Rodent stratigraphy of some Miocene fissure fillings in Gargano (prov. Foggia, Italy)

M. Freudenthal

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A new genus of Muridae, *Microtia*, is described and three species *M. magna, M. parva,* and *M. maiuscula* are ascribed to it. The size and morphology of *Microtia* molars show a very wide variation which is interpreted as an evolutionary trend, and used to establish an age sequence for a large number of fissure fillings, that show no stratigraphic correlation in the field. This sequence serves as a background for the study of the birds from Gargano by Ballmann.

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Introduction

The Gargano Upper Miocene fissure fillings were discovered in 1969 by the present author, Dr C. Beets, and Dr H. J. W. G. Schalke. Since then a number of collecting campaigns have been held, which yielded an extensive vertebrate collection from over 75 localities. These campaigns were financially supported by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.), the Italian Consiglio Nazionale delle Ricerche, and the Rijksmuseum van Geologie en Mineralogie.

The fossil vertebrates recognized so far belong to the following groups:

Amphibia		Mammalia:	Insectivora
Reptilia:	Testudinata		Chiroptera
	Crocodylia		Rodentia
	Sauria		Carnivora
	Serpentes		Artiodactyla
			Lagomorpha
Aves			

Among these only the birds, and one of the insectivores have been studied in some detail (Ballmann, 1973, Freudenthal, 1972). After Ballmann's publication a considerable amount of new bird material was collected, and a second publication on the Gargano birds appeared to be worth while. During a discussion on this

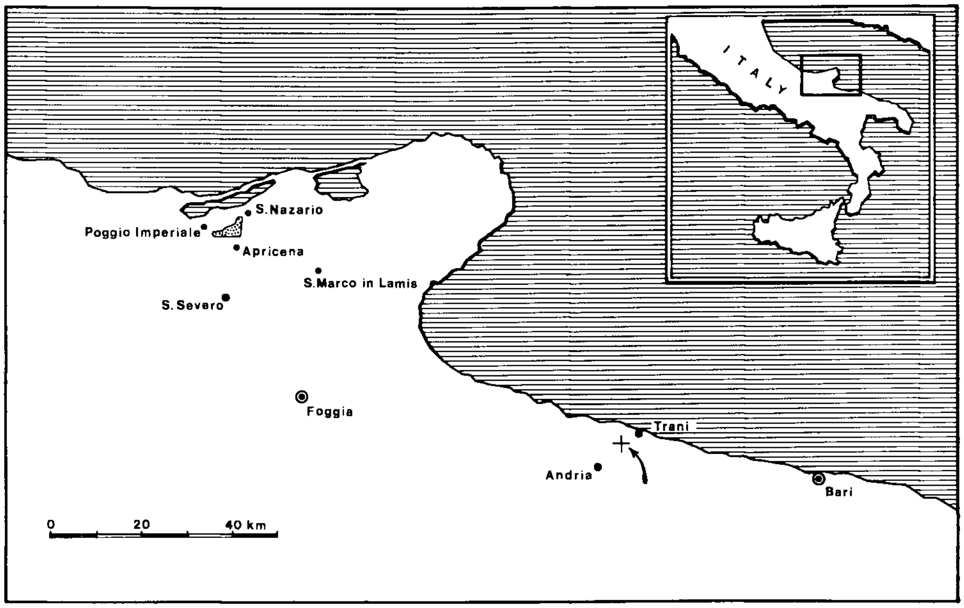


Fig. 1. Map. of Southern Italy, indicating the area under study. Most localities are in the area between Poggio Imperiale, Apricena and San Nazario. One locality between Trani and Andria is indicated by an arrow.

second publication between Ballmann and the present author we came to the conclusion, that there were age differences between the localities, and that a better knowledge of the chronological sequence would be of great help. This led to the present publication which is meant to propose a sequence for the localities where bird remains were found, by means of the degree of evolution of the rodents from these same localities.

A joint publication on the Muridae from Gargano by J. J. Michaux, R. Geesink and the present author is planned in the future, but this preliminary report is published now, in order not to hamper other lines of research.

Thanks are due to Messrs J. Timmers and T. Velthuyzen for their skilful execution of the drawings and photo work.

The Gargano Muridae

Among the fossils from the Gargano fissure fillings the Muridae constitute the most significant element. They are frequent in all localities, equalled or outnumbered by Lagomorpha only. Generally murid and lagomorph remains form over eighty percent of the faunules.

Two genera of murids may be distinguished, and these are both present in all localities sampled so far. The first one in all details answers the description of the modern genus *Apodemus,* which is quite surprising as the Gargano faunas are considered to be older than the oldest known occurrence of *Apodemus* in other areas. The second one is certainly the most conspicuous element of the Gargano faunas, and offers a good possibility to establish the chronological sequence of the localities, because it was subject to a great morphological change and increase in size during its existence in the Gargano area. In a number of features, such as the shape of the mandible, the elongation of M_1 and M^3, and its hypsodonty, it resembles Microtidae, which led to the choice of the name *Microtia* for this peculiar genus.

Microtia nov. gen.

Diagnosis — genus of Muridae with well-developed M_1 and M^3. M_1 consists of a posterior part of four cusps (two crests), as present in all murids, and an anterior part that may vary in its number of crests. The maximum number of crests so far found in a *Microtia* M_1 is seven. M^3 consists of two anterior crests in V-shape, plus a varying number of crests behind this V. The total number of crests in M_1 and M^3 is more or less equal within each population. The labial wall of M_1 and M^3 is often formed by a thin vertical enamel plate that tends to form a continuous connection between the crests. This plate is best developed in very hypsodont molars with a large number of crests. In hypsodont forms the roots may be formed long after the molar has begun to wear down.
The type species is

Microtia magna nov. sp.

Pl. 1, figs. 1-6; Pl. 2, fig. 1.

Holotype — Skull RGM 179 335, Pl. 1, figs. 1-3.
Type locality — San Giovannino, prov. Foggia, Italy. The type locality is a limestone quarry, South of the road from Poggio Imperiale to Apricena, near the farmhouse of San Giovannino. Topographic map of Italy, 1 : 25.000, Sheet 155 II NE, Apricena; co-ordinates 41°48'08" N, 2°57'37" E (zero meridian of M. Mario, Rome). During the years 1969 through 1972 there was hardly any quarrying activity, and the fossiliferous fissure remained accessible. This permitted us to collect a very fine collection from this fissure. In 1973 the quarry was reopened, and in the summer of 1975 a considerable part of the fissure filling had been removed. It is quite possible that it will soon be exhausted entirely.
Age — Late Miocene.
Cotypes — a large collection of skulls, mandibles, maxillas, isolated molars and bone material, kept at the Rijksmuseum van Geologie en Mineralogie, Leiden.
Figured cotypes — Mandible RGM 179 337, Pl. 1, figs. 4-6, Skull fragment RGM 179 336, Pl. 2, fig. 1. The skull fragment is figured because the molars in the holotype are rather worn.

Diagnosis — Very large murid, skull length 8 cm, maxillary tooth row 20 mm, mandibular tooth row 18 mm; M_1 has five crests in the figured cotype, M^3 has four crests in the holotype, four and a half in the figured cotype.

Discussion

Microtia magna is chosen as the type species for *Microtia* as it is the largest species found so far, it is extremely well represented by beautiful skull material, and it constitutes the most conspicuous species from the richest Gargano locality. Other species have a higher degree of hypsodonty, a larger number of crests in M_1 and M^3 and better developed external enamel plates, but materially these forms are not as well represented in our collection.

Measurements — So far only a number of M_1 have been measured. The results are given in Table 1.

At present only a small part of the available *Microtia* material has been studied. Over seventyfive fossiliferous localities in the area have been sampled, and all of these yielded *Microtia* material. In a few localities less than hundred specimens were found but generally we have hundreds, and in quite some cases even thousands of specimens.

One of the localities, Biancone, has been studied by Mr R. Geesink (Rijksherbarium, Leiden), which resulted in an - unpublished - thesis. I am very grateful that Mr Geesink gave me permission to use his data in this publication. In Biancone two species of *Microtia* can be distinguished quite easily by their size and these two will be described here, in order to facilitate the discussion of *Microtia* evolution hereafter.

Microtia parva nov. sp.
Pl. 2, figs. 4, 5.

Holotype — Maxilla sin. with M^1-M^3, RGM 194 344, Pl. 2, fig. 4.
Type locality — Biancone, Gargano, prov. Foggia, Italy. Topographic map of Italy, 1 : 25.000, sheet 155 II NE, Apricena; co-ordinates 41° 48' 48" N, 2° 59' 12" E (zero meridian of M. Mario, Rome). Biancone is the name of the previous owner of the quarry which was situated on the West side of the road from Apricena to San Nazario. In the summer of 1975 the site was owned by Maselli, and the quarrying activity had completely changed the aspect

of the place. In fact the fossiliferous fissure filling has only been accessible in 1970. All material collected is from a sample of about 1000 kg of matrix. Other fissure fillings in the same quarry, discovered in the years 1971 through 1975, did yield fossil material but the fissure we designate by the name of Biancone is the only one so far that produced material of *M. parva.*
Age — Late Miocene.
Cotypes — A collection of about 7000 teeth from Biancone. Some 500 have been catalogued with RGM registration numbers that lie between 149 082 and 149 761.
Figured cotype — Mandibula sin. with M_1-M_3 RGM 149 082, Pl. 2, fig. 5.

Diagnosis — Considering its upper M^1 *M. parva* could be considered as a large *Stephanomys.* The lower molars are not like those of *Stephanomys.* They resemble a common murid type like *Parapodemus,* though some alterations are definitely recognizable. M_1 is made up of three crests plus an anterior cusp that may be simple or split (level 3½ to 4 as defined in the chapter on quantified morphology). A mesolophid is often present between the posterior two crests. The anterior cusp may be connected to the next crest by one longitudinal ridge, or by two such ridges seperated by a small funnel. M^3 consists of three ridges: t_1, t_4-t_6, and t_7-t_9 (see Thaler, 1966, p. 116). In some cases t_7-t_9 shows a shallow sinus in the lingual wall, that indicates the possibility of a further subdivision. The teeth are moderately hypsodont. The vertical enamel plate on the labial side of the molars is hardly present. M_1 has two roots, M^3 has two or three roots.

Measurements — see Figs. 2, 3.

Discussion

M. parva is almost the smallest *Microtia* known. Only one form from Rinascita 1 and Trefossi 1 is smaller than *M. parva* (see Fig. 4). Yet it is still considerably larger than any contemporaneous murid known (with the exception of *M. maiuscula* to be described hereafter).

Microtia maiuscula nov. sp.
Pl. 2, figs. 2, 3.

Holotype — Maxilla sin. with M^1-M^3 RGM 149 425, Pl. 2, fig. 2.
Type locality — Biancone, Gargano, prov. Foggia, Italy. For details on the type locality see the description of *M. parva* nov. sp.
Age — Late Miocene.
Cotypes — Over hundred specimens from Biancone, catalogued under RGM registration numbers that lie between 149 080 and 149 476.
Figured cotype — Mandibula dex. with M_1-M_3 RGM 149 081, Pl. 2, fig. 3.

Diagnosis — larger than *M. parva.* All features present in *M. parva* are found in *M. maiuscula* as well, though their frequency may be different. Apart from size the only difference between *M. parva* and *M. maiuscula* may be that in the latter there is always a sinus in the lingual part of the posterior crest of M^3.

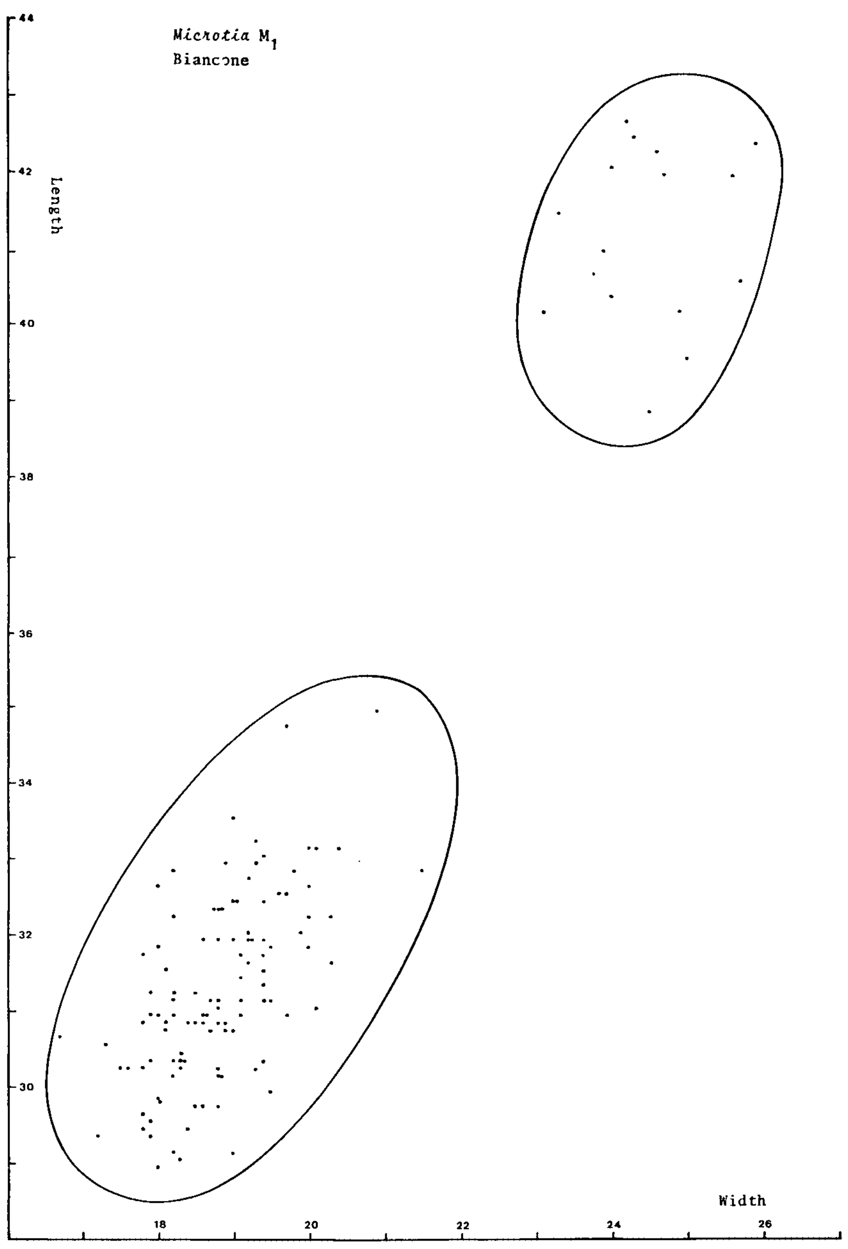


Fig. 2. Length-Width diagram of M_1 of *M. parva* and *M. maiuscula* from Biancone. Scale in tenths of millimeters.

Measurements — see Figs. 2, 3.

Quantified morphology

One of the most conspicuous features of Microtia M_1 and M^3 is the large number of crests these elements may develop. This led to an effort to quantify the morphology of these elements, as follows: for M_1 the number of crests is counted;

if the anterior cusp is simple it is counted as a half crest, if it is split it is counted as a full crest. Each of the measured specimens is given such a morphology value, and the arithmetic mean of these values is calculated for each population. In Fig. 4 the mean values of the morphology of M_1 are represented by the dashed line. The horizontal scale represents the number of crests for the morphology. For M^3 the procedure is essentially indentical to that for M_1. The number of crests is counted, the posterior crest is counted as 1 if it is simple, and a ½ is added if the posterior crest shows some trace of further subdivision. The mean morphology of M^3 is represented by the dot and dash line in Fig. 4.

The *Microtia* molars offer a splendid opportunity to approach the morphology by methods of quantification and statistics. Several features that can easily be counted show a wide range through the whole of the material available. However, the figures given in this paper are certainly not optimal, and a great deal of improvement may be expected from a further refinement of the counting method, and of the value attributed to the various morphological types. This will be the scope of a later paper.

Principles of Microtia evolution

As stated in previous papers (Freudenthal, 1971, 1972) Gargano is supposed to have been an island, well isolated from the mainland, during the time when the genus *Microtia* existed. It is not imaginable that the fauna we recovered from the Gargano fissure fillings could have existed in an area that did have any connection with the mainland. There are some indications that immigrations took place in Gargano during the existence of the *Microtia* fauna, but these can certainly not have been immigrations from the mainland. New murids that may have been introduced in the area under study do already fit the generic description of *Microtia,* so they must have undergone insular isolation on another island during some time before they reached our area. It seems most logical to assume that a number of islands existed in the South Adriatic (present Gargano and Le Murge may have been two of these islands), and these islands became connected from time to time so that faunal exchange was possible. The periods of connection were so rare that each island could develop different forms, and they were so frequent that the fauna of the entire archipelago continued to form a homogeneous unit. The main principles of evolution explained hereafter may have been valid on all islands, the details may have differed.

The genus *Microtia* is represented by a vast amount of material from over seventyfive fissure fillings in Gargano. There is a very wide variety in size and morphology among this material: the smallest M_1 measure about 2.3 mm, the largest ones reach 9 mm. The number of crests in M_1 varies between 3½ and 7. Within each sample the size variation is not larger than it is normally in murids, and if it is so, this can easily be explained by the presence of more than one species, clearly distinguished by size and morphology. The total variety, however, must be caused by evolutionary trends that can only be traced if the chronological sequence of the localities is known.

Unfortunately, all Gargano localities are fissure fillings and their chronological relation cannot be derived from the superposition of strata. So, we have to work with the assumption that a certain feature is primitive, and then we declare the locality in which it was found to be 'old'; another feature is considered to be modern, and the locality in which it was encountered is considered to be 'young'. It is evident that this is a vicious circle: if the assumption is inverted, the conclusions change automatically into their opposites.

However, it seems acceptable that the first murids that invaded Gargano should not have been too different from murids on the mainland, which means that they must have been relatively small, and that they cannot have had an excessive number of crests in M_1 and M^3. This makes populations with a large size or a complex morphology 'modern'.

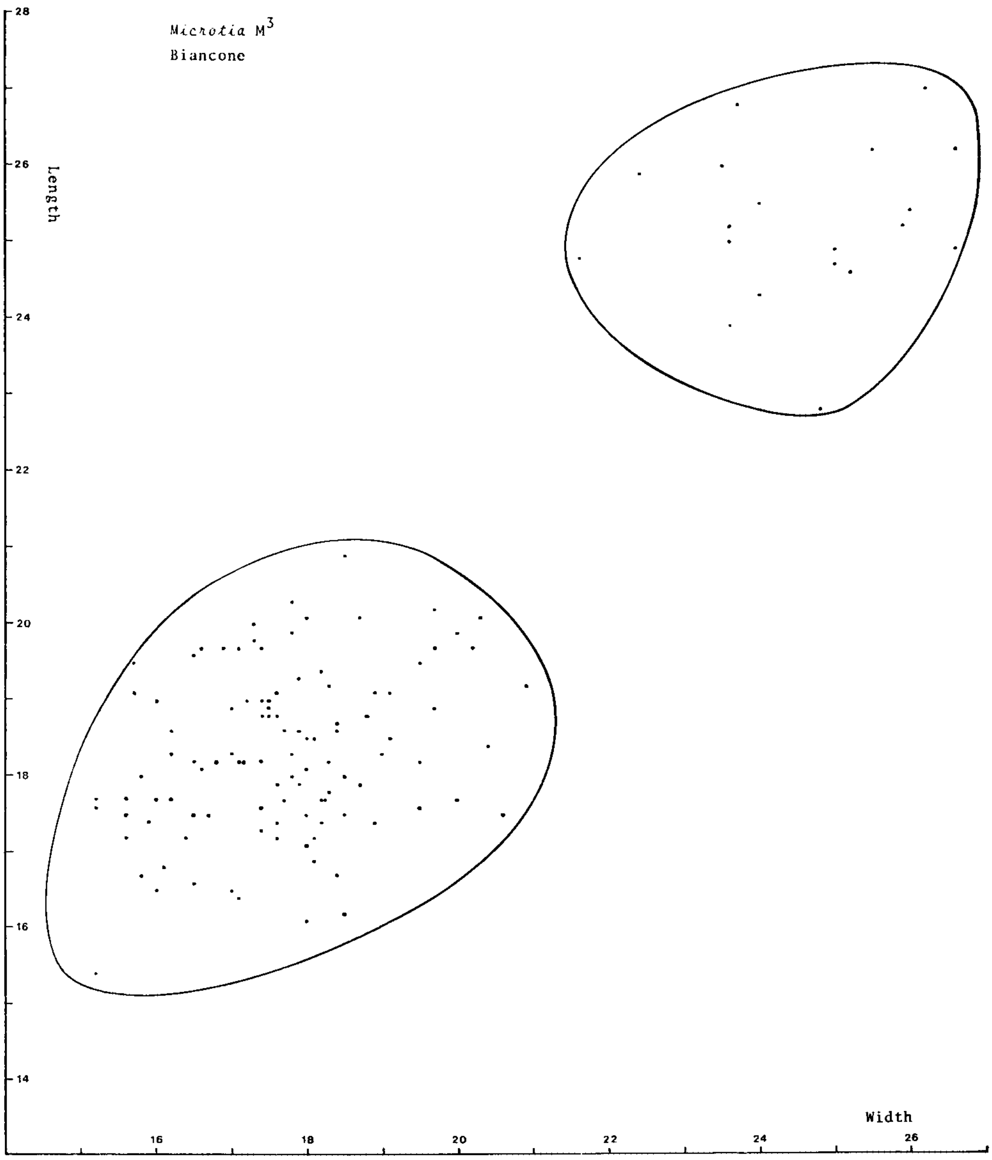


Fig. 3. Length-Width diagram of M^3 of *M. parva* and *M. maiuscula* from Biancone. Scale in tenths of millimeters.

With these principles in mind we proceeded in measuring with the vernier callipers the lengths of up to twenty specimens of M_1 per species for each of the localities considered to be important. Of course it will be necessary in a future publication to use a more refined measuring method and to measure a larger amount of material, but within the framework of this preliminary report the method used turned out to be quite satisfactory.

In the localities regarded as young in view of the presence of the very large species *M. magna*, there are generally three species: the large *magna*, a medium-sized one and a small one. Morphologically the medium one is highest developed. The smaller one varies moderately in size but the medium-sized species varies considerably throughout the localities considered to be young. These localities were then put in a sequence of ascending size of the medium species. It then appeared that other localities where only one species of *Microtia* was present formed a logical downward continuation of the sequence found so far. This led to a chronological arrangement of the fissure fillings which show no stratigraphical relationship in the field.

The next step was to take the evolution of the medium lineage as a parameter of continuous evolution. In Figure 4 the arithmetic means of the populations considered to belong to this lineage are arranged on a straight oblique line; the horizontal axis represents the absolute size of M_1. The angle of the oblique line is insignificant, which means that the vertical axis - representing the time - has a relative and not an absolute value. If the assumption of a continuous evolution in the medium lineage is valid, the vertical distances between localities in Fig. 4 represent relative time gaps between these localities. After the vertical position of each of the localities had been established in this way samples of smaller and larger *Microtia* species from the same localities — as far as available — were measured, and introduced in their proper place in Fig. 4. Furthermore the same procedure was followed for the M_1 of Cricetidae. Question marks indicate that the entry is not based on M_1, but on the lenght of M_1 estimated from other dental elements. Interrupted range lines indicate that the distribution within the range is discontinuous and that the sample may represent more than one species.

This procedure gave a satisfactory result for most of the localities studied: the medium-sized *Microtia* species show a continuous growth in size, the smaller species originates about halfway the stratigraphic sequence, and in the higher localities it is generally present without varying in size; the larger species can probably not be derived from the medium one; it is introduced in the upper part of the sequence, and after that it is present in most localities, showing a moderate increase in size, parallel to the increase in the medium lineage.

Fig. 4. Evolution of *Microtia* and stratigraphy of the Gargano localities (see pages 12 and 13). The length of M_1 is indicated on the horizontal scale in tenths of millimeters. The horizontal lines represent the ranges of the lengths of M_1 in the various populations. The continuous oblique lines connect the arithmetic means of the various populations.

B	Biancone	N4	San Nazario 4	C9	Chiro 9	C4	Chiro 4
R1	Rinascita 1	P4	Pizzicoli 4	C2S	Chiro 2 S	C20C	Chiro 20 C
T1	Trefossi 1	C27	Chiro 27	P1B	Posticchia 1 B	P11A	Pirro 11 A
C3A	Cantatore 3 A	C6	Chiro 6	C14A	Chiro 14 A	C24	Chiro 24
FD	Fina D	MG1	Mt. Granata 1	FH	Fina H	G2	Gervasio 2
C7A	Chiro 7 A	C5A	Chiro 5A	G1	Gervasio 1	SG	San Giovannino

The horizontal scale also represents the number of crests counted in M_1 and M^3.
– – – – line connecting the morphology values of M_1 of the main lineage (lineage 2).
—·—·— line connecting the morphology values of M^3 of the main lineage.

Table 1. Measurements of *Microtia* molars used for the evolution table.

locality		length M_1				morphology	
	n	min.	mean	max.	range	M_1	M^3
Main line of evolution (lineage 2 in Fig. 4)							
Biancone	118	2.9	3.15	3.5	0.6	3.80	3.50
Rinascita 1	20	3.7	3.93	4.2	0.5	3.95	3.50
Trefossi 1	20	3.8	4.15	4.5	0.7	4.00	3.50
Cantatore 3 A	20	4.4	4.75	5.3	0.9	4.18	3.50
Fina D	20	4.4	4.92	5.3	0.9	4.58	3.65
Chiro 7 A	20	4.7	5.07	5.3	0.6	4.68	3.65
Nazario 4	20	4.8	5.27	5.8	1.0	4.89	4.07
Pizzicoli 4	20	5.1	5.49	5.9	0.8	5.03	4.45
Chiro 27	20	5.2	5.59	6.3	1.1	5.05	4.45
Chiro 6	20	5.0	5.67	6.5	1.6	5.20	4.93
Mt. Granata 1	11	5.3	5.70	6.1	0.8	5.00	4.95
Chiro 5 A	20	5.4	5.75	6.2	0.8	5.13	4.50
Chiro 9	20	5.3	5.83	6.2	0.9	5.18	4.88
Chiro 2 S	30	5.4	5.84	6.2	0.8	5.18	4.87
Posticchia 1 B	10	5.5	5.86	6.4	0.9	5.65	5.78
Chiro 14 A	20	5.6	5.90	6.3	0.7	5.23	4.95
Gervasio 1	15	5.7	6.12	6.5	0.8	5.96	5.90
Chiro 20 C	20	5.9	6.26	6.5	0.6	6.05	6.32
Pirro 11 A	7	6.1	6.29	6.5	0.4	6.00	6.75
Chirro 24	20	5.9	6.31	6.7	0.8	6.10	6.38
Gervasio 2	6	6.5	6.67	7.0	0.5	6.40	7.00
Chiro 4	6	6.0	6.17	6.7	0.7	6.00	6.30
San Giovannino	20	6.4	6.75	7.2	0.8	6.23	6.32
Group of large species (lineage 3 in Fig. 4)							
Chiro 27	2	7.5	7.55	7.6	0.1	5.00	
Fina H	10	7.2	7.77	8.2	1.0	5.10	4.83
Chiro 6	5	7.3	7.70	8.2	0.9	5.10	
Mt. Granata 1	6	7.2	7.48	7.9	0.7	5.17	5.00
Posticchia 1 B	10	7.0	7.56	8.0	1.0	5.00	4.75
Gervasio 1	13	7.4	7.97	8.7	1.3	5.13	4.80
Chiro 20 C	10	7.6	7.96	8.6	1.0	5.00	
Pirro 11 A	10	7.9	8.42	9.0	1.1	5.00	4.70
Chiro 24	6	7.6	7.88	8.3	0.7	4.94	4.57
Gervasio 2	4	8.0	8.10	8.2	0.2	4.88	4.75
San Giovannino	10	7.9	8.36	8.9	1.0	5.00	4.75
Chiro 4	10	7.5	8.13	8.8	1.3	5.10	4.85
Chiro 10 B	9	7.5	7.96	8.4	0.9	5.11	5.05
Group of small modernized species (lineage 1 in Fig. 4)							
Bosco	10	3.7	3.98	4.3	0.6	4.90	4.45
Chiro 27	3	4.0	4.07	4.2	0.2	5.00	
Fina H	34	3.7	4.28	4.8	1.1	5.05	4.53
Posticchia 1 B	10	3.9	4.13	4.4	0.5	5.00	4.40
Gervasio 1	10	3.8	4.04	4.2	0.4	5.10	4.40
Chiro 20 C	4	3.8	4.06	4.3	0.5	5.20	4.45
Pirro 11 A	10	3.7	3.92	4.2	0.5	5.00	4.35

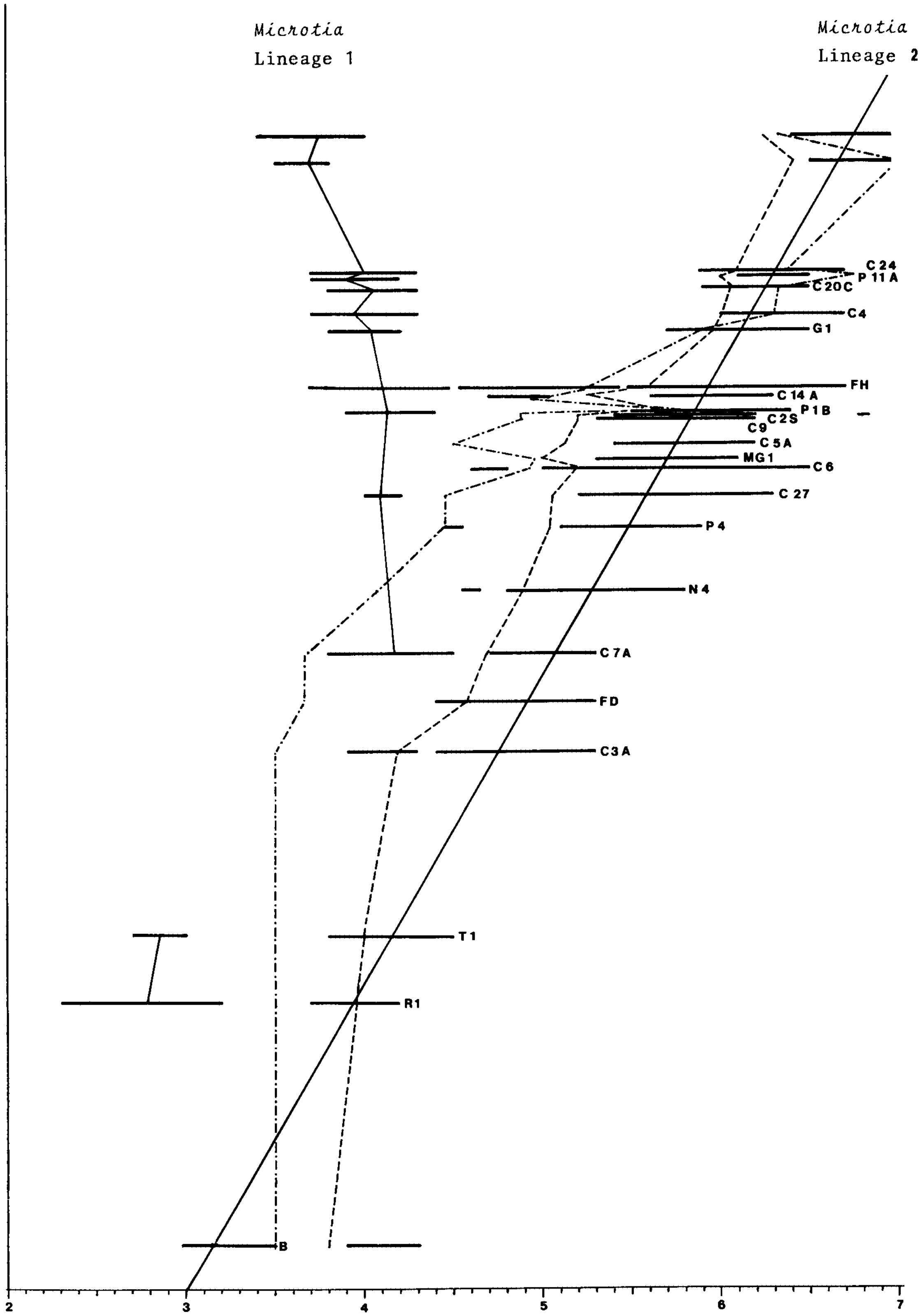
Table 1. Measurements of Microtia molars used for the evolution table (continued).

locality			length M_1			morphology	
	n	min.	mean	max.	range	M_1	M^3
Chiro 24	10	3.7	4.01	4.3	0.6	4.85	4.60
Gervasio 2	10	3.5	3.69	3.8	0.3	5.00	4.30
San Giovannino	10	3.4	3.74	4.0	0.6	4.95	4.45
Chiro 4	10	3.7	3.95	4.3	0.6	5.05	4.40
Miscellaneous							
Biancone	16	3.9	4.10	4.3	0.4	3.93	
Rinascita 1	16	2.3	2.78	3.2	0.9	3.50	3.03
Trefossi 1	4	2.7	2.85	3.0	0.3	3.50	3.13
Cantatore 3 A	3	3.9	4.03	4.2	0.3	4.00	3.50
Chiro 7 A	10	3.8	4.17	4.5	0.7	3.94	
Pizzicoli 4	1		4.50			4.50	
Nazario 4	1		4.60			4.00	
Chiro 14 A	14	4.7	4.94	5.3	0.6	4.71	3.86
Chiro 10 B	10	4.8	5.16	5.4	0.6	5.25	4.68
Chiro 2 S	1		6.80				
Chiro 10 B	2		4.35			4.00	
Chiro 6	2	4.6		4.8			

Correlation of the Gargano fissure fillings

REFERENCE LOCALITIES

We will now follow the results as presented by Figure 4. Biancone is the lowest locality in this scheme. In our interpretation *M. parva,* the smallest species from Biancone, and by far the most common one, is regarded as the source that gave rise to the main lineage of evolution. The larger species, *M. maiuscula,* is very rare. In Rinascita 1 there are also two species but in this locality the larger one is the most common. In Figure 4 we have put the most common species from these two localities on the main line of evolution, which results in the conclusion that Biancone must be older than Rinascita 1. An alternative would be to place *M. maiuscula* on the main line, and in that case Biancone would be younger than Rinascita 1 (and older than Trefossi 1). However, this appears to be quite unlikely, as the smaller species is rare in both Rinascita 1 and Trefossi 1, and the larger species in these two localities is the most common. Placing Biancone between Rinascita 1 and Trefossi 1 would mean a double switch of frequencies. Furthermore the M^3 of the larger species from Rinascita is more highly developed that it is in *M. maiuscula.* So, it is rather improbable that Biancone be younger than Rinascita 1. When Biancone is considered to be older than Rinascita 1, it is quite unlikely that *M. maiuscula* be the source of the main lineage of evolution, as in that case the continuous increase in size from Rinascita 1 upwards would be preceded by a decrease in size from Biancone to Rinascita 1. Furthermore it is not probable that *M. parva* should be linked to the smaller species from Rinascita 1,



Microtia
Lineage 1
Microtia
Lineage 2
C 24
P 11 A
C 20 C
C 4
G 1
FH
C 14 A
P 1 B
C 2 S
C 9
C 5 A
MG 1
C 6
C 27
P 4
N 4
C 7 A
FD
C 3 A
T 1
R 1
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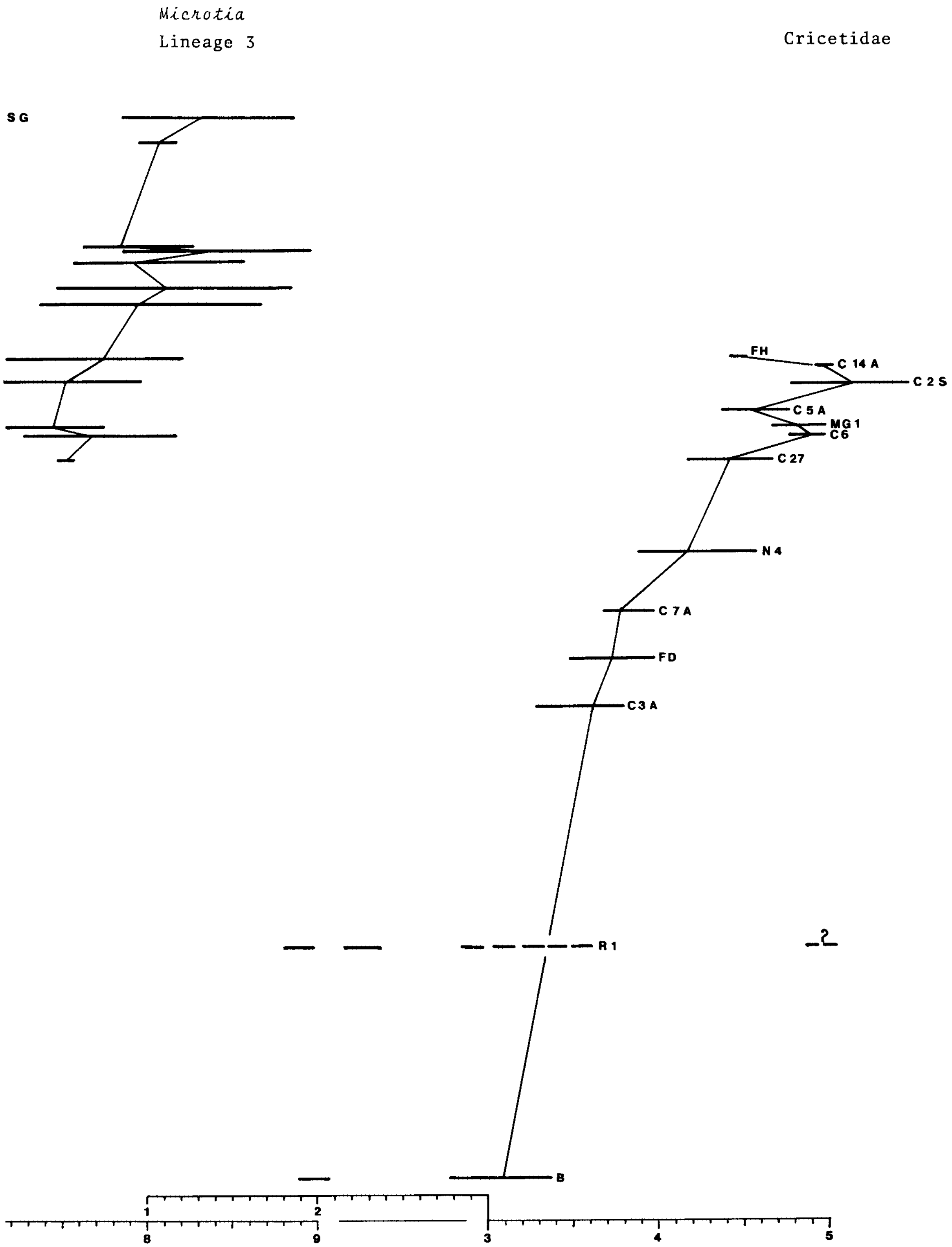
Microtia
Lineage 3
Cricetidae
SG
FH
C 14 A
C 2 S
C 5 A
MG 1
C6
C 27
N 4
C 7 A
FD
C3 A
R 1
2
B
1
2
8
9
3
4
5

as the latter is definitely smaller and morphologically less developed.

The smaller species from Rinascita 1 and Trefossi 1 resemble each other very much. They are significantly smaller than *M. parva.* Morphologically they are certainly much closer to *Stephanomys* from the mainland than *M. parva* and *M. maiuscula.* The absence of a very small *Microtia species,* close to *Stephanomys,* in the Biancone material is certainly not due to the quality of our collection: we have over 7000 *Microtia* teeth from Biancone. A possible explanation is, that a *Stephanomys* species from the mainland invaded Gargano, got isolated, and developed itself into the two species from Biancone. After this a second invasion from the mainland gave rise to the smallest lineage of *Microtia,* represented in Rinascita 1 and Trefossi 1. Whether this smallest lineage should be considered as the source for the small lineage in the upper part of the sequence (ending with San Giovannino) is impossible to say as connecting populations from intermediate levels are (still) missing. It seems, however, more probable that this small modern lineage originates at the level of Chiro 7 A or somewhat higher, and that the smallest species from Trefossi 1 has no further continuation. Equally *M. maiuscula* from Biancone seems to have no descendants. A link to *M. magna* is certainly not proven.

After Trefossi 1 the next locality is Cantatore 3 A. From Biancone to Cantatore 3 A the morphology of M_1 is slowly but gradually becoming more complex; M^3 shows no change at all. In Cantatore 3 A a small species seems to be present along with the species on the main line. This smaller one could be a first indication of the small lineage that becomes manifest in Chiro 27. In the next locality, Fina D, this small lineage is not found (the collection from Fina D is very large). In Fina D the morphology of M_1 increases somewhat faster than it did in previous localities and this acceleration continues until the level of Pizzicoli 4. Fina D shows a first increase in the morphology value of M^3.

In Chiro 7 A there is a small species that could be considered as the source of the small modernized lineage known from most young localities. The morphology values increase more or less parallel to size from Chiro 7 A to Pizzicoli 4. After Pizzicoli 4 the morphology value for M_1 seems to increase less. For M^3 the picture is less evident, but on the whole morphology appears to remain more or less constant between Chiro 9 and Chiro 2.

An important phenomenon is the first appearance of the *M. magna* lineage in Chiro 27. There is no trace of a possible ancestor of *M. magna* in any locality prior to Chiro 27. A reasonable explanation is, that *M. magna* did not develop on the island that contained the localities Biancone through Pizzicoli 4, but that it is an immigrant from another island.

The interval from Chiro 27 to Fina H presents quite a number of problems. Some of these may be caused by the fact that a large number of localities is concentrated in this interval, and the vertical distances between the localities are so small that a more refined measuring technique may alter some details. E. g., the M^3 from Monte Granata 1 is definitely more complex than the M^3 from Chiro 5 A. A better counting technique for the crests may somewhat alter the exact figures, but it is evident on first sight that the Chiro 5 A specimens are less developed. This produces a peak in the morphology line for M^3. If Chiro 5 A were older than Monte Granata 1 this peak would disappear, and such a reversal is certainly not incredible, as the difference in the arithmetic means of the two populations is only 0.05 mm; the measuring fault is in the order of 0.1 mm. From Chiro 27 to Chiro 14 A the morphology of M_1 hardly changes, M^3 becomes definitely more complex even though this is not a gradual change. The small lineage of modernized species, already present in Chiro 27 seems to be missing in the interval from Monte Granata 1 to Chiro 14 A; it reappears in Posticchia 1 B.

Chiro 2 is one of the most problematic of all our localities. The giant insectivore *Deinogalerix* (see Freudenthal, 1972) is present in all localities. In Biancone and Rinascita 1 it is relatively small, in higher levels it reaches gigantic dimensions. However, in Chiro 2 it is missing, and this certainly not due to the limitations of sampling, as Chiro 2 is one of our most intensively studied localities. The absence of *Deinogalerix* in Chiro 2 may be regarded as genuine. The same goes for *M. magna* which is present in localities older and younger than Chiro 2, but lacks in the latter. Furthermore the distribution of the *Microtia* specimens is discontinuous in Chiro 2: most M_1 range between 5.4 and 6.2 mm, and only one specimen has a lenght of 6.8 mm. This could indicate the presence of two species, the larger one of which, however, would not fit into the stream of any of the lineages recognized so far.

Chiro 14 A shows the introduction of a new lineage of *Microtia* which exists along with the main lineage. It is smaller than the main lineage, but a really small species, as well as the large *magna* are missing in this locality. This new lineage appears to have a continuation in Chiro 10 B, Fina H, and Chiro 6. In Chiro 10 B it is the only medium-sized species present. The normal main lineage is missing at this locality. At first this gave quite some problems in estimating the stratigraphic position of Chiro 10 B. On the basis of the lenght of M_1 this locality was interpreted to be slightly younger than Chiro 7 A, but the morphology values are much too high for this level. Furthermore *M. magna* and a very large cricetid are present, features that are also inconsistent with the normal situation expected for the level of Chiro 7 A. Only after the special form from Chiro 14 A was discovered it was possible to find a satisfactory position for Chiro 10 B. This locality is not represented in Figure 4, as the absence of the main lineage makes it impossible to determine its vertical position exactly. It is assumed to be somewhat younger than Chiro 14 A.

In Fina H we have a continuous range of the lenght of M_1 from 3.8 to 6.5 mm. It is quite probable that this range represents three species. The possible size limits of these three are indicated by small interruptions in the range line in Figure 4; in fact the range is continuous. Through a more detailed study it will be possible to distinguish the three species more exactly. As this has not yet been done it was difficult to calculate the arithmetic mean of the lenght for the main lineage; so, the vertical position of Fina H is not exactly determined but the interpretation in Figure 4 appears to be a reliable estimate. Chiro 6 presents roughly the same problem, though the smallest species is missing here; the other two are even more vaguely separated than they are in Fina H. Chiro 6 is estimated to be of the same age as Fina H.

In Posticchia 1 B the most remarkable feature is a very sharp increase in the morphology values, as compared to previous localities. Especially M^3 becomes much more complex, its value is even higher than the value for M_1. In all preceding localities M^3 had a lower morphology value than M_1. rmall

All this leads to the conclusion that some event intervened in the continuous insular evolution, during the period represented by Chiro 2 through Fina H. New forms are introduced and disappear again. Forms normally present in all localities are lacking in some localities of this interval. Morphology changes very rapidly, and last but not least cricetids cease to exist in the area. The best explanation for such an event seems to be that during this period the isolation of Gargano diminished and new influxes became possible; these influxes, however, did certainly not come from the mainland. They came from one or more other islands that had already been isolated for quite some time, and that contained faunas similar, though not identical, to the fauna of Gargano. Apparently the isolation of Gargano was restored after the level of Fina H. From then onwards three species of *Microtia* exist. The small one and the large one are most common, the medium-sized species is often quite rare, causing some difficulties in the correlation of a few localities. The morphology value of M^3 is larger than for M_1 in this upper part of the main lineage.

In the lineage of *M. magna* the arithmetic mean for the length of M_1 of the population of Pirro 11 A is considerably larger than it is in the adjacent localities Chiro 20 C and Chiro 24. The vertical postion of Pirro 11 A is based on a sample of M_1 from the medium-sized lineage which only contains seven specimens. Unfortunately no further material is available, but it is possible that Pirro 11 A is younger than it appears to be on the basis of our sample. It should be of about the same age as San Giovannino, in order to get a good fit for the distribution of *M. magna*.

The locality of Chiro 4 is represented in Table 1, but left out from Figure 4, as the sample size for the medium-sized lineage (6 specimens) is too small, and the distribution of this sample is too asymmetric to allow a reliable positioning. By the morphology of its molars the Chiro 4 population certainly fits into the highest part of the sequence.

The morphology of the smallest lineage of modernized species (roughly Chiro 27 through San Giovannino) seems to be stable. A slight decrease in size may be present in this lineage.

In the *magna*-lineage the gradual increase in size is obvious, if the sequence of Fig. 4 is accepted. There is certainly no increase in the morphology value, on the contrary there seems to be a slight decrease in the number of crests. This is a quite peculiar phenomenon, as it means a reversal of the typical evolutionary trend of *Microtia*.

On the whole the Cricetidae fit quite well into this pattern. Ranges of the lengths of M_1 are drawn in the righthand part of Figure 4. The vertical position is based on the main lineage of *Microtia*. On this basis the Cricetidae show a gradual increase in size, which corroborates the validity of the sequence found. Like in *Microtia*, some problems may arise at the levels shortly below and above Chiro 2. The only serious problem is a very large cricetid M^2 found in Rinascita 1. A matching M_1 is estimated to measure 5.0 mm, a size only encountered in localities like Chiro 2, and certainly not in one of the lowest levels. If this occurrence is not due to a contamination of the sample, I am not able to give an explanation. Cricetidae are absent in the higher part of the sequence.

Work in Gargano is continuing with special attention to new localities that may pad the gaps between the localities yet known, or that may extend the known sequence upwards or downwards. Another objective is the research in adjacent areas that may have been separate islands during the Upper Miocene, and so could have been the source of species that cannot have evolved in the area studied so far. A fissure filling between Trani and Andria, in the Murge area, has yielded some fragmentary *Microtia* material which proves that the theory of evolution on several separate islands is more than a hypothesis.

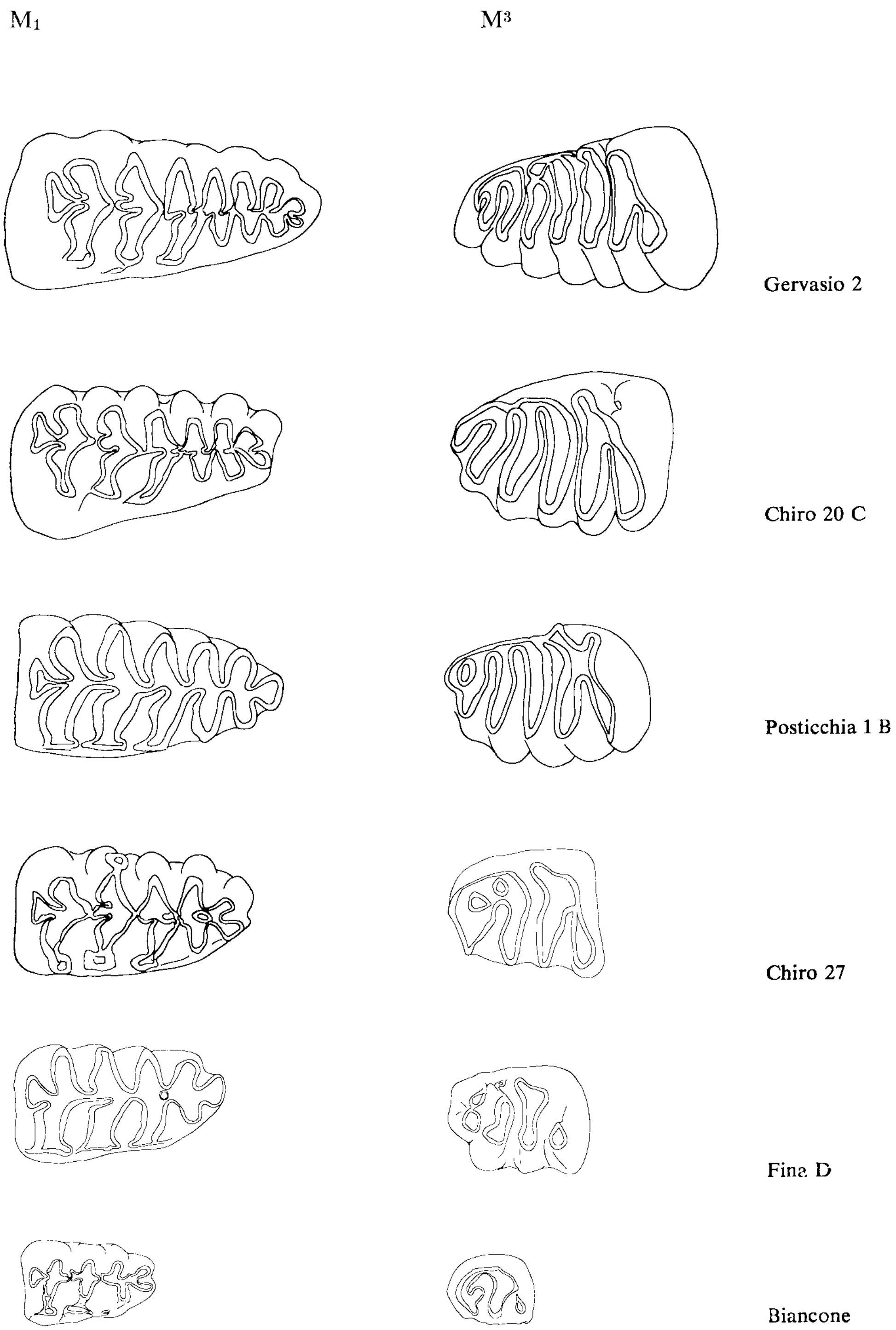

Fig. 5. Examples of various morphological types of *Microtia* molars. All specimens are from the right, or they are inverted to look like right specimens. The enlargement is about 6 x.

OTHER LOCALITIES

All localities containing bird remains and studied by Ballmann were compared with the scheme in Figure 4. The results will be given hereafter for those localities that are not represented in Figure 4:
Biancone 2 equals Nazario 4.
Chiro 2 N is the same fissure as Chiro 2 S; there are no differences between the two.
Chiro 3 is comparable to Nazario 4.
Chiro 4 is one of the highest localities; an exact correlation is not possible, due to the lack of sufficient material of the medium-sized *Microtia*.
Chiro 5 B may be comparable to Chiro 7 A.
Chiro 6 is probably very close to Fina H.
Chiro 7 C looks quite the same as Chiro 7 A, but the sample contains a mandible of *M. magna* that cannot easily be explained.
Chiro 10 A is comparable to Chiro 14 A; its cricetid is identical to the one from Chiro 2.
Chiro 10 C is equal to Chiro 10 A.
Chiro 11 A could not be correlated.
Chiro 11 B is comparable to Pizzicoli 4.
Chiro 12 is comparable to Chiro 14 A.
Chiro 14 B should be placed in the interval between Chiro 2 and Fina H.
Chiro 15 could not be correlated exactly; it is probably as high as Gervasio 1 or still higher.
Chiro 20 A through E are all from the same fissure, and no differences have been found.
Chiro 22 is difficult to correlate but could be of the level of Gervasio 1.
Falcone 2 A belongs to the interval Cantatore 3 A - Trefossi 1.
Falcone 2 B is comparable to Cantatore 3 A.
Fina E is comparable to Gervasio 1.
Nazario 2 B is similar to Chiro 7 A.
Nazario 3 is almost identical to Nazario 4; it can well be the same fissure.
Pirro 11 C is probably equal to Pirro 11 A.

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Plates

Plate 1

Figs. 1-5 natural size, fig. 6 x 2.

Microtia magna nov. sp.

Fig. 1. Holotype, skull, RGM 179 335. Ventral view. Loc. San Giovannino.

Fig. 2. Idem, dorsal view.

Fig. 3. Idem, lateral view.

Fig. 4. Mandibula sin., RGM 179 337. External view. Loc. San Giovannino.

Fig. 5. Idem, internal view.

Fig. 6. Idem, occlusal view.

Plate 1

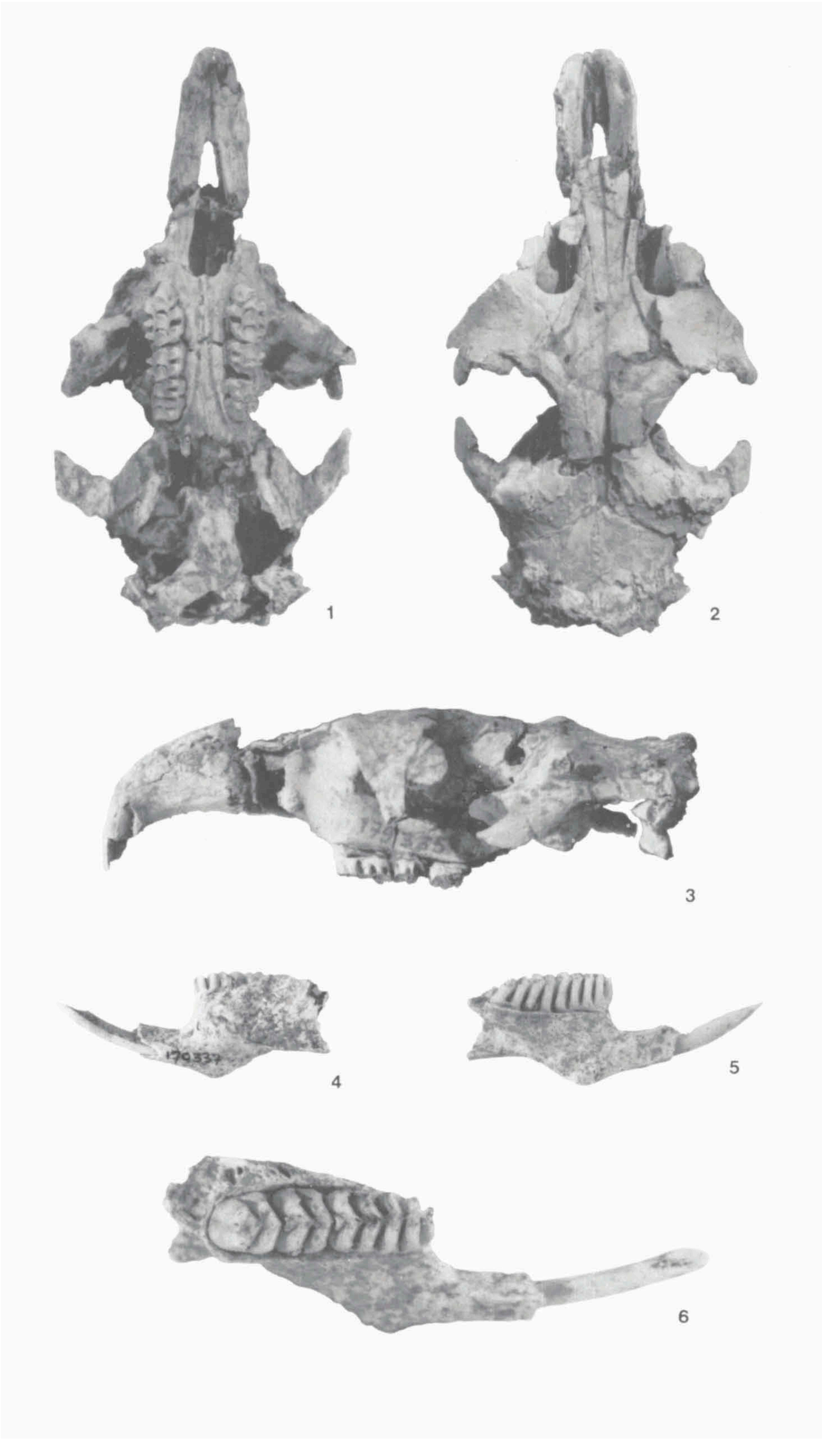

Plate 2

Fig. 1 x 2, figs. 2-5 x 10.

Microtia magna nov. sp.

Fig. 1 Skull fragment, RGM 179 336. Loc. San Giovannino.

Microtia maiuscula nov. sp.

Fig. 2. Holotype, Maxilla sin. with M^1-M^3, RGM 149 254. Loc. Biancone.

Fig. 3. Mandibula sin. with M_1-M_2, RGM 149 081. Loc. Biancone.

Microtia parva nov. sp.

Fig. 4. Holotype, Maxilla sin. with M_1-M_3, RGM 149 344. Loc. Biancone.

Fig. 5. Mandibula sin. with M_1-M_3, RGM 149 082. Loc. Biancone.

Plate 2