

Size evolution of the lower incisor of *Microtia*, a genus of endemic murine rodents from the late Neogene of Gargano, southern Italy

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Abstract.—The Neogene paleoisland from the area of Gargano, Italy, has yielded numerous fossil vertebrates, some of them showing extraordinary morphological peculiarities due to island evolution. Among them, *Microtia* (Freudenthal 1976) is the dominant rodent genus in the Gargano palaeofauna and is represented by at least three evolutionary lineages. The incisors are used to describe the size evolution in these lineages, and we come to the conclusion that these lineages did not follow the same evolutionary trend: two of them evolve toward larger size, while the third one shows a slight decrease in size. In addition, we describe the evolution of the curvature of the lower incisor, compared with that of body-size. The evolution of *Microtia* is characterized by a specialization for burrowing, which may be accompanied by either an increase or a decrease in size. Finally, we propose that the evolutionary change among these three sympatric lineages allowed *Microtia* to minimize competition between species, by avoiding size overlaps.

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Introduction

The Gargano area (province of Foggia, Southern Italy) is considered a late Neogene paleoisland and has yielded many micromammal remains from numerous karstic localities spanning a poorly constrained interval during the late Miocene and the early Pliocene (Abbazzi et al. 1996). All described species show extraordinary morphological peculiarities due to island evolution (Freudenthal 1972, 1976; Ballmann 1973, 1976; Butler 1980; Willemsen 1983; Leinders 1984).

Among the seven rodent genera, the murine *Microtia* is represented by at least three lineages characterized by different sizes and morphologies (Freudenthal 1976; Torre 1986; De Giuli et al. 1987; Abbazzi et al. 1993). The middle-sized lineage, which contains the most abundant *Microtia* species, shows an evolution toward a larger size. This evolutionary size increase is similar to that observed in other island endemic rodents (Foster 1964; Thaler 1973; Sondaar 1977; Case 1978; Heaney 1978; Lawlor 1982; Adler and Levins 1994). Two other sympatric *Microtia* lineages are also represented in the Gargano fauna, a small-sized one and a large-sized one.

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Many recent studies on extant rodent communities have pointed out the role of competition in community size structure (Brown and Lieberman 1973; Brown 1975; Dayan et al. 1989, 1990; Dayan and Simberloff 1994, 1998; Parra et al. 1999a; Millien-Parra and Loreau 2000). By community size structure, we mean the body size structure of a community that can be characterized by the degree of body size overlaps between coexisting species, or by the values of the body size ratios between these species. The effect of competition between coexisting rodent species can be revealed by the study of incisor size, as demonstrated by Dayan et al. (1989, 1990), Dayan and Simberloff (1994) and Parra et al. (1999a). Moreover, the radius of curvature may be a better indicator of species size segregation in rodent assemblages than any other dimension of the incisor (Parra et al. 1999a). The occurrence of numerous karstic localities of different age and the abundance of *Microtia* in each of these localities provide a unique opportunity

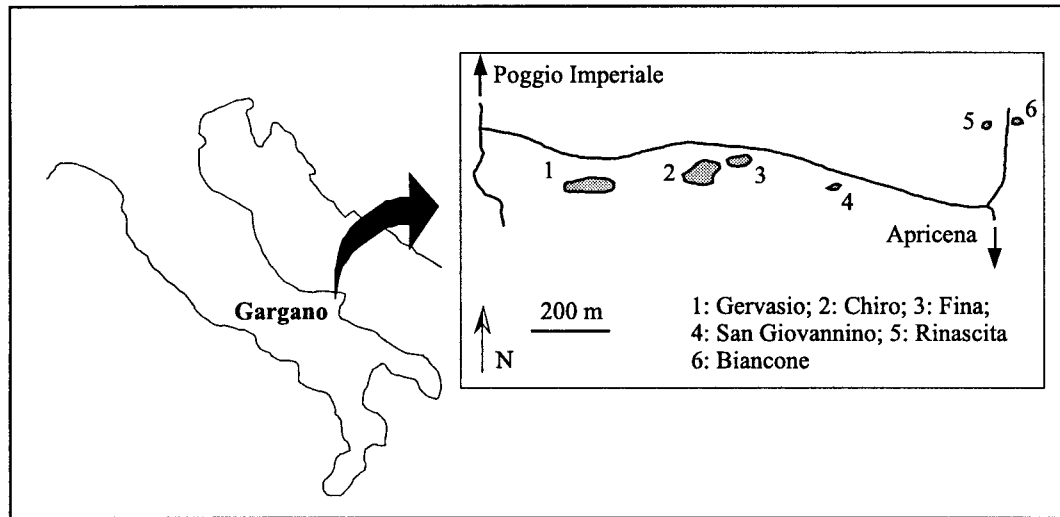


FIGURE 1. Location of the Gargano fissure fillings that were considered in this study.

nity for the investigation of the size structure in this rodent community and its evolution through time. Previously only the molars of *Microtia* have been described, and they are the basis for biostratigraphy of the different localities of the Gargano paleoisland (Freudenthal 1976). However, the endemic genus *Microtia* is represented in the Gargano fissures by many lower incisors, isolated or associated with lower-jaws, and it is the change in the size and shape of these incisors that will be used to describe *Microtia* evolutionary trends.

Material and Methods

Chronology of the Gargano Localities.—The material used in our study originates from the late Neogene of Italy, where it was collected by M. Freudenthal and stored at the National Museum of Natural History, Leiden, Netherlands. Our samples come from 11 different fissures that range from the oldest to the youngest known in the Gargano time range (Fig. 1). The fissure fillings cannot be dated by traditional methods, so the chronological succession was based on evolutionary trends of size and morphology in a number of taxa. During the time span represented by the Gargano fissures the morphology of *Microtia* molars changed markedly, with the development of additional lamellae at the anterior end of the first lower molar, M/1, and at the back of the third upper molar, M3/, and an increase in

hypso-donty, these morphological changes being accompanied by an increase in size (Freudenthal 1976; Abbazzi et al. 1993). Some evolutionary modifications in the tooth enamel microstructure have also been observed on the first lower molar for this genus (Zafonte and Masini 1992). Both the number of crests on the M/1 and M3/ and the size of the M/1 have been used by Freudenthal (1976) to determine the chronological succession of the Gargano fissures. Although the genus *Microtia* was used first to establish the relative chronological arrangement of the Gargano fissures (Freudenthal 1976), the sequence inferred using a number of other taxa from the Gargano is almost identical to the conventional one considered here. A review of this evidence now follows. Several rodent species show a progressive increase in size during the time span represented by the Gargano fissures: the glirid *Stertomys* (Daams and Freudenthal 1985), the cricetid *Hattomys* (Freudenthal 1985), and the murid *Apodemus* for which there is also an increase in the number of roots on the first upper molar (M. Freudenthal unpublished data). Freudenthal (1985) studied in detail the cricetid rodents that are found in large quantities in the Gargano fissures. In particular, the genus *Hattomys* is characterized by a considerable increase in size, in addition to great changes in molar morphology. By using the size of *Hattomys*, Freudenthal (1985) con-

structed a chronological sequence of the Gargano fissures that agreed with the morphological evolution of the genus and importantly corroborates the sequence based on the evolution of size and morphology of *Microtia*. The lagomorph *Prolagus* is represented by two lineages that also reach a larger size and display a tendency toward a complication of the dental morphology accompanied by an increase in crown height (Mazza 1987a,b), and its evolution also corroborates the chronological sequence of the Gargano fissures considered in this study (De Giuli and Torre 1984). Remains from the giant insectivore *Deinogalerix* (Freudenthal 1972) were found in a large number of different fissures, and Butler (1980) distinguished two different lineages that differed in size, both lineages evolving toward a larger size. Lastly, Ballmann (1973, 1976) recognized eight different genera among the birds from the Gargano, and the increase in size of the three species of Accipitridae (eagles) and six species of Strigiformes (owls) permitted an arrangement of the Gargano fissures into a stratigraphical sequence that independently corroborates the chronology attained with the use of the mammal taxa from the Gargano.

The use of several evolutionary lineages, the fact that the evolutionary trends in these lineages involve progressive changes in morphology and morphological complexity in addition to size changes, and the fact that reversal in these evolutionary trends is highly improbable provide an indirect determination of the relative chronology of the different fossil localities as originally established by Freudenthal (1976). Accordingly, we followed the chronological sequence of the Gargano fissure fillings proposed by Freudenthal (1976), where the 11 fissures considered are arranged in the following order, from the oldest to the youngest (abbreviations for the fissure names are given in brackets): Biancone 1 (b1), Rinascita 1 (r1), Fina D (fd), Chiro 7a (c7a), Chiro 27 (c27), Chiro 6 (c6), Chiro 5a (c5a), Fina H (fh), Gervasio 1 (g1), Chiro 24 (c24), and San Giovannino (sg) (Fig. 1).

Material.—In this study, we included both numerous lower jaws bearing incisors and isolated lower incisors. According to Freudenthal, there are three main lineages of *Microtia*

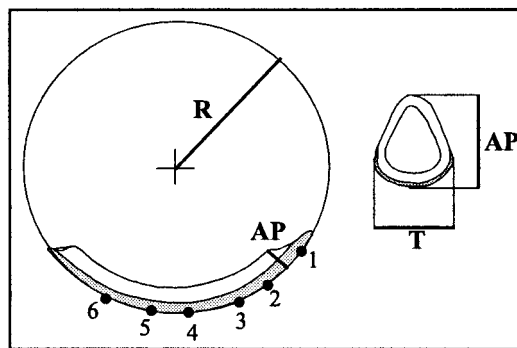


FIGURE 2. Lower incisor in lateral and in cross-sectional views showing the three measurements taken: anteroposterior diameter (AP), radius of curvature (R), and transverse diameter (T).

that were differentiated on the basis of various morphological characters of the molars, in particular the number of crests on the M/1 and M/3 and the degree of hypsodonty of the M/1 (Freudenthal 1976). The main middle-sized lineage leads from the species *M. parva* in the oldest fissure, Biancone 1, to *Microtia* sp. in the youngest fissure, San Giovannino. Two other *Microtia* lineages are present in the Gargano fauna, a small one, which occurs in fissures Chiro 7a to San Giovannino, and a larger one, *M. magna*, which occurs in fissures Chiro 27 to San Giovannino. Lastly, two other small forms were recognized in the older fissures Biancone 1 and Rinascita 1, but their position relative to the other main lineages remains unclear, and several systematic hypotheses are under discussion (Freudenthal 1976: *Microtia maiscula* and *Microtia parvula*; Abbazzi et al. 1993: *Microtia* sp.). In addition, these small forms are not well represented in our samples, and we have thus not included them in our study. According to Freudenthal (1976), it is very likely that the modern small size lineage originates in Chiro 7a and has no phylogenetic relationship with the *M. parva* from Biancone 1 or the other small forms found in older fissures, and that *M. parva* is rather the source for the middle *Microtia* size lineage.

Measurements.—We took measurements with a drawing tube coupled to a digitizer with 0.01 mm precision for three characters: the anteroposterior diameter (AP), the transverse diameter (T), and the radius of curvature (R) of the lower incisor (Fig. 2). The inci-

incisor radius was computed using six points on the anterointernal margin of the incisor.

Statistical Analyses.—Descriptive statistics (sample size, mean, and standard deviation) of each sample were computed for the three size characters (AP, R, and T) of the lower incisor. Sample variability of these three size variables for each *Microtia* species was estimated by its coefficient of variation, CV, following the formula $CV = \text{standard deviation} \times 100/\text{mean}$. Among each *Microtia* lineage and for each size character AP, R, and T, a one-way ANOVA and *t*-test mean comparison tests between successive fissures were then conducted to compare size differences among all the 11 fissures considered. Since multiple *t*-tests were performed, the significance levels were corrected using the Bonferroni method (Sokal and Rohlf 1995). To characterize the amount of total size variation through time of the three measured characters for the three *Microtia* lineages, we computed simple percentages of size change, following the formula $(X_2 - X_1) \times 100/X_1$, where X_2 is the size in the youngest fissure and X_1 the size in the oldest one. To estimate *Microtia* body mass, we used a regression analysis on log-transformed data to describe the allometric relation between lower incisor size (AP) and body mass (*W*) among 51 extant rodent species (Millien-Parra 2000). All these statistical analyses were computed using Systat software, Version 5.2.1.

To describe the *Microtia* community size structure and its evolution, we computed the interspecific size ratios between each *Microtia* lineage. To compute these ratios, for each fissure, the mean size value of the larger species was divided by that of the next smaller one, i.e., the large-sized versus the middle-sized species and the middle-sized versus the small-sized species. Lastly, to test for the equality of these size ratios, i.e., for a regular size structure, we used Barton and David (1956) statistic (Simberloff and Boecklen 1981; Dayan et al. 1989, 1990; Dayan and Simberloff 1994). This method tests for constancy of ratios between the mean sizes of paired size-ranked species in a community, and thus for a regular size structure in this community. As in Dayan and Simberloff 1994, we used the Barton and David statistic $G_{1,m}$ which is the ratio of the

smallest to the largest size ratio. The null hypothesis that the observed ratios do not differ from those produced by chance alone is rejected when the probability lies under the significance level.

Results

Sample Homogeneity

Descriptive statistics for the three size characters AP, R, and T are given in Table 1. Sample sizes range from 1 to 38 incisors. Within each sample, each size variable was tested for normality with the Kolmogorov-Smirnov test. The assumption of normality was valid in most cases (65 out of 66 samples), except for *M. parva* from fissure Biancone 1, which had a significant result for variable AP ($p < 0.002$). However, since the sample size is large enough to use parametric statistics ($n = 38$), and the assumption of normality was valid for the two other variables R and T ($p = 0.49$ and $p = 0.86$, respectively), we considered the sample *M. parva* from fissure Biancone 1 homogeneous.

CV values range from 3.8% to 12.7% for variable AP, from 5.0% to 14.8% for variable R and from 4.4% to 19.0% for variable T (Table 1). CV values computed for 117 samples of Oligocene fossil rodent species on molar length range from 1.7% to 24.8% (Vianey-Liaud et al. 1995). Similarly, CV values computed from data after Barnoski (1993) on molar measurements from fossil and extant populations of *Microtus pennsylvanicus* range from 2.5% to 15.1%. Some data on upper incisors from extant rodent populations gave values that fell between 3.2% and more than 19.0% for variables AP and R (Parra et al. 1999a). Lastly, some data obtained from lower incisors for several muroid species gave values that fell between 2% to 15% for AP (Millien-Parra 2000). All the CV values given above are comparable to those obtained in the present study for variables AP, R, and T of the lower incisor of *Microtia* populations.

Microtia Evolution

Size Evolution.—The size evolution of the three lineages for the three size characters of the lower incisor is depicted in Figure 3.

TABLE 1. Descriptive statistics for the lower incisor anteroposterior diameter (AP), radius of curvature (R), and transverse diameter (T); \bar{x} and SD in mm; CV is Simpson coefficient of variation ($CV = SD \times 100/mean$); * indicates samples for which $n = 5$. Abbreviations for the fissure names are the following: b1 = Biancone 1; r1 = Rinascita 1; fd = Fina D; c7a = Chiro 7a; c27 = Chiro 27; c6 = Chiro 6; c5a = Chiro 5a; fh = Fina H; g1 = Gervasio 1; c24 = Chiro 24; sg = San Giovannino.

	AP				R				T			
	<i>n</i>	\bar{x}	SD	CV	<i>n</i>	\bar{x}	SD	CV	<i>n</i>	\bar{x}	SD	CV
<i>Microtia</i> middle-sized lineage												
sg	4	1.98	0.20	10.2*	3	24.10	1.26	5.2*	4	1.63	0.15	9.4*
c24	10	1.86	0.11	5.7	9	24.51	1.76	7.2	10	1.60	0.13	8.3
g1	9	1.83	0.15	8.1	9	23.68	2.43	10.3	9	1.53	0.20	12.8
fh	15	1.91	0.24	12.7	12	23.27	1.87	8.0	15	1.52	0.19	12.4
c5a	21	1.87	0.18	9.8	11	22.22	2.04	9.2	21	1.49	0.17	11.3
c6	38	1.86	0.21	11.0	31	22.89	2.84	12.4	38	1.50	0.22	14.4
c27	12	1.84	0.11	5.9	8	21.08	1.08	5.1	12	1.45	0.18	12.0
c7a	33	1.82	0.22	11.9	27	18.84	2.04	10.9	33	1.36	0.20	14.6
fd	31	1.70	0.17	9.8	23	18.25	1.66	9.1	31	1.24	0.18	14.8
r1	26	1.72	0.13	7.8	25	16.39	1.20	7.3	26	1.23	0.11	9.3
b1	38	1.26	0.13	10.4	35	11.40	1.17	10.2	38	0.83	0.12	14.9
<i>Microtia</i> small-sized lineage												
sg	21	1.27	0.12	9.3	16	17.25	1.36	7.9	21	0.92	0.11	12.2
c24	15	1.32	0.14	10.6	12	16.22	2.41	14.8	15	0.98	0.15	14.8
g1	28	1.36	0.09	6.7	26	17.39	2.08	12.0	28	0.98	0.10	10.0
fh	10	1.37	0.07	5.4	9	18.84	1.05	5.6	10	1.02	0.07	7.2
c27	22	1.40	0.09	6.6	18	17.59	1.24	7.1	22	1.13	0.08	7.3
c7a	5	1.31	0.08	5.8	4	14.13	1.42	10.0*	5	0.95	0.07	7.5
<i>Microtia magna</i>												
sg	18	2.97	0.14	4.8	14	37.92	1.90	5.0	18	2.45	0.11	4.4
c24	7	2.73	0.13	4.8	6	33.90	1.69	5.0	7	2.07	0.13	6.2
g1	2	2.84	0.16	5.5*	1	27.72	—	—	2	2.16	0.41	19.0*
fh	18	2.85	0.11	3.8	16	32.54	2.03	6.2	18	2.35	0.10	4.4
c6	1	2.74	—	—	1	35.55	—	—	1	2.27	—	—
c27	1	2.70	—	—	1	31.35	—	—	1	2.24	—	—

Microtia middle-sized lineage: Results of the one-way ANOVA are highly significant for the three size characters AP, R, and T (all $p < 0.001$), which indicates a strong relation between time and size. *T*-test mean comparisons tests corrected by the Bonferroni method indicate some significant differences between Biancone 1 (b1) and the following fissure Rinascita 1 (r1) for AP, R, and T (Fig. 4). For size character R, *t*-tests indicate significant differences between fissure r1 and fd, and between fissures c7a and Chiro 27 (c27).

We can thus describe the size evolution of that lineage in two episodes (Fig. 3). The oldest one from fissure b1 to r1 is characterized by a strong increase in size for all the size characters of the lower incisor. This episode is followed by an increase in size from r1 up to c27 for size character R, whereas no significant size trend was evidenced for size characters AP and T.

Microtia small-sized lineage: Size evolution

in this lineage can be described by an increase in size in the interval of Chiro 7a (c7a) to Chiro 27 (c27) followed by a decrease in size for AP and T. For R, we observe an increase in size in the interval of c7a to Fina H (fh) similarly followed by a decrease in size (Fig. 3). Results of the one-way ANOVA are significant for the three size characters AP, R, and T ($p < 0.004$, $p < 0.001$, and $p < 0.001$, respectively), which indicates a significant relation between time and size. *T*-tests indicate significant size differences between each successive fissure from c7a until Gervasio 1 (g1) and until fh for R and T, respectively (Fig. 4). *T*-tests show no significant size differences between the successive fissures for size character AP, but since the results of the ANOVA were significant, this can be interpreted as a slight decrease in size for this variable.

Microtia magna: The one-way ANOVA gave highly significant results for the three size characters AP, R, and T (all $p < 0.001$), which

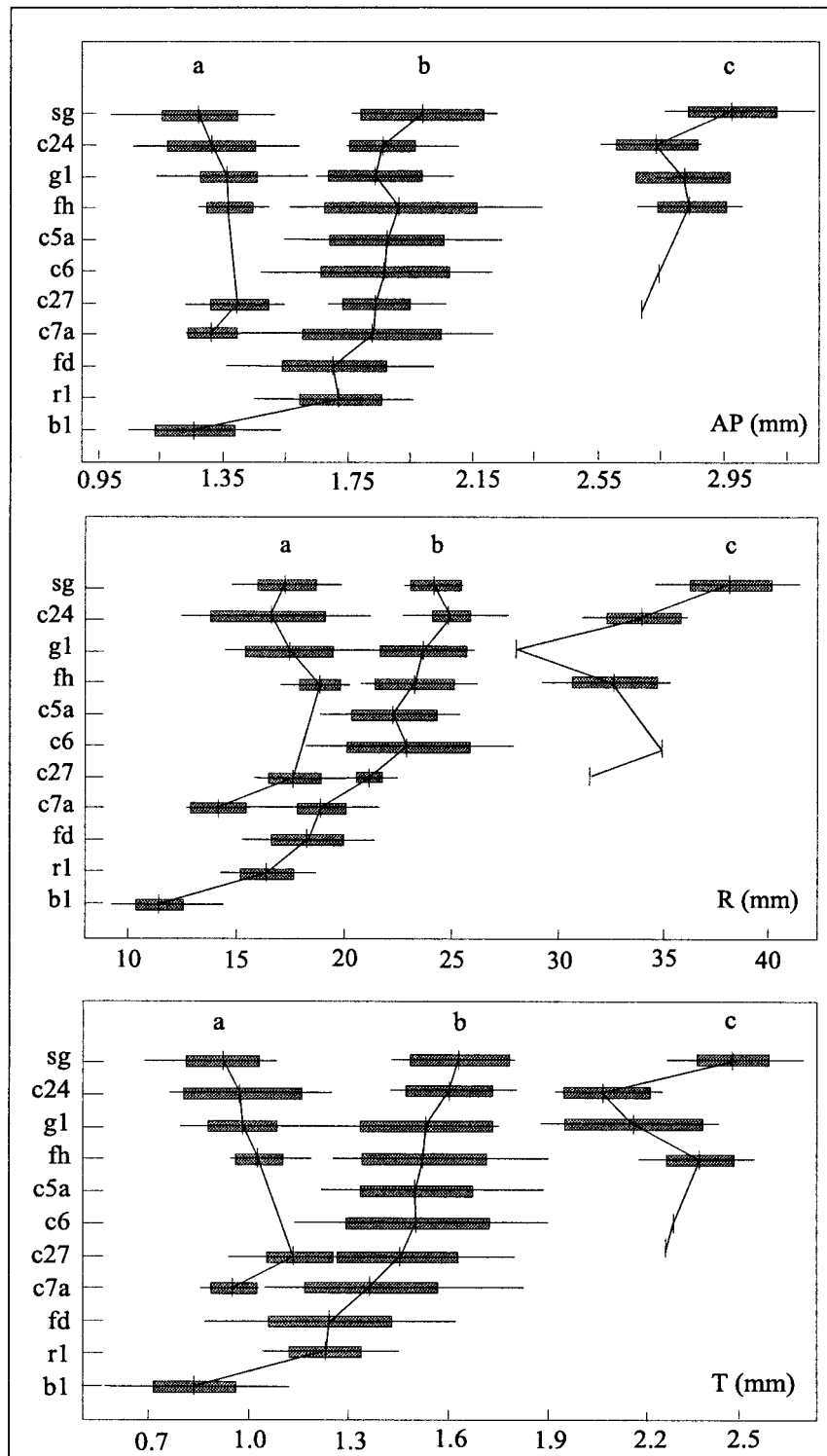


FIGURE 3. Evolution of each *Microtia* lineage for the three size characters of the lower incisor AP, R, and T; x-axis = size, in mm; y-axis = Gargano fissures arranged following Freudenthal's chronology; a = small-sized *Microtia* lineage; b = middle-sized *Microtia* lineage; c = *M. magna*; vertical line = mean; box = standard deviation; horizontal line = total range. Abbreviations for the fissure names are the same as in Table 1.

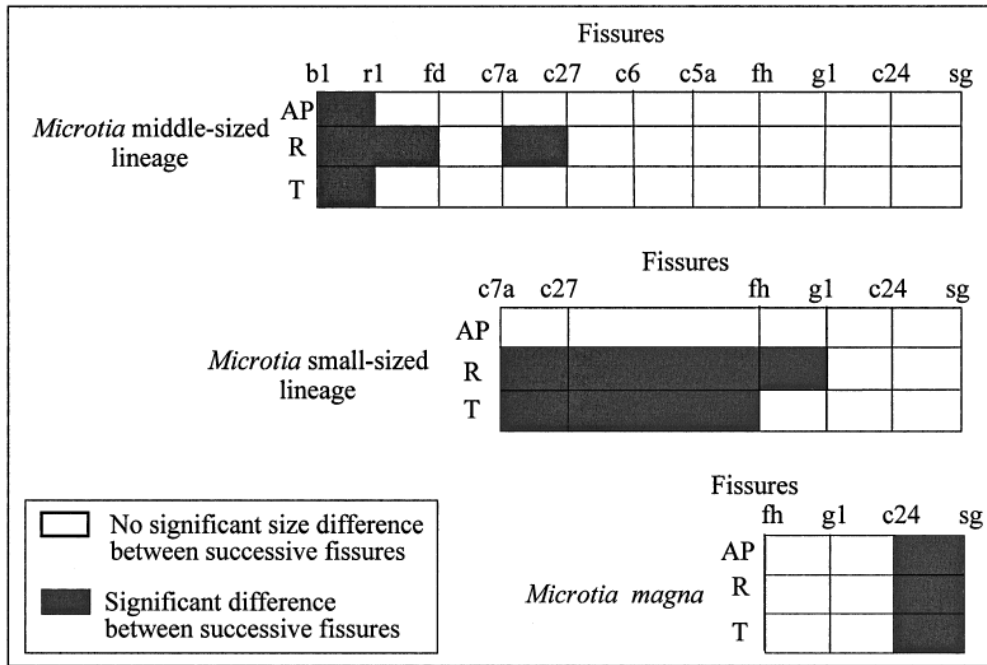


FIGURE 4. Schematic representation of the size evolution of the three *Microtia* lineages through time for samples represented in this study. All successive fissures were compared by performing a *t*-test for each size character AP, R, and T, corrected with the Bonferroni method. No test was performed for fissures c27 and c6 for *M. magna* ($n = 1$ in these samples). Abbreviations for the fissure names are the same as in Table 1.

indicates a strong effect of time on size within this lineage. After running the *t*-tests comparing all successive fissures for AP, R, and T, the only significant size trend observed was between fissures Chiro 24 (c24) and San Giovanni (sg) (Fig. 4). The *M. magna* lineage can thus be characterized by an increase in size from c24 to sg for AP, R, and T (Fig. 4). Additionally, Figure 3 shows a decrease in size from Fina H (fh) to c24 for size characters AP and T. However, the difference between these two fissures is not statistically significant, and the c24 sample is represented by only seven specimens. In addition, there was a significant difference between fh and sg for the three size characters AP, R, and T ($p < 0.01$, $p < 0.001$, and $p < 0.01$, respectively). Finally, the size decrease observed between fh and c24 was not demonstrated by Freudenthal (1976) for molar size where there was a larger sample size than that used to describe the incisor size evolution.

We can make the following conclusions from our analyses: (1) For each of the three lineages, size of the three incisor characters changes through time, as indicated by the sig-

nificant results of the ANOVA. (2) Size trends are different between the three *Microtia* lineages: we observe a strong size increase in the middle-sized lineage, a slight size decrease in the small-sized lineage, and a small size increase in *M. magna*.

Congruence among Size Variable Evolution.—Temporal trends for the three size characters AP, R, and T are usually similar, although this is not always the case. For example, in the middle-sized *Microtia* lineage, R increases later in time (until Chiro 27) than either AP or T (until Rinascita 1; Fig. 4).

Total percentage size changes of each *Microtia* lineage for each size character AP, R, and T are given in Table 2. For the middle-sized *Microtia* lineage, an increase of 57% of AP accompanies a greater increase of 111% and 96% for characters R and T. Therefore, not only has the incisor become larger, but its shape has also changed during the evolution of this lineage. The radius of curvature of the incisor has increased following an allometric evolutionary trend, i.e., the relative proportions of the three size characters of the lower incisor are

TABLE 2. Percent changes of the lower incisor anteroposterior diameter (AP), radius of curvature (R), and transverse diameter (T) for the three *Microtia* lineages between the extremes of their chronological range. Percent change is estimated following the formula $(X_2 - X_1) \times 100/X_1$, where X_1 and X_2 are measurements in mm in the oldest and youngest fissures, respectively. Abbreviations for the fissure names are the same as in Table 1.

	AP	% Change	R	% Change	T	% Change
<i>Microtia</i> middle-sized lineage						
b1	1.26		11.40		0.83	
sg	1.98	+57.14%	24.10	+111.40%	1.63	+96.39%
<i>Microtia</i> small-sized lineage						
c7a	1.31		14.13		0.95	
sg	1.27	-7.87%	17.25	+22.08%	0.92	-3.16%
<i>Microtia magna</i>						
c27	2.70		31.35		2.24	
sg	2.97	+10.15%	37.92	+20.96%	2.45	+9.38

not conserved during evolution. This pattern is shown for the *Microtia* middle-sized lineage in Figure 5, where the radius of curvature, R, was divided by the size of the incisor, AP, to eliminate the effect of size on the shape of the lower incisor. Figure 5 illustrates the decrease in the relative curvature (i.e., increase in R/AP) that accompanies the increase in size (AP) of the lower incisor. The results are similar for *M. magna*, for which R increased twice as much as AP and T, with a 21%, 10%, and 9% percent change, respectively. Finally, for the small-sized *Microtia* lineage, AP and T decreased (-8% and -3%, respectively), whereas R increased (22%). We can thus conclude that the character R shows a peculiar size trend compared with the two other characters, as it seems to evolve to a larger extent when compared with overall size, and always to-

ward an increase in the lower incisor's radius of curvature.

Estimation of Body Size Change

The length of the first lower molar is generally the measurement used to estimate body mass of fossil mammals (Creighton 1980; Gingerich et al. 1982; Legendre 1989; Martin 1990). However, this relation could not be applied to *Microtia*, as there was an evolutionary increase of the molar occlusal surface by the development of additional lamellae in front of the M/1 (Freudenthal 1976). An estimation using a model based on the M/1 length would thus greatly overestimate body mass. Indeed, using the same formula as that for the incisors, we computed the total percent size change of the first lower molar length, based on Freudenthal's published data (Freudenthal 1976). For the middle-sized *Microtia* lineage, the M/1 length shows an increase of 114% from b1 to sg, while we computed an increase of 57% for the lower incisor size of the *Microtia* middle-sized lineage (Table 2). In previous studies, we showed that the size of the upper (Parra and Jaeger 1998) and lower (Millien-Parra 2000) incisors are highly correlated with body size in extant rodents, with coefficients of correlation of 0.89 and 0.93, respectively. The regression line that best describes the relation between body mass (W) and the lower incisor anteroposterior diameter (AP) among 51 extant rodent species is the following (Millien-Parra 2000): $\text{Log}W = (2.58 \times \text{LogAP}) + 3.19$ ($p < 0.001$), giving the following allometric function: $W = 24.28 \times (\text{AP})^{2.58}$ (Fig. 6). Table 3 pro-

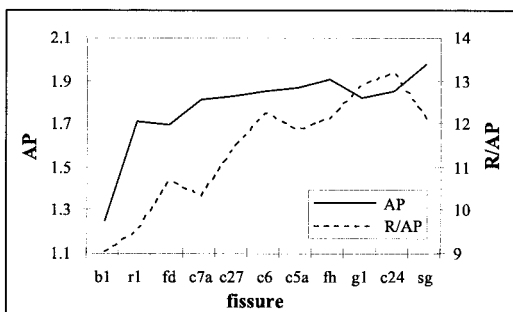


FIGURE 5. Representation of the evolution of the size and shape of the middle-sized *Microtia* lower incisor through time. This evolution is characterized by an increase in size (AP, in mm: solid line), accompanied by an increase in the relative curvature (R/AP: dotted line) of the lower incisor. Abbreviations for the fissure names are the same as in Table 1.

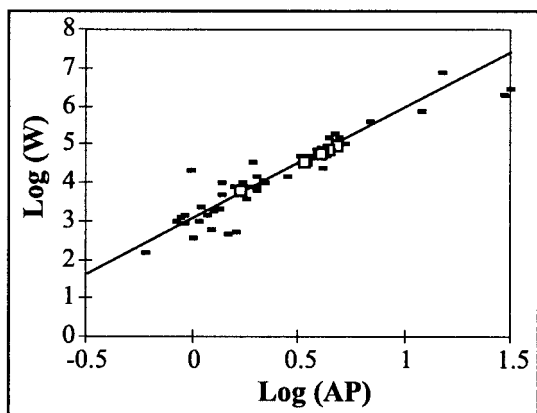


FIGURE 6. Relation between the anteroposterior diameter of the lower incisor (AP), in mm, and body weight (W), in g; $\text{Log}W = 3.19 + 2.58 \text{Log}AP$; $R = 0.93$; dashes: 51 extant rodent species (data from Millien-Parra 2000); squares: *Microtina* (mean value for each lineage for each fissure).

vides the estimated body mass of the three *Microtina* lineages at their earliest known locality and at San Giovannino. As previously, we used these body mass estimations to compute a percent body mass change for each lineage. For the middle-sized *Microtina* lineage, there is a very strong increase in body mass of 231.92%. We also observe a slight decrease in body mass for the small-sized *Microtina* lineage of 7.69% and a small increase in body mass for *M. magna* of 28.32%.

Size Divergence among the Three *Microtina* Lineages

We can define two steps during the evolution of *Microtina* (Fig. 3) (Freudenthal 1976: Fig. 4). From the beginning of the series until fissure Chiro 27 (c27), the two smaller species are well represented. The first remains of the large species *M. magna* appear in c27, and this species is rare until fissure Fina H (fh).

From the beginning of the series until Chiro 27, the two smaller species evolve toward a larger size. After the appearance of *M. magna*, the smallest species evolves toward a smaller size for size characters AP and T, until the youngest fissure, San Giovannino, where the three *Microtina* lineages are well discriminated by size. Therefore, it seems that the three *Microtina* lineages evolve in a way that increases the size differences between them. However,

TABLE 3. Lower incisor anteroposterior diameter (AP, in mm) and estimated body mass (W, in g) for the three main *Microtina* lineages at the extremes of their chronological range. Percent change is estimated following the formula: $(W_2 - W_1) \times 100/W_1$, where W_1 and W_2 are estimated body masses at the oldest and youngest fissures, respectively. The following regression was used to compute body mass: $\text{Log}(W) = 2.58 \times \text{Log}(AP) + 3.19$, where Log are natural logarithms (from Millien-Parra 2000). Abbreviations for the fissure names are the same as in Table 1.

	AP	Log(AP)	Log(W)	W	% Change
<i>Microtina</i> middle-sized lineage					
b1	1.26	0.23	3.77	42.21	
sg	1.98	0.68	4.94	140.10	+231.92%
<i>Microtina</i> small-sized lineage					
c7a	1.31	0.27	3.88	48.26	
sg	1.27	0.24	3.80	44.55	-7.69%
<i>Microtina magna</i>					
c27	2.70	0.99	5.74	311.87	
sg	2.97	1.09	5.99	400.20	+28.32%

the evolution of size character R follows a different pattern, and the two smaller lineages remain very close in size until fissure Gervasio 1.

Interspecific mean-size ratios between each *Microtina* lineage were computed for the five fissures where the three coexisting *Microtina* lineages were represented in our samples (c27, fh, g1, c24, and sg). The evolution of the mean value of these ratios for the three characters of the lower incisor (AP, R, and T) is depicted in Figure 7. From Chiro 27 to San Giovannino, there is an increase in the ratio values (Fig. 7), which illustrates the size divergence between the three *Microtina* lineages through time.

We also used the Barton and David statistic proposed by Simberloff and Boecklen (1981) to test whether the mean-size ratio of the middle-sized to the small-sized *Microtina* was equal to the ratio of *M. magna* to the middle-sized *Microtina* in each of the successive fissures where the three species coexisted. The ratios were found to be constant in only two cases: sg for character AP ($p < 0.045$) and fh for character T ($p < 0.044$). However, for size characters AP and R, there was a general tendency of a decrease in the p -values through time (Fig. 7), which can be interpreted as an evolution toward an increasingly regular size structure of the *Microtina* community. In contrast, no

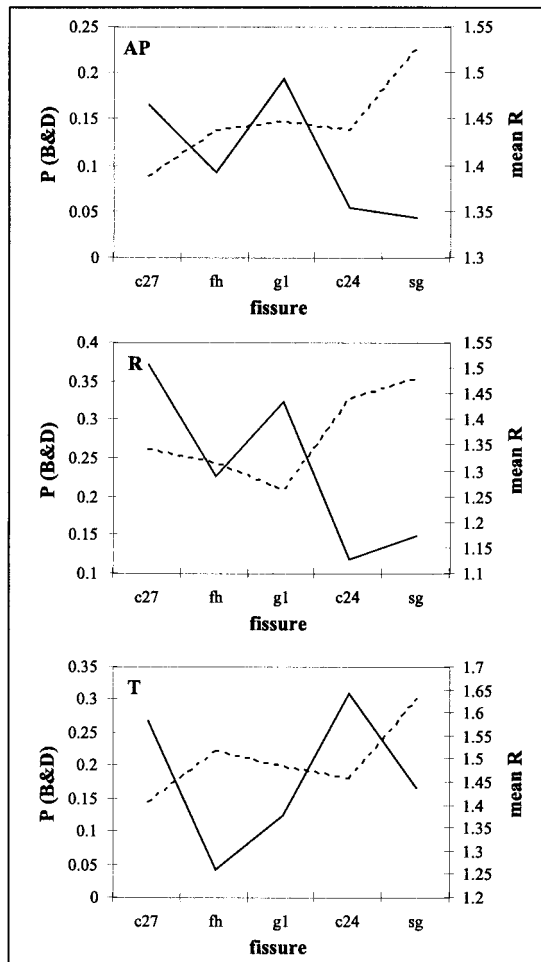


FIGURE 7. Evolution of *Microtia* community size structure in the five fissures where the three *Microtia* species were represented in our samples. Dotted line = mean value of the mean-size ratio of *Microtia* middle-sized to *Microtia* small-sized and of *M. magna* to *Microtia* middle-sized. There was an increase of this value for the three characters of the lower incisor (AP, R, and T), which illustrates the size divergence of the three *Microtia* species through time. Solid line = p -value of the B&D statistic used to test for constant size ratio between species. Overall, there was a decrease in this value through time for size characters AP and R, which can be interpreted as an evolution toward a more regular size structure for these two characters. Abbreviations for the fissure names are the same as in Table 1.

clear trend could be evidenced for size character T (Fig. 7).

Discussion

Peculiarities in the Evolution of the Lower Incisor Radius.—We pointed out that the size character R evolves to a greater extent and shows an unusual trend compared with the two oth-

er size characters of the lower incisor, AP and T. While characters AP and T might be representative of overall body size evolution, character R seems to evolve somewhat independently of body size, although it is certainly partly constrained by body size. Character R shows also the largest total percent change of the three characters. Agrawal (1967) showed that the upper and lower incisors of some fossorial rodents have a very low curvature (i.e., large radius of curvature), when compared with terrestrial or arboreal rodents. This observation was confirmed in a recent study of the lower incisor shape variability among murid rodents (Millien-Parra 2000). Additionally, the morphology of the *M. magna* skull and postcranial skeleton from San Giovannino fissure suggests that this species was a burrowing rodent (Parra et al. 1999b). We interpret the great increase in lower incisor radius of curvature (character R) revealed in the present study as an evolution toward a more specialized burrowing life in *Microtia* and a perfection of its adaptation through the allometric evolutionary trend of the lower incisor.

Amount of Change and Physiological Implications.—For the middle-sized *Microtia* lineage there is a considerable increase in body mass of 231%. Body mass has been well correlated with several physiological and ecological parameters in extant mammals, such as basal metabolic rate, gestation time, longevity, reproductive output, and population density (see reviews in Peters 1983 and in Damuth and McFadden 1990). Such a large increase in body mass might be related to a reduced reproductive output and increased gestation time, while the energetic expenditure per unit mass and the population density are reduced, all of which would enhance the probability of extinction of *Microtia* on reconnection with the mainland in the early Pleistocene.

Gigantism or Nanism?—The general pattern of insular evolution among mammals indicates that small species become larger on islands, and large species become smaller (Foster 1964; Van Valen 1973). Size trends among the three *Microtia* lineages are different, as the two larger lineages evolve toward a larger size while the smallest lineage evolves toward a smaller size. Previous studies on insular ro-

dents have mostly found a general trend toward gigantism (Musser 1981; Musser and Newcomb 1983; Hutterer et al. 1988; Biknevičius et al. 1993; Michaux et al. 1996; but see Foster 1964), making the Gargano small-sized lineage one of the few endemic island rodent lineages known to evolve toward a smaller size.

Several hypotheses have been proposed to explain the increase in size of isolated rodent species. One of these hypotheses maintains that a decrease in predation (Heaney 1978) or the absence of predators on islands (Valverde 1964) allows rodent species to evolve toward a greater size. However, the Gargano fissures yield many remains of birds of prey (Ballmann 1973, 1976) that probably preyed heavily on *Microtia*. The Gargano microfossils are indeed probably concentrated in owl pellets.

Two approaches have led to the hypothesis of the existence of an optimal body size among mammalian species. The first was based on the relation between body mass and population density among mammals (Damuth 1993), while the second was based on the existence of a compromise between the rate of resource acquisition and resource conversion among mammals (Brown et al. 1993). These two models predict that there is an optimal body size for mammalian species around 1 kg and 100 g, respectively, and it is claimed that the theory of an optimal body size provides an explanation for the evolution toward a larger size of isolated small mammals (Brown et al. 1993; Damuth 1993). However, the hypothesis of an optimal body size for each *Microtia* lineage seems unlikely given the contrasting direction of the size evolution of the small-sized *Microtia* lineage compared with that of the other two. In addition, the theory of an optimal body size has been recently criticized (Blackburn and Gaston 1996; Kozłowski 1996; Chown and Gaston 1997). We conclude that an optimal body size did not drive the evolution in *Microtia* and that other mechanisms must have had strong influences on its evolution.

Many studies of extant rodent communities have pointed out the role competition might play in determining community size structure (Brown and Lieberman 1973; Brown 1975; Da-

yan et al. 1989, 1990; Dayan and Simberloff 1994, 1998; Parra et al. 1999a; Millien-Parra and Loreau 2000). Competition between the three *Microtia* lineages may have been an important factor driving their size evolution, leading the small-sized *Microtia* lineage to evolve toward a smaller size and the two other lineages to evolve toward a larger size. In addition, we have demonstrated an evolution toward a more regular size structure of the *Microtia* community, accompanied by an increase in the interspecific mean-size ratios between species. Both of these evolutionary patterns may well have decreased interspecific competition. This argument is affirmed by the different amounts of evolutionary change computed for the three *Microtia* lineages, which result in a minimized size overlap between the species and a possible minimization of direct competitive interaction between them, an evolutionary response that would have favored their coexistence.

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