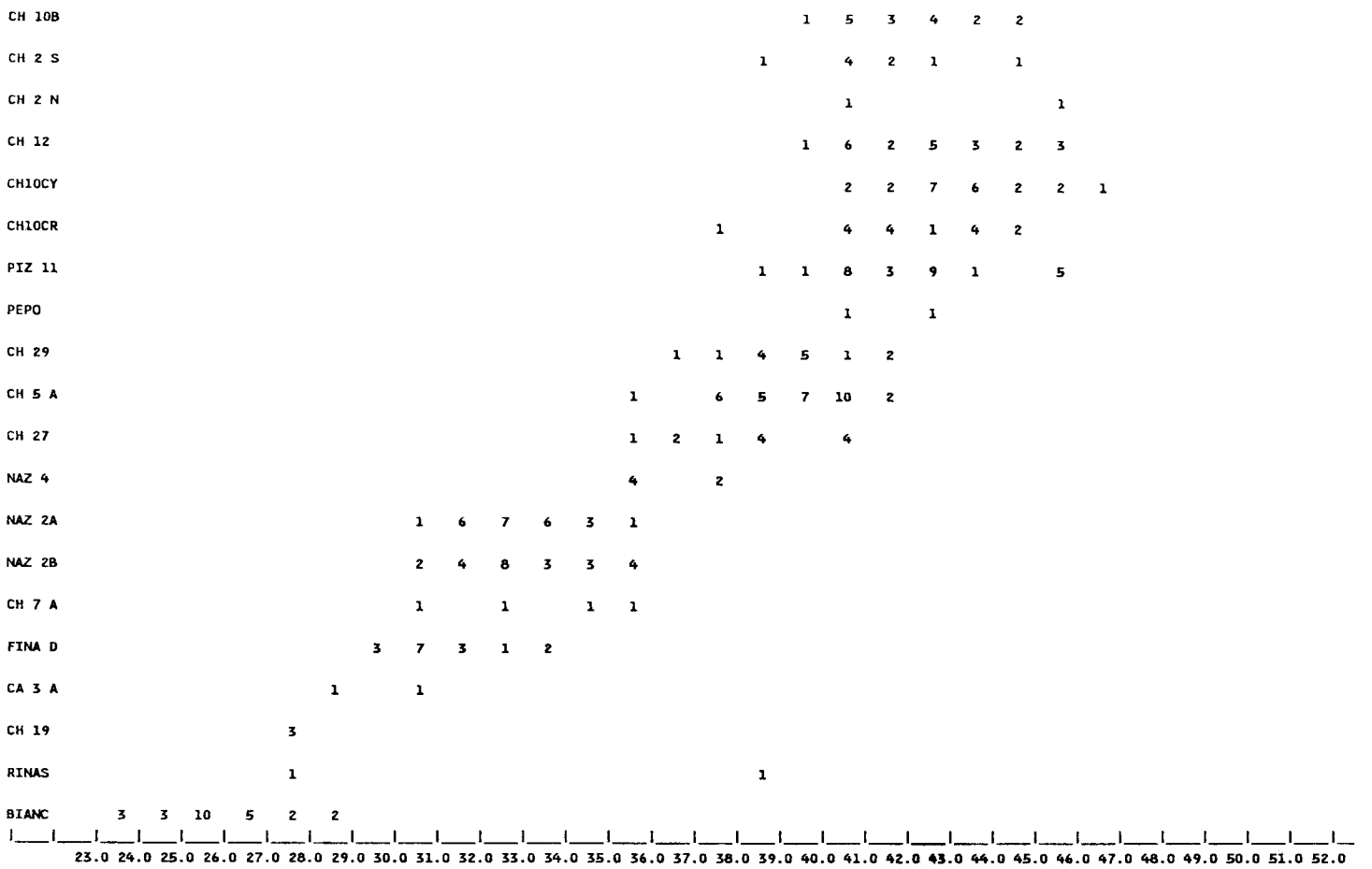

Fig. 11. Frequency distribution of the length of M^2 of *Hattomys*.

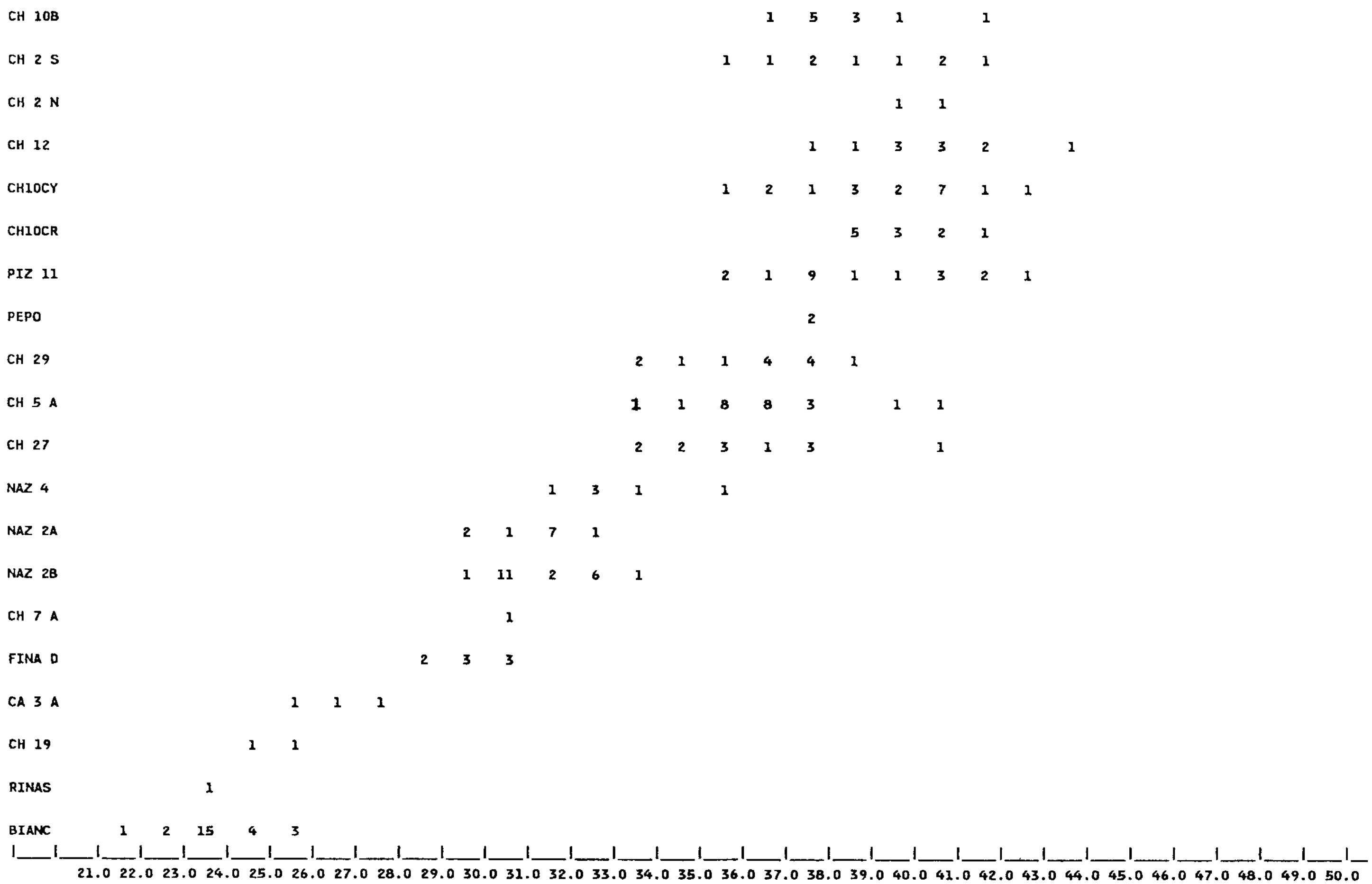

Fig. 12. Frequency distribution of the length of M^3 of *Hattomys*.

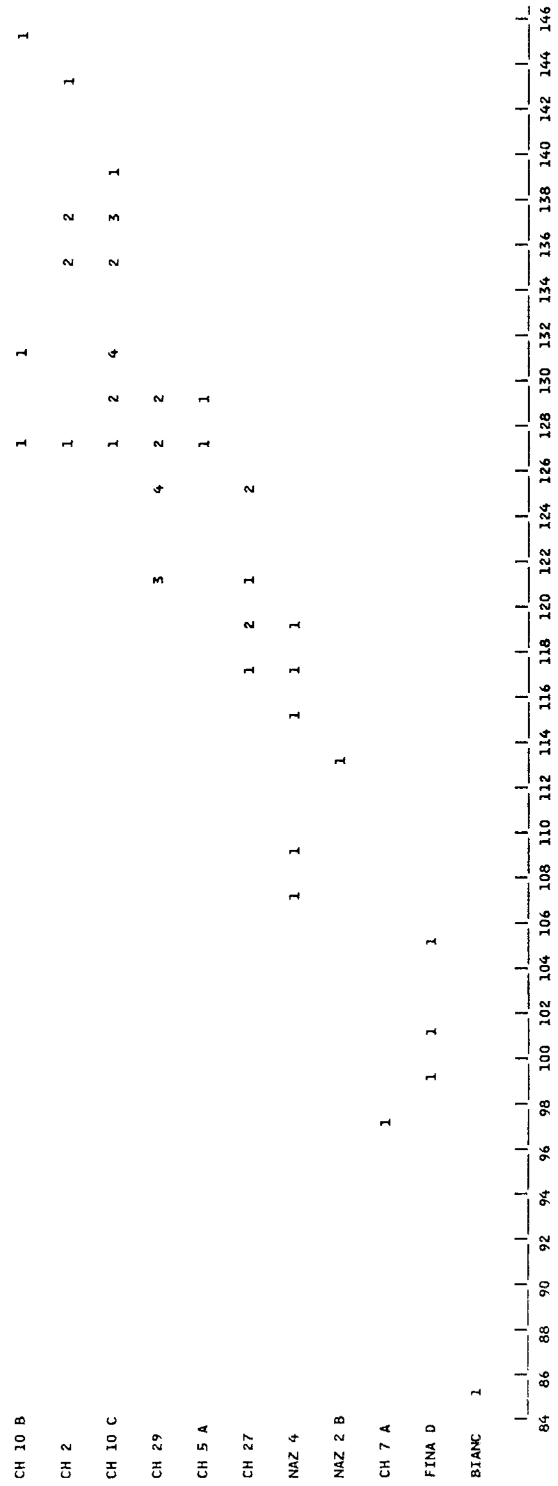

Fig. 13. Frequency distribution of the length of the lower tooth row of *Hattomys*.

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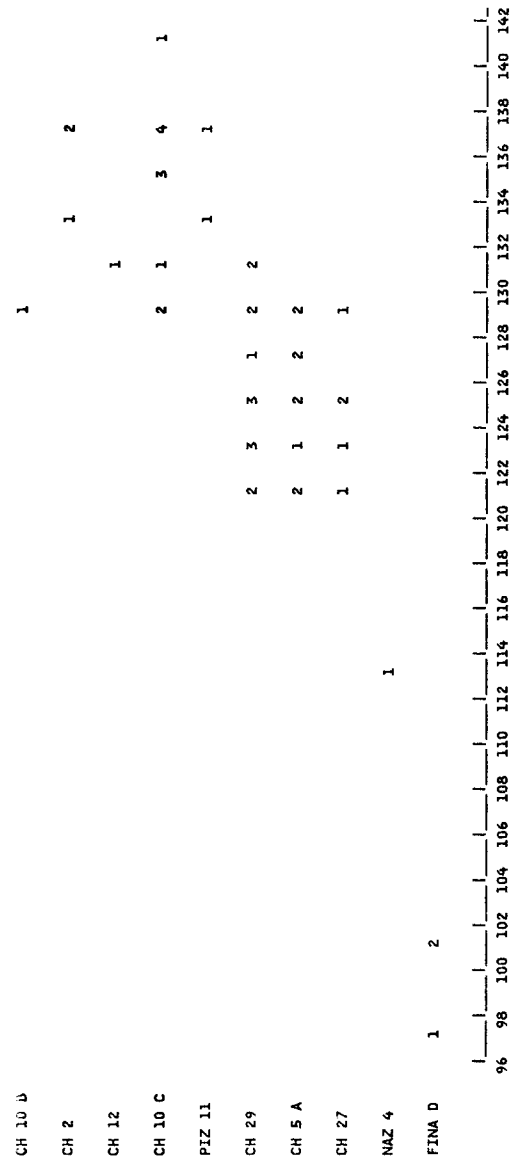

Fig. 14. Frequency distribution of the length of the upper tooth row of *Hattomys*.

CORRIGENDA SCRIPTA GEOLOGICA 77

Due to an unfortunate misunderstanding, which the editors deeply regret, three pages (pp. 69, 72, 75) have been omitted from the text. The missing pages, containing Figs. 7, 10 and 13, are given on the following pages.