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The case of an insular molarless black rat: Effects on lifestyle and mandible morphology

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ABSTRACT

We report a specimen of an insular black rat (*Rattus rattus*) from Illa den Colom (Menorca, Western Mediterranean) displaying a singular dental characteristic. It has no molar teeth but displays regular incisors. Its mere occurrence as a regular adult rat is puzzling and we attempted to evaluate what diet and morphological changes in jaw shape were promoted by the total lack of molars, and allowed the successful survival of this specimen. Two approaches were performed: first, bone tissue was analysed to obtain $\delta^{15}N$ and $\delta^{13}C$ values in order to estimate dietary preferences of the rat. Second, the shape of the jaw was analysed through elliptic Fourier analysis, using outlines as markers of diet. The values for C and N fractionation (−19.89‰ and 10.06‰, respectively) suggest that the molarless rat included animal food in the diet and not exclusively plant material as observed in other mainland rat populations. The morphometric analysis in which the shape of the molarless mandible falls into the range of omnivorous groups leads to a similar conclusion. The adult age of the specimen suggests that it fed efficiently enough with its incisors to allow a normal growth. Although displaying a lack of molar teeth, no deep changes in remodelling jaw morphology can be observed and its shape falls into the variation of regular murines. The molarless rat exemplifies that special ecological features on small islands allow the survival of aberrant morphotypes.

1. Introduction

Islands are regarded as ''laboratories of evolution'', because processes of genetic and phenotypic evolution often occur fast and may lead to pronounced intra-specific differences.[1]

Extreme morphological changes can become fixed in insular populations because accidents lead to genetic drift in small, isolated populations[2,3] and because ecological conditions, such as the absence of predators, may allow survival of variants that would not have been viable on the mainland.

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We report here a case that exemplifies an unexpected output of insular conditions. During a trapping campaign in the Balearic Islands (Western Mediterranean Sea), an outwardly normal specimen of black rat (*Rattus rattus*) revealed a surprising dental phenotype, being devoid of any molar tooth despite the occurrence of regular incisors (Fig. 1). The uniqueness of the specimen could restrict it to be considered as anecdotic; its occurrence as adult and outwardly healthy specimen however raises questions about the ecological strategy that allowed its survival despite an intuitively unfavourable phenotype. It is furthermore intriguing from a developmental point of view since cases of such molar anodontia with no further apparent abnormalities are unreported in both wild rodents and laboratory mutants.

We investigated the possible ecological characteristics of this molarless rat using two approaches: stable isotopes and morphometric analysis of its jaw shape, both likely to vary with diet changes. Mandible shape was further evaluated in what extent the occurrence of such an exceptional dental phenotype modified the jaw due to the action of mastication movement on bone remodelling.

2. Materials and methods

The molarless specimen of *R. rattus* was captured on Illa den Colom (Menorca, Balearic Islands, Western Mediterranean Sea), a small islet (60 ha) situated 200 m from the Menorcan coast, with a house only settled a few weeks during the year. Its vegetation is basically formed by a shrub community of *Launaea cervicornis*. On the islet survives an insular population of the endemic Balearic Lizard, *Podarcis lilfordi brauni*. Amongst rodents, only *R. rattus* has been reported. The European rabbit, *Oryctolagus cuniculus*, is also present in the island (García, pers. com.). No evidence exists for the presence of other land mammals, although probably the house mouse, *Mus musculus*, is also present. Rats achieve high densities, according to personal observations (JAA) and to the abundant remains of their activity (accumulations of broken shells of terrestrial snails, scats, etc.).

The specimen was captured in a small beach on the southwest coast of the islet during a unique night trapping field work in the summer of 1982 with snap traps, using bread and oil as bait. It is an adult specimen that displays a so far unrecorded full absence of molars and alveoli, with upper and

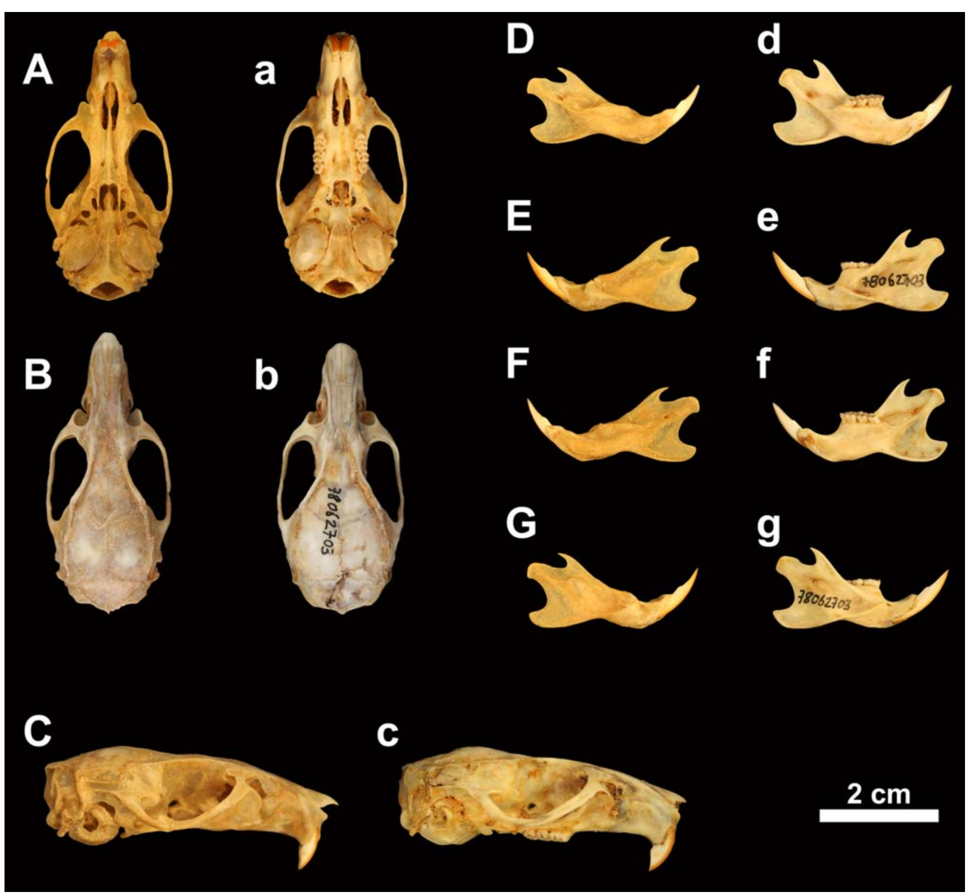

Fig. 1 – Comparison of the Illa den Colom molarless *Rattus rattus* (IMEDEA 90276, labelled with capital letters) and normal *R. rattus* from Menorca (IMEDEA 62593, labelled with small letters). (A, a) Skull, ventral view. (B, b) Skull, dorsal view. (C, c) Skull, lateral view. (D, d) Left mandible, lingual view. (E, e) Left mandible, labial view. (F, f) Right mandible, lingual view. (G, g) Right mandible, labial view. No remarkable differences in skull and mandible shape can be observed between specimens.

lower incisors being present (Fig. 1). Only its skeleton is preserved and it is currently curated at the vertebrate collection of the Institut Mediterrani d'Estudis Avançats (CSIC-UIB, Palma de Mallorca) under the accession number IMEDEA 90276. Measurements: body length, c.185 mm; tail length, c. 213 mm; ear length, 23.5 mm; posterior foot length, 32.5 mm; weight, >130 g. These values roughly fall within the known range of adult black rats in insular environments.[4]

Two approaches were used to further analyse the significance of this specimen. First, $\delta^{15}N$ and $\delta^{13}C$ values were obtained from two bones of the molarless rat in order to estimate its foraging ecology (i.e., the trophic level of this specimen and the origin, marine vs. terrestrial, of the consumed food). Data of stable isotopes measured in different body tissues of *Rattus* spp. have been obtained from the literature[5–10] for comparative purpose.

Second, we analysed the shape of the mandible through an elliptic Fourier analysis, using the mandible outline as a morphological marker of diet.[11] The Illa den Colom mandible shape has been compared with major clades of murines, including other representatives of the *Rattus* group presenting various diets. Mandible shape was quantified in each taxon for *ca*. 10 specimens,[11] the mean shape per taxon constituting the core of the dataset for mandible shape. Intra-specific variation in insular context was addressed by further considering several samples of *R. rattus*: two from Mediterranean mainland (based on 10 specimens from Greece and 9 from Sanary, France), and two from other Mediterranean islands, either small (9 specimens from Port Cros, France) or large (9 specimens from Corsica). Another Menorcan rat, with regular molars, was further included in the analysis. For this single Menorcan rat and the molarless rat, both right and left mandibles were measured, the right being mirrored and measured as left mandible, in order to get an average value per specimen that was included in the mandible shape dataset. This dataset was analysed using a principal component analysis, thus displaying the main pattern of mandible shape variance on few synthetic axes. The size of the molarless rat was further compared with its relatives based on the area of the mandibular bone. To check the molar region, internal images of the molarless rat jaw have been obtained with a Trophy Intraoral X-Ray System.

3. Results

No evidence of molar root or alveoli can be distinguished inside the mandibles of the molarless rat using X-ray images (Fig. 2), only incisors being observed: traumatic loss of molar teeth can thus be excluded.

The analysed bones present a $\delta^{15}N$ value of 10.06‰ and a $\delta^{13}C$ value of −19.89‰ (C/N: 3.3) (Fig. 3). The value of $\delta^{13}C$ corresponds to the expected in an environment of C3 vegetation, and the rather high $\delta^{15}N$ value is likely indicating an animal part in the diet of this individual.[12] Extensive bibliography on stable isotope analysis of liver, muscle, bone and other tissues of rats living in islands with seabirds colonies is available.[5–10,13] Though isotopic data from other Menorcan or Illa den Colom rats is lacking, the molarless rat displays values of $\delta^{13}C$ and $\delta^{15}N$ in the range of values measured in specimens feeding in insular areas close to the sea (shore, inter-tidal, etc.) or in areas occupied by seabird colonies.

Fig. 2 – X-ray images of both mandibles of the molarless rat (IMEDEA 90276). Just incisors can be observed inside the jaw, and no remains of molar root or alveoli are distinguishable. Scale bar 2 cm.

Mandible size may be regarded as a proxy for body size. The comparison of the molarless rat with other populations of black rats (Fig. 4) confirms that the molarless rat from Illa den Colom falls into the range of variation of mainland and insular populations of adult rats. Its mandible is slightly smaller than the one documented for its Menorcan relative, but this may be due to regular intra-population variance.

Regarding mandible shape (Fig. 5), the first axis characterises large trends in diet amongst the main groups of murine rodents. Herbivorous taxa, namely Arvicanthini, are shifted towards positive values along the first principal axis (PC1). On

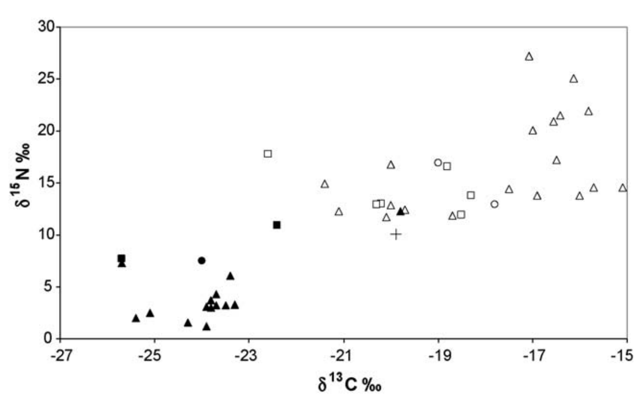

Fig. 3 – Stable isotopes signature of the molarless rat in comparison of other data published for *Rattus* spp.[5–7,9,10] White symbols: rats feeding in "marine" environments (i.e., colony of seabirds, coastal, cove and shore in literature). Black symbols: rats feeding in "terrestrial" environments (forest, inland or upland in literature). Data from liver (squares), muscle (triangles) and bone (circles). +: Illa den Colom molarless rat (data obtained from bone).

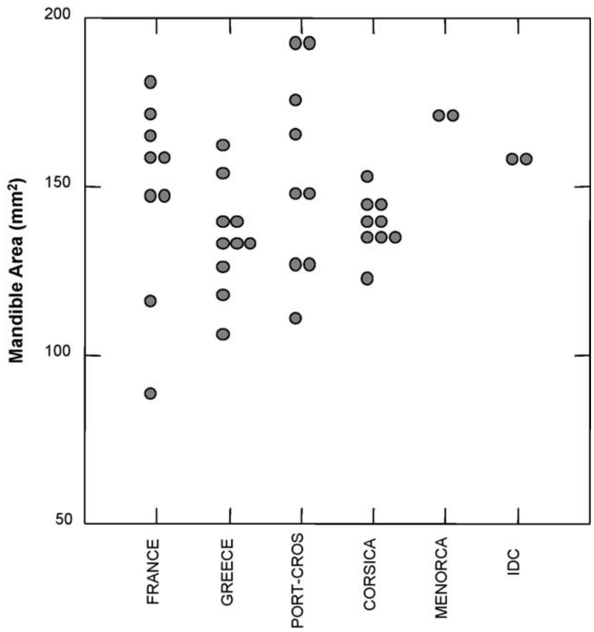

Fig. 4 – Mandible size in different black rat populations: France and Greece (mainland populations), Port Cros (small islet off Southern France), Corsica, Menorca, and the molarless rat from Illa den Colom (IDC). For Menorca and Illa den Colom, the two mandibles of a single specimen have been measured.

the contrary, diverse omnivorous murine rodents belonging to the *Apodemus*, *Mus*, and *Praomys* groups are clustered towards negative PC1 values. The group of *Rattus* is characterised by a large variation in this morphospace, including both omnivorous taxa such as *Rattus huang*, *niviventer*, or *norvegicus*, but also extremely specialised herbivorous taxa such as *Nesokia*. *R. rattus* seems rather central in this respect, but its intra-specific variation encompasses zones of the morphospace corresponding to omnivorous as well as herbivorous mandible shape. Mainland populations and the Menorcan specimen fall into the range of variation of herbivorous allies; in contrast, Corsican rats and especially the molarless rat from Illa den Colom are shifted towards more omnivorous groups. This corresponds to morphological differences that are qualitatively obvious (Fig. 1), with a more massive mandible for the Menorcan rat and a slender shape for the molarless rat.

4. Discussion

4.1. *Feeding and mastication*

Anodontic mice have been used in the laboratory to explore how mastication is induced. It is considered that teeth play an important role in the regulation of the mandible movements during the mastication. The mastication in rodents can be divided in two stages, gnawing and chewing.[14] Several studies suggest that tooth eruption promotes conversion from sucking to chewing during the early post-natal period, thus no chewing masticatory movements should be developed in absence of molars. Nevertheless, in the absence of incisors and molars, the masticatory rhythms have been demonstrated to occur almost normally,[15] mainly those associated with chewing.

This odd wild rat devoid of molars reached adulthood suggesting that it fed efficiently enough to allow at least an apparently normal growth and its survival until capture. The change from sucking to mastication behaviour should have occurred in our specimen without molars probably only stimulated by the presence of associated periodontal mechanoreceptors of the incisors.

During the feeding process, several types of rhythmic oral behaviours have been described, such as sucking, lapping, licking, and mastication. Only mastication involves the use of teeth: food is cut into small pieces by the incisors (gnawing) and these are ground by the molars (grinding). Although our specimen would have had special difficulties for grinding, it may be concluded that it reached adulthood through lapping and licking of liquid foods and biting, piercing, and gnawing solid food with the incisors.

4.2. *Ecology of the molarless rat*

Black rats have usually a vegetation-based diet[16] although their world-wide success testifies of their adaptability to various diets. This flexibility regarding the available food is particularly clear on islands, where black rats have shown niche shift depending on the insular context.[17] On various Mediterranean islands, black rats extended their niche by incorporating food of animal origin to their diet,[6,8,18–21] although vegetation matter usually remains dominant.[4] The use of animal resources as a part of the diet seems to be increased on small islets, where rats, in absence of mammalian predators, can reach very high densities.[22] Such a shift to the consumption of soft food of animal origin might have been the key of the successful survival of a molarless rat.

This hypothesis is corroborated by the stable isotopes analyses on the bones of the molarless rat. This method allowed tracing diet shifts on other insular populations of black rats[6,8] and the values obtained on the Illa den Colom specimen indeed fall within the range of variation of populations including a large proportion of small vertebrates, insects, and other animal matter in their diet. This suggests that the molarless rat should have been omnivorous, consuming a mixed terrestrial and marine food, including animal matter.

4.3. *Mandible shape change: plasticity due to missing teeth or local adaptation?*

Mandible shape has been shown to vary at the inter-specific level amongst the major clade of murines, depending on the dominant diet of each taxa.[11] Variation at the intra-specific scale have been further evidenced within the wood mouse[23] and the domestic mouse,[24] and interpreted as related to diet shifts amongst populations. It was thus tempting to investigate how the mandible shape of the molarless rat was situated in the morphospace including on one side, the diversity of the murine rodents, and on the other side, a diversity of mainland and insular black rat populations. A first striking result was

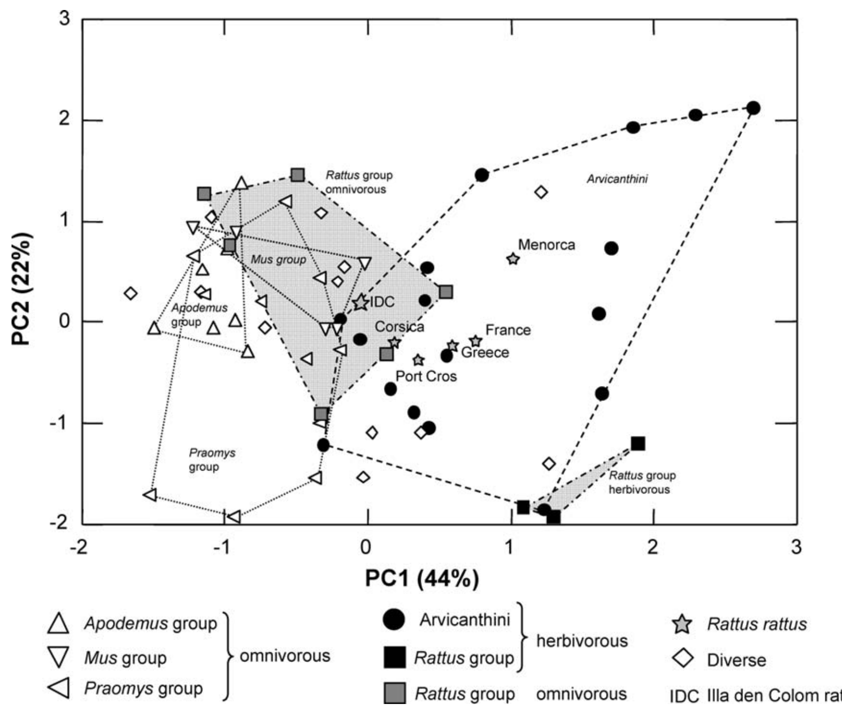

Fig. 5 – Disparity in mandible shape amongst murine rodents of various taxa and diets, and amongst mainland and insular populations of black rats. The morphospace corresponds to the first two principal axes of a PCA on the variance-covariance matrix of the Fourier coefficients of an outline analysis of the mandible (method: elliptic Fourier transform; coefficients D1–D7). The PCA has been performed on the mean values per group, the groups being the different murine taxa, or the black rat populations. Black symbols, grey symbols refer respectively to herbivorous and omnivorous diets. Triangles and rhombs refer to supra-generic taxa, and stars to *Rattus rattus* populations.

that, despite the quite unusual phenotype of a molarless animal, the mandible shape falls within the range of variation of regular murines, and close to other populations of black rats. Hence, the absence of molars was not associated with a pathological jaw morphology that may have arisen from deeply perturbed developmental pathways. Instead, the mandible shape of the molarless rat from Illa den Colom appeared as an end-member in the variation of documented black rat populations, far from the other Menorcan specimen but quite close to Corsican rats. Whereas the Menorcan rat (with molars) displayed a morphology characteristic of a herbivorous diet, the molarless rat fall into the range of variation of omnivorous members of the *Rattus* group, thus corroborating the conclusions based on isotopes analyses of an omnivorous animal.

Although seductive, this result raises the question of the process responsible for such a morphological shift in mandible morphology. Morphological differences between the omnivorous clades of *Praomys*, *Apodemus* and *Mus*, and the herbivorous Arvicanthini result of an evolutionary divergence that occurred over more than 10 million years.[25] Differences between herbivorous and omnivorous members of the *Rattus* groups are more recent but still accumulated over ~2 My.[25] Morphological evolution is often accelerated on islands[26] because of the not mutually exclusive processes of founder effect, drift, and niche shift. All these processes might have contributed to the differentiation of Menorcan and Illa den Colom rats. Alternatively, the morphological output observed on the molarless rat may not reflect the evolution of a local population, but an individual syndrome due to abnormal bone remodelling in a molarless rat. Plastic changes – slender mandibles and reduced insertion of masticatory muscles – have been evidenced in laboratory rats and mice.[24,27]

A qualitative inspection of the jaw of the molarless rat indeed points to a more posteriorly curved coronoid process, and a slender horizontal ramus. Similar trends were also evident in *Onychomys* (a carnivorous South American Cricetidae), when compared to *Peromyscus* (a more vegetarian Cricetidae), due to a less important mass of the masseter muscle and a more prominent role of the biting function of the incisors.[28] Hence, the observed jaw morphology of the molarless rat might be the result of a changed balance between the unaffected biting function and the much reduced chewing function, changing the relative development of the masticatory muscles and in turn the pattern of bone remodelling of the mandible.

4.4. *What genetic process for a molarless rat?*

Absence of molars is documented in wild rodents at different evolutionary scales. The third molar as well as a second one is regularly missing in a few lineages of Murinae from South-East Asia.[29] Third molar is occasionally missing in some species or in some individuals, e.g. in *Mus musculus* or *Mus pahari*.[29] Missing teeth are also known in mammals including rodents due to loss in old animals, or due to developmental abnormalities. Specimens of murine rodents with loss of molars due to ageing occur in the wild, but they are rare and only occur in very old animals (often obtained in environments free of carnivores); in very old specimens of *R. rattus*, usually only the third molar is missing at a stage of worn-down first upper molar (personal observations). In these specimens the complete re-absorption of the alveoli is never observed, in contrast with the jaw and skull of the molarless rat, completely devoid of any evidence of alveolus (Fig. 2). The specimen further does not display any characteristics of a very old age, since the cranial sutures are not yet completely fused. Hence, the most parsimonious explanation for the occurrence of the specimen is to consider that it was born molarless as an effect of a mutation or a developmental failure. A complete absence of molar teeth has however never been observed in wild species, and this raises the question of the genetic causes relayed by developmental processes responsible for such an exceptional phenotype.

Non-heritable absence of teeth, usually related to problems of tooth eruption, has been reported in case of exposure to toxicant substances[30] or even as a consequence of malnutrition.[31] However, in rats and mice, such defects are usually limited to the third molar. Although genetic bases of some anomalies in tooth development have been recently reviewed,[32] heritability of the genetic mutation displayed by the molarless rat here studied is unknown.

To our knowledge, rodents with total absence of molar teeth but with normal incisors and otherwise normal phenotypes are unknown as laboratory mutants. It is possible that minor mutations have altered complex developmental processes to produce the unique phenotype, which we have described. That the molarless rat survived into adulthood demonstrates that major phenotypic effects may be preserved in unusual environments, such as those found on islands, and can be a source of morphological innovations in evolution.

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