AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2821, pp. 1–25, figs. 1–11, tables 1–4 August 5, 1985

Philippine Rats: A New Species of *Crateromys* from Dinagat Island

GUY G. MUSSER,[1] LAWRENCE R. HEANEY,[2] AND DIOSCORO S. RABOR[3]

ABSTRACT

Crateromys australis, new species, is described from one specimen collected on Dinagat, a small island north of Mindanao, Republic of the Philippines. The new rat is contrasted with the larger-bodied *C. schadenbergi,* which is endemic to Luzon, and the smaller *C. paulus,* the only native murid recorded from Ilin Island. A discussion of the three species is set against the native mammals of Dinagat and the native Philippine murids.

INTRODUCTION

The Philippine Archipelago is one of the island groups east of the Sunda Shelf in which the insular distributions of rats and mice are still poorly known, the morphological and ecological traits of the species are inadequately documented, and the phylogenetic relationships among them are confused. We provide new information about the morphological and insular diversity within one group of those rats, and about the overall species diversity of murids in the Archipelago by naming and describing a new species of *Crateromys* from Dinagat Island in the southern Philippines.

Crateromys is endemic to the Philippine Islands. For more than eighty years it was thought to be monotypic, consisting of the spectacular *C. schadenbergi* from the highlands of northern Luzon (Meyer, 1896; Taylor, 1934). In 1981, Musser and Gordon described *C. paulus* from Ilin Island, just south of Mindoro. Our results presented here document a third species. We describe it and discuss its relationship to the other *Crateromys* and to the mammals known from Dinagat Island. We also discuss the three species of *Crateromys* in a framework formed by the distribution of murid rodents native to the

[1] Archbold Curator, Department of Mammalogy, American Museum of Natural History, New York.
[2] Assistant Professor, Museum of Zoology and Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan.
[3] College of Forestry, University of the Philippines, College, Laguna 3720, Republic of the Philippines.

 ISSN 0003-0082 / Price $2.80

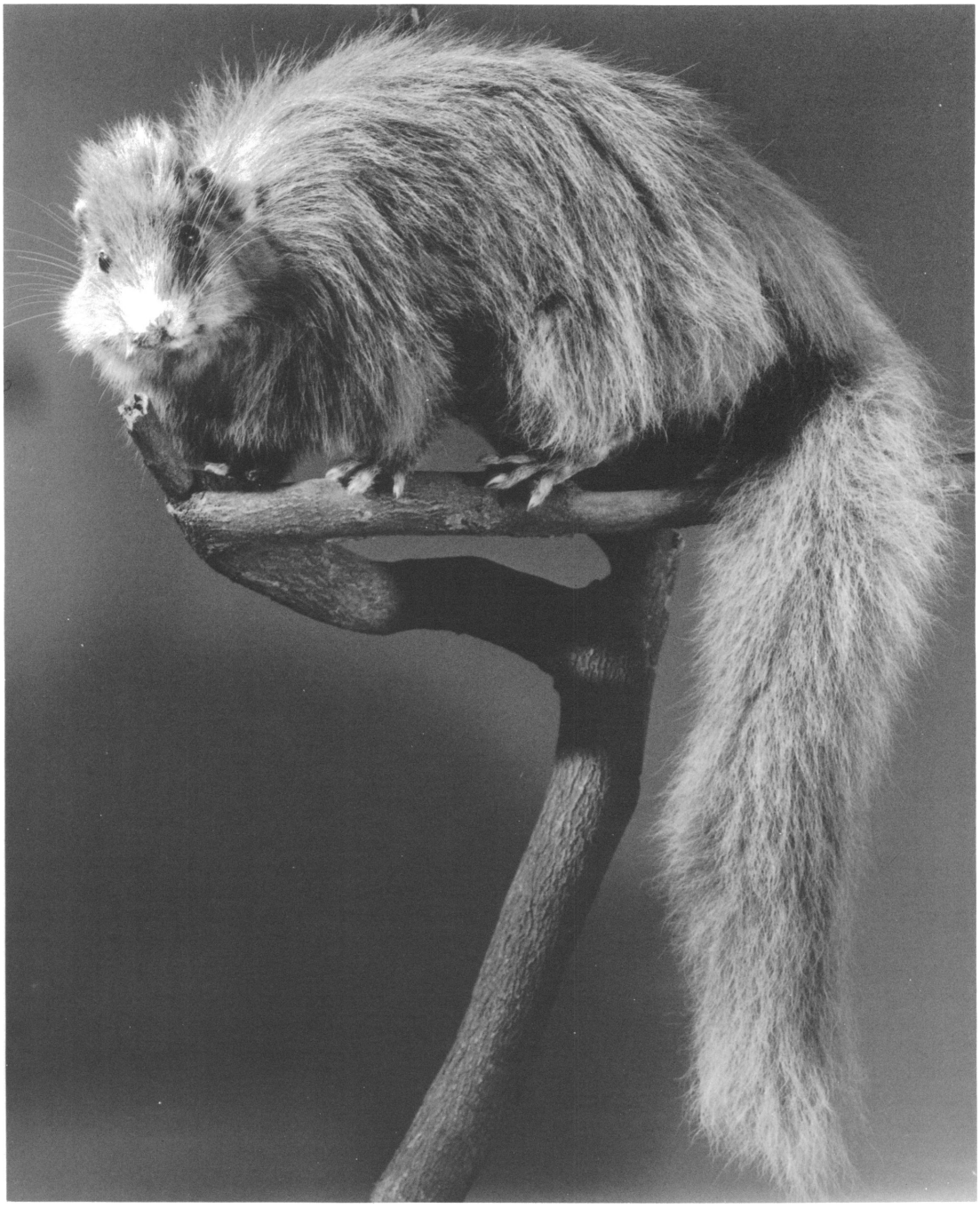

FIG. 1. *Crateromys schadenbergi.* Melanistic adult male (USNM 102546) from Mount Data on Luzon Island.

Philippine Islands. Among endemic Philippine murids, species of *Crateromys* are most similar to those of *Batomys* and *Carpomys* in morphologies of skins, skulls, and denti-

tions. The relationship among these genera will be the subject of a future paper (Musser and Heaney, MS).

Abbreviations and Methods

Specimens we studied and measured are in the Field Museum of Natural History, Chicago (FMNH); the University of Michigan Museum of Zoology, Ann Arbor (UMMZ); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

All measurements are in millimeters. Cranial measurements were taken with dial calipers graduated to 0.1 mm. See Musser and Gordon (1981) for definitions, and for an explanation about measurements of skins.

Acknowledgments

For this report we have relied upon specimens in museums; we thank curators in charge of those collections for allowing us to study and sometimes borrow material. The photographs are by Messrs. Jim Coxe, Peter Goldberg, and Frank M. Greenwell. The map was drawn by Patricia Wynne. We are especially grateful to those reviewers, both from the American Museum and at other institutions, who took the time to read our manuscript and provide critical evaluations of its contents.

The present report is No. 115 in Results of the Archbold Expeditions.

THE NEW *CRATEROMYS*

Naming and diagnosing the new species, as well as presenting its description and comparisons with other species of *Crateromys,* are the purposes of this section. Our samples of each species are small. *Crateromys paulus* is represented only by the holotype. Our sample of the Dinagat *Crateromys* also consists of one specimen. The Luzon *C. schadenbergi* is known to us by less than two dozen examples. Some of what we write here may have to be modified if more specimens of each species, especially *C. paulus* and the Dinagat animal, are ever obtained and become available for study. Some of the features that now set the new species apart from *C. paulus* and *C. schadenbergi* may not prove to be diagnostic in a larger series where the range of variation due to age, individual attributes, and secondary sexual features can be more reliably estimated for the population. However, the morphologies of the specimens in each insular sample are so distinctive that most diagnostic features we note here will likely prove to be characteristic of larger series. We are confident that the morphological contrasts we see are not associated with insular populations that are physically isolated and genetically compatible. Rather, they distinguish physically and genetically isolated populations, the definition of biological species in mammals. We express our confidence in this hypothesis by naming the Dinagat rat.

Crateromys australis, new species

Holotype: The holotype, UMMZ 161022, is an adult male obtained by Dr. D. S. Rabor and a field crew from Mindanao State University on May 16, 1975, from Balitbiton, Loreto Municipality, Dinagat Island, Surigao del Norte Province, Republic of the Philippines. The specimen consists of a stuffed study skin (fig. 4), cranium and mandible (figs. 5–7), and baculum. The holotype is the only example of the new species.

Measurements: See table 1.

Type Locality: Dinagat is a small (about 671 square km in area) and elongated island just off the tip of northeastern Mindanao (fig. 2). Dinagat, wrote duPont and Rabor (1973, p. 2), "is located at 10° north latitude and 125°45′ east longitude. It lies southeast of the southern end of Leyte Island and is north of Surigao del Norte Province on the northeastern projection of Mindanao Island. One of the smaller islands in the eastern Philippines, Dinagat lies on the Pacific Ocean side; together with Luzon, Polillo, Catanduanes, Samar, Mindanao, and Siargao, it forms a small part of the Eastern Rim of the Archipelago that directly borders the Philippine Deep." Rugged, mountainous topography characterizes Dinagat. The highest peak, Mount Redondo, is in the northern tip of the island and rises to about 3000 ft above sea level. For further descriptions of topography, as well as vegetation, read duPont and Rabor (1973) and look at the terrain diagrams in

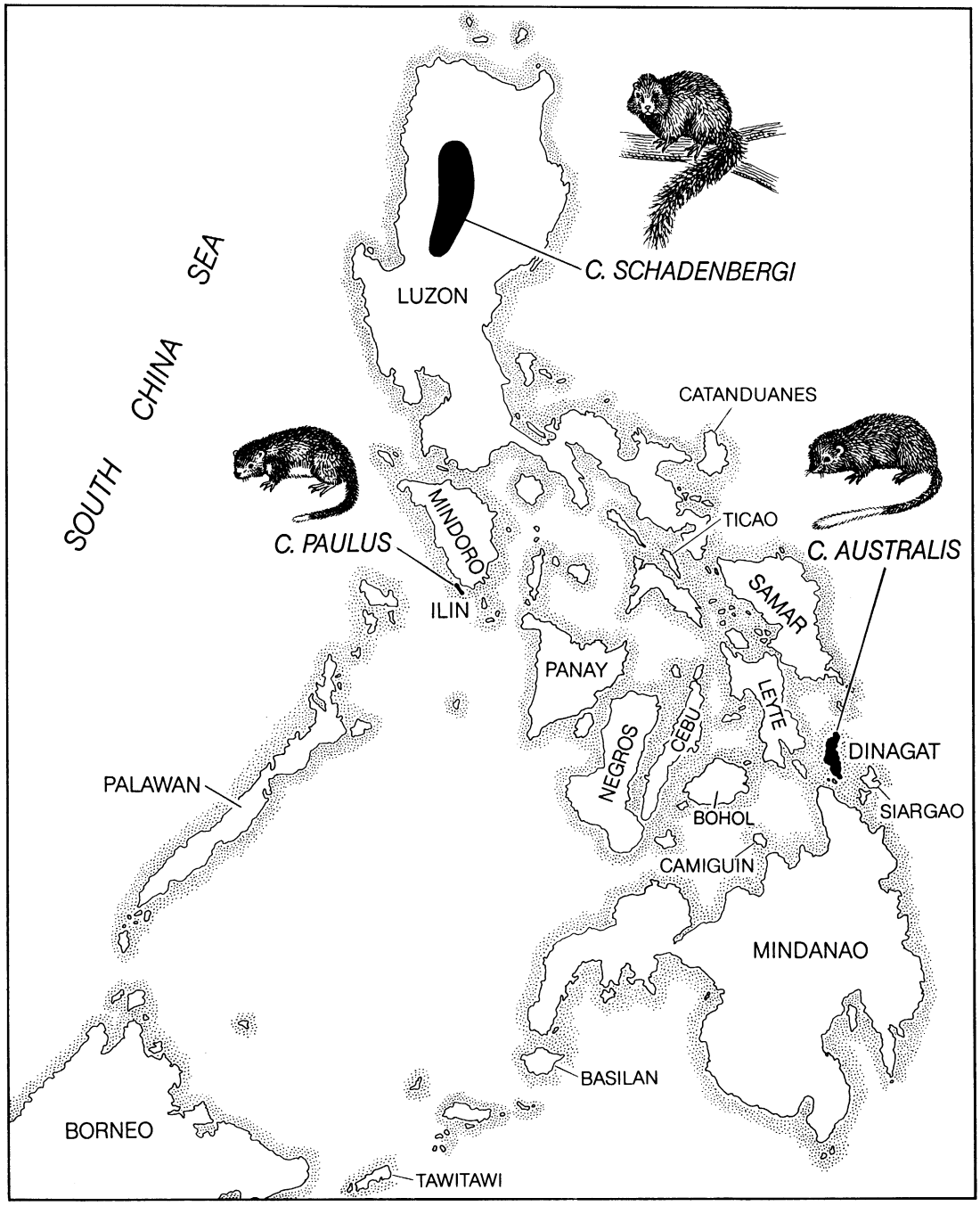

FIG. 2. The Philippine islands and the insular distribution of the known species of *Crateromys.*

King and McKee (1949). *Crateromys australis* is known only from Dinagat Island.

ETYMOLOGY: The Latin, *australis,* means southern and points to the presence of a species of *Crateromys* in the southern Philippine Islands, as contrasted with the north-

ern Philippines where two other species of *Crateromys* with different morphologies are found.

DIAGNOSIS: The following combination of characters distinguish *Crateromys australis* from either *C. schadenbergi, C. paulus,* or both (see also table 1 and figs. 1 and 3–9):

1. body size moderate;
2. tail slightly longer than combined length of head and body;
3. ears dark and moderate in size;
4. head without crest of fur;
5. dorsal pelage moderately long and slightly rough, ventral fur thin and short;
6. upperparts tawny spotted with black, underparts pale orange-brown, no apparent dorsal color pattern;
7. tail furry and tricolored, base colored like rump, proximal half of remainder of tail black, distal half white;
8. tail hairs short and stiff;
9. cranium, mandible, and molars of medium size;
10. temporal crests nearly straight, converging slightly posteriorly;
11. nasals broadest anteriorly and decreasing quickly in width posteriorly;
12. premaxillary suture on side of rostrum located at anterior margin of nasolacrimal capsule;
13. nasolacrimal capsule small relative to size of cranium;
14. squamosal roots of zygomatic arch situated high on sides of braincase;
15. interparietal wide relative to breadth of braincase;
16. incisive foramina long and wide relative to rostral breadth;
17. palatal bridge short, its posterior margin situated anterior to back edge of second upper molar;
18. width of palatal bridge greater than width of a first upper molar;
19. alisphenoid strut absent;
20. tympanic bulla small relative to cranial size, not inflated;
21. postglenoid vacuity large;
22. mental foramen moderately high on dentary;
23. anterolabial cusp (cusp t1) on each upper molar directed posteriorly, the lingual cusp just behind (cusp t4) straight on first and second molars, the posterolingual cusp (t7) of each molar moderately directed anteriorly;
24. anterolabial cusp (t3) present on each second and third upper molar;
25. front lamina of each first lower molar not connected to lamina behind it.

DESCRIPTION AND COMPARISONS: The large *Crateromys schadenbergi* and the smaller *C. paulus* are beautiful rats; *Crateromys australis* is equally handsome. It has a chunky body, long tricolored tail, and tawny and orange fur. Its overall body size is less than that of *C. schadenbergi* but greater than *C. paulus* (table 1). The upperparts are tawny peppered with black, and the fur is rough, not coarse and stiff as it is on *C. paulus* or very long, soft, and bushy, which are the qualities of *C. schadenbergi* (fig. 1). The coloration is uniform over upperparts of the body; there are no patterns as in *C. paulus* or some specimens of *C. schadenbergi* (Musser and Gordon, 1981; Meyer, 1896, pl. 14). Hairs forming the overfur are orange-brown either throughout their lengths or only near the tips and are 20–25 mm long on most regions of the body but only 10–15 mm long on the head. The top of the head is without a crest of fur; a crest is typical of *C. schadenbergi* (fig. 1). The uniform color of the head is broken up around the eyes, each of which is set within a narrow ring of darkly pigmented skin that is circled by a ring of skin with short and pale brown hairs. The underfur of the dorsum is 5–10 mm long, gray, and crinkled. Short, black guard hairs barely extend beyond the overhairs; they are most abundant in the middle of the back, decrease on the sides, and are absent from the base of the tail and sides of the head.

The ears are small and round. The skin is darkly pigmented. The top half of each ear is covered, inside and out, by short brown hairs, which form a sparse coat. The basal half lacks hair in front and is covered in back by short hairs similar to those of the dorsal body fur.

Underparts of the head and body are bright orange-brown. The color is uniform over the body except on the throat and upper chest, which are slightly paler. The ventral fur is

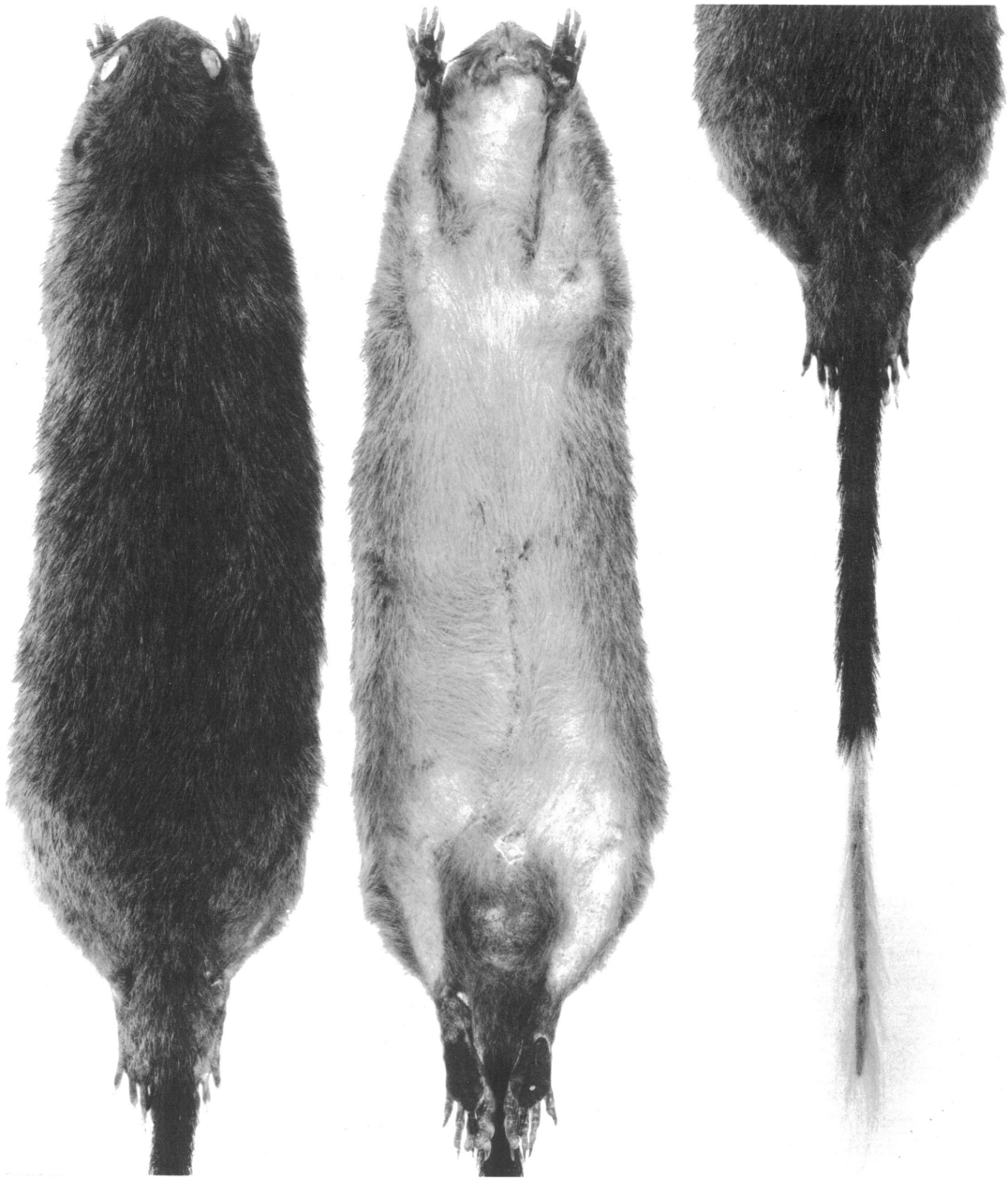

FIG. 3. Holotype of *Crateromys australis*. Adult male (UMMZ 161022) from Dinagat Island.

short (8–12 mm long) and appears closely appressed to the body. The scrotum is covered ventrally by a sparse coat of short (3 mm long), golden hairs.

Dorsal surfaces of the front and hind feet are covered with dark brown fur; ventral surfaces are naked. Palmar and plantar pads are dry and distorted in the study skin but resemble those in the other species of *Crateromys*: there are three interdigital and two palmar pads on each palmar surface, and four interdigital and two plantar pads adorning each plantar region. Fur over the front limbs is similar to that of the dorsal body surface,

FIG. 4. Holotype of *Crateromys paulus*. Adult male (USNM 522023) from Ilin Island.

TABLE 1
Measurements (in Millimeters) of *Crateromys*

Measurement	*C. schadenbergi*[a]	*C. australis*[b]	*C. paulus*[c]
Length of head and body	360.8 ± 20.1 (343–389), 4[d]	265	255[e]
Length of tail	405.7 ± 60.6 (363–475), 3	281	215
Length of hind foot	77.5 ± 3.9 (73–82), 4	54	50
Length of ear	25.3 ± 1.8 (23–28), 7	—	20
Greatest length of skull	68.5 ± 1.4 (66.6–71.4), 8	57.3	52.6
Zygomatic breadth	36.7 ± 1.5 (35.1–39.2), 7	31.0	29.4
Length of nasals	27.0 ± 0.9 (25.5–28.3), 8	24.5	21.2
Length of rostrum	20.6 ± 1.0 (19.1–21.7), 9	17.4	16.2
Breadth of rostrum	13.7 ± 0.5 (12.9–14.2), 9	11.4	12.0
Breadth of braincase	22.7 ± 1.9 (19.3–24.7), 9	20.3	17.2
Height of braincase	17.4 ± 0.5 (16.8–18.5), 9	15.1	14.2
Breadth of zygomatic plate	7.6 ± 0.8 (6.3–8.6), 9	5.9	5.3
Length of incisive foramina	12.1 ± 0.6 (11.3–13.2), 9	11.2	6.5
Length of diastema	18.3 ± 0.9 (17.0–20.1), 9	16.1	16.0
Palatal length	36.4 ± 0.6 (35.0–37.2), 9	28.5	29.1
Postpalatal length	26.5 ± 0.9 (25.8–28.3), 8	22.4	19.7
Incisive foramina to M^1	1.7 ± 0.7 (0.5–2.8), 9	0.9	4.7
Length of palatal bridge	15.4 ± 0.8 (14.4–16.5), 9	9.7	14.4
Palatal bridge to M^3	2.5 ± 0.6 (1.9–3.6), 9	3.4	1.7
Breadth of palatal bridge at M^1	3.2 ± 0.5 (2.4–4.0), 9	4.2	3.3
Breadth of palatal bridge at M^3	4.2 ± 0.5 (3.3–4.6), 9	4.6	3.7
Length of bulla	10.1 ± 1.1 (8.7–11.7), 9	6.4	7.9
Breadth across incisor tips	5.4 ± 0.4 (4.8–6.2), 8	4.4	4.2
Alveolar length of M^{1-3}	15.9 ± 0.8 (14.6–17.3), 9	12.0	11.4
Crown length of M^{1-3}	16.1 ± 0.9 (14.6–17.3), 9	12.1	11.8
Breadth of M^1	4.3 ± 0.3 (4.1–4.7), 9	3.6	3.2
Alveolar length of M_{1-3}	16.5 ± 0.8 (15.4–17.7), 9	13.3	12.3
Crown length of M_{1-3}	16.9 ± 0.9 (15.8–18.1), 9	13.2	11.9
Breadth of M_1	4.2 ± 0.3 (3.9–4.7), 9	3.2	3.1

[a] Sample consists of FMNH 62294–62296; USNM 102544–102546, 102554, 282646, 283149, and 290611.
[b] UMMZ 161022.
[c] USNM 522023.
[d] Mean, plus or minus two standard deviations, observed range in parentheses, and number of specimens.
[e] Taken from the stuffed skins, as explained by Musser and Gordon (1981).

but shorter. The brown of the hind feet, beginning at each ankle, grades gradually into hairs typical of the dorsal body coat. Claws on the front feet differ from those in the other species only in size, and that difference is proportional to body size. There is a tuft of pale brown hairs at the base of each front claw. The hallux is proportionately larger than that of *C. paulus,* and proportionately equal to (but absolutely shorter than) that of *C. schadenbergi.* A tuft of white hairs sits at the base of each claw on the hind digits.

The tail is slightly longer than the combined length of head and body (table 1), and tricolored. The base of the tail is covered for about 30 mm by tawny fur similar in color and texture to that clothing the upperparts of the body. The rest of the tail is covered by short (15–20 mm long) and bristly hairs; the basal half of this remainder is black, and the distal half white (fig. 3). Hairs at the tail tip are slightly softer and longer than elsewhere and form a tuft. Texture and color of the tail hairs are the same on both dorsal and ventral surfaces.

The distinctions in size and coloration between *C. australis* and the other two species of *Crateromys* are striking. *Crateromys australis* contrasts with *C. paulus* (figs. 3 and 4) by being larger; having tawny upperparts, orange-brown underparts, and no dorsal pattern rather than a dark, grizzled brown dor-

sum and creamy-gray venter, and a dorsal color pattern; pigmented, rather than unpigmented ears; longer tail, both absolutely and relative to length of head and body; and a tail with equal regions of black and white fur, rather than merely a white tip.

Compared with the large-bodied and bushy-tailed *C. schadenbergi* (fig. 1), *C. australis* differs in its smaller body size; absence of crest of fur on the head, as opposed to a distinct crest; rough, moderately long fur, rather than a soft, long, bushy coat; tawny dorsum and orange-brown venter, rather than a black, gray, or mottled coat in which the color is uniform over the head and body in some specimens, or the gray and black form patterns of either a white cape across the shoulders or crescents behind the shoulders in other individuals (see color plate 14 in Meyer, 1896); and tail that is tricolored and covered by short and stiff fur, rather than monocolored and covered by long and soft hairs that provide the bushy-tailed appearance.

The cranium of *Crateromys australis* is illustrated in figures 5 and 6. It is large and chunky with a moderately long rostrum, a narrow interorbital region unmarked by dorsolateral ridges or beading, a squarish braincase modestly adorned with indistinct temporal ridges, a small interparietal, a slight zygomatic notch, flaring zygomatic arches that are squarish in dorsal or ventral outline, a bony palate ending anterior to the back margins of the third molars, and small bullae relative to cranial size. The cranium of *C. australis* resembles those of *C. schadenbergi* and *C. paulus* in general configuration.

There are significant distinctions among the three species. Size is the most obvious. The cranium of *C. australis* is smaller than that of *C. schadenbergi* in nearly all dimensions, and larger than the cranium of *C. paulus* in many dimensions (table 1).

Other differences are apparent when the regions of the rostrum, interorbit, and braincase of each species are contrasted. In *C. paulus* and most specimens of *C. schadenbergi,* the posterior margin of the nasals lies only a short distance behind the dorsal premaxillary-frontal suture, about at the level of the anterior margins of the orbits. In *C. australis,* the nasals extend well beyond the premaxillaries, to a spot slightly behind the front margins of the orbits. In addition, the nasals of *C. australis* are broadest at their anterior margin and decrease evenly in width to the posterior tips; nasals of the other two species are much wider throughout their posterior two-thirds relative to the anterior third. The region of each frontal-premaxillary suture on either side of the nasals is nearly flat or slightly convex in *C. schadenbergi* and *C. australis.* In *C. paulus,* there are prominent swellings under the areas of these sutures, and a trough over the nasals separating the swellings. The shape of the nearly smooth braincase with its squarish outline and sloping sides is similar among the species. In *C. schadenbergi* and *C. paulus,* the temporal ridges are shaped like an hourglass with the waist located at the level of the anterior edge of the interparietal; the temporal ridges on the cranium of *C. australis* are nearly straight, with only a slight waist at a more posterior spot than on the other species, and only a slight outward flaring where the temporal ridges meet the occipital crest. Finally, *C. australis* has a wider interparietal than is typical of the other species. The difference is expressed by the posterior margin of the interparietal, which extends nearly all the way across from one squamosal-parietal suture to the other; the distinction is clearly seen in figure 5.

As viewed from the side, the cranium of *C. australis* is similar to those of the other species (fig. 6). Especially evident are the small bullae relative to braincase size, the robust zygomatic arches, the great height of the cranium from the molar rows to the top of the interorbital area (which helps give the cranium its chunky aspect), the hypsodont molars, and the zygomatic plate in which the anterior margin is either straight or gently concave and barely extends forward of the dorsal maxillary root of the zygomatic arch (a configuration responsible for the slight zygomatic notch, seen best from dorsal perspective).

Differences other than size are conspicuous among the three species in lateral view. In *C. schadenbergi,* the premaxillary-maxillary suture on the side of the rostrum lies on top of the nasolacrimal capsule; the comparable suture in *C. australis* lies at the anterior margin of the capsule, and in front of the capsule in

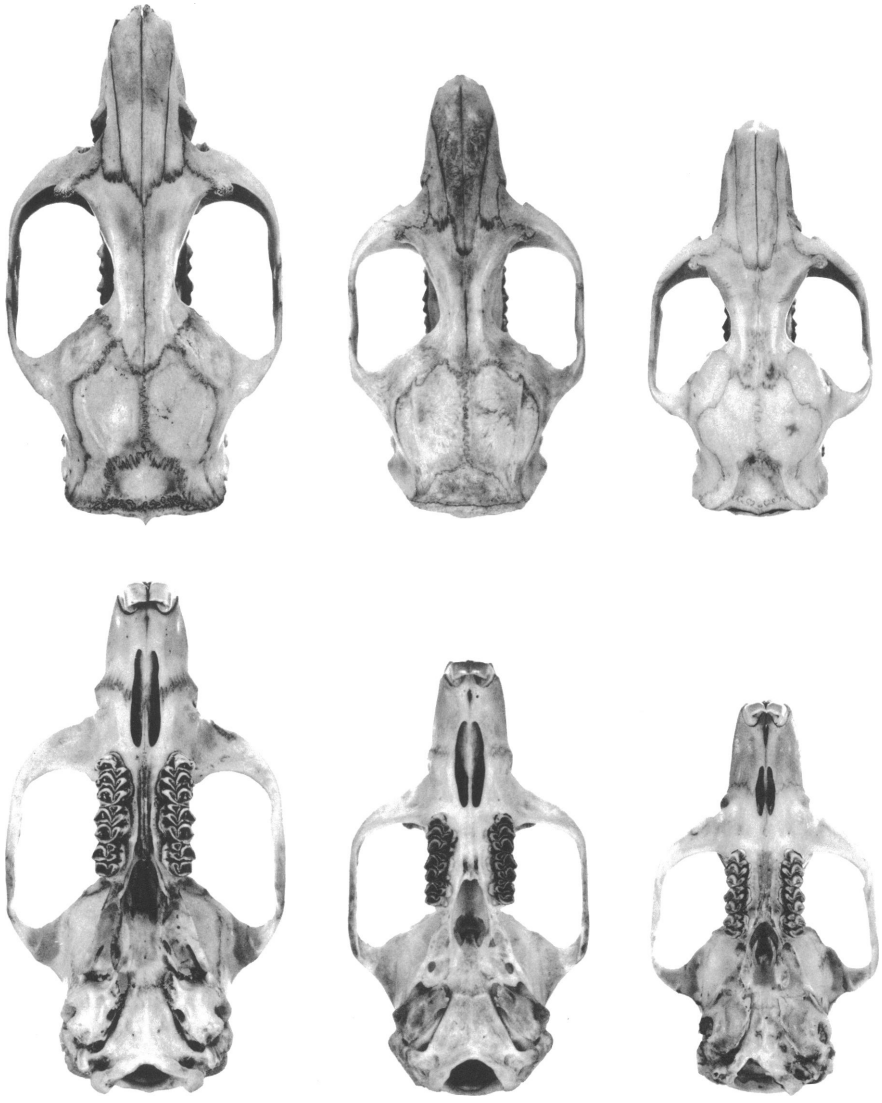

FIG. 5. Crania of adult *Crateromys*. Left, *C. schadenbergi* (USNM 102546); middle, *C. australis* (UMMZ 161022, holotype); right, *C. paulus* (USNM 522023, holotype). Natural size.

C. paulus—relationships that can be seen clearly in figure 6. The nasolacrimal capsule forms a prominent bulge on each side of the rostrum in *C. schadenbergi* and *C. paulus*; the capsules are smaller and not as swollen, but still conspicuous, in *C. australis*. Dorsal to each nasolacrimal capsule, the muscle scar of the anterior part of the medial masseter extends slightly anterior to the premaxillary-maxillary suture where it forms a deep depression on the side of the rostrum in *C. schadenbergi*. The muscle scar extends slightly farther forward but forms only a shallow depression in *C. australis*. The origin of the medial masseter ends at the premaxillary-maxillary suture and is barely evident in *C. paulus*. Finally, the squamosal roots of the zygomatic arches are situated high on the sides of the braincase in *C. australis* and *C. schadenbergi* but much lower in *C. paulus*.

Also seen in lateral view are differences among the three species in configurations of

FIG. 6. *Crateromys.* Views of same crania as shown in figure 5. Top, *C. schadenbergi*; middle, *C. australis*; bottom, *C. paulus.* Natural size.

the alisphenoid region of the braincase (fig. 7). In *C. paulus,* there is a large elliptical opening dorsal to the pterygoid ridge. This is not "the combined foramen ovale and entrance of the alisphenoid canal into the sphenoidal fissure," as Musser and Gordon (1981, p. 520) described it, but the foramen ovale. The anterior opening of the alisphenoid canal is not visible. A lateral strut of the alisphenoid is lacking and the masticatory-buccinator and accessory foramen ovale are joined as a single, broad aperture lateral to the foramen ovale. In most crania of *C. schadenbergi,* there is a strut of alisphenoid bone lateral to the large foramen ovale. With the strut present, there is a coalesced masticatory-buccinator foramen anterior to the strut and an accessory foramen ovale posterior to the strut. The area of the alisphenoid bone anterior to the foramen ovale may be complete, as it is in *C. paulus,* or it may be perforated by one or several small or large openings representing bone erosion on the side of the alisphenoid canal. In *C. australis,* the alisphenoid strut is absent and the configuration of the alisphenoid region resembles that of *C. paulus* except for one feature: there is a large opening in the alisphenoid bone anterior to the foramen ovale. This is a hole on the side of the alisphenoid canal, which is situated medial to the alisphenoid bone, and not the anterior opening of the alisphenoid canal, as such an opening would be in other genera of murid rodents (see Musser and Newcomb, 1983, for example). This pattern of strut and foramina in the alisphenoid region of *Crateromys* and the carotid circulation it reflects will be presented in detail elsewhere (Musser and Heaney, MS).

The relative size of the postglenoid foramen, also a feature in the squamosal region best observed from lateral perspective, differs among the three species (fig. 7). The foramen is large in *C. schadenbergi* but much smaller in *C. australis* and *C. paulus,* both absolutely and also relative to size of braincase.

Several distinctions among *C. schadenbergi, C. australis,* and *C. paulus* are evident when the crania are examined from a ventral perspective (figs. 5 and 8). The overall contrast in size is again apparent. A most conspicuous difference is length of the incisive foramina. In *C. schadenbergi* and *C. paulus,* the foramina are long and occupy most of the rostrum between the incisors and anterior margins of the molar rows. In *C. paulus,* the incisive foramina are short, penetrating only about the middle third of the rostrum.

The width of the palatal bridge, the position of its posterior margin, and depth of the palatal grooves differ among the three species. The palatal bridge of *C. schadenbergi* is narrower than the width of a first upper molar. In contrast, the bridge of *C. paulus* at its narrowest point (between the second molars) is about equal to the width of a first upper molar, and the palate of *C. australis* is wider than a first upper molar. Considering cranial size, the palatal bridge of *C. schadenbergi* is clearly much narrower than that of either *C. paulus* or *C. australis.* The bridge of *C. schadenbergi* is longitudinally scored by very deep palatal grooves; the grooves are shallow and inconspicuous in *C. australis* and *C. paulus.* The posterior margin of the palatal bridge is deeply notched in all three species. The anterior margin of this notch (which forms the posterior margin of the palate) is

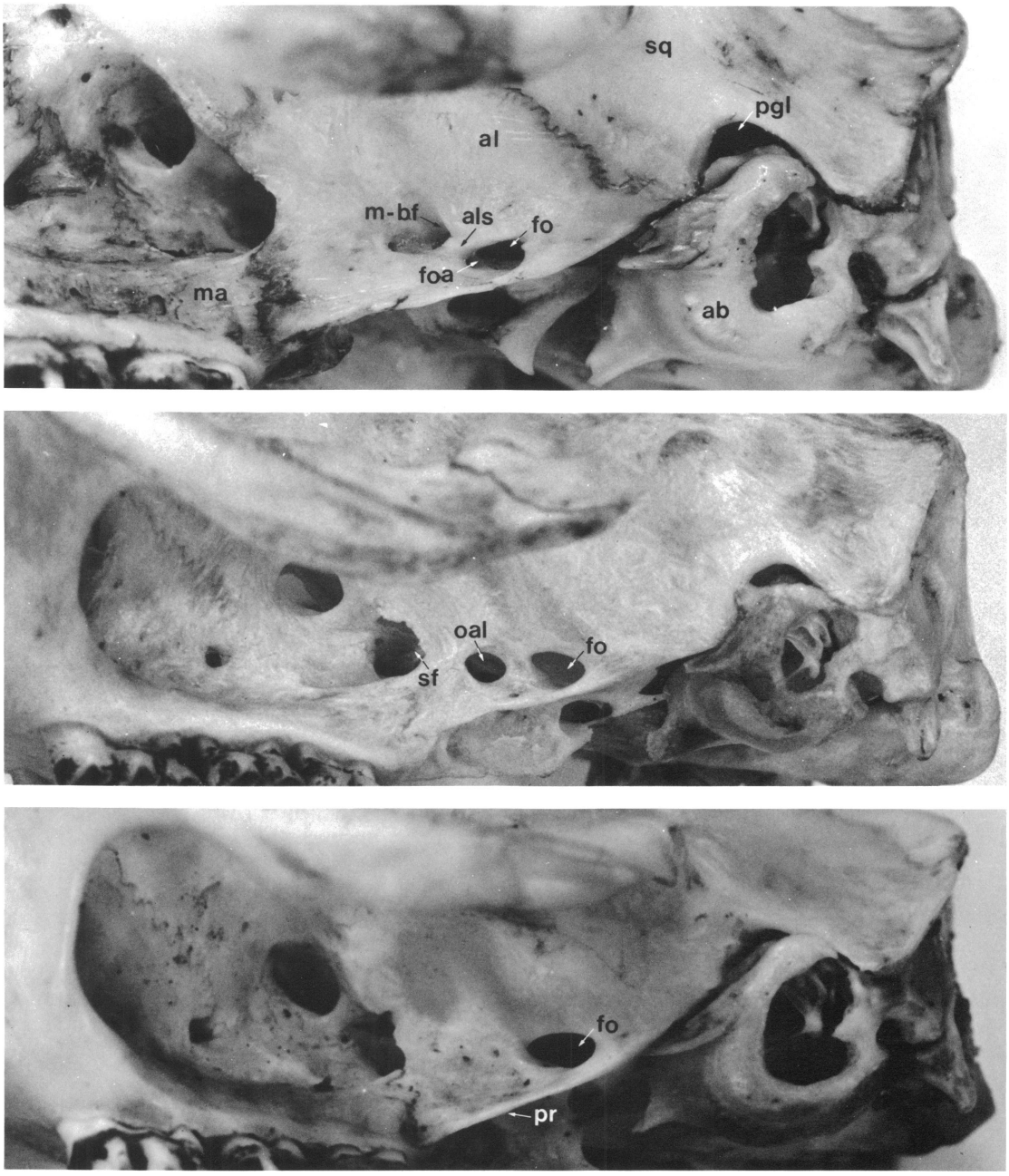

FIG. 7. *Crateromys.* Posterolateral views of same crania depicted in figures 5 and 6 focusing on alisphenoid and squamosal regions. Top, *C. schadenbergi*; middle, *C. australis*; bottom, *C. paulus.* Abbreviations: **ab**, auditory bulla; **al**, alisphenoid bone; **als**, lateral strut of alisphenoid bone; **fo**, foramen ovale; **foa**, accessory foramen ovale; **m-bf**, masticatory-buccinator foramen; **ma**, maxillary bone; **oal**, opening on side of alisphenoid canal (it is not the anterior opening of the alisphenoid canal); **pgl**, postglenoid foramen; **pr**, pterygoid ridge; **sf**, sphenoidal fissure (Wahlert, 1983, calls this the anterior alar fissure); **sq**, squamosal bone.

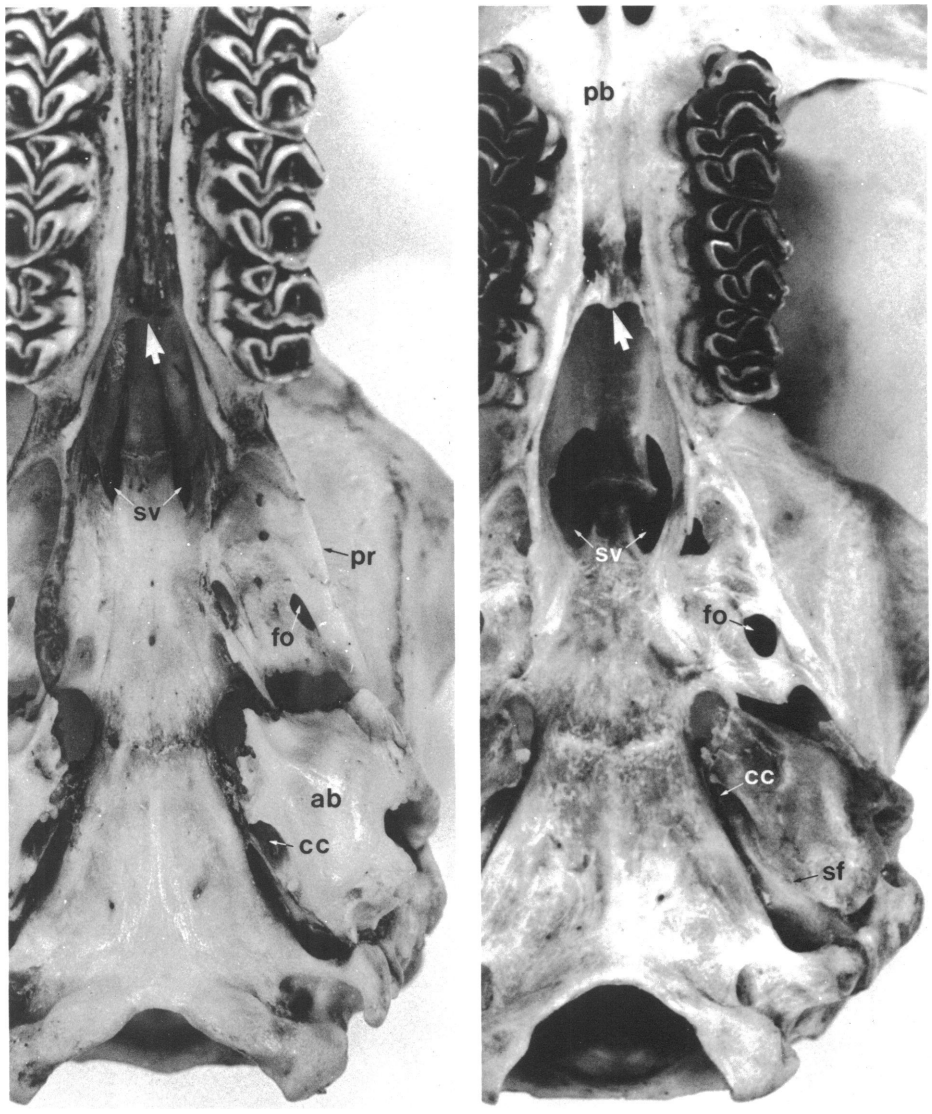

FIG. 8. *Crateromys.* Ventral views of same crania shown in figure 7. Left, *C. schadenbergi*; right, *C. australis.* Large white arrow points to posterior margin of bony palate (palatal bridge); note its position in relation to the third molars. Abbreviations: **ab**, auditory bulla; **cc**, carotid canal; **fo**, foramen ovale; **pb**, palatal bridge; **pr**, pterygoid ridge; **sf**, stapedial foramen (which is tiny and barely evident); **sv**, sphenopalatine vacuities.

located about even with the middle of the third upper molars in *C. schadenbergi* and *C. paulus* but is situated farther forward in *C. australis,* at a point just in front of the back edge of the second molars (fig. 8). Both absolutely and relative to cranial length, *C. australis* has the shortest palatal bridge and *C. paulus* the longest (the length of palatal bridge as compared to skull length is 22% in *C. schadenbergi,* 17% in *C. australis,* and 27% in *C. paulus*).

Many of the features associated with the

posterior half of the ventral cranium are shared by *C. australis* and the other two species (figs. 5 and 8). For example, the sphenopalatine vacuities are small. The stapedial foramina are minute; they and the configuration of the pterygoid plates and alisphenoid regions reflect a carotid circulation in which the internal maxillary artery branches from the internal carotid instead of the stapedial, a pattern common to species of *Crateromys, Carpomys,* and most *Batomys* (Musser and Heaney, MS).

The tympanic bullae are also similar in general aspect but differ in size and degree of inflation (fig. 5). The bullae of *C. australis* are the smallest of the three species, both absolutely (table 1) and proportionally (the length of bulla as compared to skull length is 14% for *C. schadenbergi,* 10% for *C. australis,* and 15% for *C. paulus*). The bullae of *C. australis* are not inflated and resemble those of *C. schadenbergi* in shape; in contrast, *C. paulus* has relatively inflated, globular tympanic bullae.

In their general aspect, the dentaries of *Crateromys australis* resemble those of the other two species (fig. 9); however, there are differences. Dentaries of *C. australis* are smaller than those of *C. schadenbergi* and larger than those of *C. paulus.* In *C. australis,* the coronoid process is gracile relative to the body of the dentary compared with the relatively more robust processes in the other two species. The posterior margin of each dentary is shallowly concave between condylar and angular processes in *C. australis* but deeply concave in *C. schadenbergi* and *C. paulus.* Finally, the mental foramen of *C. schadenbergi* is located at the apex of the superior and inferior masseteric ridges; in *C. australis,* the foramen is slightly above the apex, and in *C. paulus* it is still higher, just below the dorsal margin of the dentary.

Although molars of *C. australis* are actually much smaller than those of *C. schadenbergi* and slightly larger than molars in *C. paulus* (table 1), lengths of molar rows relative to cranial size are similar among the species (the crown length of molar row compared to skull length is 23% in *C. schadenbergi,* 21% in *C. australis,* and 22% in *C. paulus*). The three species also share a similar degree of hypsodonty, relative sizes of each molar within a row, number of roots anchoring each tooth, and the general pattern of occlusal surfaces (Musser and Gordon, 1981). *Crateromys schadenbergi* and *C. paulus* resemble one another closely in occlusal pattern. Other than size, the only differences, according to Musser and Gordon (1981, pp. 522–523), are:

> the labial cusp of the second lamina on each M^1 and the first lamina of each M^2 (cusp t6 on both teeth) is more discrete in *C. paulus* than *C. schadenbergi* and separated by a wide cleft from the adjacent medial cusp, whereas the two cusps are broadly merged in *C. schadenbergi*; the last row of cusps on M^3 is a broad, thick, and nearly transverse lamina in *C. paulus,* but bicuspid in *C. schadenbergi*; and the lamina at the back of M_3 in *C. paulus* has a nearly complete posterior outline with the lamina being oblong and nearly transverse, whereas the back of the lamina on each M_3 in *C. schadenbergi* is scalloped and the entire lamina ia shaped like a chevron.

Compared with the few distinctions that contrast *C. schadenbergi* and *C. paulus,* there are conspicuous differences in aspects of occlusal patterns in upper molars between *C. australis* and the other two species of *Crateromys* (fig. 10). First, the cusp at the anterolingual margin of each tooth (cusp t1) is directed strongly backwards in *C. australis,* which contrasts with the jutting anterior orientation characterizing each cusp on the first and second molars of *C. schadenbergi* and *C. paulus,* and the horizontal position of cusp t1 on each third molar of those latter two species. Second, the lingual cusp of the second lamina (cusp t4) on each first and second molar is horizontal or nearly so, again unlike the anterior projecting cusp t4 in the other species. Third, the lingual cusp of the third lamina (cusp t7) on each first and second molar does jut forward in *C. australis,* but not to the same degree as cusp t7 does in *C. schadenbergi* and *C. paulus.* Finally, there is a small but distinct cusp on the anterolabial margin (cusp t3) of each second and third molar of *C. australis*; comparable cusps are not present on the teeth of either *C. schadenbergi* or *C. paulus.*

There are differences among specimens of the three species in occlusal patterns of the lower molars, but one distinction reflects relative age: molars of *C. australis* are worn slightly more than those of *C. paulus* or most specimens of *C. schadenbergi* we have seen

FIG. 9. *Crateromys.* Views of right dentaries from same specimens illustrated in figures 5 and 6. Top, *C. schadenbergi*; middle, *C. australis*; bottom, *C. paulus.* Arrows point to mental foramina. The dentary of *C. australis* is slightly smaller than natural size; the others are about natural size.

and so the cusp surfaces appear more expansive in area, which can be seen in figure 11. The only difference not associated with age that we detected was the occlusal configuration formed by the first and second laminae of the first molars. In two of the species, there is a moderately wide (*C. schadenbergi*) or narrow (*C. paulus*) enamel and dentine bridge connecting the first and second laminae at their middles; such a structure is not present in the holotype of *C. australis* (fig. 11).

NATURAL HISTORY: Dr. Rabor remembers that the Dinagat *Crateromys* was shot from a tree; he can provide no other information about its habits or habitat. That *C. australis* is arboreal is indicated by its long tail relative to length of head and body and its short, broad feet with well developed tubercles. Arboreality is common also to *C. schadenbergi* (Musser and Gordon, 1981). Nothing is known of the habits or habitat of *C. paulus.*

CRATEROMYS AUSTRALIS AND THE PHILIPPINE MAMMALS

To provide a name, diagnosis, and description for the new species of *Crateromys* is to identify only part of its characteristics. The species is also defined by answering three other questions: What is its relationship to the other mammals native to Dinagat Island? What is the significance of its insular distribution relative to the other species of murid rodents that are native to the Philippine Islands? What are the phylogenetic relationships among *C. australis* and the other two species of *Crateromys*? We explore these aspects of *Crateromys australis* in the following discussion.

Crateromys australis and the Dinagat Mammals

Twenty-eight species of wild mammals are represented by specimens from Dinagat Island (Heaney and Rabor, 1982; table 2). Two of these, *Rattus exulans* and *R. rattus mindanensis,* also inhabit most other islands in the Philippines that have been sampled for mammals. Their presence on Dinagat likely reflects introductions, probably through inadvertent human activity (Musser, 1977a).

The other 26 species are native to Dinagat. Three of these are endemic to the island: *Podogymnura aureospinula, Crateromys australis,* and a species of *Batomys.* However, other members of these genera are not endemic to Dinagat. *Podogymnura* is

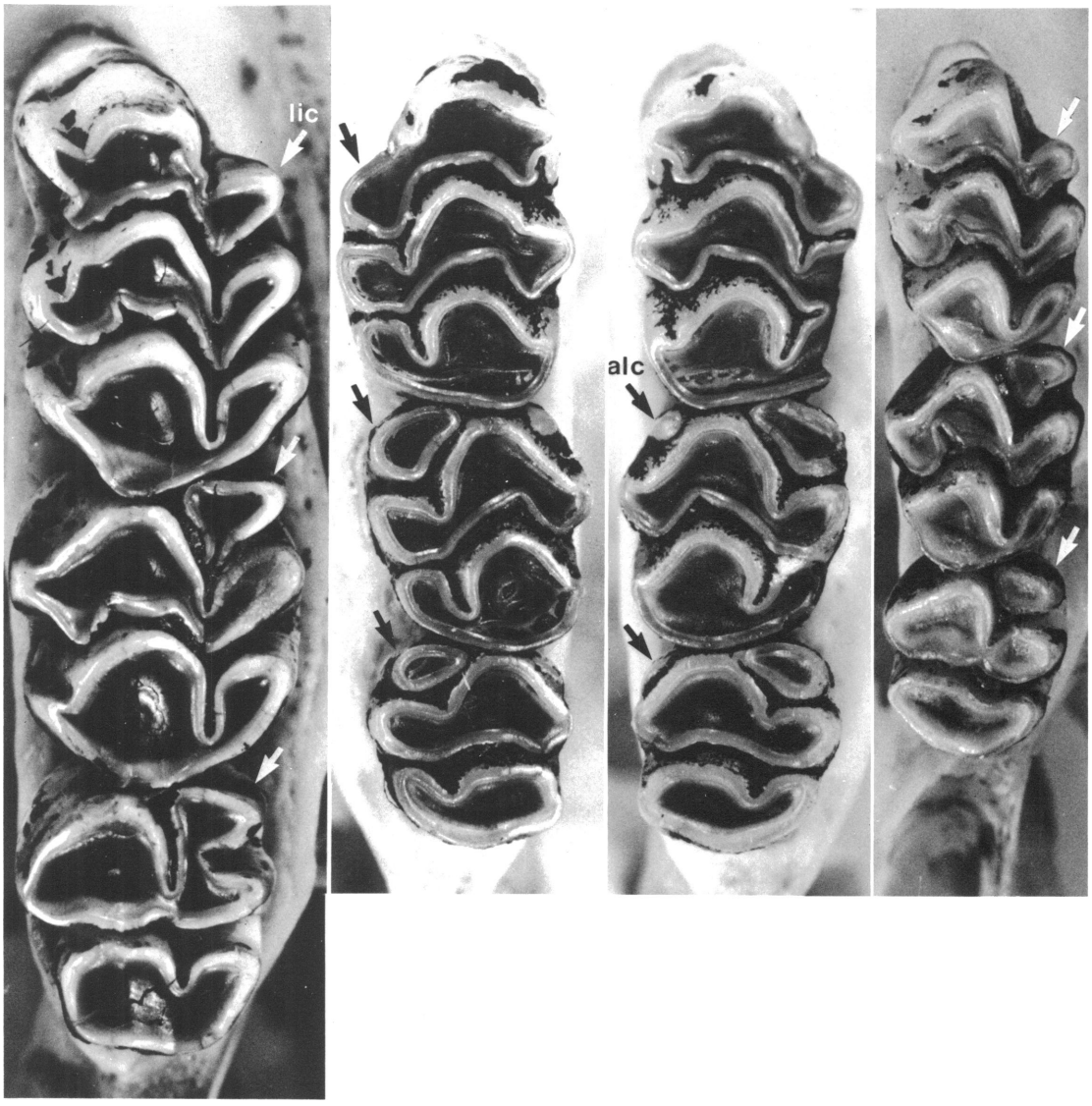

FIG. 10. *Crateromys*. Occlusal views of upper molar rows in same specimens shown in figures 5 and 6. Far left, right side of *C. schadenbergi*; middle two, left and right rows of *C. australis*; far right, right toothrow of *C. paulus*. Note the different orientation of lingual cusp rows (**lic**, cusps t1, t4, and t7; indicated by an arrow at top of each row of lingual cusps on each molar) among the species, and the presence of anterolabial cusps (**alc**, which is also cusp t3) on second and third molars in *C. australis* and their absence in the other two species. See table 1 for values from dental measurements. Approximately ×8.

represented by *P. truei* on Mindanao (Heaney and Morgan, 1982); *Crateromys* by *C. schadenbergi* on Luzon and *C. paulus* on Ilin (this report); *Batomys* by *B. dentatus* and *B. granti* on Luzon, and *B. salomonseni* on Leyte and Mindanao (Musser and Heaney, MS, which also documents the new *Batomys* from Dinagat). The Dinagat representatives of *Podogymnura, Crateromys,* and *Batomys* are morphologically unique and very different from their relatives on the other islands.

None of the other native mammals re-

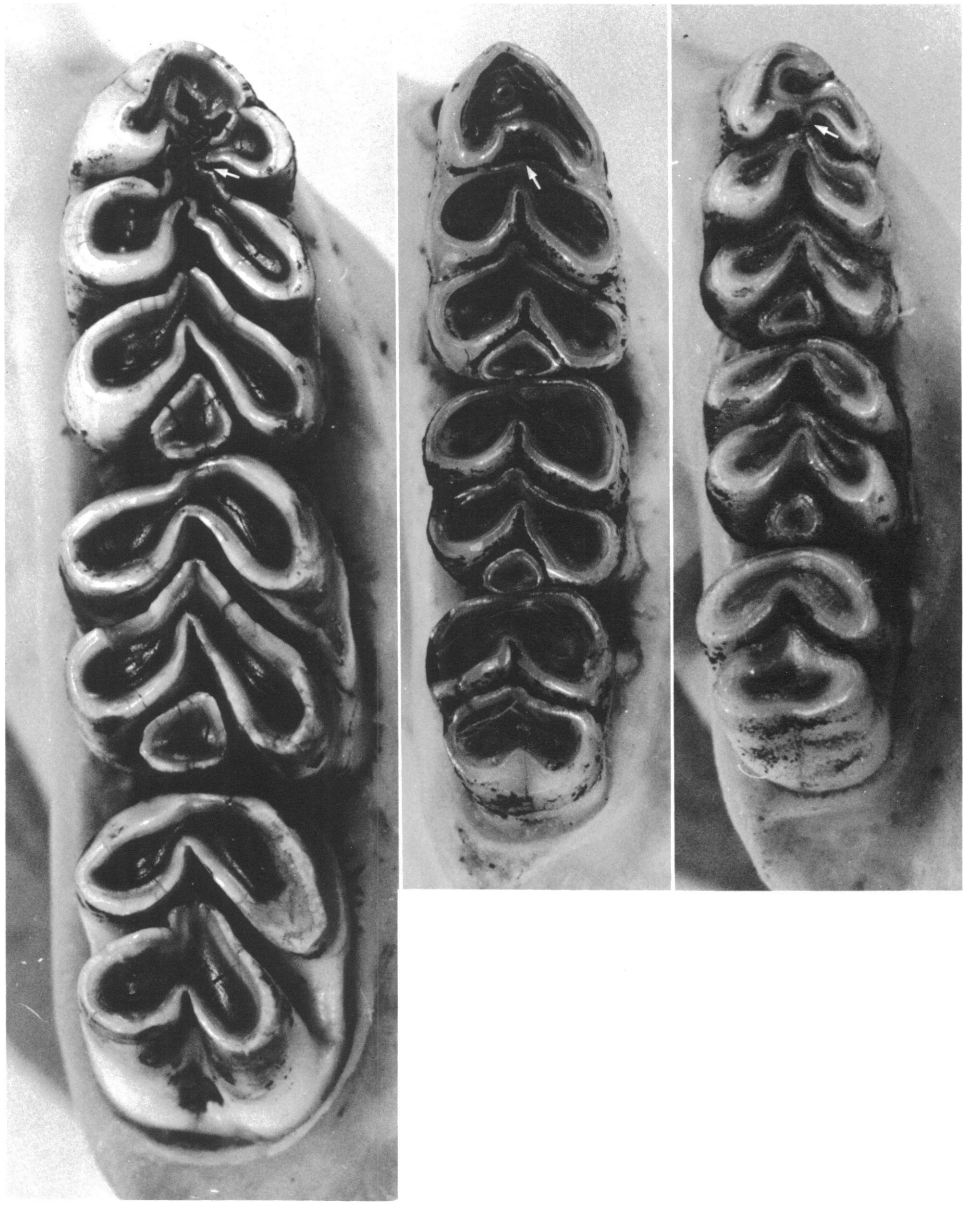

FIG. 11. *Crateromys.* Occlusal views of right lower molar rows in same specimens shown in figure 10. Left, *C. schadenbergi*; middle, *C. australis*; right, *C. paulus.* Small white arrows point to enamel and dentine bridge connecting first and second rows of cusps in *C. schadenbergi* and *C. paulus,* and absence of a comparable connection in *C. australis.* See table 1 for values from dental measurements. Approximately ×8.

corded from Dinagat are endemic to the island. Nine (a tree shrew, bat, dermopteran, primate, all three squirrels, and two rats) also occur on other islands in the Mindanao Faunal Province and nowhere else in the Philippine Archipelago. Five species of bats and one rat are found throughout the Philippines, and eight species of bats occur in the Indo-Australian region as well. Only one of the species of bats is endemic to the Mindanao

TABLE 2
Mammals Recorded from Dinagat Island[a]

Genus and Species	Distributional Status				
	Endemic	Mindanao Faunal Province[b]	Throughout Philippines[c]	Oriental Faunal Region[c]	Introduced[d]
Insectivores					
Podogymnura aureospinula	+	–	–	–	–
Tree Shrews					
Urogale everetti	–	+	–	–	–
Dermopterans					
Cynocephalus volans	–	+	–	–	–
Bats					
Acerodon jubatus jubatus	–	–	+	–	–
Cynopterus brachyotis luzoniensis	–	–	–	+	–
Haplonycteris fischeri	–	–	+	–	–
Macroglossus minimus lagochilus	–	–	–	+	–
Ptenochrius jagori	–	–	+	–	–
Ptenochirus minor[e]	–	+	–	–	–
Pteropus hypomelanus cagayanus	–	–	–	+	–
Pteropus leucopterus	–	–	+	–	–
Pteropus vampyrus lanensis	–	–	–	+	–
Rousettus amplexicaudatus amplexicaudatus	–	–	–	+	–
Emballonura alecto alecto	–	–	–	+	–
Megaderma spasma spasma	–	–	–	+	–
Hipposideros diadema griseus	–	–	–	+	–
Hipposideros obscurus	–	–	+	–	–
Primates					
Tarsius syrichta	–	+	–	–	–
Squirrels					
Exilisciurus concinnus surrutilus	–	+	–	–	–
Sundasciurus mindanensis	–	+	–	–	–
Petinomys crinitus	–	+	–	–	–
Rats and Mice					
Apomys microdon	–	+	–	–	–
Batomys sp.	+	–	–	–	–
Crateromys australis	+	–	–	–	–
Bullimus bagobus bagobus	–	+	–	–	–
Rattus everetti	–	–	+	–	–
Rattus exulans	–	–	–	–	+
Rattus rattus mindanensis	–	–	–	–	+

[a] The list is compiled from Heaney and Rabor (1982), Heaney and Morgan (1982), and Musser (1982b). We omit sight records of a viverrid, wild pigs, and deer that were included in the Dinagat fauna by Heaney and Rabor (1982). The carnivore was probably either *Paradoxurus hermaphroditus* or *Viverra tangalunga*, both of which occur throughout the Philippines. The wild pigs may have been either *Sus barbatus philippensis* or feral *Sus scrofa*; in his report on the taxonomy and phylogeny of *Sus*, Groves (1981) did not mention any records from Dinagat Island. Grubb and Groves (1983), in their notes on taxonomy of the deer known from the Philippine Islands, do not record specimens or sightings from Dinagat; the deer occurring there are likely to be *Cervus mariannus*, which is known from Mindanao and other islands in the Philippines (Grubb and Groves, 1983).

[b] The Mindanao Province includes the islands of Mindanao, Basilan, Bohol, Leyte, Samar, and many small islands.

[c] These are species native to Dinagat Island but also occurring elsewhere in the Philippines and outside of that island group.

Faunal Province; the rest are part of the widespread Philippine and Indo-Australian fauna.

The mammalian fauna of Dinagat Island is typical of small islands that are separated from Mindanao by water less than 120 m deep and thus likely to have been connected to Mindanao during the late Pleistocene. Except for *Crateromys,* all of the genera from Dinagat are also known from Mindanao, and species richness is relatively high, as is typical for land-bridge islands (Heaney, MS). Dinagat, however, is unique among these small islands near Mindanao in not only having endemic species, but possessing three of them. We do not know why. Possibly the endemicity on Dinagat reflects a unique geological history. Possibly *Crateromys australis* and the other two species now known only from Dinagat also occur on nearby islands and in northeastern Mindanao. Possibly other small islands near Mindanao also have endemic species of mammals not yet discovered. Additional and intensive collecting efforts on Mindanao and the smaller nearby islands are needed to determine the actual endemic patterns of mammals on Dinagat as well as in the Mindanao Faunal Province.

Crateromys australis and the Native Philippine Murids

Forty-four native species of rats and mice are found within the political boundaries of the Philippine Islands (table 3). Six of these (*Rattus tiomanicus, Sundamys muelleri, Palawanomys furvus, Maxomys panglima, Chiropodomys calamianus,* and a species of *Haeromys*) inhabit the Palawan region on the islands of Balabac, Culion, Busuanga, Palawan itself and nearby smaller islands. All six species are actually part of the murid fauna native to the Malay Peninsula and islands on the Sunda Shelf (Musser and Newcomb, 1983).

One species (*Rattus tawitawiensis*) is native to Tawitawi Island in the Sulu Archipelago. Its morphological affinities appear to be with populations of *Rattus* inhabiting Sulawesi and other islands that rim the Sunda Shelf in deep water beyond the 180 m bathymetric line (Musser and Heaney, 1985).

Thirty-seven species of native murids have been recorded from islands that form the backbone of the Philippines. Two of these species are endemic to Mindoro and are more closely related to the Sunda Shelf fauna than to any species in the Philippine assemblage. *Anonymomys mindorensis* is morphologically and probably phylogenetically related to *Haeromys,* a genus with representatives on Borneo, Palawan, and Sulawesi (Musser and Newcomb, 1983). *Rattus mindorensis* may be a close relative of the Sundaic *R. tiomanicus* (Musser and Califia, 1982).

Thirty-five species are native to the main chain of Philippine Islands and found nowhere else. The majority of these have been recorded from the two largest islands in the Archipelago: Luzon and Mindanao. It is also on these two islands that the highest degree of endemicity is found. Of the 22 species known from Luzon, 18 (82%) are endemic; *Crateromys schadenbergi* is one of those endemics. Six of the ten (60%) species native to Mindanao are endemic to that island. The rest of the islands for which records are available have one to five species and the endemicity is lower: 10 percent for Leyte and 40 percent for Mindoro and Dinagat; *Crateromys australis* is one of the two endemic murids on Dinagat.

Ilin Island is an exception to the low endemicity of small Philippine islands.

←

[d] Species that are not native to Dinagat but likely introduced.

[e] When Yoshiyuki (1979) described *Ptenochirus minor,* he recorded specimens from Mindanao and Palawan. The species also occurs on Dinagat, and Heaney and his field team found it to be very common in forested areas throughout Leyte; they have not collected it anywhere else but in the Mindanao Faunal Province. The sole record from outside of that region consists of one specimen from Palawan Island; the bat is part of a collection that was purchased from someone in the Philippines. The large collections we have examined from Palawan have not contained any specimens of *P. minor* and we suspect that Yoshiyuki's specimen was actually caught elsewhere but mistakenly indicated as coming from Palawan.

TABLE 3
Native Philippine Murids[a]

Genus and Species	Islands																
	Luzon	Mindoro	Ilin	Catanduanes	Ticao	Samar	Calicoan	Leyte	Dinagat	Siargao	Mindanao	Camiguin	Basilan	Bohol	Negros	Palawan Group	Sulu Archipelago
Phloemys cumingi	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apomys datae	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apomys abrae	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apomys sacobianus	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apomys musculus	I	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apomys microdon	I	–	–	I	–	–	–	I	I	–	–	–	–	–	–	–	–
Apomys insignis	–	–	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–
Apomys hylocetes	–	–	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–
Apomys littoralis	–	–	–	–	–	–	–	–	–	–	I	–	–	–	I	–	–
Batomys granti	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Batomys dentatus	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Batomys salomonseni	–	–	–	–	–	–	–	I	–	–	I	–	–	–	–	–	–
Batomys sp.	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–	–	–
Carpomys melanurus	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Carpomys phaerus	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crateromys schadenbergi	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crateromys paulus	–	–	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crateromys australis	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–	–	–
Crunomys fallax	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crunomys rabori	–	–	–	–	–	–	–	E	–	–	–	–	–	–	–	–	–
Crunomys melanius	–	–	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–
Archboldomys luzonensis	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chrotomys whiteheadi	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chrotomys mindorensis	I	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Celaenomys silaceus	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhynchomys soricoides	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhynchomys isarogensis	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Abditomys latidens	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tryphomys adustus	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Limnomys sibuanus	–	–	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–
Tarsomys apoensis	–	–	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–
Murid sp.	–	–	–	–	–	–	–	–	–	–	E	–	–	–	–	–	–
Bullimus luzonicus	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bullimus bagobus	–	–	–	–	–	I	I	I	I	I	I	–	–	I	–	–	–
Rattus everetti	I	I	–	–	I	I	I	I	I	I	I	I	I	I	–	–	–
Rattus mindorensis	–	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anonymomys mindorensis	–	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Haeromys sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	E	–
Chiropodomys calamianus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	E	–
Maxomys panglima	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	E	–
Palawanomys furvus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	E	–

TABLE 3—(*Continued*)

Genus and Species	Islands																
	Luzon	Mindoro	Ilin	Catanduanes	Ticao	Samar	Calicoan	Leyte	Dinagat	Siargao	Mindanao	Camiguin	Basilan	Bohol	Negros	Palawan Group	Sulu Archipelago
Sundamys muelleri	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	S	—
Rattus tiomanicus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	S	—
Rattus tawitawiensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E
Total species	22	5	1	1	1	2	2	5	5	2	10	1	1	2	1	6	1
Total endemic	18	2	1	—	—	—	—	1	2	—	6	—	—	—	—	4	1
Total indigenous	4	3	—	1	1	2	2	4	3	2	4	1	1	2	1	—	—
Total Sundaic	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—

[a] Data are extracted from Heaney and Rabor (1982); Musser (1977b, 1981a, 1982a, 1982b, 1982c); Musser and Gordon (1981); Musser and Freeman (1981); Musser, Gordon, and Sommer (1982); Musser and Newcomb (1983); Heaney (1984); Musser and Heaney (1985); and Musser's records filed in the Department of Mammalogy at the American Museum of Natural History.

Abbreviations: —, unrecorded, either absent or not yet collected; E, endemic to a particular island or group of islands; I, indigenous to the Philippine Islands excluding the Palawan group and the Sulu Archipelago; S, Sundaic (see Musser and Newcomb, 1983).

Rattus rattus mindanensis, R. rattus rattus, R. nitidus, R. norvegicus, R. exulans, and *Mus castaneus* occur on many islands in the Philippines, but we have excluded them from the list of native Philippine murids because all are likely introduced to the islands (Musser, 1977a).

Crateromys paulus is the only mammal that has been recorded from there.

The endemic murids are from Luzon, Mindoro, Ilin, Leyte, Dinagat, and Mindanao. Except for Ilin, these islands also have a larger murid fauna than do those islands from which only one or two nonendemic natives have been recorded: Catanduanes, Ticao, Samar, Calicoan, Siargao, Camiguin, Basilan, Bohol, and Negros. The native, nonendemic species on these nine islands are representatives of either *Apomys, Bullimus,* or *Rattus*; species of *Crateromys* are either absent or not yet discovered (table 3).

The picture of native Philippine murids can be viewed from another perspective. First, set aside the species that are more closely related to the Sundaic than to the Philippine fauna: *Anonymomys mindorensis* and *Rattus tiomanicus* from Mindoro, the native murids of the Palawan region (table 3), and *Rattus tawitawiensis* from the Sulu Archipelago. The murid fauna that is native to the islands forming the backbone of the Philippines is endemic to the Archipelago and consists of two primary groups. One is composed of species of the Old Philippine Endemic genera: *Phloeomys, Apomys, Batomys, Carpomys, Crateromys, Crunomys, Archboldomys, Chrotomys, Celaenomys,* and *Rhynchomys.* The other contains species of *Rattus* and species in genera at about the same morphological grade as *Rattus*—the New Endemics: *Abditomys, Tryphomys, Limnomys, Tarsomys,* Murid sp. (described in Musser and Heaney, MS), and *Bullimus* (Musser, 1981b).

The distribution among the islands of the species in each major assemblage is indicated in table 4. Luzon has the highest number of species in each group and the most endemics within each of the two groups. *Crateromys schadenbergi* is part of the Old Endemic fauna on Luzon and species of all the other Old Endemic genera are found on that island.

One species of *Crateromys* is the only rodent recorded from Ilin Island. Members of the New Endemics have not yet been collected there.

Species of the Old Endemics have been recorded from six of the other islands. A species

TABLE 4
Insular Distributions of Old Philippine Endemic Murids Contrasted with Philippine *Rattus* and its Endemic Relatives[a]

Island	Old Philippine Endemics (*Phloeomys, Apomys, Batomys, Carpomys, Crateromys, Crunomys, Archboldomys, Chrotomys, Celaenomys, Rhynchomys*)		*Rattus* and New Endemics (*Abditomys, Tryphomys, Limnomys, Tarsomys*, Murid sp., *Bullimus, Rattus*)	
	Total Species	Endemics	Total Species	Endemics
Luzon	18	15	4	3
Mindoro[b]	2	—	1	—
Ilin	1	1	—	—
Catanduanes	1	—	—	—
Ticao	—	—	1	—
Samar	—	—	2	—
Calicoan	—	—	2	—
Leyte	3	1	2	—
Dinagat	3	2	2	—
Siargao	—	—	2	—
Mindanao	5	3	5	3
Camiguin	—	—	1	—
Basilan	—	—	1	—
Bohol	—	—	2	—
Negros	1	—	—	—

[a] Species are listed in Table 3.

[b] *Anonymomys mindorensis* and *Rattus mindorensis* are excluded; see discussion in text.

of *Apomys* inhabits Catanduanes. One species of *Apomys* and one of *Chrotomys* are known from Mindoro. A species of *Apomys* is the only Old Endemic on Negros and the only native murid found there. One species of *Apomys*, one of *Batomys*, and one *Crunomys* inhabit Leyte—only the *Crunomys* is endemic. One species of *Apomys*, one of *Crateromys*, and one of *Batomys* are found on Dinagat—only the *Apomys* is not endemic to the island. Finally, three species of *Apomys*, one *Batomys*, and one *Crunomys* are recorded from Mindanao—two of the *Apomys* and the *Crunomys* are endemic.

No species of *Phloeomys, Carpomys, Archboldomys, Celaenomys*, or *Rhynchomys* have been discovered on any of the islands outside of Luzon. *Chrotomys*, an inhabitant of Luzon and Mindoro, is also a northern Philippine genus. Representatives of *Apomys, Crunomys, Batomys*, and *Crateromys* occur in the northern part of the Archipelago and so far they are the only Old Endemics that have been found in the Archipelago south of Luzon. One of these is the very distinctive *Crateromys australis* from Dinagat.

Members of the New Endemics are found on nearly all the islands for which records of native murids are available. Three species are restricted to Luzon and three to Mindanao. All the other islands have only *Rattus everetti* or *Bullimus bagobus*—both inhabit some of the islands, including Mindanao, and *R. everetti* is also found on Luzon (see table 3). The native murids of Ticao, Samar, Calicoan, Siargao, Camiguin, Basilan, and Bohol consist only of New Endemics; members of the Old Endemics are either absent from these islands or have simply not yet been discovered.

Relationships Among Species of *Crateromys*

We are unable to resolve phylogenetic relationships among the three species of *Crateromys*. We can state that in the characters of skins, skulls, and dentitions, all three are more closely related to one another than to any other species of Philippine murid, a proposition we will elaborate upon in a future report in which we define *Crateromys, Batomys, Carpomys*, and other genera, and discuss phylogenetic relationships among them (Musser and Heaney, MS). We can also point out that each species of *Crateromys* is very distinctive and that there is not one derived character or a combination of derivations that can be used to relate one species closer to any of the others because most characters for which polarity can be determined are unique to a single species. Our assessment of whether a feature is primitive or derived is based upon study of the distributions of characters in other murine genera and in other groups of muroid rodents (see Musser and Gordon, 1981; Musser and Newcomb, 1983).

Fur and body proportions indicate that *C. schadenbergi* and *C. paulus* are more derived relative to *C. australis*. The latter has a tail that is slightly longer than length of head and body and moderately furred. The head and body has a simple bicolored pattern with the

upperparts being one color, the underparts another, and no definite pattern of dorsal coloration or head crest. These are likely primitive features compared with characteristics of the other two species. *Crateromys schadenbergi* has long and lax pelage, a very bushy tail, conspicuous head crest, and polymorphic color patterns—features we interpret to be derived. The short and well furred tail of *C. paulus* and the dorsal pattern on its head and body are also derivations relative to those of *C. australis*; however, they do not tie *C. paulus* more closely to *C. schadenbergi* than to *C. australis.*

Most specimens of *C. schadenbergi* have an alisphenoid strut, a few either lack the strut or have a vestige on one or both sides of the cranium. The other two species lack the strut. Presence of the alisphenoid strut is a primitive condition. But, because of its variation in the series of *C. schadenbergi,* we are uneasy about using this feature to determine relationships. Both *C. australis* and *C. paulus* are known by only one specimen. We do not know if there would be variation regarding expression of the strut within a larger sample of either *C. australis* or *C. paulus* that would be similar to that seen in the sample of *C. schadenbergi.*

Squamosal roots of the zygomatic arch originate low on sides of the braincase in *C. paulus.* This is likely a derived feature (Musser and Gordon, 1981) and separates that species from *C. australis* and *C. schadenbergi,* which have the primitive condition: squamosal roots located high on the braincase.

Crateromys paulus stands apart from the other two species in another character. It has very short incisive foramina, a primitive trait, compared with the longer incisive foramina in both *C. schadenbergi* and *C. australis.*

The palatal bridge points to the opposite relationship. The palate of *C. schadenbergi* is narrow and scored by deep palatal grooves. Relative to breadth of molars and size of crania, the palatal bridge is wider in *C. australis* and *C. paulus,* and it is marked with shallow palatal grooves. The morphology of *C. australis* and *C. paulus* is primitive compared with that of *C. schadenbergi. Crateromys schadenbergi* can be set apart from the others by using the palatal bridge.

The tympanic bullae are smaller relative to cranial size in *C. australis* than in the other two species, but their shape is like that in *C. schadenbergi.* The bullae of *C. paulus* are more inflated, which is derived.

Finally, if characters of the molars are used to indicate relationships, *C. schadenbergi* and *C. paulus* possess the derived morphology and *C. australis* the primitive condition. For example, the configurations of the lingual row of cusps on each upper molar, especially the anterolingual cusp and the one just behind it, are primitive compared with the positions of lingual cusps in the other two species. The presence of an anterolabial cusp on each second and third upper molar in *C. australis* is primitive and its absence in the other two species represents a derivation. The lack of an enamel and dentine connection between the first and second laminae of each first lower molar in *C. australis* is also primitive; a prominent connection, which is characteristic of both *C. schadenbergi* and *C. paulus,* is derived.

There are other features that we used to distinguish the three species from one another but that we cannot use to assess phylogenetic relationships because we are unsure whether they are primitive or derived. The configuration of the proximal portion of the nasals, relative swelling of the region just anterior to the interorbit, relative inflation of nasolacrimal capsules, position of the premaxillary-maxillary suture relative to the nasolacrimal capsules and muscle scars of the medial masseters, shape of temporal ridges, position of the posterior margin of palatal bridge relative to third molars, and mandibular characters are some examples for which we lack information about polarity.

CONCLUSIONS

The central theme of our report has been the description of *C. australis* and comparisons of it with *C. schadenbergi* and *C. paulus.* We also discussed *C. australis* in the contexts of the mammalian fauna of Dinagat Island and the murid fauna native to the Philippines. We have contrasted the morphology of *C. australis* with those of the other two species to determine phylogenetic relationships among the three. We conclude that *C. australis* seems no more closely related to *C.*

schadenbergi than to *C. paulus,* based upon skins, skulls, and dentitions. We also point out that relative to the other two species, *C. australis* is primitive in pelage coloration and both hair and color patterns, body and tail proportions, some cranial characters (small bullae relative to cranial size, for example), and occlusal patterns of molars. There is no question that the cusp patterns of *C. schadenbergi* and *C. paulus* are derived relative to those of *C. australis.* If the latter were known by only fossil fragments of toothrows, especially upper molars, investigators would certainly conclude that *C. australis* was more primitive than either *C. schadenbergi* or *C. paulus* and possibly ancestral to those species.

LITERATURE CITED

duPont, John E., and Dioscoro S. Rabor
1973. Birds of Dinagat and Siargao, Philippines. An Expedition report. Nemouria, no. 10, pp. 1–111, figs. 1–9.

Groves, Colin P.
1981. Ancestors for the pigs: taxonomy and phylogeny of the genus *Sus.* Tech. Bull., no. 3, Dept. Prehist., Res. School Pacific Stud., Australian Nat. Univ., pp. i–iii + 1–96, figs. 1–14, pls. 1–9.

Grubb, Peter, and Colin P. Groves
1983. Notes on the taxonomy of the deer (Mammalia, Cervidae) of the Philippines. Zool. Anz., Jena, 210 1/2, pp. 119–144, 1 fig.

Heaney, Lawrence R.
1984. Mammals from Camiguin Island, Philippines. Proc. Biol. Soc. Wash., vol. 97, no. 1, pp. 119–125.

Heaney, Lawrence R., and Gary S. Morgan
1982. A new species of gymnure, *Podogymnura* (Mammalia: Erinaceidae) from Dinagat Island, Philippines. *Ibid.,* vol. 95, no. 1, pp. 13–26, figs. 1–2.

Heaney, Lawrence R., and Dioscoro S. Rabor
1982. Mammals of Dinagat and Siargao islands, Philippines. Occ. Pap. Mus. Zool. Univ. Mich., no. 699, pp. 1–30.

King, P. B., and E. M. McKee
1949. Terrain diagrams of the Philippine Islands. Bull. Geol. Soc. America, vol. 60, pp. 1829–1836, 1 fig., 5 pls.

Meyer, A. B.
1896. Säugethiere vom Celebes- und Philippinen-Archipel. I. Abh. u. Ber. d. K. Zool. u. Anthr.-Ethn. Mus. zu Dresden 1896/97, no. 6, pp. 1–36, pls. 1–15.

Musser, Guy G.
1977a. *Epimys benguetensis,* a composite, and one zoogeographic view of rat and mouse faunas in the Philippines and Celebes. Amer. Mus. Novitates, no. 2624, pp. 1–15, figs. 1–4.
1977b. Results of the Archbold Expeditions. No. 100. Notes on the Philippine Rat, *Limnomys,* and the identity of *Limnomys picinus,* a composite. *Ibid.,* no. 2636, pp. 1–14, 1 fig.
1981a. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. Bull. Amer. Mus. Nat. Hist., vol. 168, art. 3, pp. 225–334, figs. 1–51.
1981b. The giant rat of Flores and its relatives east of Borneo and Bali. *Ibid.,* vol. 169, art. 2, pp. 67–176, figs. 1–40.
1982a. Results of the Archbold Expeditions. No. 107. A new genus of arboreal rat from Luzon Island in the Philippines. Amer. Mus. Novitates, no. 2730, pp. 1–23, figs. 1–13.
1982b. Results of the Archbold Expeditions. No. 108. The definition of *Apomys,* a native rat of the Philippine Islands. *Ibid.,* no. 2746, pp. 1–43, figs. 1–19.
1982c. Results of the Archbold Expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). Bull. Amer. Mus. Nat. Hist., vol. 174, art. 1, pp. 1–95, figs. 1–60.

Musser, Guy G., and Debra Califia
1982. Results of the Archbold Expeditions. No. 106. Identities of rats from Pulau Maratua and other islands off East Borneo. Amer. Mus. Novitates, no. 2726, pp. 1–30, figs. 1–5.

Musser, Guy G., and Patricia W. Freeman
1981. A new species of *Rhynchomys* (Muridae) from the Philippines. Jour. Mammal., vol. 62, no. 1, pp. 154–159, figs. 1–2.

Musser, Guy G., and Linda K. Gordon
1981. A new species of *Crateromys* (Muridae) from the Philippines. *Ibid.,* vol. 62, no. 3, pp. 513–525, figs. 1–6.

Musser, Guy G., Linda K. Gordon, and Helmut Sommer
1982. Species-limits in the Philippine murid, *Chrotomys. Ibid.,* vol. 63, no. 3, pp. 514–521, figs. 1–4.

Musser, Guy G., and Lawrence R. Heaney
1985. Philippine *Rattus*: a new species from

the Sulu Archipelago. Amer. Mus. Novitates, no. 2818, pp. 1–32, figs. 1–19.

Musser, Guy G., and Cameron Newcomb
1983. Malaysian murids and the Giant Rat of Sumatra. Bull. Amer. Mus. Nat. Hist., vol. 174, art. 4, pp. 327–598, figs. 1–117.

Taylor, Edward H.
1934. Philippine land mammals. Monograph Bur. Sci. (Manila), no. 30, pp. 1–548, figs. 1–12, pls. 1–25.

Wahlert, John H.
1983. Relationships of the Florentimyidae (Rodentia, Geomyoidea) based on cranial and dental morphology. Amer. Mus. Novitates, no. 2769, pp. 1–23, figs. 1–10.

Yoshiyuki, Mizuko
1979. A new species of the genus *Ptenochirus* (Chiroptera, Pteropodidae) from the Philippine Islands. Bull. Natn. Sci. Mus., Ser. A (Zool.), vol. 5, no. 1, figs. 1–6.