

The skull of *Microtia*, an extinct burrowing murine rodent of the late Neogene Gargano palaeoisland

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LETHAIA



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The Neogene Gargano paleoisland (southern Italy) has yielded numerous fossil vertebrates, some of them showing extraordinary morphological peculiarities. Among these endemic species, the rodent genus *Microtia* Freudenthal, 1976, is represented by three main lineages that evolve toward gigantism. This genus is the most significant and abundant rodent represented in the Gargano palaeofaunas. Its evolutionary trends reveal an increase of size, accompanied by a complication of molar structure. Before carrying out a study on the Gargano rodent community, its structure and its evolution, it was necessary to characterize *Microtia*'s ecological adaptations. *Microtia* was adapted to burrowing life, which appears to be a unique adaptation for a murine rodent, since European burrowing Plio-Pleistocene and extant rodents are only represented by arvicolidids. Therefore, the extinction of *Microtia* is likely to be due to competition with arvicolidids after the breakdown of isolation, since they occupied very similar ecological niches. □ *Insular evolution, rodent, Gargano, Neogene, Microtia, paleodiet, stable isotopes.*

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The Gargano area is considered as a late Neogene paleoisland, and has yielded many micromammal remains from numerous karstic localities, with all described species showing extraordinary morphological peculiarities. Two taxa of large mammals, *Hoplitomeryx* (Leinders 1984) and *Deinogalerix* (Freudenthal 1972), which show tremendous morphological specializations, have also been recorded from the Gargano fossil assemblage.

Among the seven rodent genera known in the Gargano assemblage, the murine *Microtia* is represented by at least three lineages of different sizes and shows an evolution toward gigantism through time, which is similar to the observations made on other island endemic rodents (Adler & Levins 1994; Case 1978; Foster 1964; Heaney 1978; Lawlor 1982; Sondaar 1977; Thaler 1973). However, it also shows an original morphological trend with the development of additional lamellae in front of the M_1 and at the back of the M^3 , associated with the development of semihypsodonty. According to the fossil record, *Microtia* may have differentiated from a primitive late Miocene murine. The early Pliocene transgression (5.3 Ma) was responsible for the fragmentation of an endemic territory

into numerous small islands. According to that interpretation, the Gargano endemic fossil assemblage would correspond to the last episode of a long insular endemic evolution (Freudenthal 1976; Rook *et al.*, in press). Until now, only the molars of *Microtia* have been described, and they represent the basis for a biostratigraphic scale of the different localities of the Gargano province (Freudenthal 1976). The name of *Microtia* indicates a resemblance in its molar structure with the arvicolid *Microtus* (Freudenthal 1976). The genus *Microtus* is distributed over the entire Holartic region (Ellerman 1941), and some of the species show numerous adaptations to burrowing life. The arvicolidids have originated from a primitive cricetid during the late Miocene of Europe (Chaline 1980) and underwent an important adaptive radiation which allowed its members to occupy many habitats and to develop different adaptations (Wilson & Reeder 1993).

However, the resemblance between *Microtia* and the extant genus *Microtus* was based only on the molar structure and not on the skull and lower jaw anatomy.

In order to investigate the paleoecology of *Microtia*, a description of the skull and a morphometrical analysis of

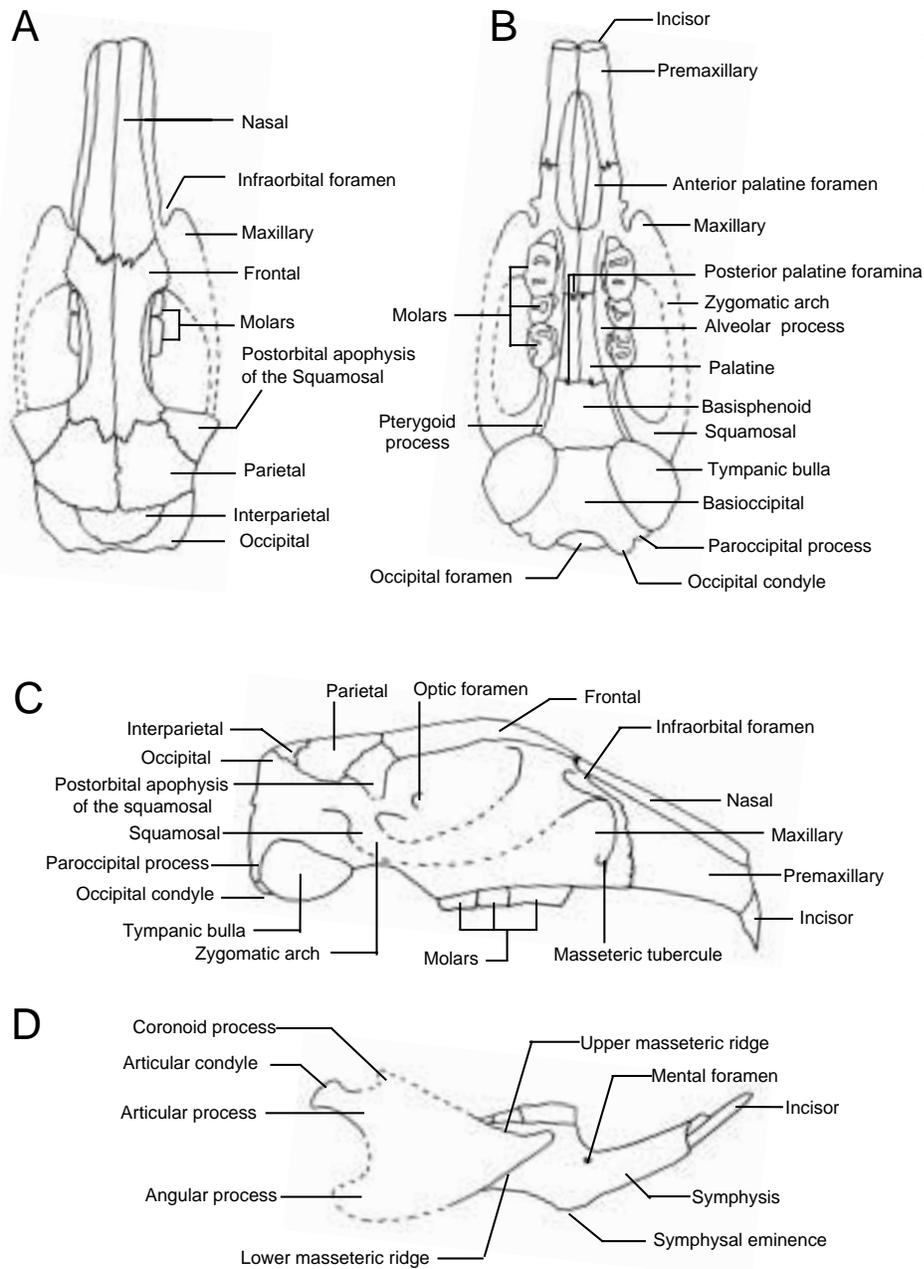


Fig. 1. Tentative reconstitution of *Microtia magna* skull, from the two specimens RGM 179335 and 426521: dorsal (A), palatine (B) and lateral (C) views of the skull, and labial view of the lower jaw (D). Dashes figure areas that were lacking on specimens examined. $\times 1$.

the skull and the postcranial skeleton of *Microtia* were performed. Some isotopic analyses on *Microtia*'s incisor enamel were also conducted to investigate its diet and to define the paleoenvironment of the Gargano paleoisland.

Material and methods

Material

The material used in our study originates from the late Neogene of Italy, where it was collected by M.

Freudenthal and deposited at the National Museum of Natural History, Leiden, The Netherlands. Our description relies on the two most complete skulls of the largest species, *Microtia magna* (Freudenthal 1976): the holotype RGM 179335 from San Giovannino locality, and another specimen from the same locality labeled RGM 426521a (where RGM stands for 'Rijksmuseum van Geologie en Mineralogie'). The specimens labeled 426521b and c are the two lower jaws that belong to the same individual as the skull RGM 426521a. In addition to these two specimens, we have studied several other maxillary and lower

jaw fragments showing complete dental rows, and also isolated incisors from the medium-sized species of an older locality named Chiro 27 (RGM 427280–90, 427292–93, 427255, 427263 and 427265). We also incorporated in our study elements of the postcranial skeleton of *M. magna* from San Giovannino (RGM 426640–43). Measurements were taken with a caliper. The material has been compared to several extant rodents, among them *Rattus rattus* because of its numerous plesiomorphic murine characters, and *Arvicola terrestris* (Arvicolidae), for its burrowing habit and its superficial resemblance to *Microtia*. The results of isotopic analyses performed on *Microtia* specimens were compared to the results obtained for *Prolagus* (Ochotonidae, Lagomorpha), which is represented in the Gargano paleofauna (Mazza 1987). Isotopic analyses were performed on isolated lower incisors of *Prolagus* labeled RGM 427256–61, 427268–69 and 427272–73.

Morphometric approach. In order to visualize the shape differences between *Microtia*, *Rattus* and *Arvicola*, we compared their average skull and lower jaw morphologies using deformation grids (non-uniform deformation with a thin-plate spline analysis) where *Arvicola* and *Rattus* were the references. In order to run these analyses, we used a reconstruction of *Microtia*'s skull (Fig. 1) as an average shape of this taxon. The program TPSLINE (Rohlf 1994) was used to visualize deformation grids between *Microtia* and the extant references, *R. rattus* and *A. terrestris*.

Twenty-five landmarks were defined on the palatine view of the skull (Fig. 2A). Landmarks 2–6, 8–11 and 22–25 are located at the intersections between bones and are type 1 landmarks in the classification of Bookstein (1991). Landmarks 1, 7, 12–15 and 18–21 are points of maximum curvature (type 3 landmarks). They are defined as follows: 1 – anterior edge of the nasal bone; 2 – anterior edge of the anterior palatine foramen; 3 – posterior edge of the anterior palatine foramen; 4 – suture between the maxillary and palatine bones; 5 – posterior edge of the palatine; 6 – suture between the basisphenoid and basioccipital bones; 7 – posteriormost point of the occipital; 8 and 9 – intersection between the upper incisor and premaxillary; 10 and 11 – suture between the premaxillary and maxillary bones, on lateral edge of the skull; 12 and 13 – anteriormost point of the zygomatic arch; 14 and 15 – posteriormost point of the zygomatic arch; 16 and 17 – intersection between the squamosal bone and the tympanic bulla, on the lateral edge of the skull; 18 and 19 – posteriormost point of the paroccipital process; 20 and 21 – posteriormost point of the occipital condyle; 22 and 24 – anteriormost point on the mesial edge of the molar row; 23 and 25 – posteriormost point on the distal edge of the molar row. Points 1–7 are located on the longitudinal axis of the skull.

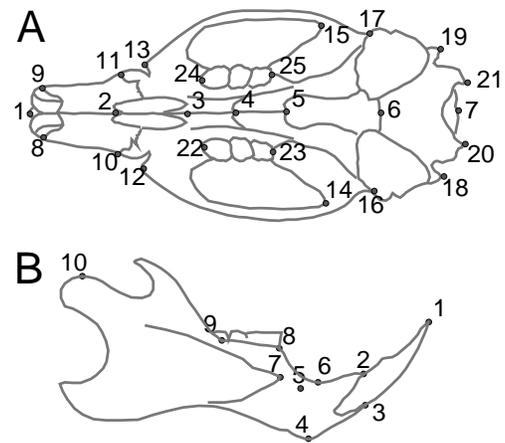


Fig. 2. Location of landmarks on the palatine view of the skull (A) and labial view of the lower jaw (B) used in the morphometric comparisons.

Ten landmarks were defined on the labial view of the lower jaw (Fig. 2B). Landmarks 2, 3, 5, 7, 8 and 9 are located at the intersections between bones and are type 1 landmarks in the classification of Bookstein (1991). Landmark 1 is located at the extremity of the incisor and is a type 2 landmark. Landmarks 4, 6 and 10 are points of maximum curvature (type 3 landmarks). They are defined as follows: 1 – anterior extremity of the lower incisor; 2 – intersection between the dentary bone and the incisor, on upper edge; 3 – intersection between the dentary bone and the incisor, on lower edge; 4 – lowermost point on the symphyseal eminence; 5 – mental foramen; 6 – lowermost point on the upper edge of the symphysis; 7 – intersection between the lower and upper masseteric ridges; 8 – lower point on the distal edge of the M_1 ; 9 – intersection between the ramus of the lower jaw and the molar row; 10 – uppermost point of the articular condyle.

Stable isotope analyses

There is some evidence that the original carbon-isotope signature in fossil tooth enamel is usually not affected by diagenesis (Bocherens *et al.* 1996; Quade *et al.* 1992; Wang & Cerling 1994). The analysis of $\delta^{13}\text{C}$ values in fossil tooth enamel is thus useful to test some hypotheses related to the paleodiet of fossil mammals (Bocherens *et al.* 1996; Gröcke 1997; Kohn *et al.* 1996; Lee-Thorp *et al.* 1989; MacFadden & Cerling 1994, 1996; Quade *et al.* 1992). Incisor enamel has been analyzed isotopically, including specimens belonging to *Microtia* and *Prolagus*, the latter being known for its herbivorous habits. Incisor enamel has been chosen because it was easier to clean mechanically than molars and there was no doubt about morphological distinction between the lower incisors from *Microtia* and *Prolagus*. However, to perform the analyses, 10–20

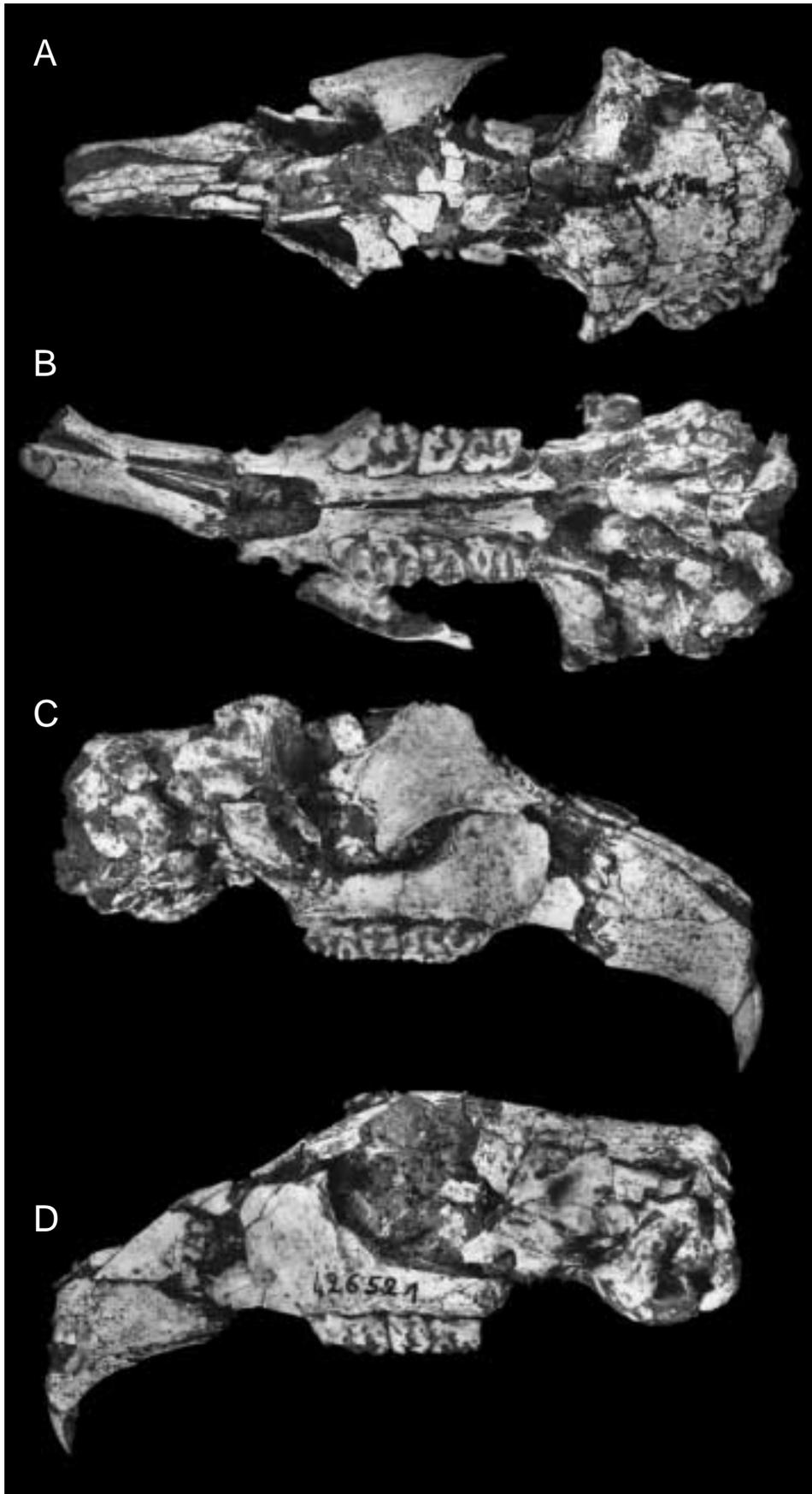


Fig. 3. *Microtia magna*. Skull RGM 426521a from San Giovannino, in dorsal view (A), palatine view (B), right (C) and left (D) lateral view. $\times 1.5$.

mg of powder was required, and several specimens had to be gathered in order to obtain enough material. The isotopic analyses were also performed on incisor dentine and bone in order to test for the possible diagenetic alteration of the isotopic signal by comparing altered tissues (dentine and bone) to tissues presumed to be unaltered (enamel). Preparation of bone and tooth carbonate hydroxylapatite was performed according to the protocol described by Bocherens *et al.* (1996) for fossil samples. The $\delta^{13}\text{C}$ values were computed relative to a standard following the formula $\delta^{13}\text{C} = [((^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}}) - 1] \cdot 1000$. The standard is PDB, and the standard error of $\delta^{13}\text{C}$ is 0.1‰.

Description

Skull

Figs. 1, 3

Measurements of the two studied specimens are given in Table 1. The main characteristics of the skull are its large size (about 8 cm in length), its elongated and narrow snout, the strong interorbital constriction and its anteriorly displaced molar row. In addition, the anterior part of the zygomatic arch is considerably enlarged and some postorbital apophyses of the squamosal that stick out above the zygomatic root are strongly enlarged and prominent (Fig. 4). These apophyses correspond to the insertion points of the powerful temporal muscles.

Upper incisors are slightly proodont, ungrooved and oval in cross section. Their anterior extremities end with a deep notch, and their tips consist almost exclusively of enamel (Fig. 5). The upper incisors extend beyond the anterior edge of the nasal.

The anterior palatine foramina are very long, extending from the level of the incisor roots to the anterior margin

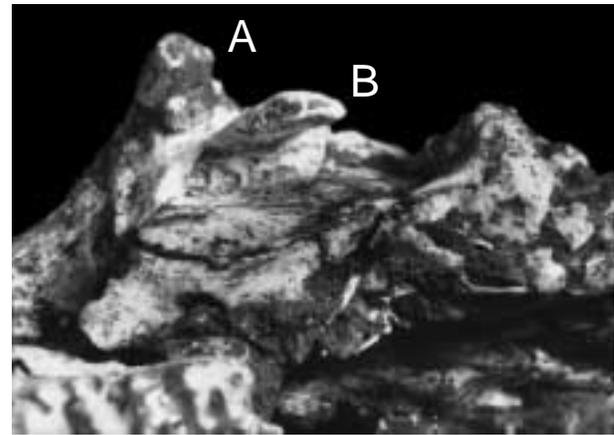


Fig. 4. *Microtia magna*. Skull RGM 426521a from San Giovannino, detailed ventro-lateral view of the skull showing the apophysis of the squamosal (A) and the posterior root of the zygomatic arch (B). $\times 3$.



Fig. 5. SEM micrograph of *Microtia* sp. from Chiro 27: tip of upper incisor RGM 427287. $\times 20$.

Table 1. Cranial measurements (in millimeters) of the two *Microtia magna* specimens from San Giovannino. LAPF – maximum anterior palatine foramen length; WAPF – maximum anterior palatine foramen width; WPAL – palatine width between t4 of M¹; WBO – basisphenoid width, on the basisphenoid–occipital suture; LPAL – distance length from the posterior edge of the anterior palatine foramina to the choanae; WROS – rostrum width, on the premaxillary–maxillary suture; LTR – maximum tooth row length; WM1 – maximum M¹ width; TLS – maximum length skull; LFT – frontal length; LPR – parietal and interparietal length, from the frontoparietal to the interparietal–occipital suture; LIPR – interparietal length; WIPR – maximum interparietal width; CIO – minimum interorbital width; WTOT – maximum skull width, including zygomatic arches; WPR – maximum skull width, on the interparietal–occipital suture; HOC – maximum occipital height, from the skull base to the highest point on the interparietal; HTOT – maximum skull height on the level of the M¹ anterior edge; LPMX – premaxillary length, from the incisor anterior edge to the premaxillary–maxillary suture; DIA – diastema length, from the incisor posterior edge to the M¹ anterior edge.

Palatine view	179335	426521	Dorsal view	179335	426521	Lateral view	179335	426521
LAPF	20.30	19.35	TLS	87.87	77.81	HOC	14.56	17.44
WAPF	3.16	4.06	LFT	31.05	24.74	HTOT	18.83	16.91
WPAL	6.26	5.68	LPR	16.62	18.90	LPMX	19.85	20.15
WBO	8.94	–	LIPR	12.05	14.02	DIA	30.96	29.41
LPAL	24.41	22.25	WIPR	16.15	13.63			
WROS	12.75	8.66	WTOT	44.92	–			
LTR	19.05	17.52	WPR	30.01	30.75			
WM1	6.47	5.50	CIO	14.82	6.74			

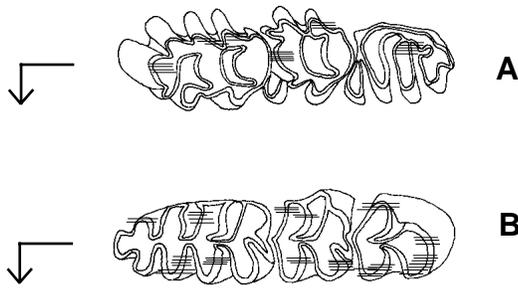


Fig. 6. *Microtia* sp. Upper (A) and lower (B) tooth rows from Chiro 27 (specimens RGM 427293 and 427290, respectively). Direction of microstriations is longitudinal, indicating a propalinal movement during mastication. $\times 3.5$.

of the M^1 . Their width increases posteriorly. Numerous and small posterior palatine foramina are distributed from the level of the M^1 – M^2 boundary to the posterior edge of the palatine. They are located in a palatal groove and show nearly vertical inclination. The huge zygomatic plate shows an anterior convex edge that bears a very strong masseteric tubercle. The molar rows have an anterior position relative to the zygomatic plate when compared to *Rattus* and *Arvicola*. Tooth rows are parallel, and their flat occlusal surfaces face ventrolaterally. Molars are incipiently hypsodont: the crowns are elevated, but the roots of molars are still present and closed (Jaeger 1989; Viriot 1994). Microstriations, which can be observed on the wear facets of both upper and lower molar occlusal surfaces, are exclusively oriented longitudinally, which demonstrates the preponderance of propalinal jaw movements (Figs. 6 and 7). The large size of the maxillary is correlated to the development and the elevation of the tooth crown. The choanas open just behind the M^3 . The optic foramen is located on half of the height of the skull, at the level of the distal edge of the molar row. The frontoparietal suture is not straight.

The upper skull roof, surrounded by the well-marked supraorbital crests, is flat in its posterior part and shows a strong slope toward the snout. The posterior part of the skull is short, the parietal being very short and the crescentic interparietal narrow and short. The tympanic bulla are small with an oval outline and are posteriorly strengthened by well-developed paroccipital processes.

Lower jaw

Figs. 1, 8

The most striking character of the lower jaw is the strong procumbency of the incisors and their very low curvature. The lower incisors are slim, oval in cross section and present no trace of groove on the enamel. They occupy a lingual position in the anterior part of the jaw, shift to the

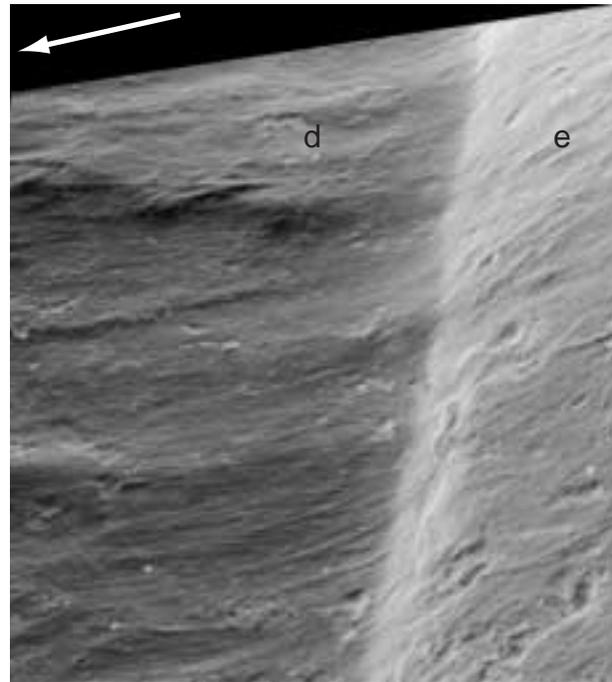
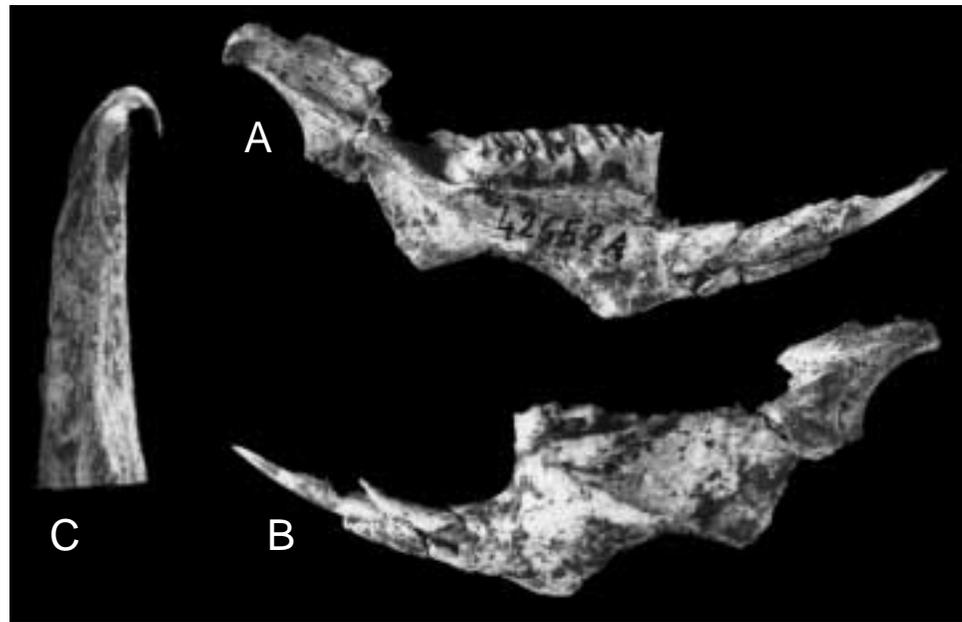


Fig. 7. SEM micrograph of *Microtia* sp. from Chiro 27; longitudinal microstriations on t9 of right M_1 RGM 427290. White arrow indicates anterior edge of the molar. d, dentine; e, enamel. $\times 670$.

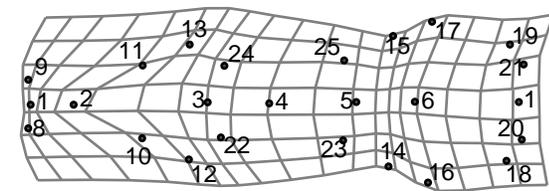
labial side between M_2 and M_3 , and end close behind the level of the posterior root of the M_3 .

The diastema is very long, and its lower edge is straight. The symphysis extends all along the diastema, as far as the highly prominent symphyseal eminence. On the posterior labial side of that process, there is a wide area for the insertion of the digastric muscles. The lower margin of the horizontal ramus is curved. The foramen mentale opens on the labial side just below the anterior edge of M_1 . The masseteric crests are strong, especially the lower one which ends into a process located just under the basis of the M_1 , behind and above the foramen mentale. The upper masseteric ridge is grooved and the anterior part of the masseteric fossa is strongly convex, due to the large and deep extent of the molar alveolus. The lingual surface, and particularly the horizontal branch of the ramus, bears many small vascular foramina, as in *Microtus*. A large retromolar basin for the insertion of the temporal muscle is present behind the M_3 . From the level of the M_3 , a straight crest extends to the lower part of the articular condyle. The mandibular foramen is well developed and sits above this crest. In one specimen (RGM 427521b) the articular condyle is preserved. It is of oval shape and is oriented toward the lingual side of the jaw (Fig. 8C). It has a low position, just above the molar occlusal surface. The coronoid process and the angular process are lacking on all examined specimens.

Fig. 8. *Microtia magna*. □A, B. Lower jaw RGM 426521b from San Giovannino, in lingual (A) and labial view (B). $\times 1.5$. □C. Articular condyle in posterior view with a lingual displacement. $\times 35$



R. rattus



A. terrestris

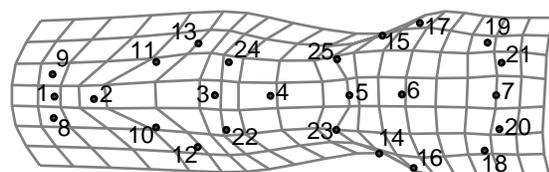
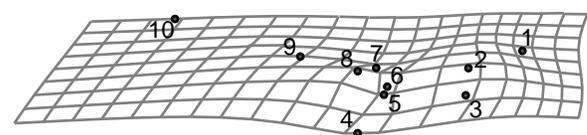


Fig. 9. Deformation grids from *Rattus rattus* to *Microtia magna* (above), and from *Arvicola terrestris* to *Microtia magna* (below) on palatine skull view. Twenty-five landmarks were considered, and the grids were computed with the TPSLINE program. The deformation is located in the median part of the skull, with an anterior displacement of the molar tooth row, and in its anterior part with an elongation of the rostrum.

Morphometric comparison with the extant taxa *R. RATTUS* and *A. TERRESTRIS*

In palatine view of the skull (Fig. 9), the elongation of the rostrum is probably the most striking difference we can observe between *Microtia* and the extant references, accompanied by the anterior displacement of the molar tooth row, and the contraction of the basisphenoid. The elongation of the rostrum is illustrated by an anterior displacement of points 1–3 and 10–13 on the deformation grids. Similarly, the anterior displacement

R. rattus



A. terrestris

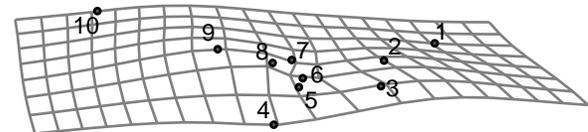


Fig. 10. Deformation grids from *Rattus rattus* to *Microtia magna* (above), and from *Arvicola terrestris* to *Microtia magna* (below) on labial lower-jaw view. Ten landmarks were considered, and the grids were computed with the TPSLINE program. The deformation is located in the symphysis area, with an elongation of the symphysis, and an extremely well-marked symphyseal eminence.

of the molar row is illustrated by the relative position of points 22 and 24. The contraction of the basisphenoid is well marked by the displacement of points 14 and 15. These main differences can be observed when we compare *Microtia* with *R. rattus*, and also *Microtia* with *A. terrestris*. These characters thus clearly represent autapomorphic features of *Microtia*. However, the deformation is greater from *Microtia* to *A. terrestris* than from *Microtia* to *R. rattus*, especially for the anterior displacement of the molar row and for the contraction of the basisphenoid.

In labial view of the lower jaw (Fig. 10), the deformation grids show that the major part of the deformation is located in the symphyseal area, with an elongation of the symphysis illustrated by the relative position of points 2 and 3 on deformation grids, and an extremely well-marked symphyseal eminence with a large displacement of point 4. Another observation concerns the low position of the articular condyle relative to the occlusal molar surface, which is marked by the displacement of point 10. These deformations can be observed when we compare *Microtia* to both *A. terrestris* and *R. rattus*.

Results of isotopic analyses

The results of isotopic analyses are given in Table 2. The $\delta^{13}\text{C}$ values range from -11.9‰ (enamel) to -9.3‰ (dentine) with an intermediate value of -9.7‰ (bone) for *Microtia* specimens. Analyses performed on *Prolagus* specimens yielded $\delta^{13}\text{C}$ values within the interval from -10.9‰ (bone) to -8.8‰ (dentine), with an intermediate value of -9.6‰ (enamel).

Microtia adaptations

Until now, most authors have focused their analyses on the original molar structure of *Microtia* and underlined its adaptation to herbivory (Zafonte & Masini 1992). It is generally recognized that there are two main types of movement used for digging among rodents: with the teeth (tooth-digging), as in *Spalax* or *Arvicola*, or with the feet (claw-digging), as in *Geomys* (Dubost 1968; Gasc *et al.* 1985; Hildebrand 1985; Laville *et al.* 1989; Lessa 1990; Lessa & Thaler 1989; Renous 1994; Wake 1993). In spite of similar habits, there is great diversity in the morphological characteristics of these rodents. Compared to claw-digging, tooth-digging is associated with more procumbent upper incisors and enlarged jaw musculature (Dubost 1968; Gasc *et al.* 1985; Hildebrand 1985; Laville *et al.* 1989; Lessa 1990; Lessa & Thaler 1989; Renous 1994; Wake 1993). A number of adaptive morphological characters in *Microtia* suggest that it was a burrowing rodent that used its incisors to dig.

Table 2. Values of $\delta^{13}\text{C}$ (‰) obtained for lower incisor enamel, dentine and bone samples from the endemic rodent *Microtia* and the lagomorph *Prolagus* of the Gargano paleofauna.

$\delta^{13}\text{C}$ (‰)	Enamel	Dentine	Bone
<i>Microtia</i>	-11.9	-9.3	-9.7
<i>Prolagus</i>	-9.6	-8.8	-10.9

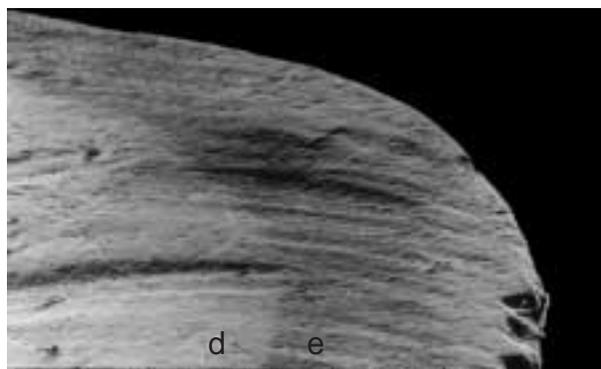


Fig. 11. *Microtia* sp. SEM micrographs from Chiro 27. Tip of lower incisor RGM 427280 with longitudinal microstriations on both dentine (d) and enamel (e). $\times 200$.

Dental characters

Molar lamellar structure and incipient hypsodonty are adaptations to an abrasive diet. Such structures are common to several burrowing rodents (Agrawal 1967). In addition, during the evolution of this genus there was an increase of the molar occlusal surface by the development of additional lamellae on the M_3 and the M^1 . Such an increase also occurs among the extant genera *Otomys* (Denys *et al.* 1987) and *Microtus* (Agrawal 1967).

The upper incisors are proodont and moderately developed. The lower incisors are very procumbent, but, unlike the situation among burrowing arvicolids (*Arvicola terrestris*, *Ellobius lutescens* and *Microtus subterraneus*) and bathyergids (Hildebrand 1985), their posterior extremities do not produce any additional lateral bulge on the lower jaw.

Von Koenigswald (1986) has shown that the uniserial incisor enamel of *Microtia* has fibers in three perpendicular directions, producing an isotropic structure which reinforces the enamel. The cross-sectional area of the lower incisor is reduced, which should decrease soil resistance during burrowing with the lower incisor (Lessa 1990).

Numerous microstriations, which can be interpreted as a consequence of burrowing habits, are present on the tip of the incisors (Fig. 11).

Skull characters

The following characters of the skull indicate a burrowing habit for *Microtia*: proodonty of the incisors, a long snout with triangular shape, and a progressive increase of size from the incisor to its posterior extremity. This general shape of the skull is considered to facilitate digging. It can be observed among numerous extant burrowing rodent families, such as spalacids (Dubost 1968; Laville *et al.*

1989), bathyergids (Dubost 1968), rhizomyids (Dubost 1968) and arvicolid (Agrawal 1967; Laville *et al.* 1989). Extremely large areas for attachment of masticatory musculature, with prominent bone processes on some of these areas, are additional characters shared with all extant burrowing rodents (Agrawal 1967; Bekele 1983; Hildebrand 1985; Laville *et al.* 1989; Lessa & Thaler 1989; Renou 1994; Wake 1993).

Among these attachments, *Microtia* has developed an extraordinarily wide anterior zygomatic arch and an extremely strong postorbital transverse apophysis on the squamosal for the attachment of the temporal muscles (Fig. 4).

Lower jaw characters

As on the skull, muscular attachment surfaces are well developed on the lower jaw. The digastric muscles, which play a major role in the depression of the lower jaw (Bekele 1983), have a strong attachment on the symphyseal eminence. The transverse mandibular muscle is also attached to that process and stabilizes the mandibular symphysis, which supports strong stress during digging (Bekele 1983). Masseteric ridges are prominent and define the attachment area for the deep posterior masseter, which is the main lower-jaw elevator.

Postcranial skeleton characters

Fig. 12

The postcranial skeleton is little specialized for digging, with similar relative proportion between posterior and anterior limbs. This is common among rodents that use their incisors to dig (Dubost 1968). Nevertheless, although there is no size reduction of the arm, muscular attachment areas are well developed, and lopsided toward the opposite part of the lever arm, in order to increase the strength of the muscle (Hildebrand 1985; Laville *et al.* 1989). This is the case for the deltoid crest, which occupies a distal position on the humerus.

However, the olecranon is short and the radius is not shorter than the humerus, indicating low specialization of the arm. The tibia is relatively short when compared to the femur, with a ratio for *Microtia* of about 1, as is the case for other burrowing rodents like *A. terrestris*, whereas surface rodents like *M. arvalis* show a ratio of about 1.4 (Laville *et al.* 1989).

Reconstruction of *Microtia* paleodiet inferred from stable-isotopic analyses

The feeding habits of *Microtia* are still unclear. On the basis of the whole set of data, we suggest that *Microtia* fed on rhizomes and roots, probably of Graminae plants.

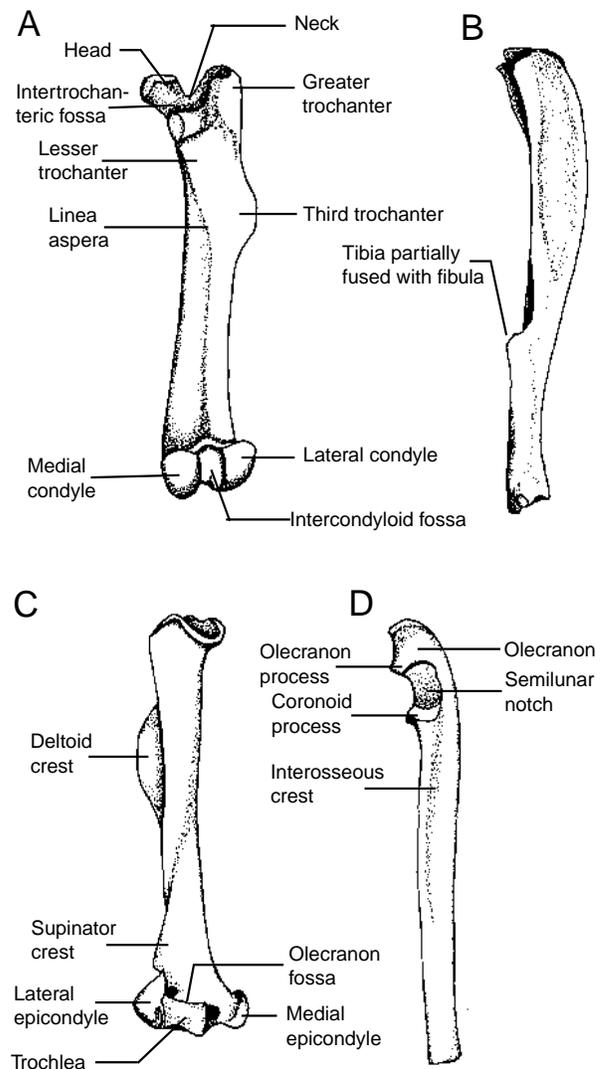


Fig. 12. Appendicular skeleton of *Microtia magna* from San Giovanni in natural size. □A. Right femur in posterior view (RGM 426641) with a well-marked third trochanter. □B. Right tibia in anterior view (RGM 426 640). □C. Right humerus in anterior view (RGM 426 642) with a deltoid crest distally displaced. □D. Left ulna in lateral view (RGM 426 643).

However, whether the Gargano area was dominated by C_3 or C_4 vegetation is unknown. The extant Mediterranean flora counts a very low proportion of native C_4 plant species (from 1% to 2%; Collins & Jones 1985). In addition, there is no evidence of the occurrence of C_4 plants in Pleistocene (Bocherens *et al.* 1996) or Neogene (Bocherens & Sen 1998; Bocherens *et al.* 1994; Quade *et al.* 1995) sites of the Mediterranean area. However, the distribution of modern C_4 plants in Europe is largely related to the ambient temperature (Collins & Jones 1985). According to the subtropical climate that occurred in Europe in the latest Miocene and earliest Pliocene (Burkle 1995; Suc

1984), it is thus not inconceivable that a higher proportion of C_4 Graminae plants may have been present during this period, since the expansion of C_4 -dominated ecosystems took place worldwide between 7 and 5 Ma ago (Cerling *et al.* 1997; Cerling *et al.* 1993; MacFadden & Cerling 1996; Quade *et al.* 1992). Our results (Table 2) show that *Microtia*'s incisor enamel has hydroxylapatite with a low $\delta^{13}C$ value (-11.9%), similar to those of large mammals feeding on C_3 plants (Bocherens *et al.* 1996; Bocherens & Mariotti 1992; Cerling *et al.* 1997).

However, before interpreting the measured carbon isotopic compositions in terms of paleodiet, it is necessary to consider possible diagenetic alteration and rodent physiology. For both *Microtia* and *Prolagus*, the $\delta^{13}C$ values obtained for enamel are very close to those obtained for dentine and bone specimens, which is not in accordance with the results obtained for large herbivorous Neogene mammals where diagenetically altered dentine and bone have isotopic values clearly different from those of unaltered enamel (Bocherens & Sen, in press). The similar $\delta^{13}C$ values obtained for enamel, dentine and bone samples could be indicative of some diagenetic alterations of the enamel that are commonly expressed in dentine and bone samples. Rodent enamel is indeed much thinner than enamel of large herbivorous mammals, which should increase the susceptibility to diagenetic alteration. However, an alternative hypothesis is that dentine and bone samples retained a non-altered isotopic signature, under the hypothesis of very low diagenesis or diagenesis with little effects on the isotopic composition of carbonate hydroxylapatite. Consequently, a significant diagenetic shift cannot be ruled out with the available data.

If isotopic values are indeed not significantly altered, the $\delta^{13}C$ values need to be compared to those of small mammals rather than large ones. The values obtained for both *Microtia* and *Prolagus* appear to be more positive than those previously obtained for specimens of small mammals. For instance, a *Prolagus* fossil specimen (10 000 BP) from Corsica yielded a $\delta^{13}C$ value of -14.5% in an exclusive C_3 -plants environment (Pouydebat & Bocherens, unpublished). Similarly, rats and mice raised under a controlled pure C_3 diet have $\delta^{13}C$ values ranging from -15.7 to -16.8% (Ambrose & Norr 1993; Tieszen & Fagre 1993). These values are actually lower than those obtained for large herbivorous mammals feeding on C_3 plants, which is probably due to physiological factors (Hedges & Van Klinken, in press). The enamel $\delta^{13}C$ values measured on the Gargano specimens should thus be indicative of a significant proportion of plants with high $\delta^{13}C$, such as C_4 plants in the paleodiet of both *Microtia* and *Prolagus*. Additional measurements performed on other fossil mammals of the Gargano fauna may be helpful to confirm this hypothesis, and the possibility of larger diagenetic effects on small teeth than on large teeth has to be investigated further.

Conclusion

Despite its name, skull characters of *Microtia* show more similarities with murids than with arvicolidids, which corroborates *Microtia* molar patterns being very close to those of a primitive murine rodent. Therefore, we interpret *Microtia* as a burrowing murine. It shares several characters with burrowing extant rodents that use their incisors to dig, but shows a unique combination of these characters, and, in addition, several original specializations. The attempt to use carbon stable-isotope composition to infer *Microtia* paleodiet did not provide unambiguous conclusions. However, it opens promising new ways of investigations on small fossil mammals, provided that the effects of diagenesis and physiology are taken into account.

Its high degree of differentiation suggests a long endemic history for *Microtia*, as already suggested by the discovery of a representative of this genus in another area of South Italy (Freudenthal 1976). It is also supported by the high endemism of other genera recorded from the Gargano localities, such as *Hoplitomeryx* and *Deinogalerix*. The extinction of such a specialized rodent as *Microtia* raises additional questions. Some authors have reported the presence of arvicolidids in the Pleistocene of the Gargano area (De Giuli 1986; Freudenthal 1971). Therefore, after the breakdown of the isolation of Gargano island and its connection to the Italian mainland, *Microtia* may have been strongly affected by competition with arvicolidids.

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