

The Relationships of
Megaoryzomys curioi, an Extinct Cricetine
Rodent (Muroidea: Muridae) from the
Galápagos Islands, Ecuador

DAVID W. STEADMAN
and
CLAYTON E. RAY

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ABSTRACT

Steadman, David W., and Clayton E. Ray. The Relationships of *Megaoryzomys curioi*, an Extinct Cricetine Rodent (Muroidea: Muridae) from the Galápagos Islands, Ecuador. *Smithsonian Contributions to Paleobiology*, number 51, 23 pages, 11 figures, 1 table, 1982.—*Megaoryzomys curioi* is a thomasomyine, not an oryzomyine as previously believed. This rodent was originally described, from three bony fragments found in a cave on Isla Santa Cruz, Galápagos, as a new species of the Antillean oryzomyine genus *Megalomys*. The genus *Megaoryzomys* was named recently for this species, based on new material from Isla Santa Cruz. Our study of additional material indicates that *Megaoryzomys curioi* is not closely related to *Oryzomys* but is most similar to large species of *Thomasomys*, a genus confined to mainland South America. The Galápagos have been colonized by cricetine rodents at least three times, once by a thomasomyine and twice by oryzomyines. Of these colonists, *Megaoryzomys curioi* is the most divergent from mainland relatives and thus is probably derived from the earliest immigrant. Although the time of extinction of *Megaoryzomys curioi* has not been determined, and it has never been recorded from life, it probably survived into historic time.

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The Relationships of *Megaoryzomys curioi*, an Extinct Cricetine Rodent (Muroidea: Muridae) from the Galápagos Islands, Ecuador

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Introduction

Megaoryzomys curioi (Niethammer, 1964) is the only species of vertebrate in the Galápagos Islands that is known only from fossils, having neither been seen alive nor collected from life by man. (*Nesoryzomys fernandinae* Hutterer and Hirsch, 1979, though not collected from life, was described from fresh owl pellets and may have been seen alive.) *Megaoryzomys curioi*, a muskrat-sized, cricetine rodent, was named on the basis of three bony fragments from a cave on Isla Santa Cruz. It was assigned originally to the Antillean genus *Megalomys*. The inadequacy of these meager fragments led us to question the validity of the assignment and to try to augment the material; Ray, beginning in 1965, and Steadman, beginning in 1978. The abundant material that resulted from our efforts immediately made it clear that the species required its own, new genus (Ray and Whitmore, 1973).

Early in 1978 we attempted to communicate

with Dr. Guy Coppoio about our long-term project, but we received no response from him; however, during final stages of preparation of this manuscript, we received from Thomas E. Simkin a copy of Lenglet and Coppoio (1979), in which the new genus *Megaoryzomys* was named for *Megalomys curioi*. We agree with Lenglet and Coppoio (1979) that the species *curioi* was not correctly placed in the genus *Megalomys*, but we do not agree that its closest affinities are with *Oryzomys*. Furthermore, we feel that the work of Lenglet and Coppoio is otherwise inadequate in its systematic treatment of this rodent. Therefore, we review here the morphology of *Megaoryzomys* based on new material and present our interpretation of its relationships. Material from Steadman's latest field work of October 1980–January 1981 will be described in his comprehensive work (in prep.) on the vertebrate paleontology of Galápagos, as will the material from Isla Isabela recorded herein as *Megaoryzomys* species.

ACKNOWLEDGMENTS.—Field work in Galápagos was supported by the Smithsonian Institution from the Walcott Fund (1968–1969), from the Fluid Research Fund (1966–1967 and 1977–1978, 1980) through the kind efforts of Dr. S. Dillon

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Ripley and Storrs L. Olson, and from the Graduate Student Program Development Fund of the University of Arizona (1980). Funds provided to Ray in 1966–1969 were used in part to defray nonpaleontological field work under the auspices of the Darwin Foundation, whereas those provided to Steadman were used strictly for paleontological work as directed by the CDRS. Permits for this latter field research were made possible through the offices of the Dirección de Desarrollo Forestal, Ministerio de Agricultura y Ganadería, Quito; Lcdo. Miguel Cifuentes, Intendente of Parque Nacional Galápagos; Craig MacFarland, Hendrick Hoeck, and David Duffy, past directors of the Charles Darwin Research Station; and Peter Kramer, Thomas E. Simkin, G.T. Corley Smith, and David W. Snow of the Charles Darwin Foundation. The personnel of the Parque Nacional Galápagos and the Charles Darwin Research Station made Steadman's field work not only possible but extremely pleasant. Marsha S. Cox, Minard L. Hall, and Thomas E. Simkin provided valuable advice on working in Galápagos. We particularly thank Miguel Pozo, Edward Steadman, and James Hill for working in the field with Steadman in Galápagos. Their companionship, hard work, and knowledge of field techniques aided immensely in this project. The De Roy's (André, Jacqueline, and Gil), the Devine's (Bud, Doris, and Steve), and the Moore's (Alan and Tui De Roy) constantly gave all sorts of advice and assistance to Steadman during field work. We also appreciate the field efforts of Srs. Camilo Calapucho, Miguel Castro, André De Roy, Michael Harris, and Tjitte de Vries, each of whom has collected fossils of *Megaoryzomys*. The late James L. Peters was instrumental in 1965 in Ray's first efforts to secure adequate material in Galápagos.

Financial support for Steadman's research at the National Museum of Natural History was provided by a Summer Visiting Student fellowship from the Smithsonian Institution and National Science Foundation grant DEB-7923840 to Paul S. Martin through the Department of Geosciences, University of Arizona. We thank the personnel of the Division of Birds, Division of

Mammals, and the Department of Paleobiology, NMNH, for the many services and courtesies put forth. Steadman's travel to the BM(NH) was financed by the National Geographic Society. We thank those in charge of collections of all institutions from which we have been permitted to examine specimens. Most especially, we thank Miss Levitt, Andrew Carrant, Anthony J. Sutcliffe, and Cyril A. Walker of the BM(NH) for allowing us to examine specimens under their care.

We thank W. Vervoort, C. Smeenk, and D.A. Hooijer, for their kindness and patience in connection with the loan of the indispensable skull of *Megalomys desmarestii* from the Leiden Museum, and Robert T. Orr of the CAS for the loan of Galápagan oryzomyines.

Discussions with Alfred L. Gardner, Michael D. Carleton, and Charles O. Handley, Jr., have enriched our knowledge of cricetine morphology and systematics. Jon A. Baskin and Michael D. Carleton provided very detailed criticisms of the manuscript. Charles O. Handley, Jr., and Paul S. Martin also read and criticized an earlier version. Naturally none of them is responsible for any remaining shortcomings. Helen F. James provided an English translation of Niethammer (1964). Karena M. Schmidt and Gene Hall helped in the sorting and cleaning of fossils. The drawings of skulls and mandibles were prepared by Lawrence B. Isham, on special funds provided by Richard S. Cowan, then director of the NMNH; the drawings of enamel patterns were kindly prepared by Molly Wing, without remuneration. The photographs are by Victor E. Krantz. This is contribution number 295 of the Charles Darwin Foundation.

Materials and Methods

ABBREVIATIONS.—The following are used to denote collections from which specimens were examined.

AMNH	American Museum of Natural History, New York
BM(NH)	British Museum (Natural History), London

CAS	California Academy of Sciences, San Francisco
CDRS	Charles Darwin Research Station, Isla Santa Cruz, Galápagos, Ecuador
CMNH	Chicago [Field] Museum of Natural History, Chicago
LSU	Louisiana State University, Baton Rouge
UF/FSM	Florida State Museum, University of Florida, Gainesville
USNM	former United States National Museum specimens deposited in the National Museum of Natural History, Smithsonian Institution

The abbreviation NMNH is used in the text to denote the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

FOSSIL MATERIAL.—Listed below are the specimens of *Megaoryzomys curioi* and *M.* species examined in this study with their collectors and dates collected. All localities are on Isla Santa Cruz and Isla Isabela (Figures 1 and 2). Except for Cueva de Kubler, Cueva de Iguana, and André's cave, we cannot vouch for the accuracy of the names or exact localities of the fossil sites in Galápagos. (MNI = minimum number of individuals represented by specimens listed.)

Megaoryzomys curioi, Isla Santa Cruz

- Cave no. 1 (= cave in Naranja Zone), different places, T. de Vries, 16 Jan 1966
USNM 284279; 5 postcranial specimens; MNI = 1
- Cave no. 1, T. de Vries, 19 Nov 1966
USNM 284280–284289; 2 maxillae, 2 cranial fragments, 2 dentaries, 1 isolated tooth, 22 postcranial specimens; MNI = 3
- Cave no. 1, place 2, T. de Vries, 16 Jan 1966
USNM 284295–284318; 1 nearly complete skull, 2 maxillae, 12 dentaries, 6 isolated teeth, 56 postcranial specimens; MNI = 9
- Cave no. 3, T. de Vries, 17 Jan 1966
USNM 284290–284294; 4 dentaries, 2 isolated teeth, 19 postcranial specimens; MNI = 3
- Cave no. 4 (= cave north of El Chato), T. de Vries, 21 Nov 1966
USNM 284348; 4 isolated teeth, 8 postcranial specimens; MNI = 2
- Cave no. 4, T. de Vries, M. Castro, 27 Jul 1967
USNM 284319–284330; 2 maxillae, 4 cranial fragments, 2 dentaries, 18 isolated teeth, approximately 80 postcranial specimens; MNI = 2
- Cave no. 5 (= cave north of Reserve in Naranja Zone), T. de Vries, 20 Nov 1966
USNM 284331–284335; 4 dentaries, 1 isolated tooth, 2 postcranial specimens; MNI = 3

- Cave near Bellavista, M. Harris, Oct 1966
CDRS 4–13; 3 dentaries, 1 isolated tooth, 6 postcranial specimens; MNI = 4
- Cave near Bellavista (not definitely the same cave as above), M. Castro, before Apr 1969
USNM 284336–284347; 1 maxilla, 6 dentaries, 4 isolated teeth, 7 postcranial specimens; MNI = 4
- Cave in Cascajo Mountains, E. Curio, 1962/1963
BM(NH) 67.1649; 1 maxilla, 2 postcranial specimens; MNI = 1
- Cueva de Kubler, D. Steadman, M. Pozo, 21, 23, 28 Jul 1979, 3 Aug 1979
USNM 284197–284270; 1 nearly complete skull, 19 maxillae, 30 cranial fragments, 16 dentaries, 116 isolated teeth, 203 postcranial specimens; MNI = 12
- Cueva de Iguana, various localities, D. Steadman, M. Pozo, 8–13 Jan 1978, 3–11 Jun 1978, 13–18 Jul 1978
USNM 284271–284278; 1 nearly complete skull, 3 cranial fragments, 1 maxilla, 9 isolated teeth, 18 postcranial specimens; MNI = 7
- André's Cave, A. De Roy, Mar 1969
CDRS 1–3; 1 nearly complete skull, 1 dentary, 1 postcranial specimen; MNI = 1

Megaoryzomys species, Isla Isabela

- Cueva de Sucre (= Cueva de Hueco Sucre), 1 km north of Pueblo Santo Tomás, M. Castro, Jan 1968
USNM 284349–284357; 2 maxillae, 4 cranial fragments, 3 dentaries, 14 isolated teeth, 8 postcranial specimens; MNI = 2

RECENT COMPARATIVE MATERIAL (skulls and mandibles).—*Thomasomys aureus*, USNM 194818, 194821, 194827 (Perú); *T. praetor*, CMNH 19255, 19256 (Perú); *T. princeps*, USNM 251957 (Colombia); *T. pyrrhonotus*, CMNH 81296, 84438, USNM 304538 (Perú); *T. cinereiventer*, AMNH 32421, 32423, 32430 (Colombia); *T. cinereus*, CMNH 81309, 81312, 81326, USNM 304537 (Perú); *T. hylophilus*, CMNH 92558, 92560, 92561 (Colombia); *T. ischyryus*, CMNH 19795, 19799, 19801, USNM 297635 (Perú); *T. kalinowskii*, CMNH 23723, 23735 (Perú); *T. rhoadsi*, CMNH 53210, 53211, 93146 (Ecuador); *Rhipidomys leucodactylus*, USNM 194495, 194496, 194499, 194501 (Perú); *R. caucensis*, USNM 387922, 387925 (Venezuela); *R. goodfellowi*, USNM 374543, 409937 (Venezuela); *R. venezuelae*, USNM 371247, 442286 (Venezuela); *R. venustus*, USNM 137507, 371242 (Venezuela); *Oryzomys palustris*, USNM 116531, 178297, 339957, (México, Alabama, Nicaragua); *Oryzomys albigularis* USNM 137509, 168229,

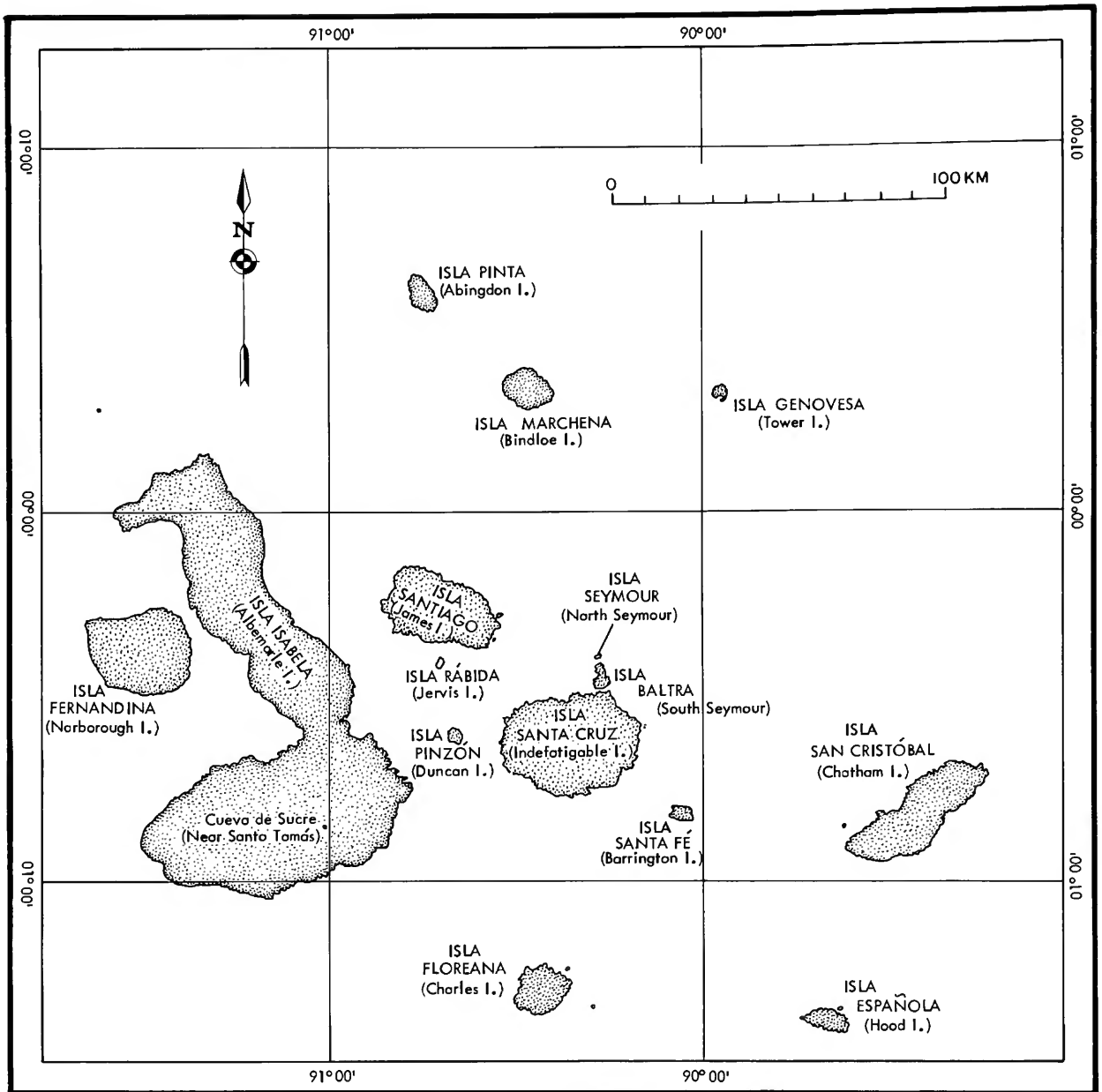


FIGURE 1.—The Galápagos Archipelago, showing major islands only. (See “Materials and Methods” and Figure 2 for details of localities on Isla Santa Cruz.)

172978 (Venezuela); *O. xantheolus*, USNM 277566, 302987, 302991 (Perú); *O. bauri*, USNM 392257 (Isla Santa Fé, Galápagos); *Nesoryzomys indefessus*, USNM 115832, 115834, 259312 (Islas Santa Cruz and Baltra, Galápagos); *N. narboroughi*, USNM 259552 (Isla Fernandina, Galápa-

gos); *N. swarthi*, CAS 2561 (Isla Santiago); *Megalomys “pilorides”* (= *desmarestii*), BM(NH) 1850.11.30.6 (Martinique); *M. desmarestii*, BM(NH) 1855.12.24.201 (Martinique), Leiden Museum “a” (Martinique); *M. luciae*, BM(NH) 1853.12.16.2 (St. Lucia); *Macruroryzomys hammondi*,

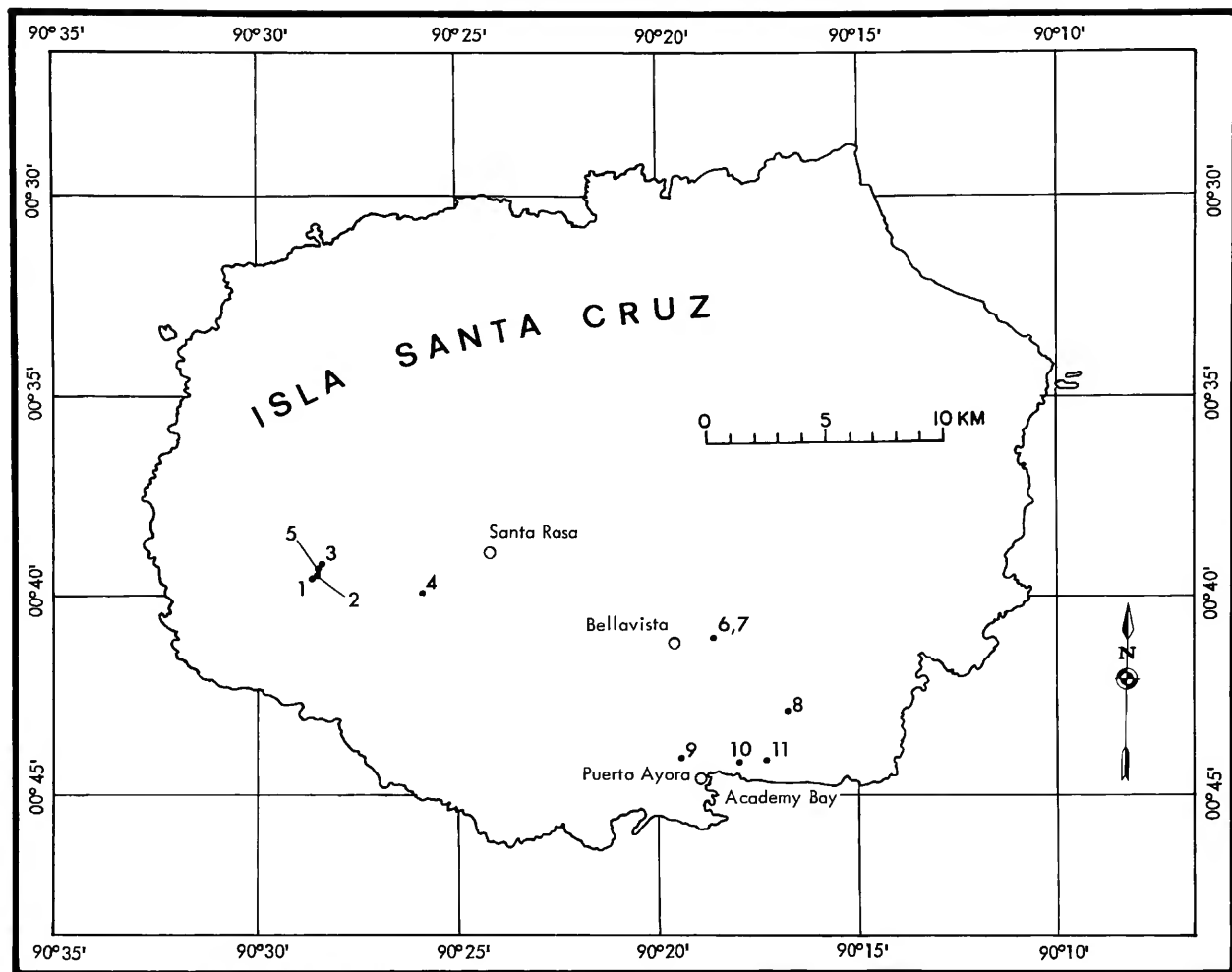


FIGURE 2.—Localities of *Megaoryzomys* on Isla Santa Cruz: 1, cave no. 1 (= cave in Naranja Zone); 2, cave no. 2 (contains no remains of *Megaoryzomys*); 3, cave no. 3; 4, cave no. 4 (= cave north of El Chato); 5, cave no. 5 (= cave north of Reserve in Naranja Zone); 6, cave near Bellavista; 7, cave near Bellavista (not definitely the same cave as no. 6); 8, cave in Cascajo Mountains (type-locality); 9, Cueva de Kubler; 10, Cueva de Iguana; 11, André's Cave. (See "Materials and Methods" for further information on these sites.)

BM(NH) 1913.10.24.55 (Ecuador); *Nectomys saturatus*, BM(NH) 1897.11.7.40 (Ecuador); *Tylomys* species, USNM 298732, 309223, 323971 (Panamá); *T. mirae*, USNM 113318 (Ecuador); *Scapteromys tumidus*, USNM 392888 (Uruguay); *S. chacoensis*, USNM 12170/8379 (Argentina); *Kunsia tomentosus*, USNM 364760 (Bolivia); *Phyllotis boliviensis*, USNM 121148, 391802 (Bolivia, Chile). In addition, the following archeological material of *Megalomys* was examined: *M. desmarestii*, USNM

293780A,B,C (dentaries; Martinique); *M. luciae*, LSU field No. 76ch, 76ci, 76cj (dentaries; St. Lucia); UF/FSM field No. 61a-39 (maxilla; St. Lucia).

MEASUREMENTS.—Statistics (mean, range, sample size) presented here are based on all adults of *Megaoryzomys curioi* examined in this study, exclusive of the holotype. Standard deviation is given for samples of 10 or more specimens. All specimens are from Isla Santa Cruz and are housed

either in the NMNH or the CDRS. Terminology for the first seven measurements follows Thomas (1905). All of the following measurements were made with dial calipers and were rounded to the nearest 0.1 mm.

greatest length between uprights 55.6, 1
 condylobasal length 54.45, 53.3–55.6, 2
 condylobasilar length 50.50, 49.3–51.7, 2
 basal length 50.25, 48.8–51.7, 2
 basilar length 46.25, 45.1–47.4, 2
 palatal length 30.30, 28.6–32.0, 3
 patatilar length 25.33, 24.6–26.5, 3
 length of diastema 16.05, 15.1–17.3, 4
 length of foramina incisivi 10.84, 9.6–11.7, 5
 length of palate 10.35, 9.9–10.6, 4
 zygomatic width 34.3+, 33.8+–34.8+, 2
 minimum width of braincase just posterior to zygomatic arch 19.03, 18.7–19.2, 3
 minimum interorbital width 8.22, 7.3–8.6, 4
 width of zygomatic plate of maxilla 8.06, 6.9–8.7, 6
 greatest width of rostrum 11.67, 11.0–12.3, 3
 depth of rostrum at anterior end of foramina incisivi 11.93, 11.8–12.1, 3
 least width of palate (between alveoli of M¹s) 4.20, 3.5–5.1, 5
 length of interparietal at midline 4.40, 4.4, 2
 width of interparietal 13.60, 12.8–14.4, 2
 width through occipital condyles 12.00, 11.8–12.2, 2
 alveolar length of upper molars 11.48±0.44, 10.9–12.3, 13
 crown length of upper molars 10.86, 10.0–11.5, 5
 length M¹ 4.92±0.28, 4.5–5.6, 20
 width M¹ 3.56±0.17, 3.3–3.9, 20
 length M² 3.31±0.17, 3.0–3.6, 14
 width M² 3.40±0.17, 3.1–3.7, 14
 length M³ 2.42, 2.3–2.5, 5
 width M³ 2.80, 2.7–2.9, 5
 length of dentary with incisor 38.10, 36.5–40.8, 7
 length of dentary without incisor 34.64, 33.4–35.5, 5
 alveolar length of lower molars 12.59±0.56, 11.7–13.6, 22
 crown length of lower molars 12.06, 11.5–12.7, 9
 length M₁ 5.17±0.18, 4.8–5.5, 15
 width M₁ 3.28±0.12, 3.1–3.5, 14
 length M₂ 3.54±0.15, 3.2–3.8, 16
 width M₂ 3.29±0.14, 3.0–3.5, 15
 length M₃ 3.35±0.23, 2.9–3.7, 11
 width M₃ 2.74±0.12, 2.6–2.9, 11

Description and Comparisons

Megaoryzomys curioi was described from a left maxilla (lacking M³) and fragments of a humerus and scapula that were found in 1962–1963 by Dr.

E. Curio in a cave (= lava tube) of unknown name or exact locality in the Cascajo Mountain area of Isla Santa Cruz (Niethammer, 1964:596, 600). Cascajo Mountain is approximately 7–8 km north of Academy Bay, although Abs et al. (1965:52) stated that the cave was approximately 15 km northeast of Academy Bay. The three original specimens of *Megaoryzomys* were found with the bones of four other species of rodents: *Nesoryzomys indefessus*, *N. darwini*, and two introduced species, *Rattus rattus* and *Mus musculus*. Unlike the remains of *Megaoryzomys*, those of the other four rodents were in the form of owl pellets, probably from the Galápagos barn owl (*Tyto punctatissima*). The bones of *Megaoryzomys*, although not mineralized, gave Niethammer the impression of being older than those of the other rodents from the same locality.

The three cotypes of *Megaoryzomys curioi* are deposited in the British Museum (Natural History), where they are housed in the Modern Mammal Section and bear the number BM(NH) 67.1649. As Niethammer (1964:598) presented no evidence to indicate that the three specimens designated as “type” represent a single individual, the maxillary fragment should be regarded as the holotype, and the scapula and humerus as paratypes. Contrary to the assertions of Lenglet and Coppo (1979:633), neither their specimens nor any others could possibly be types of their new genus, for which the species *curioi*, based on Niethammer’s specimens, is of course the type. Our measurements of the holotype, a maxilla, of *Megaoryzomys curioi* (alveolar length of upper molars 11.4 mm, length M¹ 5.1 mm, width M¹ 3.5 mm, length M² 3.3 mm, width M² 3.4 mm) are well within the range of variation of other specimens examined in this study (see “Measurements”). In addition, we could find no qualitative differences between our series of specimens and the holotype. Thus we are confident that our material represents the species described by Niethammer (1964).

Niethammer (1964:598, 599) placed his species in the West Indian genus *Megalomys* based on the following characters: (1) the similar enamel pat-

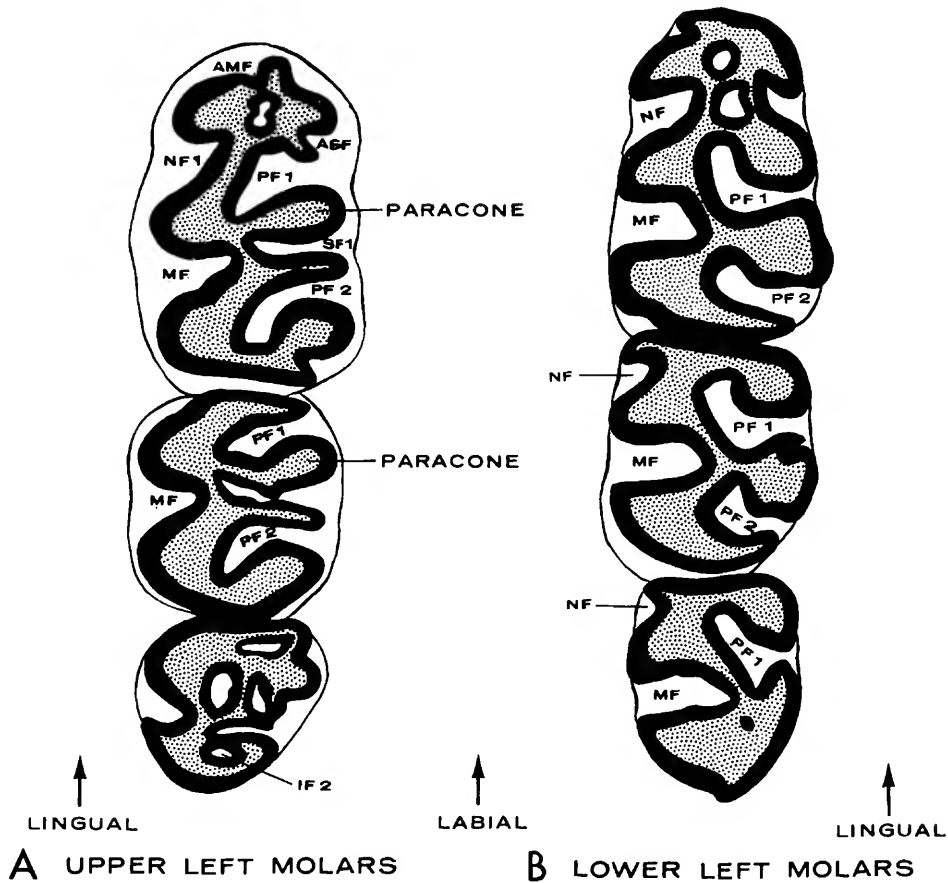


FIGURE 3.—Nomenclature of enamel patterns of molars of *Megaoryzomys*, including only those names used in the text: A, upper left molars (USNM 284317, reversed); B, lower left molars (USNM 284290, reversed). (Terminology follows Hershkovitz (1967); AMF = anterior median fold; ASF = anterior secondary fold; IF2 = 2nd internal fold; MF = major fold; NF = minor fold; PF1 = 1st primary fold; PF2 = 2nd primary fold; SF1 = 1st secondary fold.)

terns of its upper molars, (2) the similar pattern of the roots of the upper molars, (3) foramina incisivi that terminate anterior to the molars, (4) its large size. We will now re-analyze these characters, demonstrating that they do not suffice to place *curioi* in the oryzomyine genus *Megalomys*.

1. The similar enamel pattern of its upper molars. Niethammer (1964) said that the positions of enamel folds 1 and 3–8 of M^{1-2} (as shown in figure 4 of Niethammer) in *Megaoryzomys* are similar to those in *Megalomys desmarestii* of Martinique, Lesser Antilles. Niethammer's enamel folds 1–8 correspond sequentially to the following terms used herein (Figure 3): M^1 —PF.1, SF.1,

PF.2, NF, MF; M^2 —PF.1, PF.2, MF. The positions of enamel folds in *Megaoryzomys* generally resemble those in *Megalomys* (Figure 4), but *Megaoryzomys* differs from *Megalomys* and resembles the Neotropical cricetine *Thomasomys* in lacking IF.2 on M^{1-2} and in the presence of AMF and ASF. *Thomasomys* differs from both *Megaoryzomys* and *Megalomys* in its more nearly circular paracone on M^{1-2} . We agree with Niethammer that the "labial grooves" (major and minor folds) are deeper in *Megaoryzomys* than in specimens of *Megalomys* at a similar stage of wear.

Niethammer (1964) did not have any lower molars of *Megaoryzomys*. Our examination of

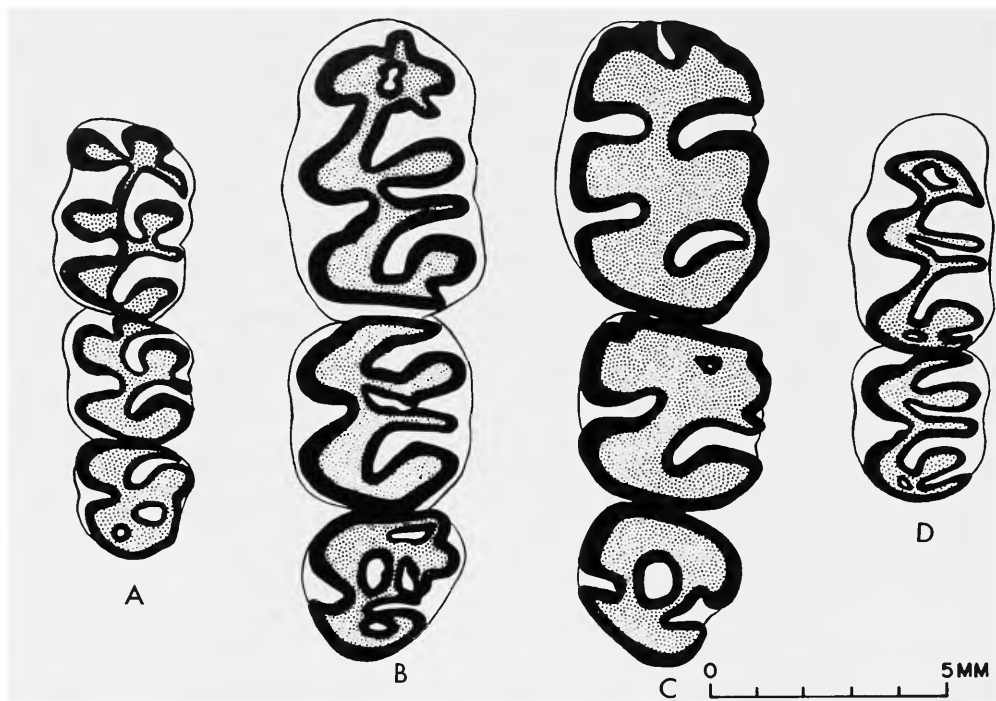


FIGURE 4.—Comparison of enamel patterns in left upper molars: A, *Thomasomys aureus*, USNM 194827; B, *Megaoryzomys curioi*, USNM 284317 (reversed); C, *Megaoryzomys curioi*, USNM 284318; D, *Megalomys luciae*, UF/FSM field no. 61a-39.

enamel patterns of the lower molars of *Megaoryzomys* (Figure 5) reveals more similarities to those of *Thomasomys* than to *Megalomys*. All primary, minor, and major folds in M_{1-3} are deeper and wider in *Megaoryzomys* and *Thomasomys* than in *Megalomys* at a similar stage of wear. The MF of M_2 is located more anteriorly in *Megalomys* than in the other two genera. *Thomasomys* differs from both in its prominent AMF.

2. The similar pattern of the roots of the upper molars. Because we have no specimens of *Megalomys* in which the alveoli of the upper molars are exposed, we cannot comment in detail on the status of this character, which is additionally obscured by Niethammer's (1964) failure to identify the taxa represented by alveolar patterns A, B, and C in his figure 3. We have, however, found the alveolar pattern of the upper molars in *Megaoryzomys* (seven specimens) to be identical to those in the only specimens of *Thomasomys* available with exposed alveoli—one specimen each of *T. cinereus* and *T. ischyrius*.

3. Foramina incisivi that terminate anterior to the molars. In *Megaoryzomys*, *Thomasomys*, and *Rhipidomys*, the posterior border of the foramina incisivi is even with, or only very slightly anterior to, the anterior border of M^1 , whereas in *Megalomys* the foramina incisivi terminate well anterior to the molars (Figures 6 and 9). Thus Niethammer's character actually supports a thomomyine allocation of *Megaoryzomys*, which differs greatly from *Megalomys* in this regard.

4. Its large size. Large size is of little value in assigning a cricetine rodent to genus or tribe. Among the mainland cricetines that are comparable in size to true *Megalomys* are *Tylomys mirae* (Peromyscini), *Nectomys squamipes* (Oryzomyini), *Kunsia tomentosus* (Scapteromyini), and *Holochilus magnus* (Sigmodontini), each of which is, like *Megalomys*, very different from *Megaoryzomys*. In addition, gigantism is a common occurrence in insular rodents, and thus the nearest mainland relative of any well-differentiated insular rodent

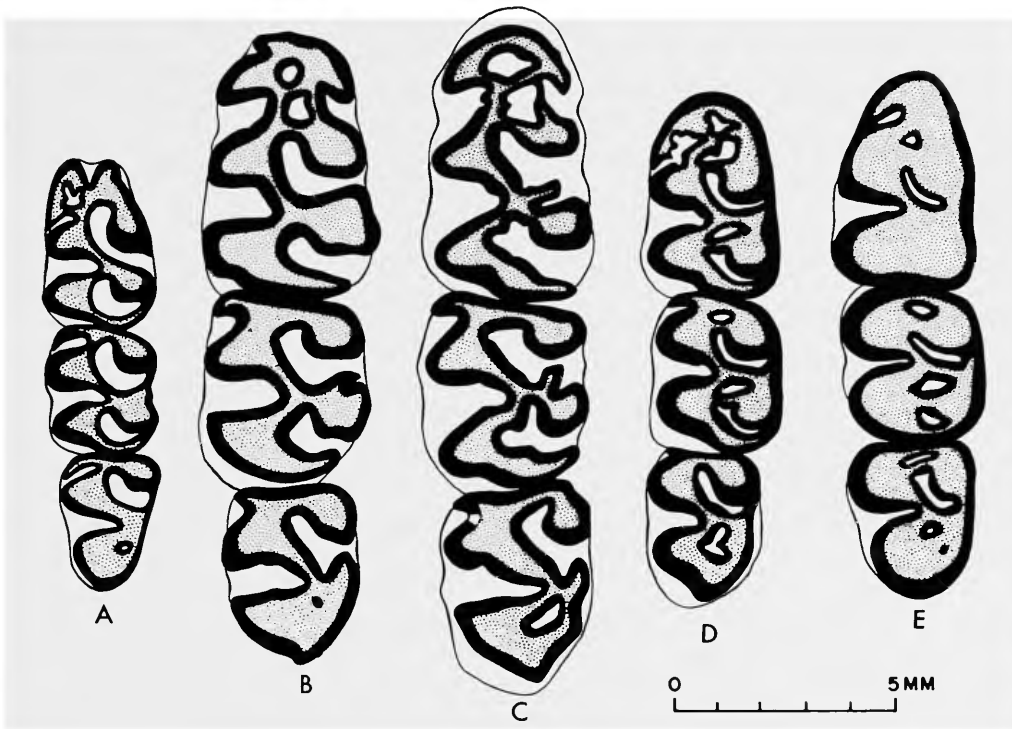


FIGURE 5.—Comparison of enamel patterns of left lower molars: A, *Thomasomys aureus*, USNM 194827; B, *Megaoryzomys curioi*, USNM 284290 (reversed); C, *Megaoryzomys curioi*, USNM 284299 (reversed); D, *Megalomys luciae*, LSU field no. 76ch (reversed); E, *Megalomys desmarestii*, USNM 293780c.

may well be smaller than its insular derivative. Gigantism in muroid rodents on islands has been abundantly documented, for example, in living species by Berry (1964, 1981) and Foster (1964), and in the Quaternary of the East Indies (Musser, 1981) and West Indies (Ray, 1962), the Canary Islands (Crusafont-Pairo and Petter, 1964), and the California Channel Islands (Gill, 1980; Walker, 1980). Certain Quaternary caviomorph rodents of the West Indies (systematically listed in Varona, 1974) also attained very large size, as did dormice in the Mediterranean (Petronio, 1970).

Thus the characters used by Niethammer (1964) to refer *curioi* to the genus *Megalomys* are invalid. Except for Lenglet and Coppois (1979), no author since Niethammer (1964) has seriously questioned its original assignment to the oryzomyine genus *Megalomys*. Abs et al. (1965), Orr

(1966), Peterson (1966), Hooijer (1967), Hershkovitz (1970, 1972), Müller (1973), Hutterer and Hirsch (1979), and Patton and Hafner (in press) mention the existence of “*Megalomys*” in Galápagos without systematic comment. To evaluate its affinities further, we compared *Megaoryzomys* to all genera and most species of Neotropical Cricetinae represented in the collections of the Division of Mammals, NMNH, supplemented by additional forms from the other museums. The majority of these species could be eliminated readily as near relatives of *Megaoryzomys* because of their relatively long palate, relatively small teeth, and differently shaped interorbital region. Table 1 includes only those species whose size or morphology are such that they deserved more serious consideration.

Megaoryzomys is not closely related to *Megalomys*; in addition to the characters in Table 1, *Megalomys*

Table 1.—Comparison of cranial characteristics of *Megaoryzomys curioi* and certain other species of cricetine rodents

Species	Depression along median suture of frontals	Shape of interorbital region (Figures 7, 9)	Length and width of palate relative to length of tooth row (Figures 6, 9)	Size of teeth relative to size of entire skull (Figures 6, 8, 9)	Dorsolateral ridge of braincase	Palatal foramina (Figures 6, 9)
<i>Megaoryzomys curioi</i>	deep	strongly constricted, with abrupt lateral expansion of squamosals	short, narrow	large	well developed, but not sharp or laterally expanded	large; numerous
<i>Thomasomys aureus</i>	shallow to deep	as in <i>M. curioi</i>	short, narrow	large	as in <i>M. curioi</i> , but slightly less developed in parietal region	small; few
<i>T. praetor</i>	deep	as in <i>M. curioi</i>	short, narrow to intermediate in width	large	as in <i>M. curioi</i>	small to medium sized; few
<i>T. princeps</i>	intermediate	as in <i>M. curioi</i>	short, narrow	large	as in <i>T. aureus</i>	small to medium sized; few
<i>T. pyrrhonotus</i>	shallow	as in <i>M. curioi</i>	short, narrow	large	as in <i>T. aureus</i>	small to medium sized; few
<i>T. cinereiventer</i>	shallow	wider than in <i>M. curioi</i>	short, wide	large	very small	small; few
<i>T. cinereus</i>	shallow	as in <i>M. curioi</i> , but more bulbous	short, wide	intermediate	very small	extremely small; very few
<i>T. hylophilus</i>	shallow	as in <i>M. curioi</i>	short, wide	intermediate	between <i>T. aureus</i> and <i>T. cinereus</i>	small; numerous
<i>T. ischyrys</i> and <i>T. kalinowskii</i>	shallow	wider and more bulbous than in <i>M. curioi</i>	short, wide	intermediate	very small	small; few
<i>T. rhoadsi</i>	shallow	wider than in <i>M. curioi</i>	short, wide	intermediate	very small	small; few
<i>Rhipidomys leucodactylus</i>	shallow	wider than in <i>M. curioi</i> , especially in posterior half	short, wide	intermediate	sharper with more lateral flare in interorbital region than in <i>Thomasomys</i> or <i>M. curioi</i>	small; few
<i>R. caucensis</i>	shallow	wider than in <i>M. curioi</i>	short, wide	intermediate	as in <i>R. leucodactylus</i>	absent or small and few
<i>R. goodfellowi</i>	shallow	wider than in <i>M. curioi</i>	short, wide	intermediate	as in <i>R. leucodactylus</i>	small; few
<i>R. venezuelae</i>	shallow	as in <i>M. curioi</i>	short, wide or narrow	intermediate	as in <i>M. curioi</i>	small to medium sized; rather numerous
<i>R. venustus</i>	shallow	wider than in <i>M. curioi</i> , with more gradual posterior expansion	short, wide	intermediate	as in <i>R. leucodactylus</i>	absent or very small and few
<i>Oryzomys palustris</i>	shallow	wider than in <i>M. curioi</i> , with gradual lateral expansion of frontals	long, intermediate in width	intermediate	very large and sharp; oriented diagonally or laterally	at least two large foramina, with varying number of smaller foramina

TABLE 1.—Continued

Species	Depression along median suture of frontals	Shape of interorbital region (Figures 7, 9)	Length and width of palate relative to length of tooth row (Figures 6, 9)	Size of teeth relative to size of entire skull (Figures 6, 8, 9)	Dorsolateral ridge of braincase	Palatal foramina (Figures 6, 9)
<i>O. albicularis</i>	shallow or absent	as in <i>M. curioi</i>	as in <i>O. palustris</i>	large to intermediate in size	not well developed in interorbital region	as in <i>O. palustris</i>
<i>O. xantheolus</i>	shallow	as in <i>O. palustris</i>	as in <i>O. palustris</i>	intermediate	as in <i>O. palustris</i>	as in <i>O. palustris</i>
<i>O. bauri</i>	shallow	as in <i>O. palustris</i>	short, intermediate in width	intermediate	as in <i>O. palustris</i>	large; numerous
<i>Nesoryzomys indefessus</i> and <i>N. narboroughi</i>	shallow	as in <i>M. curioi</i>	long, intermediate in width	intermediate	less distinct than in <i>M. curioi</i> , especially in posterior half	large; numerous
<i>Megalomys "pilorides"</i> (= <i>M. desmarestii</i>)	absent	basically as in <i>M. curioi</i> , but wider	long, intermediate in width	intermediate	extremely large; oriented mainly dorsally; not sharp	large; numerous
<i>M. desmarestii</i>	absent	wider than in <i>M. curioi</i> , with more gradual posterior expansion of frontals	as in <i>Megalomys "pilorides"</i>	intermediate	large; diagonally oriented; sharp	large; numerous
<i>M. luciae</i>	absent	as in <i>Megalomys desmarestii</i>	as in <i>Megalomys "pilorides"</i>	small	very large; oriented mainly diagonally; sharp	large; numerous
<i>Macruroryzomys hammondi</i>	shallow	as in <i>Megalomys desmarestii</i>	as in <i>Megalomys "pilorides"</i>	small	medium sized; diagonally oriented; sharp	large; numerous
<i>Nectomys saturatus</i>	absent	as in <i>Megalomys desmarestii</i>	intermediate in length and width	intermediate	medium sized; oriented diagonally; sharp	large; numerous
<i>Tylomys</i> species and <i>T. mirae</i>	very shallow	wider than in <i>M. curioi</i>	short, intermediate in width	intermediate	larger and more distinct than in <i>M. curioi</i> ; laterally oriented; sharp	very small; few
<i>Scapteromys tumidus</i>	absent	as in <i>M. curioi</i>	intermediate in length, narrow	intermediate	extremely small	very small; few
<i>S. chacoensis</i>	absent	as in <i>M. curioi</i>	as in <i>S. tumidus</i>	intermediate	extremely small	very small; few
<i>Kunsia tomentosus</i>	absent	as in <i>M. curioi</i>	short, narrow	intermediate	less distinct than in <i>M. curioi</i> in interorbital region only	small; few
<i>Phyllotis boliviensis</i>	shallow	as in <i>M. curioi</i>	short, wide	intermediate	less distinct overall than in <i>M. curioi</i>	small to large; few

is different from *Megaoryzomys* in that its zygomatic process of the squamosal joins the braincase at a more acute angle, its occipital condyles and foramen magnum are much smaller, and the masseteric crests on the dentary terminate more anteriorly (see Figure 10). Among cricetine rodents, *Megaoryzomys* differs in at least several important ways (Table 1) from other large oryzo-

myines (*Macruroryzomys*, *Nectomys*), as well as *Tylomys*, *Scapteromys*, *Kunsia*, and *Phyllotis*. The endemic oryzomyine rodents of Galápagos (*Oryzomys galapagoensis*, *O. bauri*, *Nesoryzomys indefessus*, *N. narboroughi*, *N. fernandinae*, *N. darwini*, and *N. swarthi*) also are very different from *Megaoryzomys* in several characters (Table 1) and may be ruled out as close relatives of the latter.

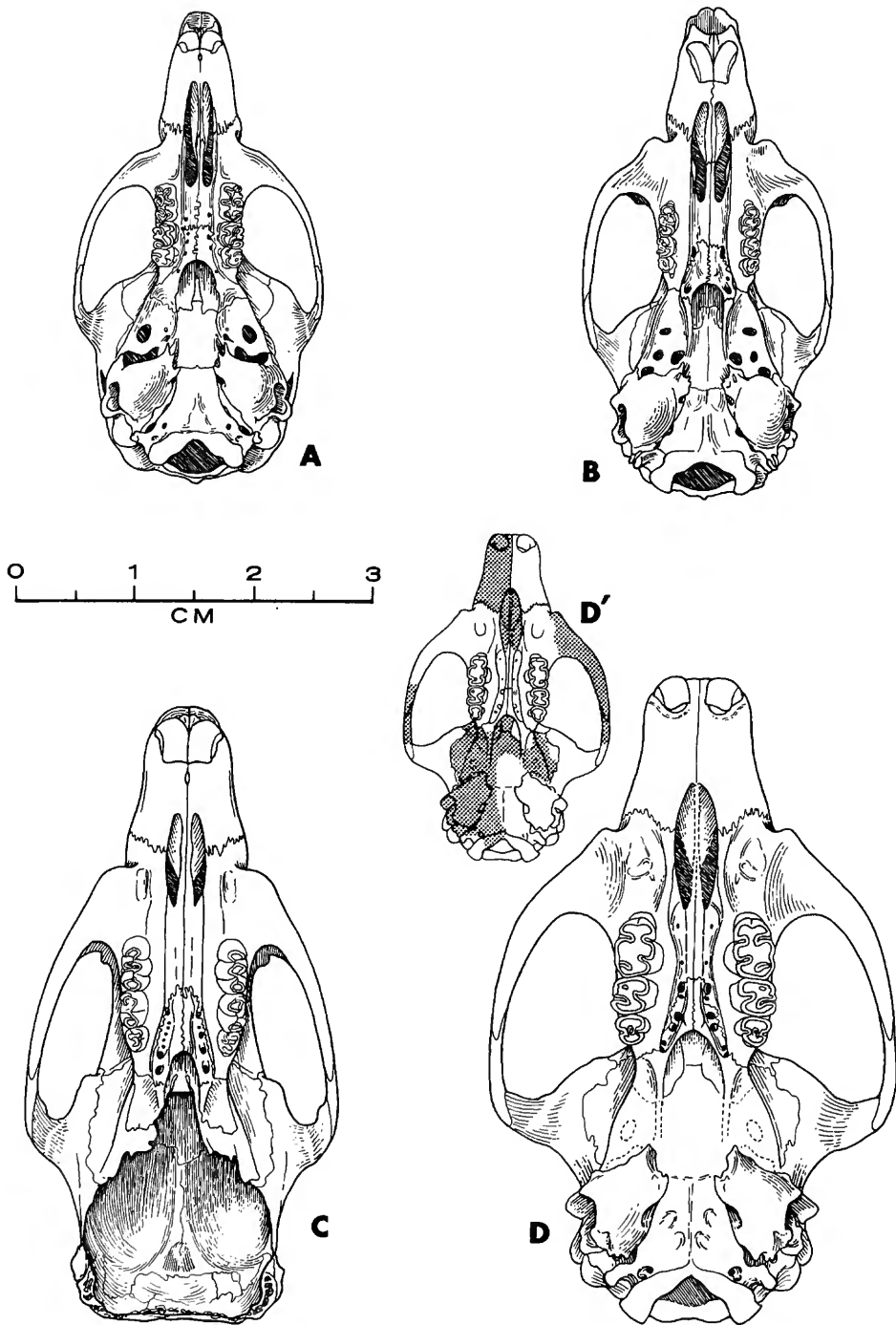


FIGURE 6.—Skulls in ventral aspect: A, *Thomasomys aureus*, female, USNM 194827; B, *Nesoryzomys swarthi*, male, CAS 2561, Isla Santiago; C, *Megalomys desmarestii*, Leiden Museum "a," Martinique; D, *Megaoryzomys curioi*, USNM 284318 (certain details of the palate are from USNM 284199); D', *Megaoryzomys curioi*, USNM 284318 (missing parts indicated by stippling, scale 1/2 that of Figures A–D).

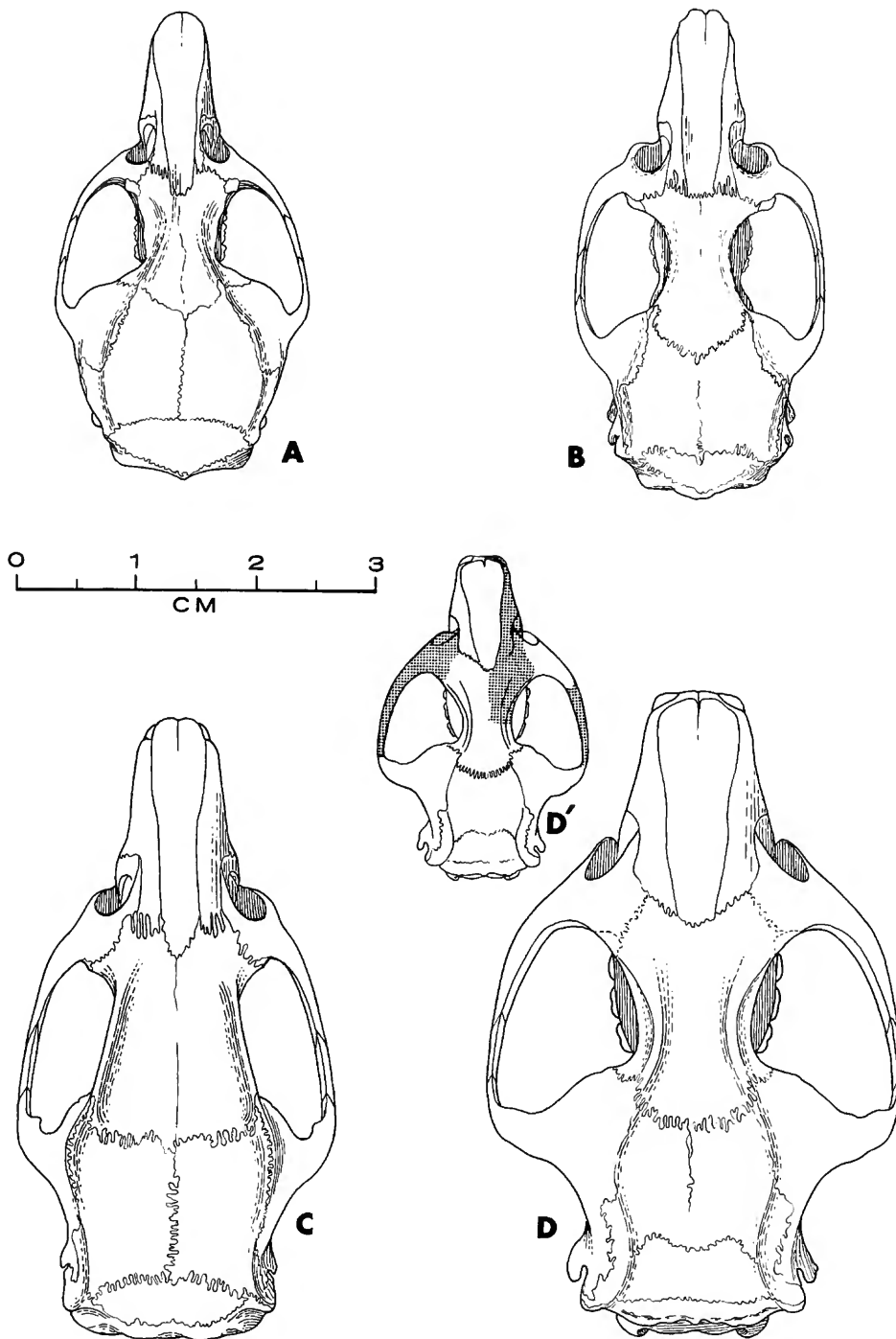


FIGURE 7.—Skulls in dorsal aspect: A, *Thomasomys aureus*, female, USNM 194827; B, *Nesoryzomys swarthi*, male, CAS 2561, Isla Santiago; C, *Megalomys desmarestii*, Leiden Museum "a," Martinique; D, *Megaoryzomys curioi*, USNM 284318; D', *Megaoryzomys curioi*, USNM 284318 (missing parts indicated by stippling, scale 1/2 that of Figures A-D).

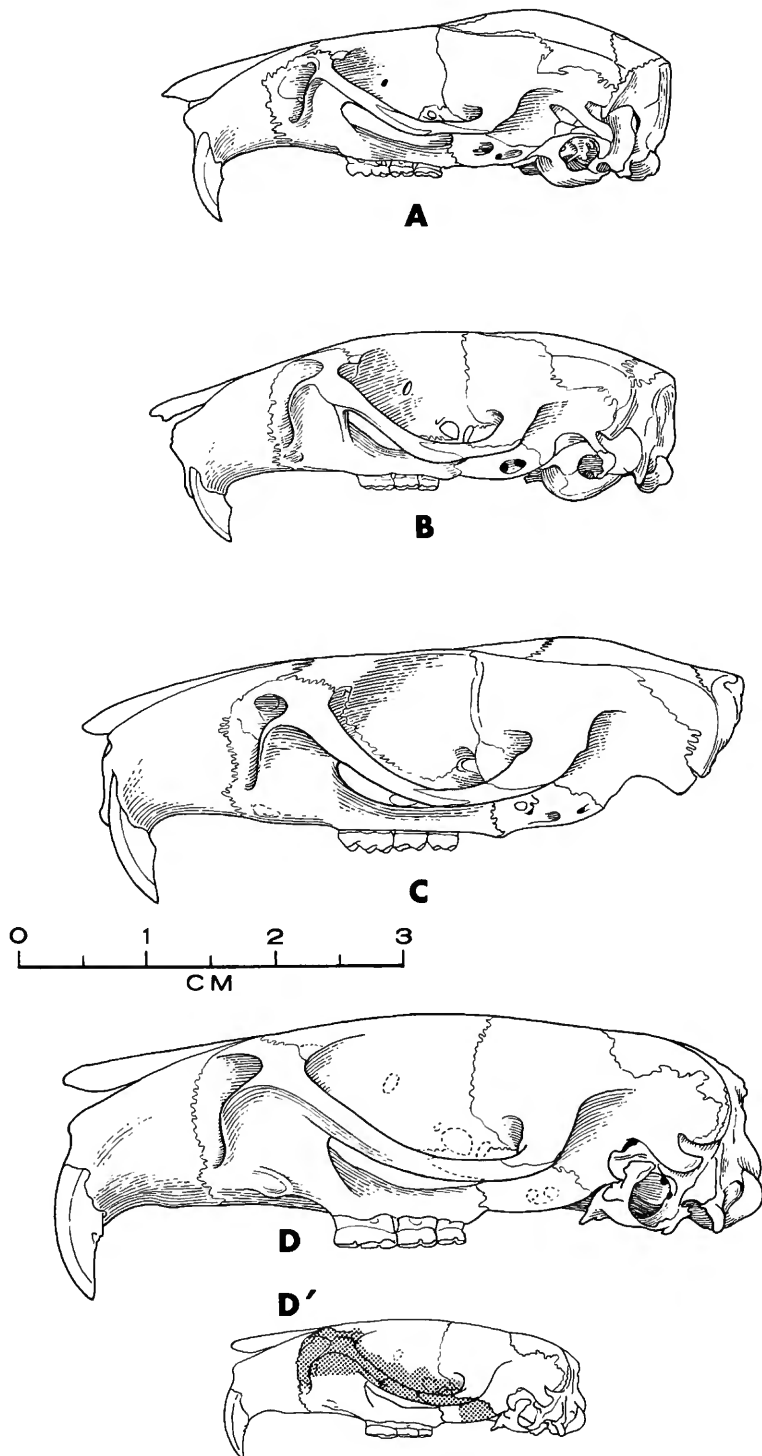


FIGURE 8.—Skulls in lateral aspect: A, *Thomasomys aureus*, female, USNM 194827; B, *Nesoryzomys swarthi*, male, CAS 2561, Isla Santiago; C, *Megalomys desmarestii*, Leiden Museum "a," Martinique; D, *Megaoryzomys curioi*, USNM 284318; D', *Megaoryzomys curioi*, USNM 284318 (missing parts indicated by stippling, scale 1/2 that of Figures A–D).

Certain species of *Thomasomys*, however, are very similar to *Megaoryzomys*. The three largest species of *Thomasomys* that we examined (*aureus*, *praetor*, and *princeps*) show a particularly strong resemblance to *Megaoryzomys*. (The skull of *T. aureus* is not aberrant within *Thomasomys*, although Hooper and Musser (1964) regarded the phallic characters of *T. aureus* to be unlike those of other *Thomasomys*.) In Table 1, *Megaoryzomys* consistently differs from these three species of *Thomasomys* only in the size and number of palatal foramina. The strongly constricted interorbital region, the short and narrow palate, and the large teeth are particularly diagnostic characters of large species of *Thomasomys* that are also shared with *Megaoryzomys*, leaving little doubt that *Megaoryzomys* is a member of the tribe Thomasomyini. Reig (1980:263) has advocated merging the thomasomyine and oryzomyine groups, but we follow the more widely accepted arrangement at least for the present, because of the closer relationship of *Thomasomys* and *Rhipidomys* (the only other genus of living thomasomyine) to each other than to any oryzomyine.

The skull of *Megaoryzomys* resembles that of the larger species of *Thomasomys* and differs from that of *Rhipidomys* in its deeper depression along the sagittal suture of the frontals, its strongly constricted interorbital region (except in *R. venezuelae*), its narrow palate (except in *R. venezuelae*), its larger teeth, and its more rounded, less laterally expanded dorsolateral ridge of the braincase (except in *R. venezuelae*). Meanwhile, we can find only two characters in which *Megaoryzomys* resembles *Rhipidomys* more than *Thomasomys*, namely their shorter, deeper rostrum and their more angular (less-domed) braincase. The truncated, deep rostrum of *Megaoryzomys* and *Rhipidomys* is closely approached, however, by an adult and an immature specimen of *Thomasomys praetor* (CMNH 19255, 19256). It is unfortunate that we do not as yet have a baculum of *Megaoryzomys*, as its morphology in neotropical cricetines appears to have taxonomic value at both the tribal and generic levels (Hooper and Musser, 1964). We feel that *Megaoryzomys* is different enough from other thomasomyines to maintain its status as a separate genus, although the name *Megaoryzomys* is an infelicitous choice for a member of the Thomasomyini.

Systematics

Order RODENTIA
 Superfamily MUROIDEA
 Family MURIDAE
 Subfamily CRICETINAE

Tribe THOMASOMYINI

OSTEOLOGICAL DIAGNOSIS.—Small to large cricetine rodents that differ from other tribes of Cricetinae in having the following unique combination of characters: (1) short palate, (2) molars pentalophodont (fide Hershkovitz, 1962, 1967), (3) molars medium-sized to large relative to size of skull.

Genus *Megaoryzomys* Lenglet and Coppois, 1979

Megaoryzomys Lenglet and Coppois, 1979.

TYPE-SPECIES.—*Megalomys curioi* Niethammer, 1964.

AMENDED DIAGNOSIS.—Large thomasomyine rodents that differ from *Thomasomys* and *Rhipidomys* in possessing the following unique combination of characters: (1) very large size (condylobasal length of skull more than 50 mm, zygomatic width more than 30 mm, crown length of upper molars more than 9 mm, length of dentary without incisor more than 30 mm, crown length of lower molars more than 10 mm), (2) deep depression along median suture of frontals (shared with certain species of *Thomasomys*), (3) palatal foramina large and numerous, (4) zygomatic plate of maxilla very wide, (5) zygomatic process of squamosal joining braincase at more obtuse angle, (6) braincase more rectangular (parietals flatter, less domed) in posterior aspect, (7) posterior margin of interparietal straight, (8) molars planar.

Megaoryzomys curioi (Niethammer, 1964)

FIGURES 3–11

Megalomys curioi Niethammer, 1964:596 [original description].

Megalomys spec. nov.—Abs et al., 1965:53.

Megaoryzomys curioi.—Lenglet and Coppois, 1979:635 [generic re-assignment].

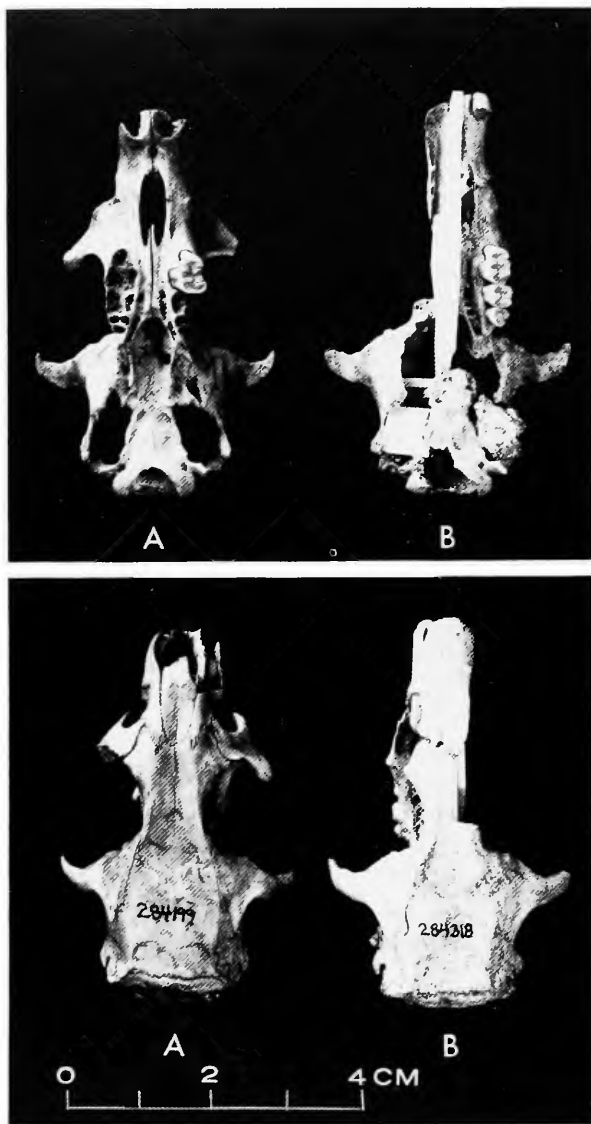


FIGURE 9.—Skulls of *Megaoryzomys curioi* from Isla Santa Cruz in dorsal and ventral aspects: A, USNM 284199; B, USNM 284318.

HOLOTYPE.—Left maxilla with M^{1-2} , BM(NH) 67.1649 (Modern Mammal Section).

PARATYPES.—A partial humerus and a partial scapula, collected with the holotype and bearing the same catalog number.

DISTRIBUTION.—Isla Santa Cruz, Galápagos, Ecuador. See Figure 2 for a map of localities.

AGE.—Quaternary. Probably both Pleistocene

and Holocene, but absolute age determinations are not available for sites containing *Megaoryzomys*.

DIAGNOSIS.—As for the genus.

Discussion

Zoogeography: Our removal of *Megaoryzomys* from the tribe Oryzomyini and its placement in the Thomasomyini necessitates a reassessment of its zoogeographic implications. By showing that *Megaoryzomys* is not closely related to *Megalomys*, a genus actually confined to the West Indies, *Megaoryzomys* can no longer be used as evidence for the supposed high degree of faunal resemblance between the terrestrial vertebrates of Galápagos and the West Indies, an idea championed by Niethammer (1964) and many other authors, nor can one refer any longer to “the present relict Caribbean and Pacific distribution of the [giant oryzomyine] group” (Hershkovitz, 1970:794). Thus the following statements of Müller (1973:114) are untenable because of reliance on erroneous systematic conclusions.

The genus *Megalomys* was previously known only . . . in the Antilles. . . . The range is therefore a relict range indicating a wider distribution in former times. The fact that the Galapagos form differs very little from those of the Antilles indicates that the Galapagos populations probably reached those islands during the Pleistocene.

Steadman (in press) has shown that proposed West Indian affinity for terrestrial organisms in Galápagos is illogical in light of the approximately synchronous emergence of the Galápagos and the Panamanian land bridge. Whereas the supposed occurrence of *Megalomys* in Galápagos is not supported on either a morphological or a zoogeographical basis, the relationship of *Megaoryzomys* to *Thomasomys* in fact fits perfectly into the biogeographical conclusions of Porter (1976), who refuted any supposed relationships between the floras of Galápagos and the West Indies and stated (p. 745): “The geographical evidence is overwhelming that the indigenous Galapagos flora has been derived almost totally from South America, most probably from the Andean region.”

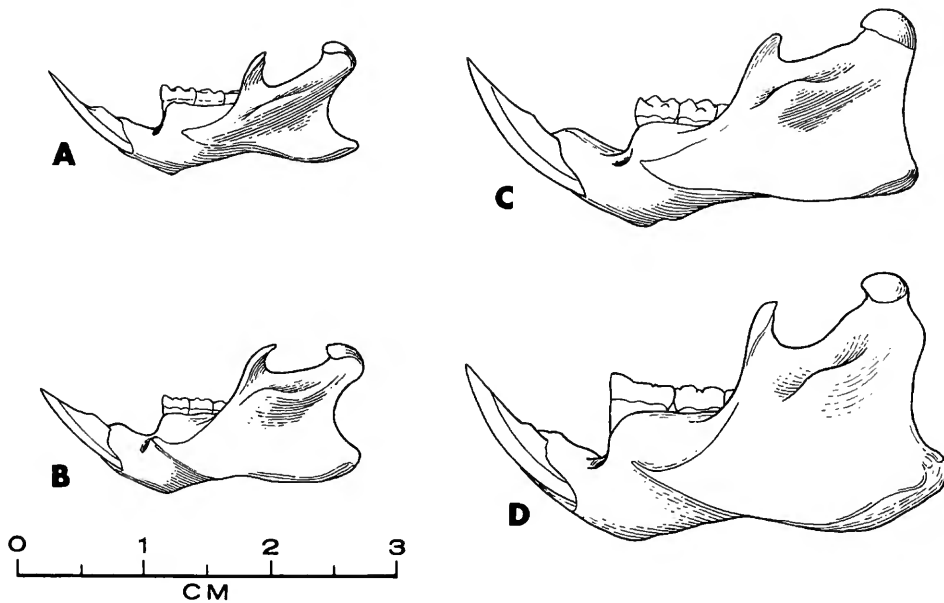


FIGURE 10.—Left dentaries in lateral aspect: A, *Thomasomys aureus*, female, USNM 194827; B, *Nesoryzomys swarthi*, male, CAS 2561, Isla Santiago; C, *Megalomys desmarestii*, Leiden Museum "a," Martinique; D, *Megaoryzomys curioi*, USNM 284290 (reversed).

Thomasomyine rodents are characterized by Hershkovitz (1972:386) as being

closely related to, but less diverse than, the oryzomyines. Some of its species are the most primitive of living myomorphs. The forms of *Thomasomys* are mainly terrestrial-scansorial. Others, especially those of the thomasomyine genus *Rhipidomys*, are specialized for arboreal life.

Within the Thomasomyini, *Megaoryzomys* has its closest living relatives in the larger species of *Thomasomys*, a genus of approximately 27 species confined to South America between 8°N and 35°S latitude (Patterson and Pascual, 1972), where they inhabit forests from approximately 1200 to 4000 m elevation. None of the living species of *Thomasomys* inhabits coastal areas; however, in proposing that a species of *Thomasomys* was the ancestor of *Megaoryzomys*, we must attempt to explain how such a species reached the Pacific coast of South America. No matter which of the competing scenarios for the biogeographic and geological history of northwestern South America proves to approach reality more closely (McKenna, 1981:63, 64), it would seem that a primitive thomasomyine must have been avail-

able at low elevation in the right place for early, possibly even pre-Pleistocene, colonization of Galápagos. It seems very unlikely that this was accomplished through rafting for long distances down a river from the highlands and then out to sea, such as would necessarily be the case if a species of *Thomasomys* were to colonize Galápagos today. Instead it seems more reasonable to suppose that a species of *Thomasomys*, very likely now extinct, did indeed live in the coastal lowlands of northwestern South America in the past and drifted out to Galápagos on a floating mat of vegetation. Orr (1966:280, fig. 4) figured and briefly discussed floating mats of vegetation in the Guayas River of southwestern Ecuador, and King (1962) recorded an abundance of similar rafts in the Rio Tortuguero, a sluggish stream of low gradient in Costa Rica. Mats such as these could easily support a small population of rodents for many days.

Evolution: Neither *Thomasomys* or *Rhipidomys* has a fossil record in mainland South America, so we do not know the range of morphological variation in Pleistocene thomasomyines, the probable ancestral group for *Megaoryzomys*.

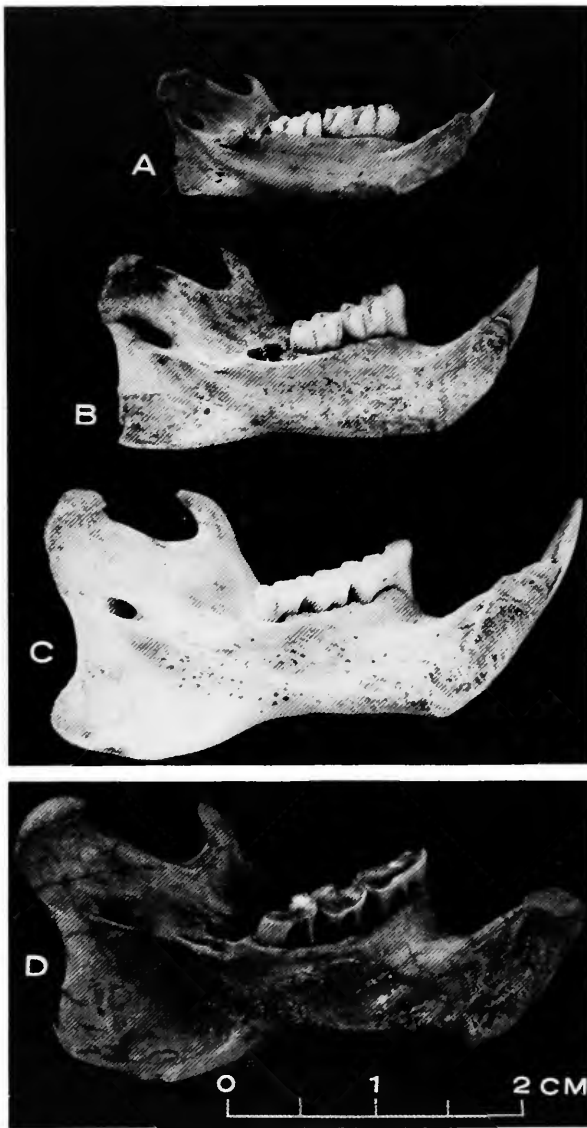


FIGURE 11.—Left dentaries of *Megaoryzomys curioi* in medial aspect: A, USNM 284207, Cueva de Kubler; B, USNM 284306, cave no. 1, place 2; C, USNM 284333, cave no. 5; D, USNM 284245, Cueva de Kubler.

Hooijer (1959, 1966) and Husson (1960) provided evidence that *Thomasomys* once occurred in the coastal lowlands of northern South America, where *Thomasomys* species is recorded in a Quaternary fossil site on the southern Caribbean island of Bonaire, near Venezuela. These specimens were more conservatively treated by Hooijer

(1967:400) as “very similar to *Thomasomys*, to which genus it may or may not belong.” The combined effects of Plio-Pleistocene uplift of the Andes and the probable altitudinal lowering of vegetational zones during glaciation (see Simpson 1975, 1979) give additional credibility to the suggestion that *Thomasomys* occurred at much lower elevations in the past than it does today. It may be noted in passing that the derivation of *Megaoryzomys* from *Thomasomys*, now restricted to higher elevations on the mainland, is analogous to the derivation of *Megalomys* from its close mainland relative, *Macruroryzomys*, now restricted to the Ecuadorean Andes (Ray, 1962; followed by Hershkovitz, 1970).

The large fossil vertebrate faunas of La Carolina, Ecuador, and Talara, Perú (Campbell, 1976, 1979, and references therein), provide evidence for the late Pleistocene existence of a more forested habitat than exists today at low elevations on the west coast of tropical South America. Certain birds at Talara are strong indicators of “at least a heavy scrub or riparian forest” (Campbell 1979:140), in an area that is extremely barren today with only widely scattered small shrubs (see figure 2 of Campbell, 1979).

The wetter, more forested conditions that existed during glacial times in coastal Perú and Ecuador are contrasted with apparent glacial aridity in Galápagos (Colinvaux 1972; Colinvaux and Schofield 1976a,b). The possible effects of these past arid conditions on the evolution and past altitudinal distribution of *Megaoryzomys* are difficult to state in our present lack of chronological control on its fossil sites. We do know that *Megaoryzomys* probably was widespread on Islas Santa Cruz and Isabela. Its known occurrences on Santa Cruz (Figure 2) range in elevation from near sea level to approximately 200 m, and the single record of *Megaoryzomys* from Isabela (Figure 1) is at approximately 300 m elevation. This rodent therefore lived in a variety of habitats ranging from arid coastal scrub to moist highland forest. Because of the very poor preservation of bones in caves on Santa Cruz and southern Isabela that are above 300 m elevation (Steadman, pers. observ.), we may never know the highest

altitudes inhabited by *Megaoryzomys*. The species of *Thomasomys* are strictly forest-dwellers, and so it may be that *Megaoryzomys* did not occur in the open areas of the highest regions of Santa Cruz and Isabela, where the vegetation is variously dominated by the shrub *Miconia* and a variety of ferns, grasses, and sedges (Wiggins and Porter, 1971).

Gigantism frequently occurs in rodents on islands, and most of the differences between *Megaoryzomys* and *Thomasomys* may be due to allometric changes associated with an increase in size. This possibility is in harmony with the closer resemblance of *Megaoryzomys* to the larger species of *Thomasomys* than to the smaller species. Insular gigantism in rodents is generally attributed to the following causes (Sondaar, 1977; Wassersug et al., 1979, and references therein): (1) predator avoidance, (2) drift toward larger size in the absence of predators because of no need to avoid them, (3) interspecific competition with other rodents, (4) selection for larger size in the absence of larger herbivores, regardless of the presence or absence of other rodents. Some combination of any of these reasons may have been involved in the attainment of large size in *Megaoryzomys*.

It is now apparent that Galápagos has been colonized successfully by cricetine rodents at least three different times, once by a thomomyine and twice by oryzomyines. The colonizations that produced the endemic genera *Megaoryzomys* and *Nesoryzomys* presumably occurred much earlier than that of *Oryzomys* (Patton and Hafner, in press). We agree with Patton and Hafner that *Nesoryzomys* is best maintained as a distinct genus, at least until its relationships to mainland cricetines are resolved. Certainly *Nesoryzomys* is not part of the same colonization that produced *Oryzomys bauri* and *O. galapagoensis*. Cabrera (1961) and Orr (1966) regarded *Nesoryzomys* as a subgenus of *Oryzomys*, although Orr (1966) correctly noted that these taxa are very different in the shape of their interorbital regions and in their development of supraorbital ridges (see plate xxiii of Heller, 1904). In addition, the karyotypic data of Gardner and Patton (1976:20) showed *Nesoryzomys* to be "so aberrant chromosomally as to

demand recognition as a full genus," whereas *Oryzomys bauri* was indistinguishable from *O. xanthaeolus* of coastal Perú. Gyldenstolpe (1932) and Patton and Hafner (in press) also noted that *O. bauri* and *O. galapagoensis* are allied to *O. xanthaeolus*. The marked similarity of *O. bauri* to *O. galapagoensis* led Cabrera (1961) and Patton and Hafner (in press) to recommend their synonymy.

Paleoecology: Niethammer (1964) indicated that both the Galápagos barn owl (*Tyto punctatissima*) and the short-eared owl (*Asio flammeus galapagoensis*) were responsible for the owl pellets associated with the three cotypes of *Megaoryzomys*. These pellets contained two species of bats and four species of small rodents, but Niethammer justifiably doubted that the remains of *Megaoryzomys* were also the remnants of owl pellets, because they represented an animal too large to be a prey item for either *Tyto* or *Asio*. Each of these owls preys heavily on rodents when available, although *Tyto* is much more prone to roost in caves than is *Asio*. Remains of *Megaoryzomys* also occur in caves that are not ancient roosting sites of *Tyto* but instead are either natural traps or simply places where *Megaoryzomys* died (Steadman, pers. observ.). Thus it may be that some of the fossils of *Megaoryzomys* in Cueva de Kubler were not prey items of *Tyto*. We believe that adults of *Megaoryzomys* could have been prey items of *Tyto punctatissima* only if they were killed and eaten within the roosting cave, whereas small, young individuals of *Megaoryzomys* apparently were preyed upon more frequently than adults and were not necessarily taken within a cave.

Extinction: The chronology of extinction of *Megaoryzomys* is very speculative. There are no absolute age determinations available as yet for any mammal-bearing fossil deposit in Galápagos, although this situation may be remedied soon by several radiocarbon samples (carbonized wood) from Cueva de Kubler that have been submitted for age determination. Both *Nesoryzomys indefessus* and *N. darwini* survived until 1935–1945 on Isla Santa Cruz (Eckhardt, 1972), although they are now presumed to be extinct through predation by introduced mammals or competition from the introduced black rat, *Rattus rattus* (Brosset, 1963;

Niethammer, 1964; Clark, 1981), which did not reach Santa Cruz until the 1930's or 1940's (Eckhardt, 1972; Patton et al., 1975). If *Rattus* or other introduced mammals had also recently caused the extinction of *Megaoryzomys*, it seems inexplicable that such a large rodent would have escaped the notice of sailors, explorers, residents, and scientific collectors who have combed Santa Cruz for the past 100 years. Thus it seems likely that *Megaoryzomys* became extinct before the other native rodents died out on Santa Cruz, even though we cannot yet assign an age to this event.

We have no evidence of contemporaneity of *Megaoryzomys* and *Rattus*. Niethammer (1964) noted that the bones of *Megaoryzomys* from the type-locality were not in the form of owl pellets as were those of *Rattus* and *Nesoryzomys*. In addition, these remains of *Megaoryzomys* gave Niethammer the impression of being older than those of the other rodents, as he stated (1964:605): "Presumably, the remains [of *Megaoryzomys*] were of a more remote origin than the recent pellets with which they might have been mixed by pure chance [our translation]." *Megaoryzomys* occurs in excavations IIB and IIC of Cueva de Kubler, where the sediments also contain bones of introduced *Rattus* and mice (*Mus musculus*), with much more numerous fossils of a large and small species of *Nesoryzomys* (probably *N. indefessus* and *N. darwini*, respectively). Although all five species of rodents may occur at the same stratigraphic levels in the unlaminated, loose cave sediments of Cueva de Kubler, the bones of *Rattus* and *Mus* are less mineralized, much lighter in color, and therefore apparently significantly younger than those of *Nesoryzomys* or *Megaoryzomys* (Steadman, 1981).

Bones of *Megaoryzomys* occur commonly on the surfaces of floors of lava tubes, small rock shelters, and ledges on the walls of fissures, suggesting to us that *Megaoryzomys* became extinct probably within the past several centuries. The possibility of the involvement of feral dogs, cats, and pigs in the extinction of *Megaoryzomys*, as stated by Niethammer (1964), is also suggestive of a recent extinction. Slevin (1959:7) listed dogs, cats, pigs, and burros as the introduced mammals of Santa

Cruz, exclusive of rodents. Eckhardt (1972) added goats and cattle to this list. Steadman has seen dogs, cats, rats, mice, goats, pigs, cattle, and burros on Santa Cruz from 1978 to 1981, with the first four species very common at least locally. Nearly all of these animals became established only after the initial period of human settlement on Santa Cruz, placed at early in the 20th century by Slevin (1959:108). It is not difficult to imagine how people and feral dogs, cats, rats, and pigs could devastate the population of a large rodent that evolved in the absence of mammalian predators and that, like the other vertebrates of Galápagos, would not have been wary when approached by an alien mammal.

Rattus has lived on Isla Isabela for a longer time than on Santa Cruz; the first definite record of any rodent on Isabela is that of a specimen of *Rattus* taken in 1891 by G. Baur (Allen, 1892). Charles Darwin did not mention the presence of *Rattus* or any other rodent on Isabela during his brief visit there in 1835 (Patton et al., 1975), although he noted *Oryzomys galapagoensis* on San Cristóbal and *Rattus* on Santiago. According to Slevin (1959:107) the first permanent human settlement of Isabela occurred in 1893 with the establishment of the villages of Villamil on the southern coast and Santo Tomás in the southern highlands. Thus 1893 is the last probable date for the establishment on Isabela of many of its feral mammals, which include dogs, cats, cattle, and burros (Slevin, 1959:7). It seems reasonable to suggest that *Megaoryzomys* species became extinct on Isabela within the past two centuries, unnoticed by man. As noted by Heller (1904), the fact that no species of *Nesoryzomys* has been recorded living on Isabela (members of this genus occur on Santa Cruz, Baltra, Santiago, and Fernandina) strongly suggests an early colonization of Isabela by *Rattus* and resultant extinction of *Nesoryzomys* prior to any thorough scientific surveys. This suggestion has recently been confirmed by Steadman's field work on Isabela in 1980, which produced remains of a small species of *Nesoryzomys* as well as additional material of *Megaoryzomys*. This material will be treated in detail in another paper.

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