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

VIRGINIE PARRA, JEAN-JACQUES JAEGER AND HERVÉ BOCHERENS

The skull of Microtia, an extinct burrowing murine rodent of the late Neogene Gargano palaeoisland. Lethaia, Vol. 32, pp. •••–•••. Oslo. ISSN 0024-1164.

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 arvicolids. Therefore, the extinction of Microtia is likely to be due to competition with arvicolids after the breakdown of isolation, since they occupied very similar ecological niches.

Virginie Parra [parra@isem.univ-montp2.fr] and Jean-Jacques Jaeger [jaeger@isem.univ-montp2.fr], Institut des Sciences de l’Évolution, UMR 5554, Université Montpellier II, cc 64 place Eugène Bataillon, 34095 Montpellier cedex 5, France; Hervé Bocherens [bocheren@ccr.jussieu.fr], Laboratoire de Biogéochimie isotopique, UMR 7618, Université Pierre et Marie Curie, case 120, 4 place Jussieu, 75252 Paris cedex 5, France; 5th August, 1998; revised 11th March, 1999.
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
been compared to several extant rodents, among them Rattus rattus because of its numerous plesiomorphic murine characters, and Arvicoloida's (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 Arvicoloida, we compared their average skull and lower jaw morphologies using deformation grids (non-uniform deformation with a thin-plate spline analysis) where Arvicoloida 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 basiocipital bones; 7 – posterioriormost 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 – anterioriormost point of the zygomatic arch; 14 and 15 – posterioriormost 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 – posterioriormost point of the paroccipital process; 20 and 21 – posterioriormost point of the occipital condyle; 22 and 24 – anterioriormost point on the mesial edge of the molar row; 23 and 25 – posterioriormost 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 – lowest point on the symphysal eminence; 5 – mental foramen; 6 – lowest point on the upper edge of the symphysis; 7 – intersection between the lower and upper maseteric ridges; 8 – lower point on the distal edge of the M1; 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 δ13C 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. ×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 diageneric 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 hydroxyapatite was performed according to the protocol described by Bocherens et al. (1996) for fossil samples. The $\delta^{13}C$ values were computed relative to a standard following the formula $\delta^{13}C = \left[ \frac{(^{13}C/^{12}C)_{\text{sample}}}{(^{13}C/^{12}C)_{\text{standard}}} - 1 \right] \cdot 1000$. The standard is PDB, and the standard error of $\delta^{13}C$ 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 of the skull.

![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). x3.](image)

**Table 1. Cranial measurements (in millimeters) of the two Microtia magna specimens from San Giovannino.**

<table>
<thead>
<tr>
<th>Palatine view</th>
<th>179335</th>
<th>426521a</th>
<th>Dorsal view</th>
<th>179335</th>
<th>426521a</th>
<th>Lateral view</th>
<th>179335</th>
<th>426521a</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAPF</td>
<td>20.30</td>
<td>19.35</td>
<td>TLS</td>
<td>87.87</td>
<td>77.81</td>
<td>HOC</td>
<td>14.36</td>
<td>17.44</td>
</tr>
<tr>
<td>WAPF</td>
<td>3.16</td>
<td>4.06</td>
<td>LFT</td>
<td>31.05</td>
<td>24.74</td>
<td>HTOT</td>
<td>18.83</td>
<td>16.91</td>
</tr>
<tr>
<td>WPAL</td>
<td>6.26</td>
<td>5.68</td>
<td>LPR</td>
<td>16.62</td>
<td>14.02</td>
<td>LPMX</td>
<td>14.02</td>
<td>29.41</td>
</tr>
<tr>
<td>WBO</td>
<td>8.94</td>
<td>-</td>
<td>LIPR</td>
<td>12.05</td>
<td>-</td>
<td>DIA</td>
<td>30.96</td>
<td>24.1</td>
</tr>
<tr>
<td>LPAL</td>
<td>24.41</td>
<td>22.25</td>
<td>WIPR</td>
<td>16.15</td>
<td>13.63</td>
<td>CIO</td>
<td>14.82</td>
<td>6.74</td>
</tr>
<tr>
<td>WROS</td>
<td>12.75</td>
<td>8.66</td>
<td>WTOT</td>
<td>44.92</td>
<td>-</td>
<td>WM1</td>
<td>6.47</td>
<td>5.50</td>
</tr>
<tr>
<td>LTR</td>
<td>19.05</td>
<td>17.52</td>
<td>WPR</td>
<td>30.01</td>
<td>30.75</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>WM1</td>
<td>6.47</td>
<td>5.50</td>
<td>CIO</td>
<td>14.82</td>
<td>6.74</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

![Fig. 5. SEM micrograph of Microtia sp. from Chiro 27: tip of upper incisor RGM 427287. x20.](image)
of the M\textsuperscript{1}. Their width increases posteriorly. Numerous and small posterior palatine foramina are distributed from the level of the M\textsuperscript{1}–M\textsuperscript{2} boundary to the posterior edge of the palate. 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\textsuperscript{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 labial side between M\textsubscript{2} and M\textsubscript{3}, and end close behind the level of the posterior root of the M\textsubscript{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 symphysal eminence. On the posterior labial side of that process, there is a wide area for the insertion of the digastic 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\textsubscript{1}. The masseteric crests are strong, especially the lower one which ends into a process located just under the basis of the M\textsubscript{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\textsubscript{3}. From the level of the M\textsubscript{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.
The skull of Microtia

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

<table>
<thead>
<tr>
<th></th>
<th>Enamel</th>
<th>Dentine</th>
<th>Bone</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Microtia</em></td>
<td>$-11.9$</td>
<td>$-9.3$</td>
<td>$-9.7$</td>
</tr>
<tr>
<td><em>Prolagus</em></td>
<td>$-9.6$</td>
<td>$-8.8$</td>
<td>$-10.9$</td>
</tr>
</tbody>
</table>

**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 M3 and the M1. 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 arvicolids (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 & Thader 1989; Renous 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 symphysal 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 Gramineae plants.

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 C₄ Graminae plants may have been present during this period, since the expansion of C₄-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 δ¹³C value (–11.9‰), similar to those of large mammalian feeding on C₃ 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 δ¹³C 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 diagnostically altered dentine and bone have isotopic values clearly different from those of unaltered enamel (Bocherens & Sen, in press). The similar δ¹³C 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 diagenetic shift cannot be ruled out with the available data.

If isotopic values are indeed not significantly altered, the δ¹³C 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 (10000 BP) from Corsica yielded a δ¹³C value of –14.5‰ in an exclusive C₃-plants environment (Pouydebat & Bocherens, unpublished). Similarly, rats and mice raised under a controlled pure C₃ diet have δ¹³C 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 C₃ plants, which is probably due to physiological factors (Hedges & Van Klinken, in press). The enamel δ¹³C values measured on the Gargano specimens should thus be indicative of a significant proportion of plants with high δ¹³C, such as C₄ 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 arvicolids, 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 endemcity 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 arvicolids 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 arvicolids.

Acknowledgements. – The authors wish to thank M. Freudenthal (Natuurhistorisches Museum, Leiden) for providing us with the Gargano material and for helpful discussions, M. Tranier and J. Cuisin (Museum d’Histoire Naturelle, Paris) for the extant comparative material, and C. Denys for her help with the interpretation of SEM micrographs. Some X-ray micrographs were made by J.P. Gasc (Museum d’Histoire Naturelle, Paris), SEM micrographs by C. Chaucogne (Museum d’Histoire Naturelle, Paris), other photographs by M. Martin and M. Pons (Institut des Sciences de l’Evolution, Montpellier). Isotopic analyses were performed at the Laboratoire de Géochimie isotopique of Paris VI, with the help of Daniel Billiou. The authors wish to thank two anonymous reviewers for their constructive comments on this manuscript. This is publication ISEM nº 99-•••.

References


