

THE GIANT RAT OF FLORES  
AND ITS RELATIVES  
EAST OF BORNEO AND BALI

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## ABSTRACT

Five murids are known only from Flores: *Papagomys armandvillei*; *P. theodorverhoeveni*, new species; *Hooijeromys nusatenggara*, new genus and species; *Floresomys naso*, new genus and species; and *Spelaeomys florensis*. One kind, *Komodomys rintjanus*, occurs on Flores as well as the Komodo Islands of Rintja and Padar. *Papagomys armandvillei* still lives on Flores and is also represented by subfossil specimens; *P. theodorverhoeveni*, *F. naso*, *S. florensis*, and *K. rintjanus* are known by subfossil fragments, the last still lives on the Komodo Islands; and *Hooijeromys* is based on specimens from sediments thought to be Pleistocene. Characteristics of the species are described. The morphological diver-

sity among them indicates adaptations to different habitats and habits, as well as a bipartite arrangement of phylogenetic affinities. *Spelaeomys* may be part of a group that includes the genera native to New Guinea. *Papagomys* clusters with *Hooijeromys*, *Komodomys*, and probably *Floresomys* to form a separate assemblage that has its affinities with *Eropeplus* and *Lenomys* on Sulawesi. The postulated relationships of the Floresian rats is set in a framework of possible paleogeographic reconstructions in the Indo-Australian region. The native murids are also contrasted with the rest of the mammalian fauna now known to occur on Flores.

## INTRODUCTION

Rats (Muridae) comprise most of the native mammalian fauna on Flores, that elongate Indonesian island in the Lesser Sunda chain (Nusatenggara) east of Bali and south of Sulawesi. The giant rat of Flores, *Papagomys armandvillei*, now lives on the island and is also represented by subfossils. They were part of a batch of cranial and mandibular fragments collected by Dr. Th. Verhoeven from Liang Toge, a cave in western Flores. The sediments in Liang Toge have been radiocarbon-dated at between 3000 and 4000 years old (Jacob, 1967). Hooijer (1957b) studied Dr. Verhoeven's material and described a subspecies of *P. armandvillei*, another species of *Papagomys*, and *Spelaeomys florensis*. There are two additional species in the lot from Liang Toge, both represented by dentary fragments and lower molars, and both originally and incorrectly identified as examples of *Rattus rattus* (Hooijer, 1967b; Musser, 1972). Hooijer (1967a) also had a few pieces of maxillae and upper tooththrows as well as isolated lower molars that came from sandstone thought to be Pleistocene in age, which he never described. These specimens along with all the material from Liang Toge that Hooijer had under his charge were studied by me and form the basis for results presented here.

The lot of subfossils and fossils contains six species in four genera, two of them new. Five of the species are known only from Flores, and only one of these has been recorded as still living on the island. The sixth species is represented by a subfossil from Flores and still lives on the Komodo Islands of Rintja and Padar. I discuss the reidentification of Hooijer's material and the new species in a context framed by a taxonomic review of the murids, both native and commensal, on Flores, and by speculations about the relationships among the native murids and between them and the native rats from other places in that vast region of islands and continent east of the Sunda Shelf (fig. 1).

## ABBREVIATIONS AND METHODS

Specimens of skins and skulls I cite in this report are in collections of the American Museum of Natural History, New York (AMNH); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); the Museum Zoologicum Bogoriense, Bogor (MZB); the Museum of Comparative Zoology at Harvard College, Cambridge (MCZ); the Field Museum of Natural History, Chicago (FMNH); and the University of Florida, Gainesville (UF). The subfossil and fossil fragments, in-

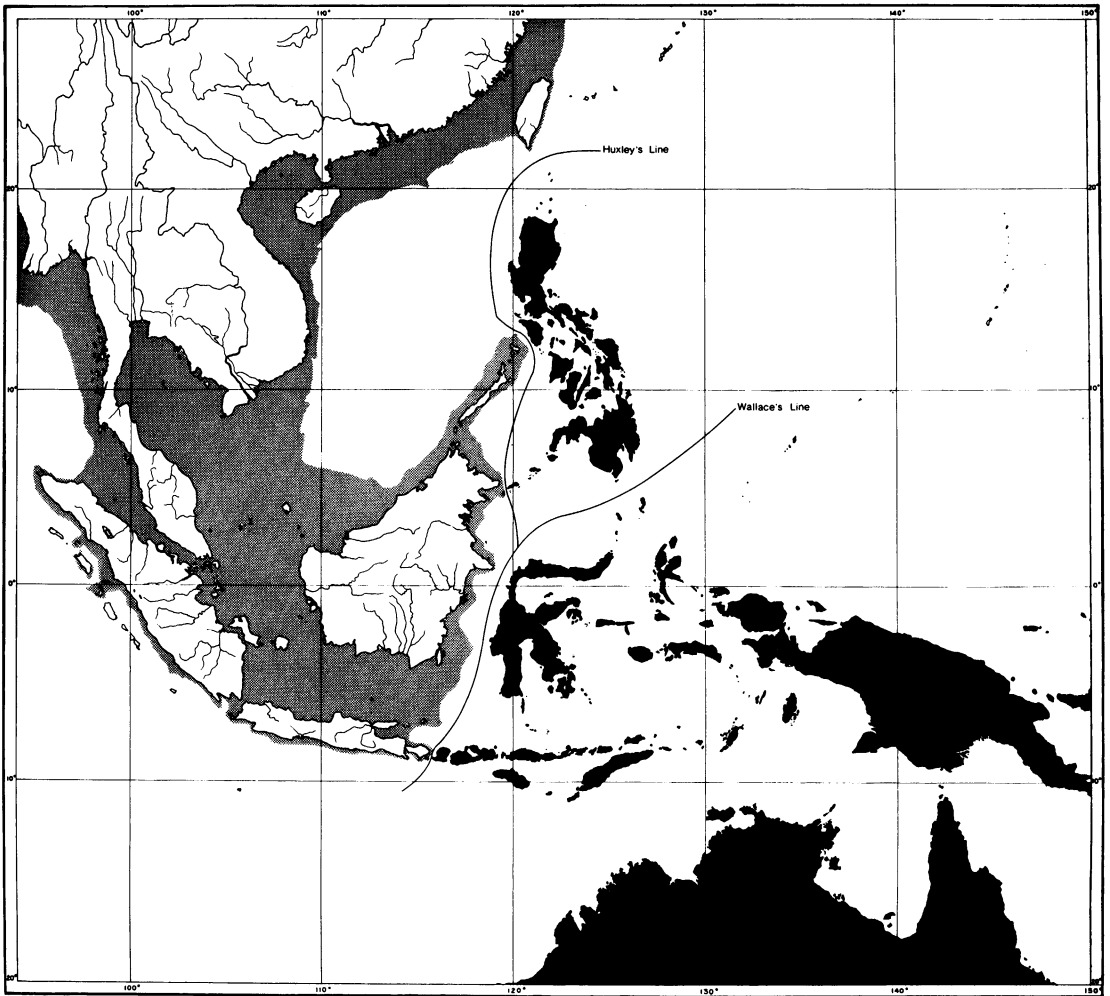


FIG. 1. Map of the Indo-Australian region. The gray area to the west of Wallace's and Huxley's lines denotes approximate margins of the continental shelf; that part of it with the Malay Peninsula and the islands of Sumatra, Java, and Borneo is the Sunda Shelf. Shown in black are the islands and continent east of the Sunda Shelf on which are found the native murid genera I discuss in this report.

cluding all holotypes, are in the collection at the Rijksmuseum van Natuurlijke Historie. Subfossil and fossil are the imprecise terms I use for, respectively, the material from Liang Toge where the sediments were dated at between 3000 and 4000 years old, and those specimens from deposits thought to be Pleistocene in age.

Measurements are in millimeters. Lengths of head and body, tail, and ear of each Recent specimen of *Papagomys armandvillei*

are those made by collectors and were taken from labels attached to skins; I measured lengths of hind feet (including claws). Dial calipers, graduated to 0.1 mm., were used to measure the skulls of those specimens; limits of the cranial measurements are defined elsewhere (Musser, 1970a).

Teeth were measured with dial calipers or Anderson's Craniometer attached to a Wild M5 Stereomicroscope. Endpoints for the length of each molar row are from the front

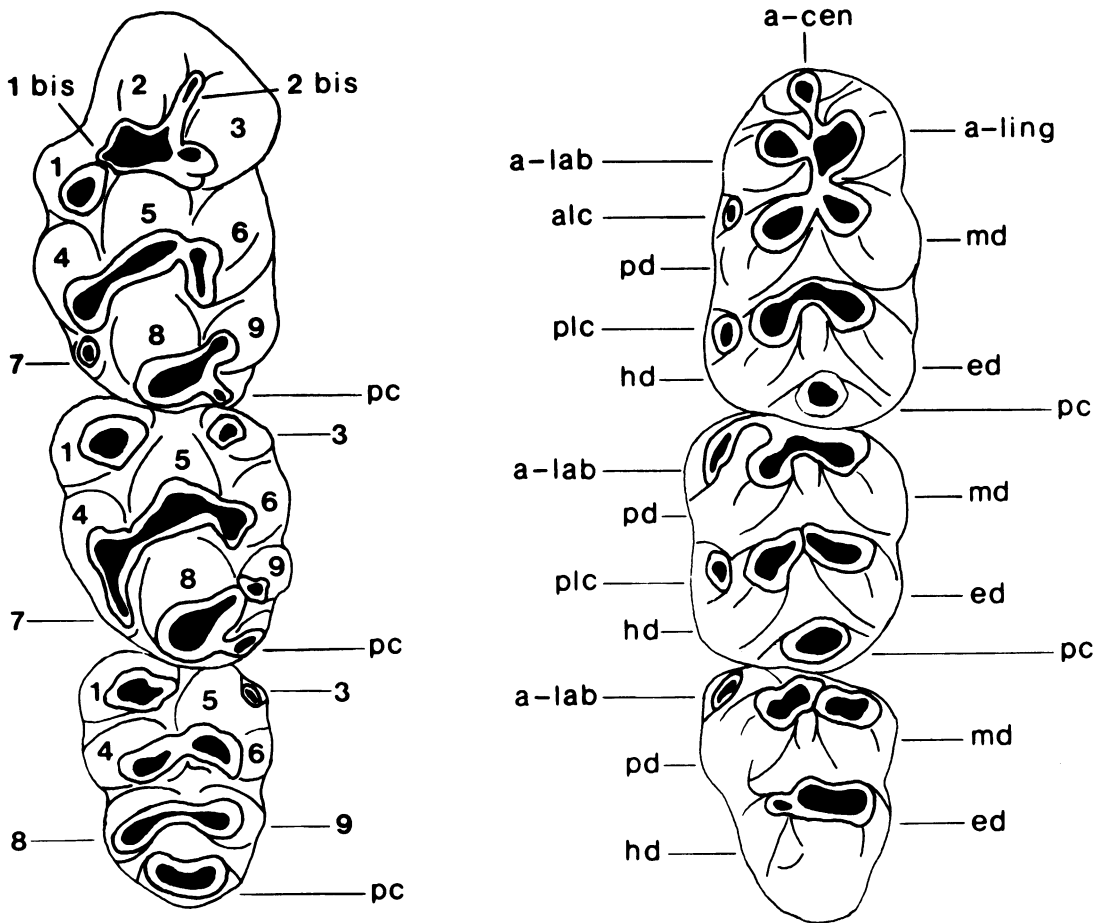


FIG. 2. Nomenclature of dental structures using right upper and lower molars of *Lenothrix canus*. Upper molars: cusps are numbered according to Miller's (1912) scheme and referred to in text with the prefix t; pc, posterior cingulum. Lower molars: a-cen, antero-central cusp; a-lab, anterolabial cusp; a-ling, anterolingual cusp; pd, protoconid; hd, hypoconid; md, metaconid; ed, entoconid; pc, posterior cingulum; alc, anterior labial cusplet; plc, posterior labial cusplet.

of the crown of the first molar (excluding the anterior root) to the back of the third; I did not use alveolar distances. I measured lengths of some molars and widths of all of them; these measurements were taken between points that defined their greatest length or width.

Occlusal structures of murid molars have received various names (Miller, 1912; Misonne, 1969; Michaux, 1971; van de Weerd, 1976; Jacobs, 1978, for example). The nomenclature I use for positions of cusps (also

called cones or tubercles) on upper molars is based on the numbering system developed by Miller (1912) and modified by Misonne (1969); it is diagrammed in figure 2. There are 10 primary cusps on each first molar of a species such as *Lenothrix canus* (the example portrayed in fig. 2), arranged in three rows, with three cusps to each row, and the tenth cusp by itself at the back of the tooth. The numbering begins with the lingual cusp of the first row and extends across to the labial cusp (t1, t2, t3), then continues across

the second row from the lingual to the labial side (t4, t5, t6), and across the third row beginning at the lingual cusp again (t7, t8, t9); the single cusp at the back of each tooth is the posterior cingulum (designated Z, t9, t10, or t12 by other authors—see Jacobs, 1978). The same numbering sequence is followed for cusps on the second and third molars. In some species (*L. canus*, for example) there is a small cusp between cusps t1 and t2 (t1bis) and between t2 and t3 (t2bis) on each first molar and a small accessory cusp behind cusp t6 on the first and second molars.

Nomenclature for the lower teeth (fig. 2) with slight modifications is that used by van de Weerd (1976, p. 44). Each first lower molar has an occlusal surface formed of three rows of large cusps (cones or tubercles), two in each row, sometimes a small anterocentral cusp at the front of the tooth, and usually a posterior cingulum. An anterolabial cusp, two rows of primary cusps, a posterior cingulum, and a cusplet form the surface of the second molar. An anterolabial cusp and two rows of cusps are present on the third molar. Any cusplets (conulids) occur usually along the labial margins of the molars, rarely along the lingual edges.

Throughout the text I often use older names of places; below is a list of those names and their counterparts found on current maps.

MALAY PENINSULA: West Malaysia

SUMATRA: Sumatera

JAVA: Jawa

BORNEO: Sarawak, Sabah, Brunei (East Malaysia); Kalimantan (Indonesian Borneo)

CELEBES: Sulawesi

MOLUCCAS: Maluku

NEW GUINEA: Irian Jaya (Indonesian New Guinea); Papua

LESSER SUNDA ISLANDS: Nusatenggara

## ACKNOWLEDGMENTS

Light from the lamp above my typewriter is the only counterpoint to the bleak grayness of this January day pressing against the museum windows in New York as I write these lines. Eleven years ago, the windows of the Rijksmuseum van Natuurlijke Historie

at Leiden were also shadowed by the gray of winter but I was distracted from that bleakness by the fascination inside where I hovered over a microscope peering at subfossils from Flores—specimens I had known before only secondhand from published accounts—that Dr. D. A. Hooijer had allowed me to examine and measure. Dr. Hooijer also showed me some Pleistocene molars from Flores, which he had not described. Did I know what they might be, he asked, and would I be interested in reporting on the material? Yes, I thought I knew what they were, and yes, I promised to publish on the specimens—and soon. I borrowed the fragments and brought them to New York. Other projects intervened and I procrastinated my report on Dr. Hooijer's fossils until after returning from a three-year expedition to Sulawesi. I regret the long delay. But during that time and through that distance I have learned more about murid rodents of the Far East than I knew 11 years ago; this report is better now than it would have been had I completed it before my trip to Indonesia. In the meantime, Dr. Hooijer has contained himself and exercised the patience of Job. I thank him for retaining confidence in me, and more importantly, for giving me, on that day in Leiden the bits of rats from Flores, material that enabled me to learn more about the remarkable diversity of murids in those archipelagos east of Borneo and Bali.

The curators in charge of collections in the museums listed above allowed me to study specimens and lent me material. I am grateful to them. Drs. J. de Vos kindly provided me with information about specimens of *Spelaomys*.

The photographs are the work of Mr. R. E. Logan, Mr. A. Singer, Mr. P. Goldberg, and the staff photographers at the Rijksmuseum van Natuurlijke Historie. Mr. Sukaeri, at the U.S. Navy Medical Research Unit No. 2 in Jakarta, provided the print in figure 3. Drawings were made by Ms. C. Miller, Ms. F. Stiles, Ms. M. Shepatin, and Ms. P. Wynne. I appreciate the talented efforts of these photographers and artists.

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## THE NATIVE RATS OF FLORES

Twelve species of rats and mice in the family Muridae are recorded from Flores (table 15). Five of these are known only from the island, one also occurs on the Komodo Islands of Rintja and Padar, and five out of the six species are represented only by subfossil and fossil fragments. Hooijer (1957b) has discussed the dental morphology of *Papagomys armandvillei*, the best known and the largest of the Floresian rats, and the first to be discovered by Europeans and described in the literature. Hooijer also named and characterized *verhoeveni*, a species he placed in the same genus with *armandvillei*, and *Spelaeomys florensis*, a third unique Floresian rat. In the following pages I review the morphology of *P. armandvillei* and *S. florensis*; demonstrate that while the holotype of *verhoeveni*, a maxillary toothrow, is an example of *P. armandvillei*, the mandibular toothrows do represent a different species of *Papagomys*, one which will be renamed; name and describe two new genera and species, both known only from Flores; and characterize a Floresian sample of *Komodomys*, a genus that was known only from the Komodo Islands.

### *Papagomys armandvillei*

CHARACTERISTICS OF RECENT AND SUBFOSSIL SPECIMENS: The giant rat of Flo-

res, *Papagomys armandvillei*, is represented in collections of museums by a few recent specimens (table 1), and is also known by subfossil fragments obtained from Liang Toge, a cave near Warukia, 1 km. south of Lepa, in Menggarai Province, western Flores. The sediments at Liang Toge have been determined by radiocarbon dating to be  $3550 \pm 525$  years old (Jacob, 1967). To Hooijer (1957b), the dental fragments represented an extinct population of *P. armandvillei* in which the individuals had larger teeth, thus were presumably larger animals, than the living rats, a difference he expressed by naming the Liang Toge sample *P. a. besar* (a Malay word that means large). Although only bits of dentaries and teeth from the extinct rats exist, there are good specimens of the living animal from which we can visualize the kind of animal the fragments represent.

The living *P. armandvillei* are huge rats (table 1), with small ears, a chunky body and short tail (fig. 3). The body structure is that of a rat adapted for life on the ground and refuge in burrows. Upperparts of the head and body (from muzzle to base of tail), legs, and tops of the front and hind feet out to bases of the claws, are dark brown or tan; the middle of the head and body is darker than the sides. The underparts are pale gray with a slight tan suffusion; they are the palest and contrast with the upperparts most sharp-



FIG. 3. Two adult *Papagomys armandvillei* from Ruteng, Flores. Photographed by M. Sukaeri, October 1973.

ly on the chin and throat, underneath the front and hind legs, and in the middle of the belly.

The pelage is dense and harsh, especially over the upperparts. That covering the upper surfaces of the head and body consists mostly of flattened flexible spines mixed among regular overhairs forming a coat 30–35 mm. thick over the back. Fine underhairs are concealed in the fur and abundant guard hairs extend 15 to 20 mm. beyond the overhairs. The vibrissae on the muzzle are black and long, some reaching 120 mm. The vibrissae over each eye are also long; those behind the cheeks are short and inconspicuous.

The ears are round and small (both abso-

lutely and relative to size of the head), dark brown, and covered with fine brown hairs.

The front feet are short and wide; their naked palmar surfaces are either unpigmented or pale brown and consist of five large and fleshy pads. The hind feet are long and wide, naked from heel to bases of the claws; each plantar surface may be pale or dark brown, and about two-thirds of its anterior portion is taken up by six large pads. Except for the vestigial thumbs that bear nails, as do those of all other murids, the front and hind digits all have long, strong claws.

The tail is stout and shorter than the head and body. It is covered with large scales (6–7 rows per cm.) with three hairs emerging

TABLE 1  
External and Cranial Measurements (in Millimeters) Along With Other Data from Specimens of  
*Papagomys armandvillei*<sup>a</sup>

	MCZ 51098	RMNH 18301 (Holotype)	MZB 8308	MZB 2394	MZB 2395	MZB 99	UF 9125
Sex	M	F	F	M	M	M	M
Age	Yg. Ad.	Yg. Ad.	Ad.	Ad.	Ad.	Yg. Ad.	Ad.
Locality	Potjong	Sika	Flores	Mboera	Mboera	Ruteng	Nunang
Year collected	1959	1892	?	1929	1929	1920	1970
Length of head and body	—	275	—	422	435	400	—
Length of tail	—	265	—	345	360	350	330
Length of hind foot	—	75	81	86	88	83	88
Length of ear	—	24	30	31	31	26	—
Scale rows/cm on tail	—	7	6	6	6	6	6
Greatest length of skull	76.9	67.8	—	78.2	81.5	75.2	—
Zygomatic breadth	37.2	31.1	—	41.5	40.1	—	38.3
Interorbital breadth	7.7	8.1	9.4	8.9	8.9	9.8	9.4
Length of nasals	28.3	24.5	29.5	29.3	32.0	29.0	31.1
Length of rostrum	25.3	21.9	25.3	25.7	26.4	25.2	26.1
Breadth of rostrum	13.5	11.7	14.9	14.3	14.4	15.0	14.2
Breadth of braincase	24.2	21.8	—	24.2	25.2	24.7	23.7
Height of braincase	18.2	18.1	—	19.0	18.5	19.0	19.0
Breadth of zygomatic plate	8.6	6.9	11.1	10.3	9.2	8.5	7.7
Depth of zygomatic notch	4.0	2.8	6.1	3.8	4.8	4.5	3.5
Breadth across incisor tips	5.3	4.7	5.8	5.3	5.2	5.0	5.7
Length of diastema	22.8	17.4	22.1	22.0	24.3	21.5	22.1
Palatilar length	38.5	33.0	38.3	38.0	39.4	37.4	38.6
Palatal length	42.9	36.6	42.9	42.6	44.1	41.6	43.0
Length of palatal bridge	19.0	17.7	19.7	17.7	17.9	20.1	18.5
Length of incisive foramina	13.2	9.8	—	—	14.4	—	14.1
Breadth of incisive foramina	4.5	3.8	—	—	3.9	—	4.5
Breadth of mesopterygoid fossa	4.9	3.5	4.8	5.2	5.6	5.6	4.4
Length of bulla	11.4	11.0	—	11.1	11.1	10.6	10.2
Height of bulla	9.4	10.2	—	8.4	9.6	8.7	10.2

<sup>a</sup> I also examined an adult male from Wewo Pongkor (MCZ 51099) collected in 1958, and an adult male without data (MCZ 51101); these specimens are incomplete, and I measured the teeth of the latter only (table 2).

from the base of each scale; the tail appears naked because the scale hairs are so fine and short. The basal two-thirds of the tail is blackish brown on all surfaces. The distal one-third is variable in color: it may be white on all surfaces, or pale brown but still contrasting conspicuously with the darker basal two-thirds, or blackish brown like the rest of the tail with only small unpigmented spots scattered over the ventral surface.

Distinctive features of the cranium and dentaries of *P. armandvillei* (figs. 4 and 6–8) are large size (table 1); a long and slender

rostrum; moderately wide zygomatic plates that project forward beyond the dorsal anterior roots of the zygomatic arches; strongly built, flaring zygomatic arches, the squamosal roots originating low on sides of the braincase and extending in the form of ridges along sides of the braincase to the occiput; rectangular braincase with sloping sides; high ridges bordering the interorbital region that sweep back and out to form wide shelves, which change to prominent parallel ridges outlining dorsolateral sides of the braincase; narrow, squarish interparietal that

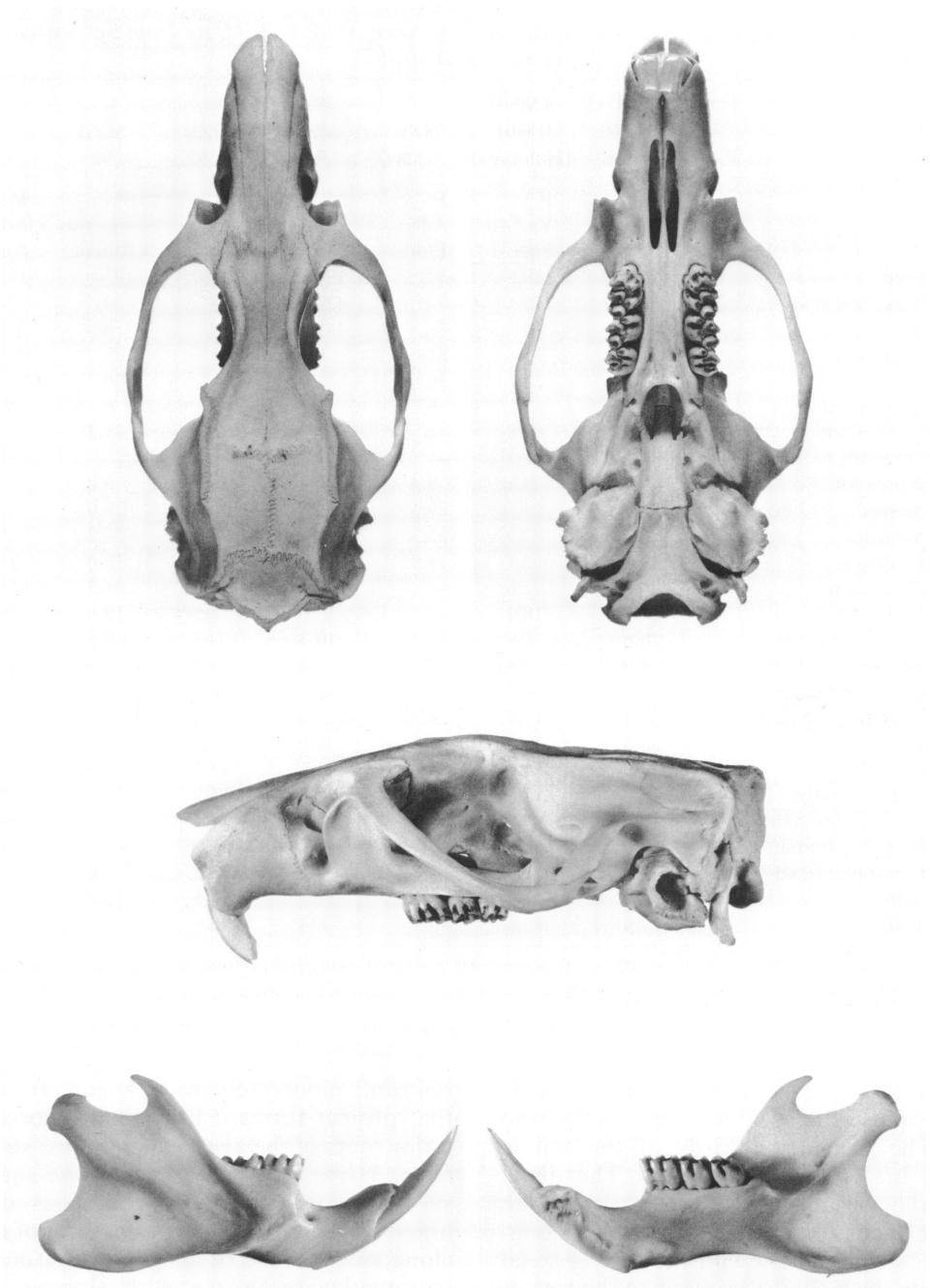


FIG. 4. Adult *Papagomys armandvillei* (MZB 2395) from Mboera, Flores. Dorsal, ventral, and side views of cranium; labial and lingual views of right dentary. All natural size.

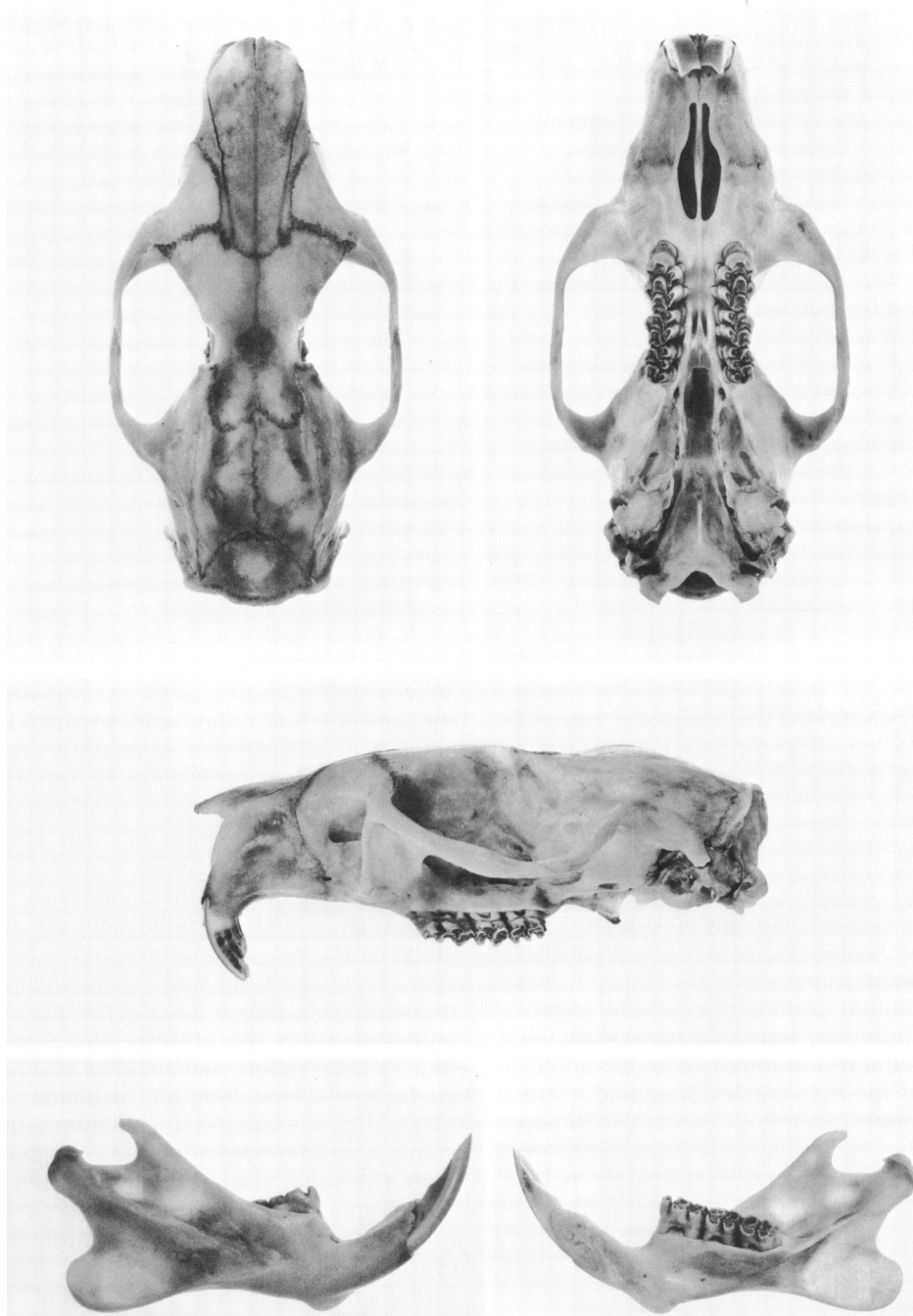


FIG. 5. Adult *Mallomys rothschildi* (AMNH 194913) from the Cromwell Mountains of northeastern New Guinea. Dorsal, ventral, and side views of cranium; labial and lingual views of right dentary. All natural size.

TABLE 2  
Lengths and Breadths (in Millimeters) of Upper Molars from Recent and Subfossil Adult *Papagomys armandvillei*, and from Holotype of *Papagomys verhoeveni*

	Length of M <sub>1-3</sub>	Breadths		
		M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<i>P. armandvillei</i>				
RECENT				
RMNH 18301 (Holotype)	15.4	4.7	4.6	4.1
MCZ 51098	14.6	4.8	4.4	3.6
MCZ 51101	14.9	4.5	4.5	3.9
MZB 8038	15.5	4.6	4.5	3.8
MZB 2394	16.0	4.9	4.5	4.0
MZB 2395	15.2	4.3	4.3	3.8
MZB 99	15.7	4.9	4.6	3.8
UF 9125	15.8	5.0	4.9	4.2
$\bar{X} \pm SD$	15.4 $\pm$ 0.5	4.7 $\pm$ 0.2	4.5 $\pm$ 0.2	3.9 $\pm$ 0.2
LIANG TOGE				
Specimen 10	—	5.2	5.0	—
<i>P. verhoeveni</i>				
Holotype	14.1	4.6	4.4	3.6

is mostly contained between the parietals with only a small posterior segment forming the roof of the occiput; an alisphenoid configuration in which a bony strut of alisphenoid bone is absent so the alisphenoid canal is open between the foramen ovale and the opening of the alisphenoid canal into the sphenoidal fissure, and the masticatory and buccinator foramina are absent, as well as the foramen ovale accessorius (fig. 7); large optic foramina; round or elliptical sphenopalatine foramina; long and narrow incisive foramina ending 1–4 mm. before the anterior margins of the first molars; long and narrow palatal bridge extending about a millimeter beyond the back edges of the toothrows, most of its length scored by two deep palatal grooves; wide, horseshoe-shaped mesopterygoid fossa in which the walls are breached by long, wide, and spacious sphenopalatine vacuities so that the anterior part of the basisphenoid and the presphenoid seem suspended in air; deep pterygoid fossae, the floor of each sloping toward the midline of

the cranium, not flat, and breached by a small but conspicuous sphenopterygoid canal (also called interpterygoid foramen); a large medial lacerate foramen in front of each bulla; the lateral margin of each pterygoid fossa that is formed by a definite ridge extending from behind the molar row to the bulla (figs. 7 and 8); bullae that are moderately large, both absolutely and relative to size of the cranium; and so attached to the braincase that only a narrow postglenoid vacuity separates the pterotic and squamosal (fig. 7); very short and inconspicuous bony eustachian tubes; long and prominent paramastoid processes; inconspicuous squamoso-mastoid foramen, not large enough to separate the squamosal above each bulla into a dorsal and ventral portion (tympanic hook); robust dentaries with small coronoid processes, wide angular processes, high and prominent masseteric ridges, and deeply concave posterior margins.

The upper incisors appear strong, either emerge from the rostrum at nearly a right

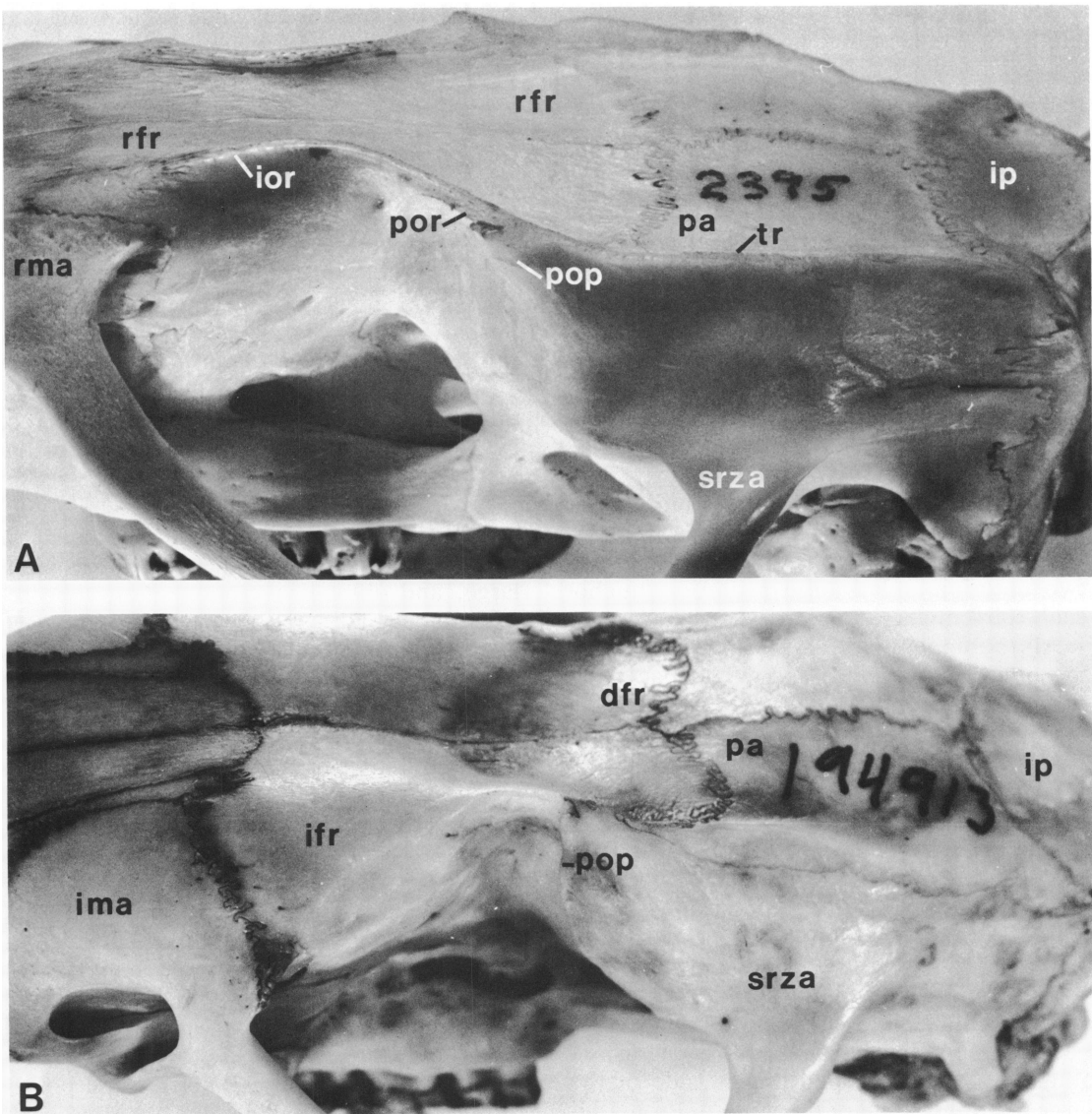


FIG. 6. Orbital views of *Papagomys armandvillei* (A, MZB 2395) and *Mallomys rothschildi* (B, AMNH 194913). The regular configurations of the dorsal maxillary (rma) and frontal bones (rfr) in *Papagomys* contrast with the highly inflated maxillary (ima) and frontals (ifr) adjacent to the orbits, and the depressed frontals (dfr) roofing the postorbital region in *Mallomys*. *Papagomys* has high ridges that border the interorbital (ior), postorbital (por), and temporal (tr) areas; comparable ridging is absent or indistinct in *Mallomys*. Each postorbital process (pop) is small, angular, and confined to the dorso-lateral margin of the postorbital and temporal areas in *Papagomys*, but consists of a long vertical ridge that projects into the posterior part of the orbital region in *Mallomys*. Each squamosal root of the zygomatic arch (srza) is low on the braincase in *Papagomys*, high in *Mallomys*. Other abbreviations are: ip, interparietal; and pa, parietal.

angle (orthodont) or curve back (opisthodont), and have orange or yellow enamel layers. The lowers are also pigmented orange or yellow.

The simple occlusal configurations of the upper and lower molars of *P. armandvillei* are illustrated in figures 9, 10, and 12; values for dental measurements are listed in tables 2 and 3, ratios in tables 6 and 7. The upper molars are wide and appear robust. The first upper molars are the widest, the second molars are as wide or only slightly narrower relative to the first, and the third molars are narrower relative to either the first or second (table 7). Each first upper molar is anchored by five roots: a large anterior, small labial, large posterior, and divided lingual. Four roots anchor each second upper molar: two anterior (which are fused into one in a few specimens) and two posterior. Three roots, two anterior and a large posterior, anchor each third molar.

All the uppers have high cusps. Those on the first and second molars slant backward so that the first molar overlaps 18–22 percent of the second molar, and the second overlaps 17–21 percent of the third (table 6). This configuration reflects an interlocking among the teeth that is characteristic of species without a posterolingual cusp t7 on any of the molars (Misonne, 1969). The interlocking is accomplished by cusp t8 of each first and second molar overlapping the large central cusp t5 on each second and third molar. In most specimens, the large cusp t1 on each second and third molar forms part of the connection because the anterolabial side of each cusp t1 abuts against the sloped lingual side of the large central cusp t8 of the molar in front (fig. 12A, B, and E). In a few rats, cusp t1 on each second and third molar is situated so far out to the lingual side that it stands by itself, does not abut against cusp t8, and is not involved in the interlocking (fig. 12C). The interlocking structure provides a strong union among the molars and represents a specialization (Misonne, 1969).

The occlusal surface of each first upper molar consists of three rows of large cusps. The central cusp in each row (t2, t5, and t8) are large and thick; the first and second rows

have large cylindrical lingual cusps (t1 and t4, respectively), but such a cusp (t7) is absent from the third row. The labial cusp of each row (t3, t6, and t9) is wide and thin, each projecting forward at an angle from the central cusp. There is no posterior cingulum and no cusps t1bis, t2bis, or cusp behind cusp t6.

Each second upper molar is longer than wide in occlusal outline. A tall, large, and cylindrical cusp t1 is present, and cusp t2 is absent, and usually cusp t3; if the cusp t3 is present, as on UF 9125 and MCZ 51098 (fig. 12B and C), it is very small. The rest of the occlusal surface consists of two rows of cusps that resemble the configuration of the last two rows in the preceding molar.

Each third upper molar has a squarish occlusal outline. Cusp t3 is usually absent (if present, it is minute), and cusp t1 is high, large, and oblong in cross-section. The remaining occlusal surface is formed by two thick and high laminae: the front one consists of cusps t4, t5, and t6 merged into either a transverse (fig. 12A and B) or boomerang-shaped (fig. 12C) structure; the chunky posterior lamina is wide, thick, transverse, and probably composed of cusps t8 and t9, although it is difficult to tell because the lamina is complete and without indication of cuspidation even in young rats.

The lower molars are wide, appear strong, and have simple occlusal patterns formed of chevron-shaped or transverse laminae set close to one another (fig. 10). The first and third molars are the same width, the second molar is wider relative to either of those (table 7). Four roots (large anterior and posterior, small labial and lingual) anchor each first lower molar, and each second and third molar has three roots (two anterior and large posterior).

The occlusal outline of each first lower molar is nearly rectangular and its surface is formed of three rows of high cusps—two cusps in each row—and a single cusp at the back of the tooth, the posterior cingulum. The front row consists of a large anterolingual cusp, angular in cross-section, and a smaller oblong anterolabial cusp; both meet in the center of the tooth to form a shallow

TABLE 3  
Lengths and Breadths (in Millimeters) of Lower Molars: Comparisons Between Mean Values from Recent and Subfossil Adult *Papagomys arandvillei*

		Breadths		
	Length of M <sub>1-3</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
RECENT				
RMNH 18301 (Holotype)	14.9	4.0	4.3	4.2
MCZ 51098	14.2	4.1	4.3	4.0
MCZ 51101	14.7	4.0	4.3	3.9
MZB 8038	16.0	4.1	4.4	4.2
MZB 2394	15.3	4.0	4.4	4.0
MZB 2395	13.8	3.7	4.1	3.9
MZB 99	15.8	4.1	4.3	4.1
UF 9125	16.0	4.4	4.8	4.5
$\bar{X} \pm SD$	15.1 $\pm$ .8	4.1 $\pm$ .2	4.4 $\pm$ .2	4.1 $\pm$ .2
Probability value	<.2	<.05	<.01	<.01
LIANG TOGE				
Specimen 1	15.9	4.5	4.9	4.6
2	16.1	4.5	4.9	4.7
3	15.3	4.1	4.5	4.3
4	—	4.1	—	4.5
5	15.7	4.3	4.5	4.2
6	—	4.1	4.6	—
7	—	4.3	4.8	—
8	—	4.3	—	—
9	—	4.1	—	—
17	—	3.9	—	—
$\bar{X} \pm SD$	15.8 $\pm$ .3	4.2 $\pm$ .2	4.7 $\pm$ .2	4.5 $\pm$ .2

V-shaped lamina that becomes elliptical after the tooth is worn down to the point where the cusps merge. The second and third rows are formed of wide oblong cusps that meet along the midline of the tooth to form chevron-shaped laminae. The posterior cingulum is large, cylindrical, and situated at the center of the back margin. There is no cusp at the front of the tooth (anterocentral cusp) such as exists on the first lower molars of *Spelaeomys florensis* (Hooijer, 1957b) or *Coryphomys buehleri* (Hooijer, 1965), nor is there a cusplet at the anterolabial edge of the second row of cusps (anterior labial cusplet) or at the anterolabial margin of the third row (posterior labial cusplet).

Each second lower molar is about as broad as long and also has a simple occlusal surface. The high cusps form chevron-shaped

rows similar in configuration to the back two rows on the first molar. The posterior cingulum is large and oblong in cross-section. There is a large anterolabial cusp. Labial cusplets are absent.

The third lower molars have squarish occlusal outlines. Their surfaces, like those of the third upper molars, are simple and formed of two laminae. The front one is thick and slightly arcuate in some specimens, transverse in most. An anterolabial cusp, defining the anterolabial margin of the lamina, is present and merges with the lamina after wear. The transverse second lamina is thick and wide, oval or oblong in cross-section. Cusplets are absent from the labial margin of each tooth.

The cuspidation of the lower molars is not elaborate partly because there are usually no

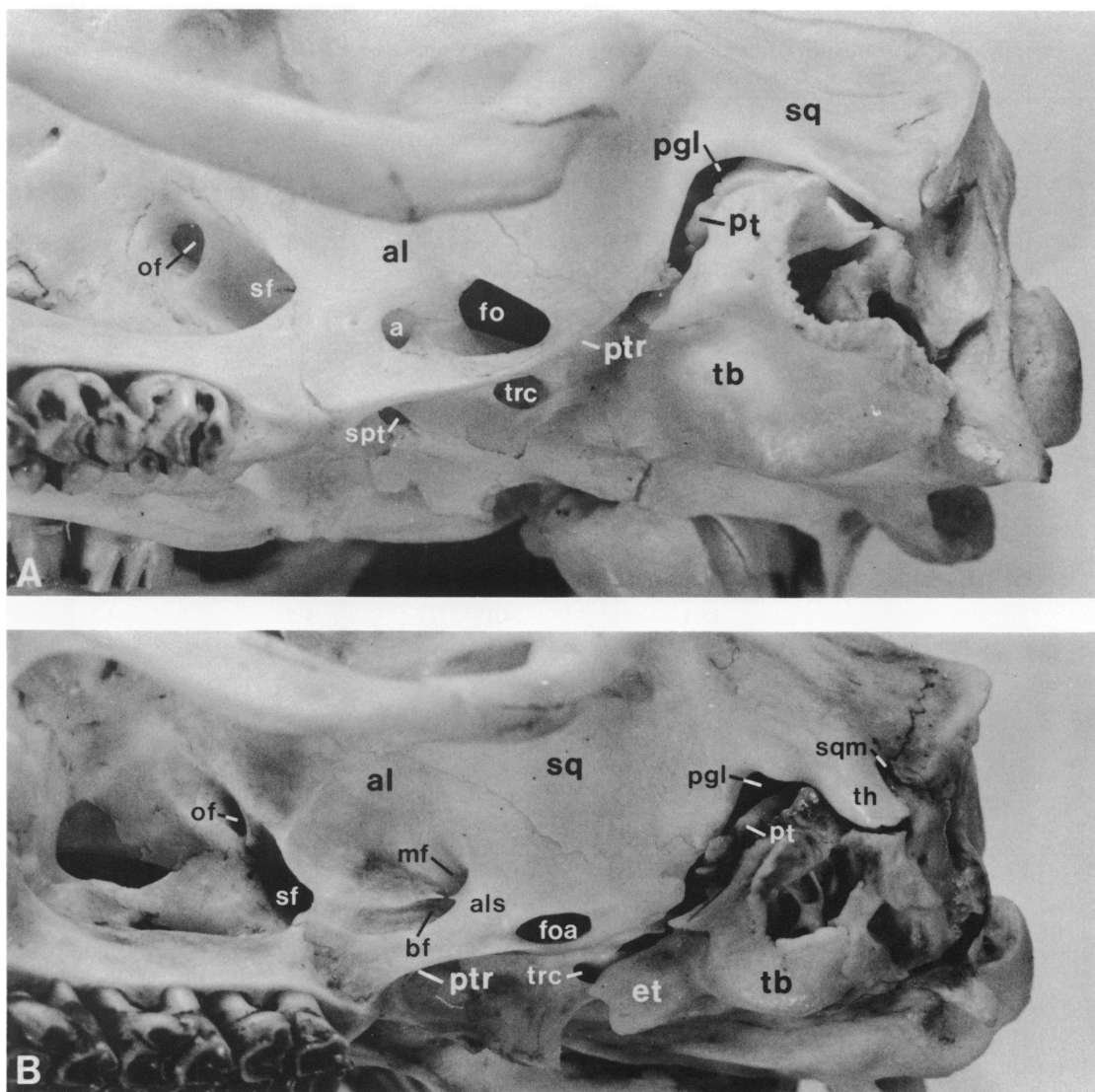


FIG. 7. Parts of the orbit, alisphenoid area, and bullar region compared with *Papagomys armandvillei* (A, MZB 2395) and *Mallomys rothschildi* (B, AMNH 194913).

**Abbreviations:** a, alisphenoid canal; al, alisphenoid bone; als, strut of alisphenoid bone concealing alisphenoid canal and foramen ovale; bf, buccinator foramen; et, bony eustachian tube; fo, foramen ovale; foa, foramen ovale accessorius; mf, masticatory foramen; of, optic foramen; pgl, postglenoid vacuity; pt, periotic bone; ptr, pterygoid ridge; sf, sphenoidal fissure; spt, sphenopterygoid canal; sq, squamosal bone; sqm, squamoso-mastoid foramen; tb, tympanic bulla; th, tympanic hook, the ventral portion of the squamosal below the squamoso-mastoid foramen; trc, transverse canal.

See text for discussions. Hill (1935), Klingener (1968), Wahlert (1974), and Musser (1981) provide additional information about the foramina and significance of the various configurations.

cusplets (designated conules by Misonne, 1969, and buccal tubercles by Hooijer,

1957b) along the labial margins of the teeth. There is an anterolabial cusp on each second

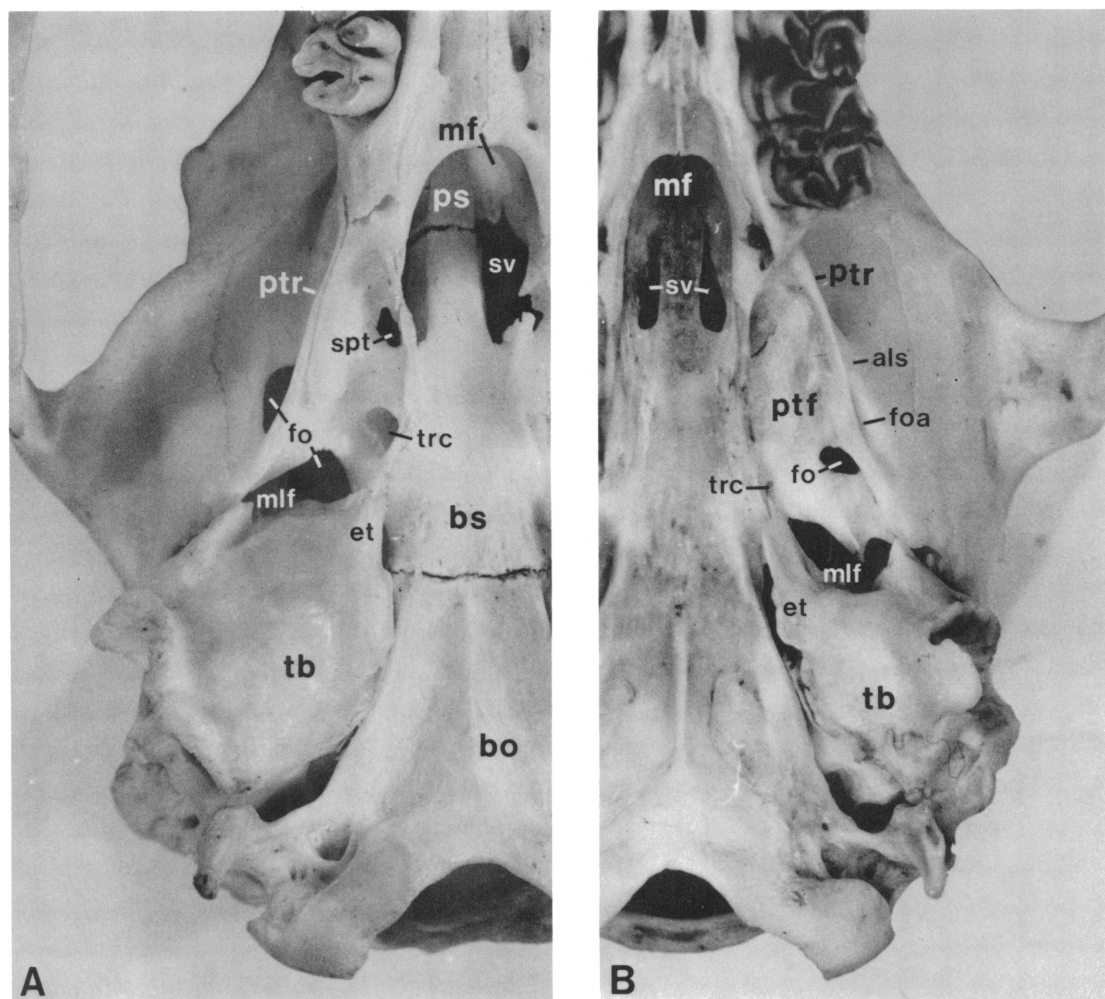


FIG. 8. Ventral views of crania: *Papagomys armandvillei* (A, MZB 2395) contrasted with *Mallomys rothschildi* (B, AMNH 194913).

**Abbreviations:** als, strut of alisphenoid bone; bo, basioccipital bone; bs, basisphenoid bone; et, bony eustachian tube; fo, foramen ovale; foa, foramen ovale accessorius; mf, mesopterygoid fossa; mlf, middle lacerate foramen; ps, presphenoid bone; ptf, pterygoid fossa; ptr, pterygoid ridge; spt, sphenopterygoid canal; sv, sphenopalatine vacuity; tb, tympanic bulla; and trc, transverse canal.

See text for further explanation. Refer to Hill (1935), Klingener (1968), and Wahlert (1974) for additional information about foramina, and Musser (1981) for other discussion about the cranial features.

and third molar in samples from both Recent and subfossil specimens. Hooijer (1957b, p. 302) reported a tiny posterior labial cusplet on the second molar of specimens 5 and 8 in the sample of subfossils, and "a tiny enamel point" at the anterolabial edge of the third row of cusps on the first molar of specimen 5; aside from these variants, labial cusplets

are absent from toothrows of *P. armandvillei*.

The subfossil pieces of *P. armandvillei* from Liang Toge consist of 11 specimens representing as many individuals: the first and second upper molars from the right tooththrow of a young rat, five mandibular fragments with complete tooththrows showing



FIG. 9. Maxillary toothrows of *Papagomys* and *Mallomys*. A, *P. armandvillei*, young adult (holotype, RMNH 18301); B, *M. rothschildi*, adult (AMNH 191525); C, *M. rothschildi*, juvenile (AMNH 194916). Approximately  $\times 8$ .

various stages of wear, which indicate different ages (three of these toothrows are illustrated in Hooijer, 1957b, plate 14, figs. 1–3), two mandibular pieces containing the first and second molars, and three fragments with only the first lower molars intact (one of these, specimen 17, was originally identified

as *P. verhoeveni* by Hooijer, 1957b, but it is a small example of *P. armandvillei*). Hooijer (1957b) has enumerated and described these dental fragments and also provided values from measurements of them. To Hooijer, "These specimens agree with the holotype of *Papagomys armandvillei* (Jentink) in the

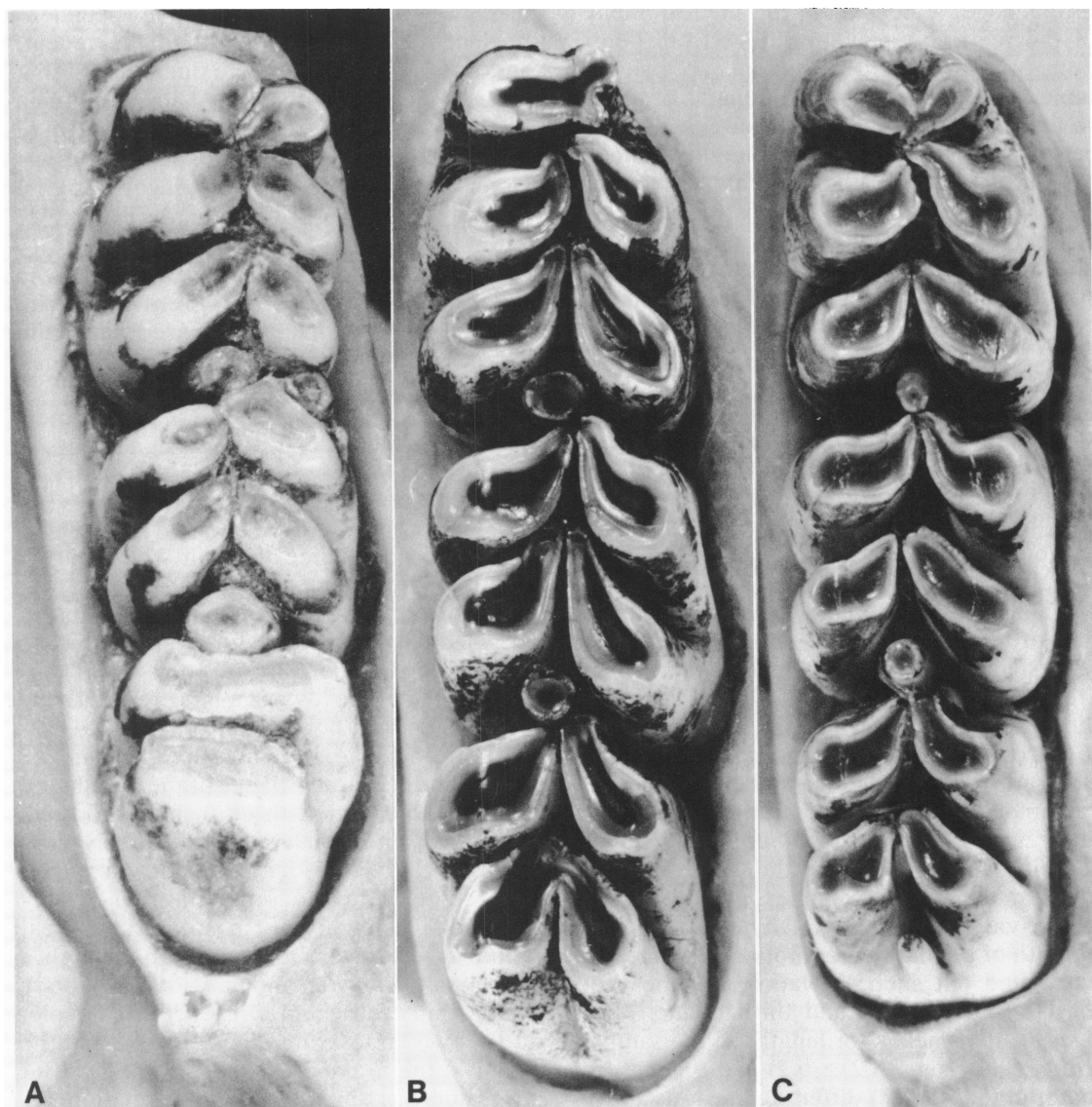


FIG. 10. Mandibular tooththrows of *Papagomys* and *Mallomys*. A, *P. armandvillei*, young adult (holotype, RMNH 18301); B, *M. rothschildi*, adult (AMNH 191525); C, *M. rothschildi*, juvenile (AMNH 194916). Approximately  $\times 8$ .

Leiden Museum (cat. ost. a) in every detail of their structure''; but, he did not think they represented the same population as the rats which now live on Flores. Based on values derived from his measurements of the teeth, Hooijer concluded that those specimens represented a population of larger animals than

the Recent ones and named it *Papagomys armandvillei besar*, an extinct subspecies he diagnosed by "Teeth larger than those of recent *Papagomys armandvillei armandvillei* (Jentink) but not identical in specific characters."

I have examined the 11 fragments from

Liang Toge. Values from my measurements of the teeth, along with values from dentitions of eight Recent specimens, are listed in table 3. There is variation in lengths of toothrows and breadths of individual teeth within each sample. Part of the variability reflects natural variation in the population, whether individual or sexual; part is attributable to different degrees of wear on the occlusal surfaces, thus affecting endpoints of the measurements. There is also a slight difference between some of my values from the Liang Toge teeth and some of the values obtained by Hooijer. He was certainly careful, as I tried to be, but the teeth are difficult to measure, and any slight differences in the endpoints of a measurement or in the instrument each of us used would result in different values. The data in table 3, however, are comparable because I measured teeth from both samples in the same way.

I agree with Hooijer's specific identification of the material from Liang Toge; these teeth and those from Recent *P. armandvillei* are alike in morphology; they also do not differ significantly in lengths of mandibular toothrows. The lower molars from Liang Toge are wider than those in the eight Recent specimens and this is the primary significant difference I could detect between the two samples. I also measured the length of each lower molar in both samples but did not list those values in table 3. The length and breadth of the first lower molar are positively correlated but such a relationship does not exist for the second and third molars. The result is that means for lengths in the sample from Liang Toge ( $6.2 \pm 0.2$ ) and the Recent material ( $5.7 \pm 0.3$ ) differ significantly ( $P = .01-.001$ ), indicating that the first lower molars of the former are significantly larger and wider than those of the latter. Differences between means for lengths of either the second ( $4.7 \pm 0.3$ ;  $4.4 \pm 0.4$ ;  $P = 0.2-0.1$ ) or third ( $4.8 \pm 0.1$ ;  $4.5 \pm 0.7$ ;  $P = 0.4-0.3$ ) lower molars are not significant; the second and third molars in the Liang Toge sample are significantly wider (table 3) than those in Recent specimens but do not differ in length.

What do these differences in size of teeth indicate? To Hooijer (1957b, p. 302) the

meaning was clear: "All the cave specimens present dimensions larger than the recent, and evidently belonged to individuals that exceed the recent in size. This is quite in harmony with the general rule that subfossil and fossil remains of recent species average larger than their recent homologues . . . . I have no doubt that *Papagomys armandvillei besar* nov. subsp. should be regarded as directly ancestral to the living *Papagomys armandvillei armandvillei* (Jentink). The amount of time that has elapsed since the deposition of the remains in the cave deposit has been sufficient for a subspecific differentiation to have taken place." If this interpretation be correct we have significant information about the magnitude of change in body size in *P. armandvillei* over a period of three to four thousand years, and an estimate of the length of time through which partial genetic isolation occurred; that is, assuming a reasonably rigorous definition of subspecies. The available data force me to a more cautious conclusion.

If widths of the lower molars are positively correlated with body size, and if the remnants from Liang Toge are a reliable sample of the dental characteristics of the population living in that region three to four thousand years ago, then that population likely consisted of individuals larger in body size than rats comprising the population of *P. armandvillei* now living in western Flores. There is, however, no indication of such a correlation between molar width and body size within the Recent sample. For example, of the two largest adults, MZB 2395 has the smallest teeth and UF 9125 the largest. But my sample is small and any correlation between body size and breadths of lower molars will have to be tested with a larger sample consisting of individuals comparable in age and sex.

The greater breadths of the lower molars in the sample from Liang Toge may reflect, rather than larger body size, some other characteristic of the population, perhaps the result of selection for foods common in the diet of the rats at that time and not present in the environment of the living animals. I would conclude only that the lower molars

in the sample from Liang Toge are significantly wider, on the average, than those from the eight Recent specimens, individuals I brought together from different localities to form one sample. Whether the observed difference actually represents a real distinction between nearly genetically isolated populations (my sense of subspecies), and actually reflects an ancestral-descendent relationship between the early population and the living rats cannot, in my opinion, be determined with the data that are now available.

**TAXONOMIC HISTORY AND CONTRASTS WITH *MALLOMYS*:** *Papagomys armandvillei* was originally described as a species of *Mus* by Jentink in 1892 and based on a young adult, RMNH 18301 (fig. 11). Through the years up to 1936, the species came to be associated with *Mallomys*, a giant rat endemic to New Guinea (Thomas, 1898; Mertens, 1936; Tate, 1936), but in 1941 Sody pointed out some of the distinctive body and cranial characters of *armandvillei* when he proposed the genus *Papagomys* to embrace it. Subsequently, Tate (1951, p. 274), in reference to his report published in 1936, wrote, "I put forth the suggestion that *Mus armandvillei* Jentink of Flores might also be related to *Mallomys*. I now find that any close relationship is invalidated by the large *Rattus*-like bullae of *armandvillei* and its very different temporal area." Hooijer (1957b) later described the dentition of *P. armandvillei*, noting features that he thought reinforced its morphological and generic separation from all other kinds of murids, and enumerated the many significant differences between the occlusal patterns of *Papagomys* and *Mallomys*. Then Misonne (1969), who focused only on the differences in dental characteristics between *Papagomys* and *Mallomys*, substantiated Sody's and Hooijer's assessments, and Tate's later conclusion that *armandvillei* was not a species of *Mallomys*. Despite those evaluations, Simpson (1977, p. 112) has recently implied that *Papagomys* was not that distinct from *Mallomys* when he summarized the fossil mammals from Flores reported by Hooijer—in the context of attempting to define limits of the Oriental and Australian zoogeographic



FIG. 11. The holotype of *Papagomys armandvillei*, RMNH 18301, a young adult. Dorsal, ventral, and side views of the cranium; labial and lingual views of the right dentary. All natural size.

regions—and wrote that "*Papagomys*, if considered a distinct genus, is endemic to Flores, but it is close to *Mallomys* of New

Guinea. Its differentiation nearly or quite to generic level suggests that its ancestors reached Flores from the east in the Pleistocene or even earlier."

I stress that Sody correctly assessed the distinctiveness of Jentink's *Mus armandvillei* when he proposed a new genus to contain it. That species does not belong in *Mallomys* and is not even phylogenetically closely related to it, judged by morphology of skin, skull, and teeth. Before continuing discussion of the Floresian rats, it is important here to point out the striking contrasts between *Papagomys* and *Mallomys*. Specimens of *Mallomys rothschildi* (the only documented species in the genus) possess the following features that distinguish them from examples of *Papagomys armandvillei*.

1. The body size of *Mallomys* is smaller (compare the measurements from *M. rothschildi* listed by Laurie, 1952, p. 302, with those from *P. armandvillei* in table 1).

2. The tail is longer than combined lengths of head and body (instead of shorter, as in *P. armandvillei*).

3. The pelage is softer, longer, and woolly (not short and harsh, as in *Papagomys*).

4. The rostrum is short, wide, and highly inflated (long, slender, and not inflated in *Papagomys*; contrast figs. 4 and 5).

5. The wide, fan-shaped interorbital region (as seen from dorsal view) is situated in front of a narrow postorbital waist (narrow interorbital region with concave margins in *Papagomys*; figs. 4 and 5).

6. The frontal bones adjacent to the orbits and the dorsal parts of the maxillaries are strongly inflated (instead of flat, not inflated; figs. 4-6).

7. The lacrimal bones are small and incorporated into the anterior walls of the orbits (large and discrete in *Papagomys*).

8. Tall, bony postorbital processes, formed from the frontals and parietals, project anteriorly into the back part of the orbital region (small angular processes, each located only at the dorsolateral margin of the postorbital and temporal regions in *P. armandvillei*; fig. 6).

9. The braincase is long and low, and arches down toward the occiput (braincase is flat on top in *Papagomys*; figs. 4 and 5).

10. There are no ridges or shelves bordering the interorbital and postorbital regions or dorsolateral sides of the braincase (wide and prominent ridges in *Papagomys*; figs. 4 and 5).

11. The walls of the braincase are smooth between the back margins of the squamosal roots of the zygoma and the occiput (low ridges here in *Papagomys*; figs. 4 and 5).

12. Squamosal roots of the zygomatic arches originate much higher on sides of the braincase (figs. 4 and 5).

13. The zygomatic plates do not project forward beyond the dorsal maxillary roots of the zygomatic roots (they extend beyond the roots in the form of a conspicuous anterior spine in *Papagomys*; figs. 4 and 5).

14. There is a posterior hook-shaped process of the squamosal above each bulla that separates the postglenoid vacuity from the squamoso-mastoid foramen (fused with the squamosal and indistinguishable in *Papagomys*; fig. 7).

15. The alisphenoid region consists of a wide alisphenoid strut, which conceals the alisphenoid canal and foramen ovale, and separates the foramen ovale accessorius posterior to the strut from the buccinator and masticatory foramina anterior to it (the alisphenoid strut is absent in *Papagomys*, as are the foramen ovale accessorius and the masticatory and buccinator foramina; the lateral side of the alisphenoid canal is open, revealing the foramen ovale and the opening of the canal into the sphenoidal fissure; fig. 7).

16. The orbital foramina are tiny (large in *Papagomys*), and the sphenopalatine foramina are long, narrow, and slitlike (round or oblong in *Papagomys*; fig. 7).

17. The incisive foramina are narrow in their anterior third, then widely dilated in the posterior two-thirds (long and slender throughout in *Papagomys*; figs. 4 and 5).

18. The palatal bridge is long and narrow, ends well in front of the backs of the molar rows, and has shallow palatal grooves except just in front of the long posterior palatine foramina (the bridge is wider in *Papagomys*, ends behind the molar rows, is scored with deep palatal grooves, and has small posterior palatine foramina; figs. 4 and 5).

19. The mesopterygoid fossa is narrow and deep, and its walls are breached by short, narrow, and slitlike sphenopalatine vacuities (wide fossa in *Papagomys*, its walls breached by spacious vacuities; fig. 8).

20. Surfaces of the pterygoid fossae are flat, the anterior two-thirds of each is complete and without a sphenopterygoid canal (the fossae floors are inclined in *Papagomys* and perforated by small but conspicuous sphenopterygoid canals; fig. 8).

21. The bullae are tiny, both absolutely and relative to size of the braincase, and each one has a long and bony eustachian tube (the bullae are much larger in *Papagomys*, both absolutely and relatively, and the tubes are short and inconspicuous; figs. 4 and 5).

22. The paramastoid processes are small (very large in *Papagomys*; figs. 4 and 5).

23. The dentaries are more slender, with larger coronoid processes, and lower inconspicuous masseteric ridges (figs. 4 and 5).

24. The anterior margins of the nasals and rostrum are set back behind the front faces of the upper incisors (the nasals and rostrum project anterior to the faces of the incisors in *Papagomys*; figs. 4 and 5).

25. Each first upper molar is anchored by four roots: large anterior and lingual, and two small posterior (first molars are five-rooted in *Papagomys*).

26. Each first lower molar has three roots: a large anterior, and two small posterior (four roots in *Papagomys*: a large anterior and posterior, and small labial and lingual).

27. The upper and lower molars are larger, more massive in appearance, and have higher cusps.

28. Each second upper molar is about as long as broad (longer than broad in *Papagomys*; fig. 9).

29. Each third upper molar is larger relative to the other molars in the row and rectangular in occlusal outline (relatively smaller in *Papagomys*, with a squarish occlusal outline; fig. 9).

30. Cusp t9 on all upper molars is either absent or incorporated into cusp t8 (Misonne's, 1969, interpretation); the posterior margin of cusp t8 on the first and second molars is bifurcate and the labial curl may

represent the merged cusp t9, or possibly cusp t7 (cusp t9 is large and prominent on the first and second molars of *Papagomys*; fig. 9).

31. Each third upper molar has a very large and discrete cusp t7 (absent from the third molars of *Papagomys*; fig. 9).

32. Cusps on all the upper molars are discrete and do not merge until after appreciable wear, that found in old adults (cusps on molars of *Papagomys* are discrete only in juveniles; most cusps are merged, particularly the labial row with the central row, in young adults and always in adults; figs. 9 and 12).

33. The occlusal surface of each third upper molar is composed of a large cusp t1, a row formed of two discrete cusps (t4 and t5), and a posterior row formed of cusps t7 and t8, each discrete—the surface is cuspidate, not laminar (behind cusp t1 in *Papagomys*, there is a thick transverse or boomerang-shaped lamina formed of cusps t4, t5, and t6, cusps so completely merged that their individual limits are lost; and a posterior transverse lamina that is elliptical in cross-section and without indication of cuspidation; figs. 9 and 12).

34. The front lamina on each first lower molar is composed of a very large anterolingual cusp that is an elongate ellipsoid in cross-section and an anterolabial cusp that is tiny (fig. 10B) or small, fig. 10C (anterolingual and anterolabial cusps of *Papagomys* are large and shaped as shown in fig. 10A).

35. There is a small anterocentral cusp at the front of each first molar in some specimens, illustrated in figure 10C (absent in *Papagomys*; fig. 10A).

36. The primary cusps on the first and second lower molars are shaped like tear drops in cross-section, with the tapered ends oriented toward the midline of each molar and projecting forward, as shown in figure 10B and C; the anteromedial edges of each cusp usually do not touch and the cusps merge only after much wear, that associated with old adults (the primary cusps are elliptical in cross-section, their anteromedial margins abut against each other, and the cusps merge after relatively much less wear; fig. 10A).

37. The occlusal surface of each third low-

er molar consists of four cusps, their shapes like the cusps on the first and second molars; the cusps merge only after much wear (in *Papagomys*, the occlusal surface of each third molar consists of two thick, transverse laminae, each without evidence of cuspidation; fig. 10).

38. The posterior cingulum on each first and second lower molar is smaller, both absolutely and especially relative to sizes of the molars and other cusps; posterior cingula occur on the third molars in some specimens, as seen in figure 10C (posterior cingula are larger in *Papagomys*, and absent from the third lower molars).

39. An anterolabial cusp is absent from each second and third lower molar (present on the second and third molars of *Papagomys*; fig. 10).

The significance of some of these morphological distinctions between *Papagomys* and *Mallomys* is discussed in another section of this report. The contrasts reflect major structural differences between the giant rats, as well as phylogenetic alliances with species other than one another.

THE HOLOTYPE OF *PAPAGOMYS VERHOEVENI*: Fragments of another kind of large rat from Liang Toge were described by Hooijer (1957b) under the name *verhoeveni*, a species he included in *Papagomys*, and one he thought was closely related to *P. armandvillei*. To *verhoeveni*, Hooijer referred a right maxillary fragment with a complete tooththrow and 18 mandibular pieces with either partial or intact tooththrows. He diagnosed the species on the basis of distinctions in the lower molars between *P. armandvillei* and *P. verhoeveni*, but designated the maxillary fragment and contained tooththrow as the holotype. Seventeen out of the 18 mandibular fragments do represent a species other than *P. armandvillei*; one mandibular portion, specimen 17, is an example of *P. armandvillei*; and the maxillary portion, the holotype, is also a fragment of *P. armandvillei*. The identity of the latter is discussed below.

The portion of the right maxillary contains a complete tooththrow (figs. 12D and 13B; tables 2, 4, 6, and 7). Half of the palatal bridge

is intact, and part of the back of the ventral root of the zygomatic plate is present. Judged by this fragment, the palatal bridge and base of the zygomatic plates must have been similar in configuration and proportions to examples of *P. armandvillei* (fig. 13) and only slightly smaller in size than the large examples of that species. I measured the width of the palatal bridge on the maxillary fragment at the levels of the first and third molars, doubled the values, and determined the breadth of the bony palate to be 4.8 mm. at the level of the first molar, and 6.4 mm. at the level of the third molar, values that fall within the range of variation of those obtained from adults of *P. armandvillei* (table 4). I could also determine that the incisive foramina of the fragment were not long enough to penetrate the palatal bridge past the front margins of the first molars, and that the bridge extended behind the back edges of the third molars by 1–2 mm., the configuration also found in specimens of *P. armandvillei*. The height of the maxilla from the base of the teeth to the lip of the orbit is about the same as it is in examples of *P. armandvillei* (I measured the height at two places: the end of the first molar, and the midpoint of the third molar. The measurements were taken between the bone at the base of the respective tooth and the lip of the orbit. For the maxillary fragment, the height at the end of the first molar is 4.8 mm., that at the midpoint of the third molar is 4.3 mm.; values for a specimen of *P. armandvillei* (MZB 2395) are 4.7 mm. and 4.1 mm., respectively). The back edge of the base of the zygomatic plate sweeps up from a point near the front of the second molar, another characteristic found in *P. armandvillei* (fig. 13). No feature of the maxillary fragment indicates it to come from anything else but a specimen of *P. armandvillei*.

The tooththrow in the maxillary fragment is also similar to those in my sample of Recent *P. armandvillei* in size (table 2), the amount of overlapping among the molars (table 6), proportions of the first and second molars (table 7), occlusal pattern (fig. 12), and number of roots beneath the first molar.

The first upper molar in the fragment is

longer than wide and has five roots. Three rows of cusps form the occlusal surface: the first consists of a large angular central cusp (t2) flanked by smaller, round lingual (t1) and oblong labial cusps (t3); the second row is formed by a large triangular cusp t5, an angular and thick cusp t4 and a wide elongate cusp t6; a large, thick cusp t8 and wide cusp t9 comprise the third row which is nearly transverse; there is no cusp t7 or a posterior cingulum.

The second upper molar is longer than wide, and 20 percent of its length is overlapped by cusp t8 of the first molar. The occlusal surface consists of a large cylindrical cusp t1 and two rows of cusps. Cusp t1 is set off to the lingual side so far that it stands isolated and does not participate in the interlocking between the first and second molars. The first row of cusps is arcuate in configuration and formed by cusps t4, t5, and t6; the second row consists of a large oblong cusp t8 and a wide, thick cusp t9 that together form a nearly transverse structure. There is no cusp t3 at the front of the tooth, but there is a ridgelike thickening of the enamel at the anterolabial corner of cusp t5, forming an angular extension of the front enamel face of that large central cusp; it is this broad surface that is leaned upon by the back of cusp t8 from the front molar, in this way forming the overlapping between the molars. There is no posterior cingulum or cusp t7.

Each third upper molar is slightly longer than wide and 15 percent of its length is overlapped by the chunky cusp t8 of the second molar, which leans against cusp t5. A large, cylindrical cusp t1 stands at the anterolingual corner of the tooth, and like its counterpart in the second molar, is situated to the lingual side and is not involved in the interlocking between the second and third molars. The rest of the occlusal surface is formed by a boomerang-shaped lamina (resulting from the merging of cusps t4, t5, and t6), and a thick, nearly transverse posterior lamina (probably cusps t8 and t9 merged) that is wide, but narrower than the one in front of it. Cusp t3 is absent but there is an enamel ridgelike thickening at the anterolabial cor-

TABLE 4  
Breadths (in Millimeters) of the Palatal Bridge at the First and Third Molars in Samples of *Papagomys armandvillei*, the Holotype of *Papagomys verhoeveni*, and *Hooijeromys nusatenggara*  
(Values for the fossils and subfossils were obtained by the method described in the text)

	Breadth at M <sup>1</sup>	Breadth at M <sup>3</sup>
<i>Papagomys armandvillei</i>		
RMNH 18301, young adult	3.1	5.2
MZB 8308, adult	3.9	6.2
MZB 2394, adult	5.1	6.8
MZB 2395, adult	5.1	6.7
MZB 99, young adult	4.4	5.7
MCZ 51098, young adult	3.2	5.6
<i>Papagomys verhoeveni</i>		
Holotype, adult	4.8	6.4
<i>Hooijeromys nusatenggara</i>		
Specimen 1, young adult	3.8	4.6
Specimen 2, old adult	5.0	6.4

ner of the large cusp t5, forming a configuration similar to that on the second molar and involved in the overlap of the second molar onto the third in a way comparable to the overlap between the first and second teeth. There are no signs of a posterior cingulum or cusp t7.

No part of the occlusal configuration of the tooththrow will distinguish it from the sample of Recent *P. armandvillei* that is available to me. Even among the other characteristics, the only difference I could find that set the tooththrow apart from those in the Recent sample is the relative size of the third molar, which is narrower relative to either the first or second molar than in *P. armandvillei* (table 7), but the difference is slight. For me, the piece of right maxilla and tooththrow that is the holotype of *P. verhoeveni* is simply a fragment from an individual of *P. armandvillei*. The name, *verhoeveni*, is a synonym of *armandvillei*. Hooijer should not be faulted for his identification. Any determination is a hypothesis, and his was based on a very few maxillary tooththrows of *P. armandvillei*, the only ones available to him for compari-

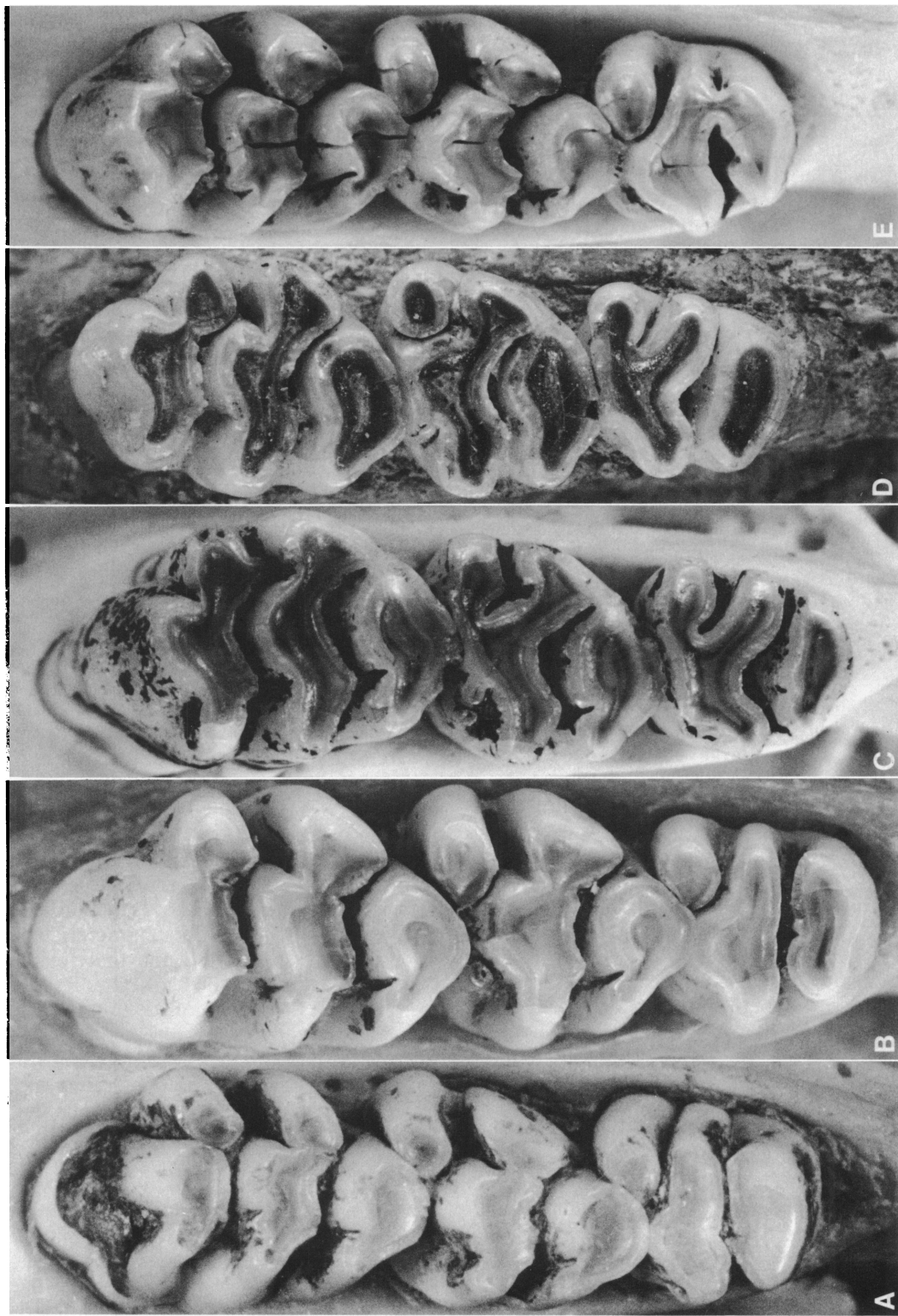


FIG. 12. Variation in occlusal pattern and size among right maxillary tooththrows of young adult and adult *Papagomys armandvillei*. A, RMNH 18301 (holotype); B, UF 9125; C, MCZ 51098; D, the holotype of *Papagomys verhoeveni*; and E, MZB 2395. Approximately  $\times 8$ .

son at the time. I initially agreed with Hooijer's determination until I eventually brought together a much larger sample of Recent *P. armandvillei* than Hooijer was able to study.

Most of the mandibular fragments referred by Hooijer (1957b) to *verhoeveni* do come from individuals of a species related, as Hooijer indicated, to *Papagomys armandvillei*. Because the name, *verhoeveni*, is no longer valid for this species, I propose a new name and provide an emended diagnosis, description, and comparison.

#### ***Papagomys theodorverhoeveni*, new species**

**DIAGNOSIS:** A species of *Papagomys* that is distinguished from *P. armandvillei* by the following features of the lower molars: the molars are smaller; the laminae on each molar are thinner, spaced far from each other, and nearly erect (the laminae are thick, set close together, and slant forward in *P. armandvillei*); the configuration of the anterolabial and anterolingual cusps at the front of each first molar is different, and an antero-central cusp is present (absent from *P. armandvillei*); large and prominent anterolabial cusps on the second and third molars; and prominent labial cusplets on the first and second molars, cusplets that are erect and discrete, not pressed against the adjacent lamina, each shaped more like a large cylindrical cusp rather than a cusplet (anterolabial and anterolingual cusps are smaller and inconspicuous relative to size of the primary cusps in *P. armandvillei*, labial cusplets are absent from nearly all specimens, minute if present).

**HOLOTYPE:** Specimen 12, a piece of right dentary containing a complete molar row from a young adult (fig. 15; table 5). The molars are moderately worn. All are intact except for the third molar where a small chip is lost from the lingual edge of the front lamina.

**LOCALITY AND POSSIBLE AGE:** The fragments are from Liang Toge, a cave near Warukia, 1 km. south of Lepa, in Menggarai Province, western Flores. The deposit at Liang Toge, but not necessarily the precise layer which forms the matrix adhering to the

specimens, has been determined by radiocarbon-dating to be  $3550 \pm 525$  years old (Jacob, 1967).

**REFERRED MATERIAL:** Seventeen mandibular fragments with either partial or intact toothrows, representing as many individuals. Hooijer (1957b) has listed all the specimens (specimen 17 in his table 2 is an example of *P. armandvillei*), described the variation in size and wear among them, and illustrated three mandibular toothrows (pl. 15, figs. 1–3) showing different stages of wear. Molar rows from a young adult and adult are illustrated in figure 15. No examples of maxillary toothrows are known.

**ETYMOLOGY:** Hooijer named this species in honor of Dr. Th. Verhoeven, who collected the material. By combining Dr. Verhoeven's first name with his last, I retain the spirit of Hooijer's intent, as well as his accolade.

**DESCRIPTION AND COMPARISON:** The lower molars of *P. theodorverhoeveni* resemble those of *P. armandvillei* (figs. 15 and 16), including the possession of four-rooted first lower molars, and three-rooted second and third molars. The primary distinctions between them are that *P. theodorverhoeveni* has smaller teeth than *P. armandvillei* (compare the values listed in tables 3 and 5) and the occlusal patterns are more elaborate and differ in other details. The rows of cusps on the lower molars of *P. theodorverhoeveni* are set farther apart than those in *P. armandvillei*, and they are nearly erect, not slanting forward so much as do the rows in *P. armandvillei*. The laminae formed by the rows of cusps are thinner, not only absolutely but relative to size of each tooth, than the thick laminae of *P. armandvillei*.

Shapes of the cusps forming the front lamina on each first lower molar differ between the two species. This lamina is formed by three cusps in *P. theodorverhoeveni*: a large anterolingual cusp, angular in cross-section, in which the enamel of the labial side joins the enamel of the back face to form a ridge running up the posterolabial side of the cusp; an anterolabial cusp, smaller than the anterolingual and elliptical in cross-section, with its long axis meeting the lingual cusp at nearly a right angle; and a small but promi-

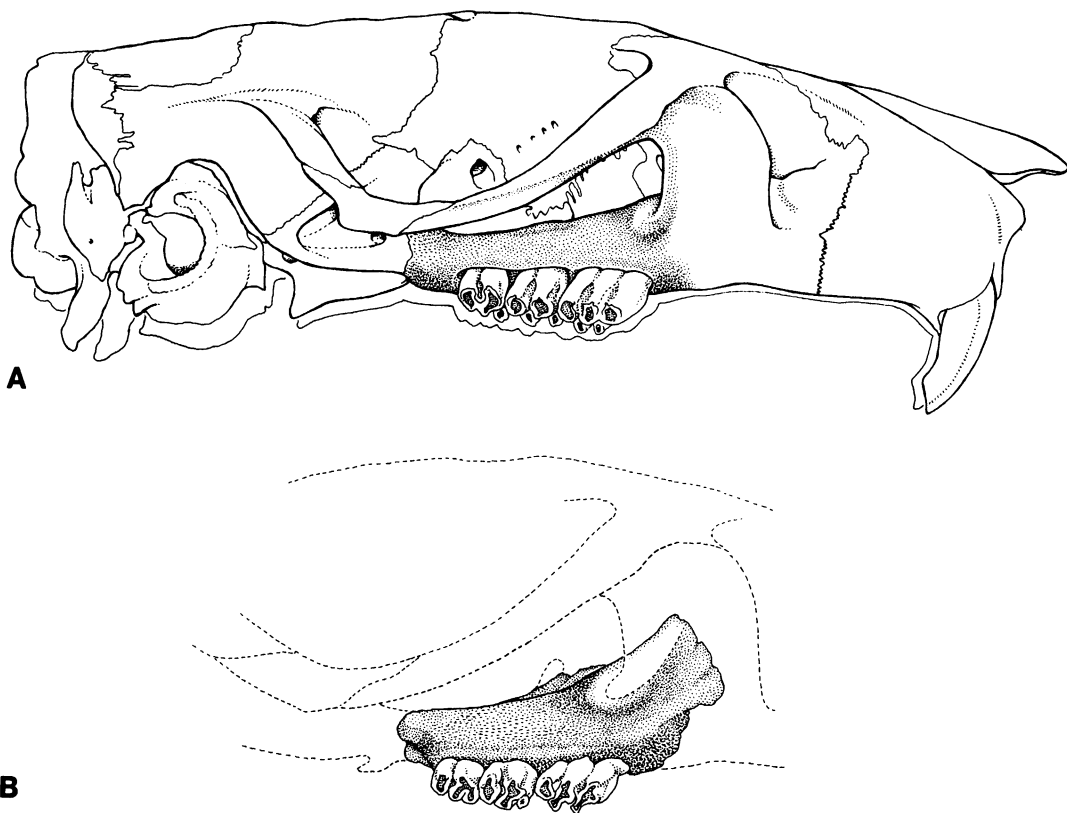


FIG. 13. Views accentuating the maxilla above each toothrow, and the base of each zygomatic plate in *Papagomys*. A, *P. armandvillei*, which has a narrow zygomatic plate. B, the maxillary fragment and reconstruction of the plate in the holotype of *P. verhoeveni*; the configuration is closely similar to that in examples of *P. armandvillei*. The stippled portion in B indicates the shape of the subfossil fragment; that in A is its counterpart. See text for further explanation.

nent anterocentral cusp. This cusp is absent from specimen 10 but occurs on all the others that are complete and not too worn (fig. 15). The anterolingual and anterolabial cusps are discrete and merge only after they are worn nearly to their bases; both form a row set far enough in front of the second row that the posterior enamel ridge rarely joins with that second row, even after much wear; and both form a lamina that is shaped like a right angle after appreciable wear. The front row in *P. armandvillei* is also formed of a large anterolingual cusp and a smaller anterolabial cusp, both shaped like tear drops in cross-section and join along their inner surfaces so the tapered ends lay tightly against each oth-

er and meet the anterior tapered ends of the two elongate cusps from the second row (fig. 15). The two rows of cusps are in contact with each other at their centers in most specimens, whether the teeth are slightly or very worn; the rows may be slightly separated in a few others, but never as far as those in *P. theodorverhoeveni*. The two cusps of the front row in *P. armandvillei* are so tightly pressed against each other that they merge after little wear and form an elongate lamina parallel to the second lamina (fig. 16), rather than one shaped like a right angle, as in *P. theodorverhoeveni*. No anterocentral cusp occurs on the first molars of *P. armandvillei*.

There is also a conspicuous difference be-

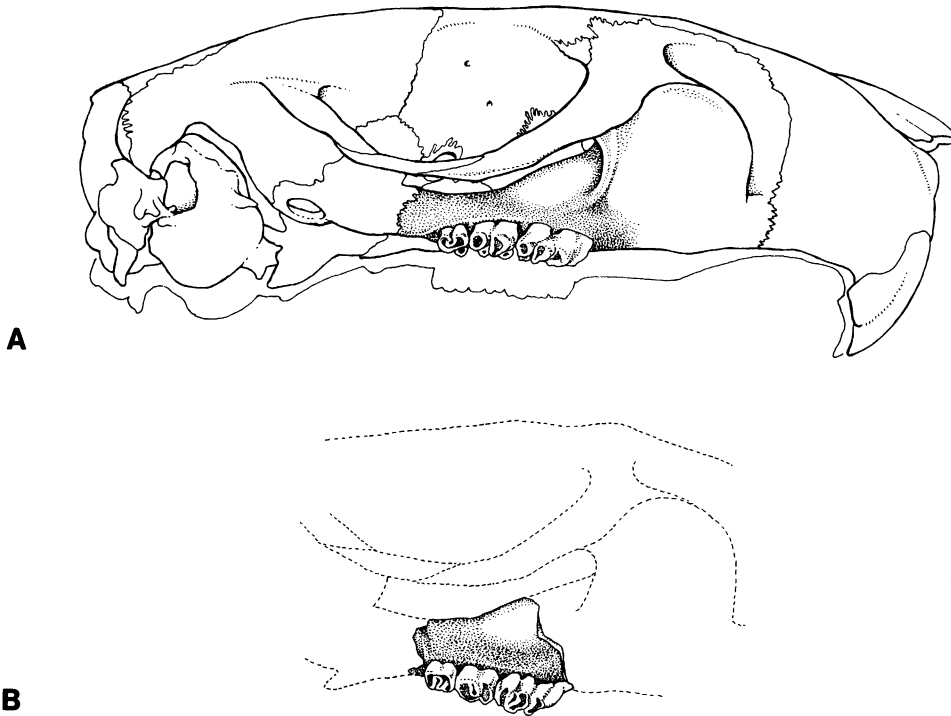


FIG. 14. Configuration of the maxilla above each toothrow, and base of each zygomatic plate in Recent *Mesembriomys* and fossil *Hooijeromys*. A, *Mesembriomys*, with a wide, expansive zygomatic plate and thick maxillary zygomatic root. B, reconstruction of the zygomatic plate and anterior part of the maxilla in *Hooijeromys*, which has a conformation similar to that in *Mesembriomys* and unlike the narrow zygomatic plate and thin maxilla in *Papagomys* (fig. 13A). The stippled portion in B indicates the fossil piece; the stippling in A is its counterpart. See text for further explanation.

tween the two species in shapes of the first laminae on the third molars. In *P. theodorverhoeveni*, this lamina is obviously composed of two elongate cusps that remain distinct after wear; in *P. armandvillei*, the cusps are indistinct and form a thick transverse lamina (figs. 15 and 16).

The two species also differ by the size of the anterolabial cusps on the second and third molars, and the number and size of the labial cusplets on the first and second molars, the primary features used by Hooijer (1957b; he called them buccal tubercles), to distinguish what he had named *verhoeveni* from *P. armandvillei*. A large anterolabial cusp occurs on each second molar in examples of *P. theodorverhoeveni*; it is larger relative to the adjacent primary cusps than is

the anterolabial cusp on each second molar of *P. armandvillei*. There is also an anterolabial cusp on each third molar that may be large and conspicuous (fig. 15B) or small and nearly incorporated into the adjacent lamina (fig. 15C). In the sample of *P. theodorverhoeveni*, there is an anterior labial cusplet on each first molar of all specimens except specimens 9, 10, and 18; a posterior labial cusplet that is found on the first molar in all the specimens; and a posterior labial cusplet on the second molar in each of the specimens. The posterior labial cusplet on each first and second molar is large, cylindrical, and discrete, forming a prominent part of the occlusal surface. Specimens of *P. armandvillei* usually lack labial cusplets; if present, which is rare, they are minute. The large anterolabial

TABLE 5  
Lengths and Breadths (in Millimeters) of Lower Molars from Adult *Papagomys theodorverhoeveni*

Specimen	Length of M <sub>1-3</sub>	Breadths		
		M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
1	13.4	4.1	4.1	3.4
2	13.7	4.0	4.1	3.6
3	13.2	3.8	4.0	3.7
4	13.8	3.9	4.1	3.7
5	—	4.0	4.2	3.6
6	14.0	3.8	4.1	—
7	12.3	3.6	—	3.3
8	—	3.9	—	—
9	—	4.2	—	—
10	—	3.8	—	—
11	13.4	3.7	3.9	3.6
12 (Holotype)	13.0	3.7	3.9	3.6
13	14.0	3.7	4.1	4.0
14	12.2	3.5	3.6	—
15	—	3.5	—	—
16	12.0	—	—	—
18	—	4.2	—	—
$\bar{X} \pm SD$ (all specimens)		13.2 $\pm$ .7	3.8 $\pm$ .2	4.0 $\pm$ .2
$\bar{X} \pm SD$ (N = 8; specimens 1-5 and 11-13)			3.9 $\pm$ .1	4.1 $\pm$ .1

cusps, anteroventral cusps, anterolingual cusps, and labial cusplets are partly responsible for the complex occlusal patterns in *P. theodorverhoeveni*. In contrast, *P. armandvillei* does not have such elaborate occlusal surfaces because there is no anteroventral cusp, the anterolabial cusps on the second molars are relatively smaller, and labial cusplets are absent.

Other than being smaller, the dentaries and lower incisors of *P. theodorverhoeveni* do not differ significantly from those in *P. armandvillei*. The enamel layers of the few intact lower incisors in my sample of *P. theodorverhoeveni* are orange, as they are in *P. armandvillei*. Study of dentaries that are better preserved than those I studied may reveal mandibular distinctions between the two species.

The laminae on the molars in *P. theodorverhoeveni* are set far apart and this configuration may be associated with the presence of relatively large anterolabial cusps and

prominent labial cusplets. Located as they are at the anterolabial margins of the laminae, the anterolabial cusps and labial cusplets add surface area to the labial sides of the laminae, extending the width of each and increasing its bulk from front to back. *Papagomys theodorverhoeveni* must have been an animal that in body size was a bit smaller than the larger examples of *P. armandvillei* or about the same size as smaller individuals of that species. The combination of smaller molars with more complex occlusal configurations than are found in *P. armandvillei* suggests that *P. theodorverhoeveni* probably utilized different foods than *P. armandvillei*, and exploited a different part of the ecosystem.

The third species endemic to Flores is smaller than either *Papagomys armandvillei* or *P. theodorverhoeveni* and is known by a few fragments from older deposits. Hooijer (1967a, p. 154) referred to them when he wrote, "The fauna associated with the two

stegodonts at Ola Bula in Flores (another site is Boa Leza) consists only of a tantalizing, as yet unidentified, murine rodent presumably related to the giant prehistoric cave rats of the island . . . it is smaller than the smallest of the cave forms (*Papagomys verhoeveni* Hooijer) and possibly directly ancestral to it, but as yet poorly represented." That unidentified murid is named and characterized below.

#### HOOIJEROMYS, NEW GENUS

**DIAGNOSIS:** A murid of moderately large body size that is morphologically more similar to *Papagomys armandvillei* and *P. theodorverhoeveni* than to any other species, but that is distinguished from *Papagomys* by the following features: the maxilla above each toothrow is higher; the basal posterior root of the zygomatic plate is chunky and arises from the maxilla at a point near the end of the second molar, a structure suggesting a large zygomatic plate in which the anterior spine is convex in outline and juts forward well anterior to the dorsal root of the zygomatic arch; small teeth set in a very wide bony palate; long incisive foramina extending posterior to the front margins of the molar rows; upper toothrows in which the second molar is broader than long; low cusps; cusp t2 large and gourd-shaped, with its bulging base at the root and its body slanting back from the maxillary surface at a 45-degree angle; simple cusp patterns on the upper molars; thin, wide rows of cusps forming transverse laminae; the third upper molar narrower relative to the second; and the lower molars (if correctly associated with the genus) also with low cusps and wide simple laminae.

**TYPE SPECIES:** *Hooijeromys nusatenggara*, new species.

**INCLUDED SPECIES:** The type species only.

**ETYMOLOGY:** I name the genus in honor of Dr. D. A. Hooijer, whose careful and intelligent research with fossils from Indonesia in general and Flores in particular has helped to elucidate the morphological and adaptive

diversity of the mammalian fauna that once lived in the Far East.

#### *Hooijeromys nusatenggara*, new species

**DIAGNOSIS:** Because there is only one species in the genus the specific and generic diagnoses are the same.

**HOLOTYPE:** Specimen 1, a piece of right maxilla containing all three molars (the third tooth is slightly separated from the rest of the toothrow; if intact, it would press directly against the back of the second molar). The toothrow and part of the maxillary fragment is illustrated in figure 17; values from measurements of the teeth, and ratios, are listed in tables 6–9.

**LOCALITY:** Olabula (also spelled Ola Bula), on the Soa Plateau, between Olakile and Mengeruda (lat. 8°30' to 8°45' S, long. 121°15' E) in Central Ngada Province, Flores (a map and photographs of the site are in Maringer and Verhoeven, 1970). Remains of *Stegodon trigonocephalus florensis* were found at Olabula and according to Hooijer (1957a, p. 119), those fossils "were found lying on the grass-covered surface of a partially eroded sandstone layer, and occur over an area almost one kilometer long by a width of several hundred meters. Along the Ai Sissa, which intersects the upland plain, the fossils protrude from the river banks. Fossils were collected both . . . from the surface of the plain as well as from the river banks and from the foot of a hill rising above the plain at Ola Bula." Dr. Th. Verhoeven told me that all the pieces I have identified as *Hooijeromys* were excavated out of sandstone—none of them were found on the surface. Sandstone matrix still adheres to the maxillary fragments of the holotype and specimen 2.

**AGE:** Hooijer (1957a, p. 120) gives "Middle or Upper Pleistocene" for the age of the sediments at Olabula. No radiometric dates are yet available.

**REFERRED MATERIAL:** In addition to the holotype, there is another right maxillary fragment from Olabula containing a complete toothrow with teeth so worn that the original

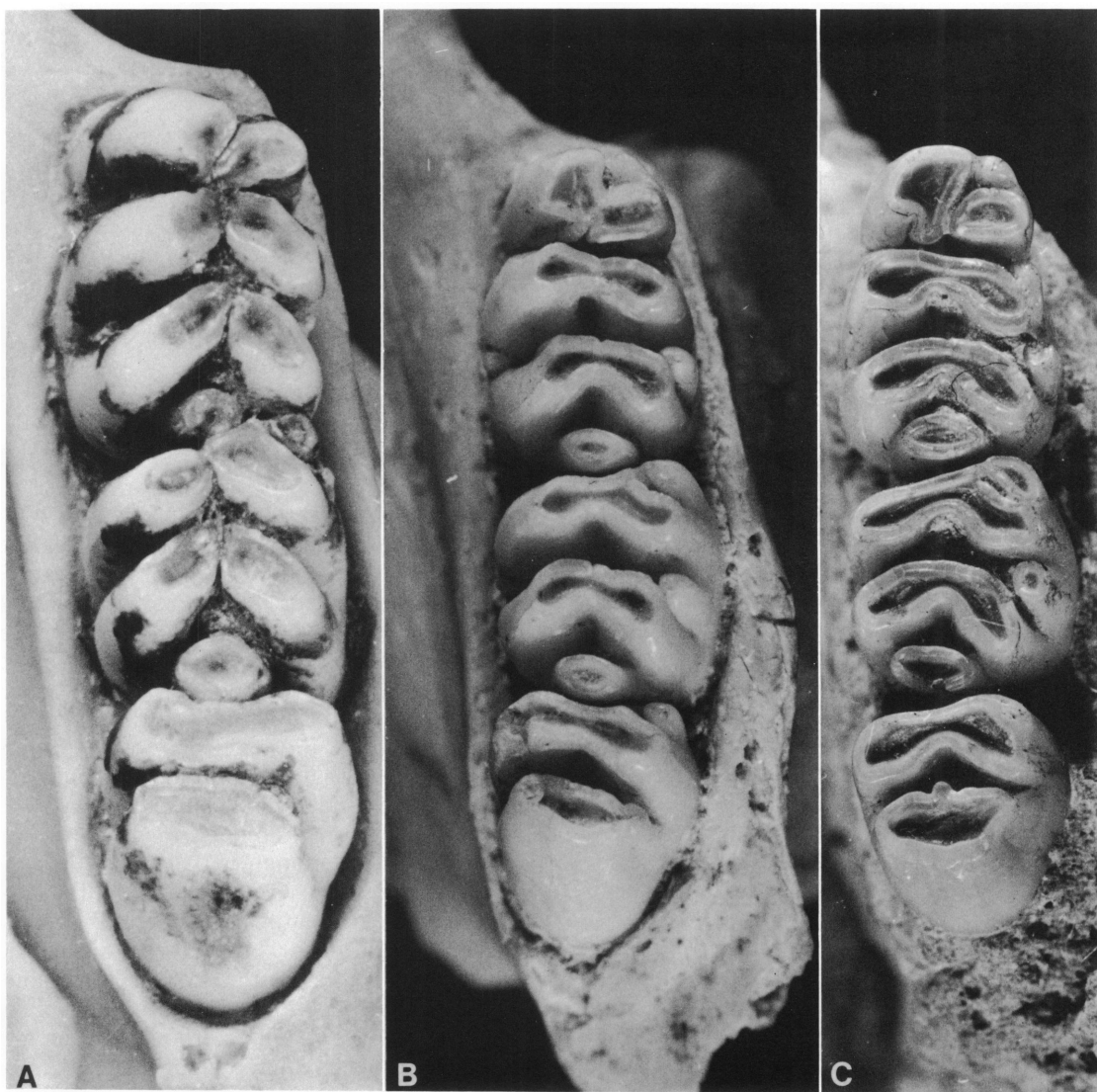


FIG. 15. Right mandibular tooththrows of *Papagomys*. A, *P. armandvillei*, young adult (RMNH 18301, holotype); B, *P. theodorverhoeveni*, young adult (specimen 12, holotype); and C, *P. theodorverhoeveni*, adult (specimen 4). All approximately  $\times 8$ .

Note in B and C: the anterocentral cusps, the configuration formed by the anterolabial and anterolingual cusps on each first molar, the labial cusplets, and the laminae spaced far apart—all contrasts with the molars of A, and with the molar rows in figure 16.

occlusal patterns of the cusps are no longer evident (specimen 2, fig. 17). There is also an isolated right upper third molar (specimen 3) obtained at Boaleza (also spelled Boa Leza). Boaleza is, according to Hooijer

(1972), a hill a few miles west of Olabula (see the map in Maringer and Verhoeven, 1970). There are also three lower molars from Boaleza that I cautiously associate with *H. nusatenggara*.



FIG. 16. Variation in occlusal pattern and size among right mandibular tooththrows of adult *Papagomys armandvillei*. A, MCZ 51098; B, UF 9125; and C, MZB 2395. All approximately  $\times 8$ . Contrast these occlusal patterns with those of *P. theodorverhoeveni*, particularly the adult (specimen 4), in figure 15.

**ETYMOLOGY:** The specific name, *nusatenggara*, originally derives from Malay; it means southeast islands and is the Indonesian designation for the Lesser Sunda Islands, that chain which includes the island of Flores. *Hooijeromys nusatenggara* is, therefore, Hooijer's rat of the Southeast Islands.

**DESCRIPTION AND COMPARISONS:** Each of the three specimens that can be definitely identified as *Hooijeromys nusatenggara* contains different information. The holotype shows what the shapes and occlusal patterns of the upper teeth were like in young adults in which the teeth are moderately worn.

TABLE 6  
Lengths (in Millimeters) of M<sup>2</sup> (LM<sup>2</sup>) and M<sup>3</sup> (LM<sup>3</sup>), Amount M<sup>1</sup> Overlaps M<sup>2</sup> (OM<sup>1</sup>) and M<sup>2</sup> Overlaps M<sup>3</sup> (OM<sup>3</sup>) and Dental Ratios (in Percent) from Samples of *Papagomys*, *Hooijeromys*, and *Komodomys*

	LM <sup>2</sup>	LM <sup>3</sup>	OM <sup>1</sup>	OM <sup>2</sup>	$\frac{OM^1}{LM^2}$	$\frac{OM^2}{LM^3}$
<i>Papagomys armandvillei</i>						
MCZ 51098	4.9	3.9	0.9	0.8	18	21
MZB 2395	4.8	3.9	0.9	1.1	18	17
UF 9125	5.2	4.1	0.7	0.9	22	21
Liang Toge (M <sup>1-2</sup> )	5.3	—	1.0	—	19	—
<i>Papagomys verhoeveni</i>						
holotype	4.6	3.9	0.9	0.6	20	15
<i>Hooijeromys nusatenggara</i>						
holotype	3.7	3.2	0.6	0.6	16	19
<i>Komodomys rintjanus</i>						
$\bar{X} \pm SD$ (N = 9)	2.6 $\pm$ .1	2.1 $\pm$ .1	0.5 $\pm$ 0.1	0.5 $\pm$ 0.1	19	19
Range	2.5–2.6	1.9–2.4	0.4–0.6	0.4–0.6	15–24	19–30

Widths for the palatal bridge can be determined from that specimen, as can an image of the configuration of the zygomatic plate at its base. The second specimen illustrates the upper toothrow of *H. nusatenggara* when the occlusal area is worn down to nearly a flat surface, the degree of wear typical of old adults. Values for measurements of the palatal bridge can also be obtained from that specimen, and the base of the zygomatic plate is preserved well enough to indicate what the zygomatic plate was probably like in the species. Specimen 3, the upper third molar from Boaleza, resembles the third molar of the holotype in size and shape. Cusp t1 is missing but the two laminae are intact and shaped like those in the holotype, differing by being worn down slightly farther, which indicates the rat was probably older than the animal represented by the holotype.

There is enough of the palatal bridge on the left side of each maxillary fragment, and enough of the maxilla and base of the zygomatic plate above each toothrow to indicate that the molar rows were short and set in a wide bony palate penetrated by incisive foramina; and that each zygomatic plate was robust and probably very wide, expansive enough to project well anterior to the dorsal root of each zygomatic arch—a configura-

tion, size, and proportion dissimilar to the shapes, dimensions, and proportions in *P. armandvillei*. Those maxillary features, combined with the dental characters, point to a species in the murid fauna on Flores that was ecologically different from *P. armandvillei*, *P. theodorverhoeveni*, and probably any other known Floresian native rat.

I was able to obtain values for breadths of the palatal bridge at levels of the first and third molars from the holotype and from specimen 2. In each fragment, the palatal bridge between the toothrows was absolutely as wide or wider than the palatal bridges in specimens of *P. armandvillei* of approximately comparable age (table 4). Thus, the teeth of *H. nusatenggara* are not only absolutely smaller than those in *P. armandvillei* (tables 4 and 8), but also much smaller relative to the breadth of the bony palate. Enough is left of the anterior portion of each palatal bridge to indicate that the posterior limits of the incisive foramina ended 1–1.5 mm. past the anterior alveolar margins of the first molars in each specimen; the incisive foramina were relatively longer in *H. nusatenggara* than they are in *P. armandvillei*—in the latter, the foramina end 1–4 mm. in front of the anterior alveolar edges of the first molars. Not enough of the bony palate

TABLE 7  
 Ratios (in Percent) Involving Lengths and Breadths of Molars from Samples of *Papagomys*, *Hooijeromys*,  
*Spelaeomys*, and *Floresomys*  
 (Based on data in tables 3, 4, 6, 8, 10–12)

	$\frac{BM^2}{LM^2}$	$\frac{BM^2}{BM^1}$	$\frac{BM^3}{BM^1}$	$\frac{BM^3}{BM^2}$	$\frac{BM_2}{BM_1}$	$\frac{BM_3}{BM_1}$	$\frac{BM_3}{BM_2}$
<i>Papagomys armandvillei</i>							
MCZ 51098	90	—	—	—	—	—	—
MZB 2395	89	—	—	—	—	—	—
UF 9125	96	—	—	—	—	—	—
Liang Toge	94	96	—	—	—	—	—
Recent (N = 8)	—	96	83	87	107	100	93
<i>Papagomys verhoeveni</i>							
holotype	96	96	78	82	—	—	—
<i>Papagomys theodorverhoeveni</i>							
M <sub>1-3</sub> (N = 8)	—	—	—	—	105	95	90
<i>Hooijeromys nusatenggara</i>							
holotype	103	93	71	76	—	—	—
specimen 2	103	95	76	78	—	—	—
<i>Spelaeomys florensis</i>							
holotype	—	95	75	79	—	—	—
specimen 2	—	95	75	79	—	—	—
M <sub>1-3</sub> (N = 16)	—	—	—	—	105	91	86
<i>Floresomys naso</i>							
M <sub>1-3</sub> (N = 2)	—	—	—	—	105	91	87
<i>Komodomys rintjanus</i>							
M <sub>1-3</sub> (N = 13)	96	76	79	—	—	—	—
M <sub>1-3</sub> (N = 13)	—	—	—	—	116	105	91

remains on either specimen of *H. nusatenggara* to determine where the back margin of the palatal bridge was situated relative to the toothrows. When viewed from a ventral perspective, *H. nusatenggara* had a wide palatal bridge—as wide as in specimens of the large-bodied *P. armandvillei*—separating narrow teeth in short toothrows, and incisive foramina penetrating past the fronts of the first molars, a configuration different from that in *Papagomys*.

The back portion of the zygomatic plate at its base is distinctively shaped in the two specimens of *H. nusatenggara*, and different from the shape in *P. armandvillei*. Part of the maxillary between the bases of the teeth and the lip of the orbit is intact and undistorted in specimen 2 of *H. nusatenggara*,

and includes a piece of the back root of the zygomatic plate. A similar piece is present on specimen 1, but the matrix has pushed out the walls of the maxillary fragment and its actual shape is distorted. Judged from the configuration in specimen 2, that portion of the maxillary between the base of the toothrow and the lip of the orbit was high and the back root of the zygomatic plate was thick and robust. In specimen 2, the height of the maxillary fragment from the base of the teeth to the lip of the orbit at a point near the end of the first molar is 5.2 mm., the height at the midpoint of the third molar is 4.3 mm.; values for a specimen of *P. armandvillei* (MZB 2395) are 4.7 mm. and 4.1 mm., respectively (I explained how I took these measurements in the account of *P. theo-*

TABLE 8  
Lengths and Breadths (in Millimeters) of Upper  
Molars from Adult *Hooijeromys nusatenggara*

	Specimen 1 (Holotype)	Specimen 2	Specimen 3
Length of M <sup>1-3</sup>	12.4	11.5	—
Breadth of M <sup>1</sup>	4.1	3.7	—
Breadth of M <sup>2</sup>	3.8	3.6 <sup>a</sup>	—
Breadth of M <sup>3</sup>	2.9	2.8	3.0

<sup>a</sup> An estimate; the tooth is incomplete.

*dorverhoeveni*). The maxillary segment in specimen 2 is much higher than in examples of *P. armandvillei*. And though specimen 1 of *H. nusatenggara* is slightly distorted, it is evident that the section of the maxilla between the base of the toothrow and the lip of the orbit was nearly as high as that in specimen 2. Part of the maxillary portion is a large swelling representing the posterior root of the base of the zygomatic plate. The swelling begins at a point near the back of the second molar and expands to form the high, thick, and robust base forming the back of the zygomatic plate. In specimens of *P. armandvillei*, the back root of the zygomatic plate is gracile, not as thick and high, and begins to curve up from a point farther up the toothrow, near the end of the first molar. The configuration in *P. armandvillei* is that associated with a moderately narrow zygomatic plate in which the anterior edge is usually erect and projects anterior to the dorsal root of the zygomatic arch by only a few millimeters (fig. 13A). The thick and chunky base in specimen 2 of *H. nusatenggara* was likely associated with a very wide zygomatic plate in which the anterior edge extended appreciably anterior to the front of the dorsal root of the zygomatic arch (fig. 14B). The shape of the zygomatic plate in *Mesembriomys gouldii* from Australia, and the projection of its anterior spine beyond the dorsal root of the zygomatic arch (fig. 14A) are examples of the configuration; the posterior base of the zygomatic plate in that species may be a good approximation of what the

zygomatic plate was like in *H. nusatenggara*.

The following description of upper molars is based on the moderately worn teeth of the holotype of *H. nusatenggara*. The teeth have some features that are like those in the upper molars of *P. armandvillei* but are unlike that species in many details. There are five distinct roots under each first upper molar in *H. nusatenggara*, four under each second molar, and three under each third molar. The cusps slant backward so the first tooth overlaps 16 percent of the second molar and the second overlaps 19 percent of the third, features also shared by *P. armandvillei* (table 6). The second molar of *H. nusatenggara* is squarish, slightly wider than long, whereas the second molar is definitely longer than wide in *P. armandvillei* (table 7). The third molar of *H. nusatenggara* is narrower relative to the second molar than in samples of the other species (table 7). The length of the third molar in *H. nusatenggara* (28 percent, mean of two specimens) is similar to the relative length of the third molar in *P. armandvillei* (25 percent, mean of eight specimens). Finally, *H. nusatenggara* has low cusps relative to those in *P. armandvillei*.

The occlusal configurations on the upper molars of *H. nusatenggara* resemble those in *P. armandvillei*, but differ in details. As in the latter species, there is no cusp t7 or posterior cingulum on any of the teeth in *H. nusatenggara*. But unlike those in *P. armandvillei*, the rows of cusps on the first and second molars are straighter and form transverse laminae, especially on the second molar.

Among examples of the two species, the front row of cusps on the first molar in *H. nusatenggara* is unique. It is formed of a small round labial cusp and a larger oblong lingual cusp flanking a large round central cusp that slopes out and forward from its small wear surface to a thick bulging base; the anterior face of the cusp slants outward from between the adjacent cusps at about a 45-degree angle from the occlusal surface to the surface of the maxilla. The three cusps are discrete and would remain so after con-



FIG. 17. Maxillary fragments and molar rows of *Hooijeromys nusatenggara* collected at Olabula, Flores. A, adult (specimen 1, the holotype); B, old adult (specimen 2). The anterior edge of the palatal bridge in specimen 1 marks the approximate posterior boundary of the incisive foramina. Approximately  $\times 8$ .

siderable wear, and their wear surfaces are aligned nearly straight so the occlusal area of the lamina they form is transverse. The cusps are less distinct in *P. armandvillei*, the lamina slants back and toward the lingual side, and the central cusp of that species is slanted at about a 30-degree angle from wear surface to maxilla. Cusp t4 in the second lamina on the first molar in *H. nusatenggara* is directed forward so it is about on the same line as the opposite labial cusp, whereas it is set farther back in *P. armandvillei*; the result is a straighter row of cusps in *H. nusatenggara* than in *P. armandvillei*, and thus a nearly transverse lamina. The third lamina on the first molar of *H. nusatenggara* is thin-

ner and straighter than the lamina in *P. armandvillei*.

The two laminae on the second upper molar of *H. nusatenggara* are thin, wide and transverse, their width accentuating the wide tooth and its squarish occlusal outline. The first lamina is nearly straight—only gently arched in the middle—in *H. nusatenggara* because the boundaries of the cusps are less discrete and the labial cusp is set forward nearly in line with the middle and lingual cusps. The first lamina on the second molar of *P. armandvillei* is clearly arcuate and slanted back toward the lingual side because the cusp boundaries are more evident and the labial cusp is set more posterior relative

TABLE 9  
Breadths of Isolated Lower Molars (in Millimeters) from Adult *Hooijeromys* Collected at Boaleza

	Specimen 1	Specimen 2	Specimen 3
Breadth of M <sub>1</sub>	3.2 <sup>a</sup>	—	—
Breadth of M <sub>2</sub>	—	—	—
Breadth of M <sub>3</sub>	—	3.5	3.1

<sup>a</sup> An estimate: the tooth is incomplete.

to the other two cusps forming the lamina. The second lamina on the tooth in *H. nusatenggara* is also straighter—essentially transverse—than its counterpart in *P. armandvillei*. There is a small low tubercle-like mound on the front and labial side of the second molar of *H. nusatenggara* that probably represents cusp t3.

The occlusal surface of the third upper molar of *H. nusatenggara* resembles that in some specimens of *P. armandvillei*, those examples in which the front lamina is shaped like a boomerang, but differs in that there is a small but distinct anterolabial tubercle that represents cusp t3 (a cusp that is usually absent in *P. armandvillei*); and the posterior lamina is narrower relative to the front lamina, and transverse in position (it is nearly the same width as the first lamina and directed back and to the lingual side in *P. armandvillei*.)

The interlocking configuration among the upper molars of *H. nusatenggara* is like that I described for the upper tooththrows in some examples of *P. armandvillei*: the back margin of cusp t8 leans against the front face of cusp t5 and the anterolabial surface of the adjacent cusp t1. Cusp t8, t5, and t1 form the interlocking between the first and second teeth, and between the second and third molars.

In table 9 I have listed measurements of three lower teeth that were found at Boaleza: a partial left first molar (specimen 4; fig. 18) from an adult, a left third molar (specimen 5) from a very young adult, and a right third molar (specimen 6; fig. 18) from an adult. The anterior half of the first molar is simple

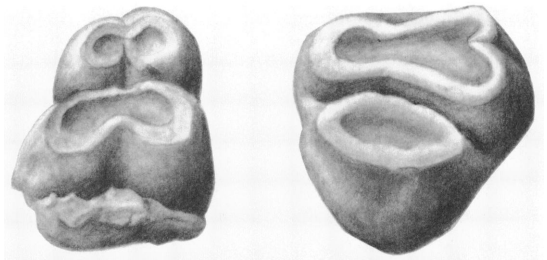


FIG. 18. Isolated lower molars of *Hooijeromys* collected at Boaleza, Flores. Left side: partial left first molar from an adult (specimen 1, breadth is 3.2 mm.). Right side: right third molar from an adult (specimen 3, breadth is 3.1 mm.).

in occlusal configuration, consisting of two rows of low cusps. The first is formed of a large squarish anterolingual cusp and a smaller anterolabial one. There is an enamel mound at the posterior base of the anterolingual cusp. The second row consists of two thick and elongate cusps; both rows are straighter than their counterparts on the molars of *P. armandvillei*. There is no antero-central cusp on the anterior margin of the tooth or cusplets on the labial margin. Each lower third molar has two low and thick transverse laminae, with no distinction between the cusps forming them. The front lamina is thick and supports a small anterolabial cusp. The second lamina, a thin oval in cross-section, is narrower than the front one. The two third molars are similar in shape, differ in amount of wear on their occlusal surfaces, and slightly in size; certainly they are from the same species. The fragment of first molar is probably also from the same species.

I cannot definitely identify the lower molars as being part of tooththrows from *H. nusatenggara*, but each is the right size for a lower molar of that species, each has low cusps that go along with the low cusps on the upper molars, and each has simple laminae that complement the shapes of the laminae on the upper teeth. The lowers are not from a species of *Rattus*, or from any other murid besides *H. nusatenggara*, that has been found on Flores. That they belong to a simple-toothed rat with a *Papagomys*-like

structure, is evidenced by the shapes of the front cusps on the first molar, which though low and simple, are reminiscent of the shapes in the front cusps on the first molars of *P. armandvillei*. The isolated lowers may represent a different, yet undescribed species, but I think not. I cautiously associate them with *H. nusatenggara*. If they do represent the lower molars of that species, then they are shorter-cusped and do not have occlusal patterns as elaborate as those in *P. theodorverhoeveni*, and are more like the simpler occlusal patterns on the lower molars in *P. armandvillei*.

*Hooijeromys nusatenggara* was apparently quite a different rat from either *Papagomys armandvillei* or *P. theodorverhoeveni* if my reconstruction of parts of the animal are correct. Based on the remnants of the maxillae associated with the toothrows, I estimate that the species was a rat of moderately large body size, something similar to *Mesembriomys gouldii* of Australia or *Uromys anak* of New Guinea, in which adults would have a combined head and body length of 275–350 mm., and a skull length of 60–70 mm. The toothrows were set in a wide bony palate, a configuration similar to that in *Mesembriomys* or *Uromys*, for example. The incisive foramina were long enough to penetrate between the toothrows. The zygomatic plates were very wide; their anterior spines were probably convex in outline, and must have projected far anterior to the front margins of the dorsal roots of the zygomatic arches (fig. 14). The teeth were low-crowned, simple in cuspidation, with broad second molars, and rows of thin and wide cusps forming transverse laminae. I cannot discern whether the rat was terrestrial or arboreal in habitus.

*Papagomys armandvillei*, *P. theodorverhoeveni*, and *Hooijeromys nusatenggara* are, or were, rats of large body size with simple or moderately complex occlusal patterns on the upper and lower molars. There is a fourth species of large-bodied rat represented by subfossil fragments found in the same cave deposits at Liang Toge that yielded the samples of *P. armandvillei* and *P. theodorverhoeveni*. *Spelaeomys florensis* is the

name Hooijer (1957b) gave it. The species contrasts sharply with the other three because of the very complex occlusal surfaces on its molars, which form some of the most elaborate patterns among murids from the Indo-Australian region. I summarize its characteristics below.

#### *Spelaeomys florensis*

Two maxillary fragments and 30 pieces of mandibles (representing 32 individuals), all with teeth, comprise the sample of *Spelaeomys florensis*. The holotype is a right maxillary fragment with a complete tooththrow from a young adult; the cusps are slightly worn. The other piece of maxilla is from the left side of an adult and also contains a complete tooththrow, one in which the occlusal surface is worn more than the holotype. Hooijer (1957b, pl. XIV, figs. 5 and 6) provided clear illustrations of both specimens as well as data from measurements of the toothrows and individual molars, values I have listed in table 10.

Nineteen of the 30 mandibular fragments of *S. florensis* contain complete tooththrows; the other pieces lack particular molars. Summaries of values for lengths of tooththrows and breadths of molars, all obtained by Hooijer (1957b), are listed in table 11.

*Spelaeomys florensis* was probably similar to *Papagomys theodorverhoeveni* in body size, for the lengths of lower tooththrows and breadths of individual molars in both species are close (tables 5 and 11). There is enough of the maxilla associated with each tooththrow of *S. florensis* to indicate that the palatal bridge and basal root of the zygomatic plate of that species were similar in configuration and proportion to those structures in *P. armandvillei*. The small fragment of palatal bridge on the older of the two specimens of *S. florensis* is about as wide as that part of the bridge in examples of *P. armandvillei*; since the teeth of those two species are also similar in size, the hard palate of each was like the other in the size of tooththrows relative to breadth of bony palate. In both specimens of *S. florensis*, the back of the zygomatic plate at its base begins to sweep out from a point near the back of the first molar; likely

TABLE 10  
Lengths and Breadths (in Millimeters) of Upper  
Molars from Adult *Spelaomys florensis*  
(Values from Hooijer, 1957b)

	Specimen 1 (Holotype)	Specimen 2
Length of M <sup>1-3</sup>	13.4	14.6
Breadth of M <sup>1</sup>	4.0	4.3
Breadth of M <sup>2</sup>	3.9	4.1
Breadth of M <sup>3</sup>	3.1	3.2

the zygomatic plates of *S. florensis* were narrow, resembling the configuration in *P. armandvillei*.

Any similarities between *S. florensis* and *P. armandvillei* end with maxillary features because the occlusal patterns formed by cusps on the teeth of *S. florensis* are elaborate compared with the simple patterns of *P. armandvillei*, or even *P. theodorverhoeveni* and *H. nusatenggara*. The cusp patterns on molars of *S. florensis* are the most elaborate of the large rats native to Flores, and even more complex than the occlusal designs in *Mallomys rothschildi* from New Guinea, *Lenomys meyeri* of Sulawesi, *Crateromys schadenbergi* from the Philippines, or *Coryphomys buehleri* of Timor, the other species of giant complex-toothed rats that Hooijer (1957b) compared with *S. florensis*.

All three upper molars of *S. florensis* are longer than wide, nearly rectangular in occlusal outline. The width of the second molar relative to the first is similar to the proportions of these teeth in samples of *P. armandvillei* and *H. nusatenggara*, but the third molar is narrower, relative to either the first or third, than in samples of those other two genera (table 7). Each first molar in *Spelaomys* has four roots: a large bilobed anterior root extending from lingual to labial side, a small lingual root, and two small posterior roots. Each second molar is anchored by four roots, two anterior and two posterior; and each third molar has three roots, two anterior and a wide posterior. Cusps on all the upper teeth are high, discrete, and nearly erect so the first molar abuts against the second, and the second against the third

with only slight overlapping (fig. 19). The cusps are distinct and remain so even after appreciable wear.

There are 11 cusps on each first upper molar in Hooijer's sample. Nine of these are large and arranged in series of three in three rows; a smaller cusp t1bis (clearly shown in Hooijer's illustrations, but absent from the molar depicted in fig. 19) sits between cusp t1 and cusp t2 of the first row; and a small oblong posterior cingulum is situated at the posterolabial margin. The lingual cusps are oval in cross-section; each labial cusp is wide at its outer side and attenuate at its other end; both labial and lingual cusps are positioned so they slant back and inward. The central cusps are large, thick and either oblong or triangular in cross-section.

Each second upper molar has nine cusps; cusp t1bis and cusp t2, both present on the first molar, are absent. Except for cusp t1 and cusp t3, cusps are shaped and positioned like their counterparts in the first molar. Cusp t1 is large, round in cross-section, and sits back from the cingular margin of the tooth; it is discrete and set back far enough so it does not lean against the posterior margin of the first molar. Cusp t3 is small, erect, and cylindrical. It is nestled between the large central and labial cusps of the row behind, and its anterolingual margin presses against the posterolabial margin of the posterior cingulum on the first molar.

Seven cusps form most of the occlusal surface of each third upper molar: a large elongate cusp t1; a small, cylindrical cusp t3; an elongate cusp t4, which is positioned so its long axis is nearly transverse; a large cusp t5, which is a smaller version of each central cusp on the first and second molars; an elongate and transverse cusp t6 that sits just back of cusp t5; a large cusp t7 on the lingual side, and a cusp t8 on the posterolabial side, each elongate in cross-section, and forming the back of the tooth. Cusp t2 is absent from the third molar, as well as a cusp t9 and a posterior cingulum, if my interpretation of the cusp sequence is correct.

The upper molars of *S. florensis* abut against each other with only slight overlap; the overlap is not as extensive, or the inter-

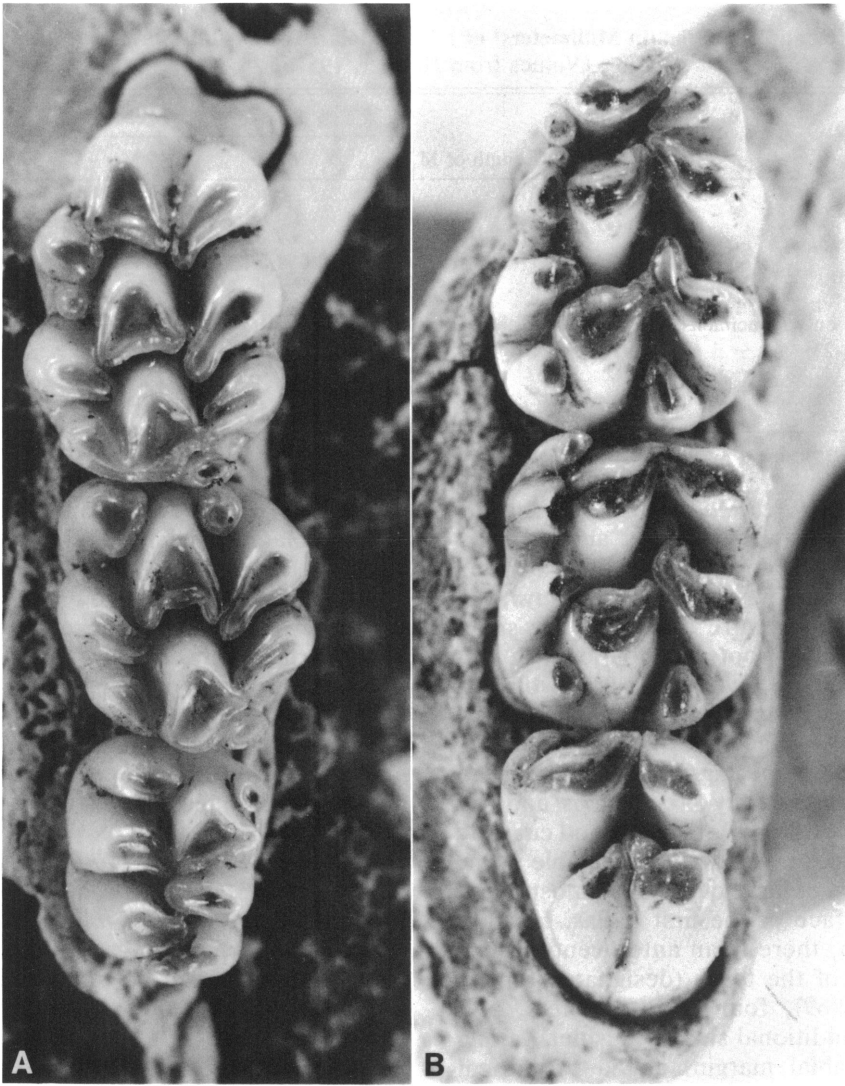


FIG. 19. Left maxillary (A) and mandibular (B) subfossil toothrows from adults of *Spelaeomys florensis*. Approximately  $\times 8$ . The upper molar row is from LT 205, the lower from LT 85, specimens in the Rijksuniversiteit Utrecht that were lent to me by Dr. A. van de Weerd. The occlusal patterns of these specimens are typical of *S. florensis* except that a cusp t1bis is missing (usually present) and there is an auxillary cusp in back of cusp p1 (usually absent) on the first upper molar.

locking among the molars as tight as it is among the upper molars of either *P. armandvillei* or *H. nusatenggara*. In *S. florensis*, the backs of cusp t7, cusp t8, and the posterior cingulum lean against the fronts of cusp t1, t5, and t3 of the molar behind.

The lower molars of *S. florensis* have been

illustrated by Hooijer (1957b: pl. 15, figs. 4–6). The first and third molars are longer than wide and the second molar is squarish in occlusal outline. The second lower molar is narrower than the first, and the third narrower than either the first or second, than are those respective teeth in samples of either *P.*

TABLE 11  
Lengths and Breadths (in Millimeters) of Lower Molars from Adult *Spelaeomys florensis*  
(Values from Hooijer, 1957b)

	Length of M <sub>1-3</sub>	Breadths		
		M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
All specimens				
$\bar{X}$	14.6	4.2	4.3	3.8
Range	13.8–15.4	4.0–4.5	4.1–4.6	3.6–4.0
N	19	29	26	20
Complete M <sub>1-3</sub> only (specimens 1–7, 13, 15, and 17–23)				
$\bar{X} \pm \text{SD}$ (N = 16)	14.5 $\pm$ .5	4.2 $\pm$ .1	4.4 $\pm$ .2	3.8 $\pm$ .1
Range	13.8–15.2	4.0–4.5	4.1–4.6	3.6–3.9

*armandvillei* or *P. theodorverhoeveni* (table 7). Each first lower molar is anchored by three roots, a wide anterior and a divided posterior; in the four-rooted *Papagomys*, the posterior root is entire and there are small labial and lingual roots not found in *S. florensis*. Each third lower molar has two roots only, a large anterior and large posterior. The occlusal surfaces of the lower molars appear complex and highly cuspidate due to the high, large, nearly erect cusps and the many large cusplets. Both cusps and cusplets remain discrete even after appreciable wear.

Three pairs of large cusps form most of the occlusal surface of the first molar. In addition to them, there is an anterocentral cusp at the front of the tooth (designated Sm by Misonne, 1969), four large cusplets, and sometimes additional smaller cusplets, along the entire labial margin, and a cylindrical posterior cingulum at the posterolingual edge of the molar. The surface of the second molar consists of two pairs of large, primary cusps, a small anterolabial cusp, three large labial cusplets, and a cylindrical posterior cingulum. Two pairs of large primary cusps form most of the third molar, and a small anterolabial cusp is present, and either one or two labial cusplets. There is no posterior cingulum at the back of each third lower molar. The back row of primary cusps on the third molar forms a lamina with a configuration similar to that in *Mallomys* and *Crateromys* (Misonne, 1969), and dissimilar to

the oblong, transverse laminae in the third lower molars of *Papagomys* and *Hooijeromys*.

When worn, the front row of anterolingual and anterolabial cusps on each first lower molar forms a thin, bilobed lamina. The second and third pairs of cusps on the first lower molar, and all the pairs on the second and third molars, form laminae with deeply scalloped posterior faces, a configuration resulting from the shape of the cusps. Each cusp has a thick, round back part and tapers to an attenuate front which slants inward toward the midline of each tooth, a shape very similar to the cusps in *Mallomys* (figs. 9 and 10). After sufficient wear, the two cusps join along their slim anteromedial borders to form a deeply incised lamina. These thick laminae, combined with a prominent anterocentral cusp on the anterior margin of the first molar, large cusplets along the labial margins of all molars, and prominent posterior cingula, form occlusal surfaces with extensive surface area for masticating food.

In summary, some of the distinctive and diagnostic features of *Spelaeomys florensis* are in the upper molars: many large, tall, erect, and discrete cusps, which remain separate even after appreciable wear; a large cusp between cusps t1 and t2 on each first molar; a large cusp t7 on the first and second molars; a prominent posterior cingulum at the back of each first and second molar (all absent from *Papagomys* and *Hooijeromys*);

a large cusp t3 on the second and third molars (absent or minute in the other two genera); and the slight overlap among the molars. Other diagnostic characters are in the lower molars: large, high, discrete cusps and the configurations of the laminae they form; large and numerous cusplets along the labial margin of each tooth; and a prominent anterocentral cusp at the front of each first molar (most cusplets are absent from lower molars of *Papagomys armandvillei*, there are half as many on the lowers of *P. theodorverhoeveni*, the cusps in *Papagomys* are shaped differently, begin to merge after less wear and form laminae of different shapes than in *Spelaeomys*).

The dentition of *Spelaeomys* is unique, not only in contrast to those of *Papagomys* and *Hooijeromys*, but also to other genera of giant rats from outside of Flores. When he originally described *S. florensis*, Hooijer (1957b) compared its dentitions with those of *Papagomys*, *Mallomys*, *Lenomys*, *Crateromys*, *Pogonomys*, *Chiropodomys*, and *Coryphomys*. Misonne (1969, p. 76) wrote the "*Spelaeomys* is apparently sharply distinguished by the presence of a large t1bis on M<sup>1</sup>; the size of this cone is quite unusual, as also are the large cingular outer conules in M<sub>1</sub> and M<sub>2</sub>, but otherwise it is not very different from the *Papagomys*-*Mallomys* series." Misonne considered *Spelaeomys* to be a member of his "*Lenothrix* group," which besides *Spelaeomys*, was composed of *Lenothrix*, *Lenomys*, *Pogonomys*, *Pithecheir*, *Crateromys*, *Mallomys*, *Papagomys*, *Coryphomys*, *Hyomys*, *Batomys*, *Carpomys*, *Tokudaia*, and *Eropeplus*. To Misonne (1969, p. 77), *Spelaeomys* "is, on the whole, not very different from the *Lenomys* type. This indicates a rather close relationship between all these genera sharing in common many primitive characters." But, *Spelaeomys* is quite different from the *Lenomys* type, as I shall point out in a later section of this report.

In addition to the specimens of *Papagomys* and *Spelaeomys*, Dr. Verhoeven collected five other dentary fragments from the deposits in the cave at Liang Toge. The pieces are from rats that were about the body

size of large-sized species of *Rattus*. *Rattus rattus*, in fact, was the identification Hooijer (1967b, p. 160) applied to the partial mandibles, and he wrote that they may "represent *diardi* as well as *argentiventer* (= *brevicaudatus*), both known in the recent state from Flores." I also studied the fragments and reported them to be examples of *R. rattus*, but referable to *R. r. sumbae*, the subspecies that nowadays lives on Flores (Musser, 1972). Both Hooijer and I were wrong. Specimens 1 to 4 are from rats that had simple *Rattus*-like lower molars and elongate slender mandibular segments in front of the molar rows; they represent a genus and species found nowhere else outside of Flores. Specimen 5 is a sample of *Komodomys* (Musser and Boeadi, 1980) from Flores. In the pages to follow, I first name and characterize the genus and species to which the first four fragments belong, then discuss my determination of the fifth specimen.

#### FLORESOMYS, NEW GENUS

**DIAGNOSIS:** A genus of murid distinguished from all others by the following combination of features: body size probably about like that of *Rattus norvegicus*; dentaries robust with prominent masseteric ridges; a slender and elongate ramus between the front of the molar row and tip of the dentary; narrow lower incisor, both absolutely and relative to width of each dentary; tooththrows short and molars narrow relative to size of dentaries; occlusal surfaces of molars consisting mostly of thick and chunky laminae; front of first molar composed of a lamina bounded on its anterior margin by high arched enamel rims and shaped like an inverted chevron, contacting the second lamina at or slightly off the center of its anterior face so the two laminae are separated by wide angular spaces on labial and lingual sides of the tooth; a nearly transverse second lamina on each first molar, and a transverse front lamina on each third molar; no anterocentral cusp on the front of the first molar; no anterior labial cusplet on any of the first molars; a large anterolabial cusp on each second molar, but usually not on the third mo-

lars; large posterior labial cusplets on the first and second molars; and posterior cingula of first and second molars wide and oval, erect and separated from lamina in front of it.

GENOTYPE: *Floresomys naso*, new species.

INCLUDED SPECIES: Only the type species.

ETYMOLOGY: I have combined the name of the island with the Greek *mys* for mouse (or rat) to formally associate the rat with Flores, the only island in Nusatenggara where specimens of this medium-sized, long-nosed animal have been found

#### *Floresomys naso*, new species

DIAGNOSIS: Same as for the genus.

HOLOTYPE: Specimen 1, a piece of right dentary with a complete molar row and part of the incisor (figs. 20 and 21) from an adult. Measurements of the molars are listed in table 12. A piece of labial corner at the front of the second molar is missing; otherwise, the toothrow is intact.

LOCALITY AND POSSIBLE AGE: All the specimens are from sediments in Liang Toge, a cave near Warukia, 1 km. south of Lepa, in Menggarai Province, western Flores. The deposit, but not necessarily the precise layer forming the matrix adhering to the specimens, has been determined by radiocarbon dating to be  $3550 \pm 525$  years old (Jacob, 1967).

REFERRED MATERIAL: In addition to the holotype there is a right mandibular fragment with a complete toothrow (specimen 2), part of a right dentary containing the first and second molars (specimen 3) and a mandibular piece with intact first and third molars (specimen 4). All the fragments are from adults but different ages, judged by wear of the molars, are represented among the specimens (fig. 20): Specimens 1, 3, and 4 are moderately worn; specimen 2 is worn down farther than the holotype. Measurements of the molars, as well as some proportions, are listed in tables 12 and 13. Part of an incisor is still attached to each piece of mandible.

ETYMOLOGY: The specific name refers to the probable long nose of the species, a feature I attribute to it inferred from the shape

of the dentaries and relative sizes of the molars and incisors. *Floresomys naso* then, is the long-nosed rat from the island of Flores.

DESCRIPTION AND COMPARISONS: The toothrow of the holotype (specimen 1) is straight, the teeth are large and their occlusal patterns are simple. The first molar is rectangular in occlusal outline, the second is squarish and wider than either the first or third molar (table 13). The occlusal surface of the first lower molar consists of three thick and stocky laminae, positioned close to one another, each composed of two high cusps; a large posterior labial cusplet; and a large wide cusp—the posterior cingulum—situated on the back margin of the tooth. The front row of cusps is composed of a large antero-lingual cusp united with a slightly smaller anterolabial cusp to form an erect lamina shaped like an inverted chevron. The second lamina is gently bowed and slants forward to abut against the posterior margin of the front lamina to the left of its center so the two laminae are separated on the labial and lingual sides by wide triangular spaces. The enamel front and sides of cusps forming the first lamina are much higher than the enamel outlines of the second lamina, so the occlusal area of the front lamina is a broad surface sloping down and back to meet the flat surface of the second lamina, which slopes down and forward. The result is a basin, bounded at the back by the low posterior enamel wall of the second lamina, and at the front by the two high arcuate enamel rims of the front row of cusps. The third lamina is chevron-shaped, slants forward, and most of its labial margin presses against a large and distinct labial cusplet, oval in cross-section, that is discrete, not merged with the labial cusp against which it is tightly pressed. The posterior cingulum at the back of the tooth is large, oval, nearly erect, and separated from the posterior face of the third lamina. There is no anterior labial cusplet on the side of the second lamina nor is there an antero-medial cusp on the anterior margin of the tooth.

The occlusal surface of the second lower molar consists of two thick and high laminae, each broadly chevron-shaped, slanting

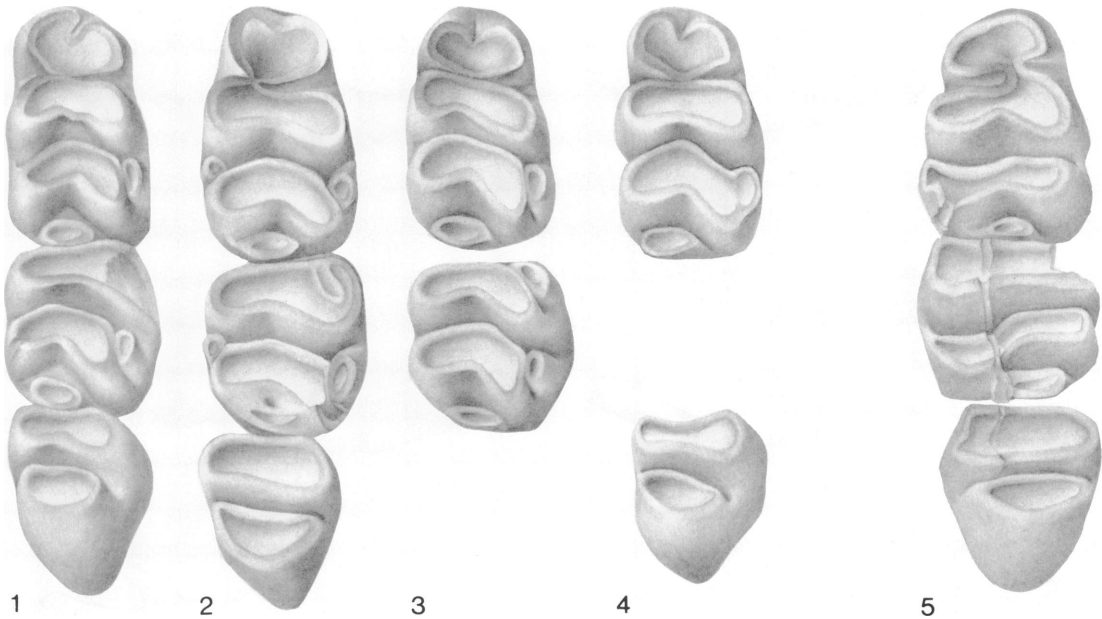


FIG. 20. Occlusal views of right (1-4) and left (5) subfossil mandibular tooththrows of adults collected at Liang Toge, Flores. Specimens 1-4: *Floresomys naso* (specimen 1 is the holotype). Specimen 5: *Komodomys rintjanus*. Measurements are listed in table 12.

slightly forward and set close together. A small chunk is missing from the labial side of the front lamina, but judged from the outline of the remaining enamel face, there was a large anterolabial cusp at the corner of the lamina. There is a large cusplet, oval in cross-section, pressed against the labial side of the second lamina. This posterior labial cusplet, like its counterpart on the first molar, is distinct and not merged with the labial side of the second lamina. The large oval posterior cingulum is nearly erect, separate from the lamina behind which it sits and resembles the posterior cingulum of the first molar in size and shape.

The occlusal surface of the third molar is formed from two high laminae. The front one is thick and transverse. Pressed against its posterior margin is the back lamina, a wide and thick structure, oblong in cross-section and forming the posterior half of the tooth. There is no anterolabial cusp, or any labial cusplets on the margin of the tooth.

Each first molar has four roots: a large an-

terior one, smaller but prominent labial and lingual roots in the middle of the molar, and one large posterior root. Each second and third molar has three roots, two anterior and a single wide posterior root. Likely the first upper molars had five roots because other murids with five-rooted first upper molars have four roots on the first lower molars.

Size (table 12) and occlusal patterns of the teeth in specimens 1 to 4, all right tooththrows, are closely similar but the shape and position of the anterior lamina on each first molar varies slightly, as does the occurrence of cusplets (fig. 20). In specimens 1 and 2, the lingual cusp of the front lamina is slightly larger than the labial cusp and they touch the second lamina to the left of its center; in specimen 3, the lingual and labial cusps are equal in size and touch the second lamina at its center; in specimen 4 the lingual cusp is slightly larger than the labial and the two contact the middle of the second lamina.

Specimen 2 contrasts with the other three in that it has extra cusplets: in addition to

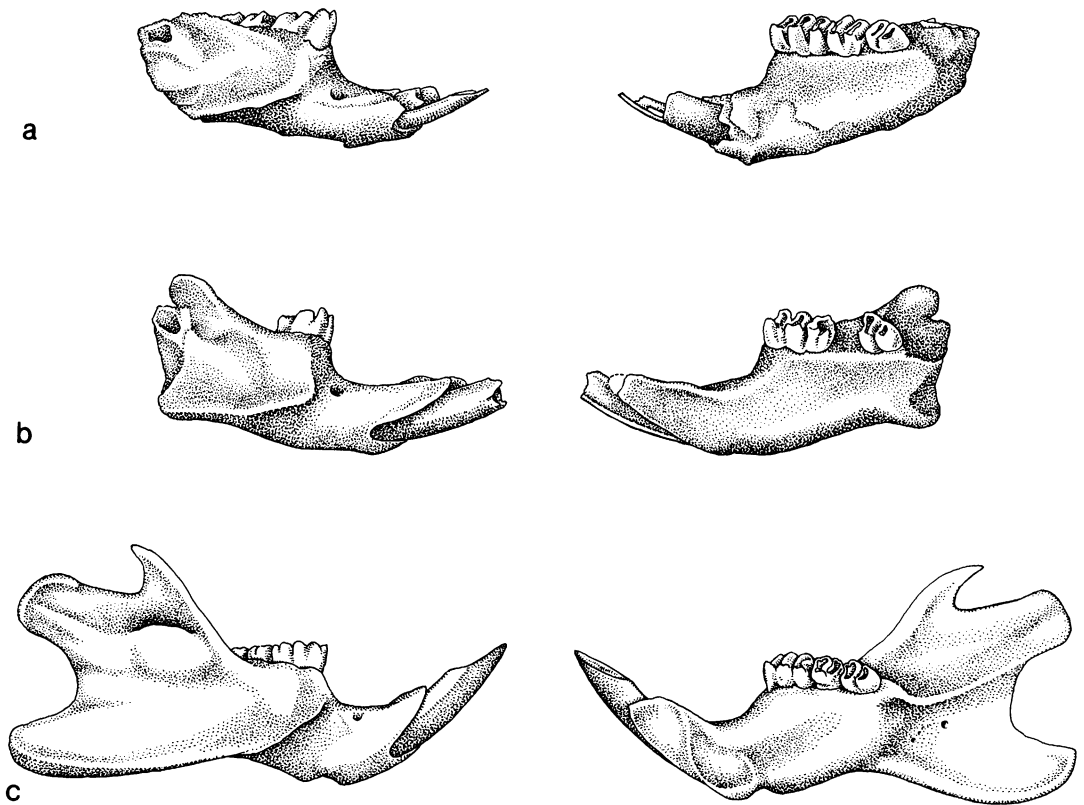


FIG. 21. Subfossil dentary fragments of *Floresomys naso* (a and b) contrasted with the dentary of a Recent *Rattus rattus* (c). *Floresomys naso*: a, specimen 1 (the holotype); b, specimen 4; both are adults from Liang Toge. *Rattus rattus*: c, an adult from Flores. Labial views are on the left side, lingual on the right side. Note the part of each dentary that is anterior to the molar row, a segment which is elongate in *F. naso* compared with that in *R. rattus*.

the labial cusplets on the first and second molars, there are two conspicuous posterior lingual cusplets, one on the first molar, another on the second.

Each specimen consists of not only molars and incisors, but part of the dentary as well. Only the body of the ramus is present in specimens 1 and 2. The body of the ramus, part of the back blade from which the alveolar capsule of the incisor still protrudes and most of the ramus between the toothrow and the front tip of the mandible is present in specimen 3, though much of the fragment is still coated by matrix. The posterior half of the dentary, from about the end of the toothrow back, is missing from specimen 4, the rest of the ramus is mostly intact.

The mandibles and incisors of *F. naso* are distinctive. Each dentary is thick and appears robust. The body of the ramus below the first molar is high (6.5 mm. in specimen 4, measured from the lip of the alveolus to the ventral surface of the ramus at the level of the front face of the first molar). The masseteric ridges, especially the longer inferior ridge, are high, prominent, and outline a large area for the origin of the masseteric musculature. The ramus between the front of the toothrow and the anterior tip of the mandible is gently curved and elongate. Out of the four specimens, the anterior portion of specimen 4 is most complete; only about 1 mm. of the tip is missing. It is illustrated in figure 21 and compared there with a den-

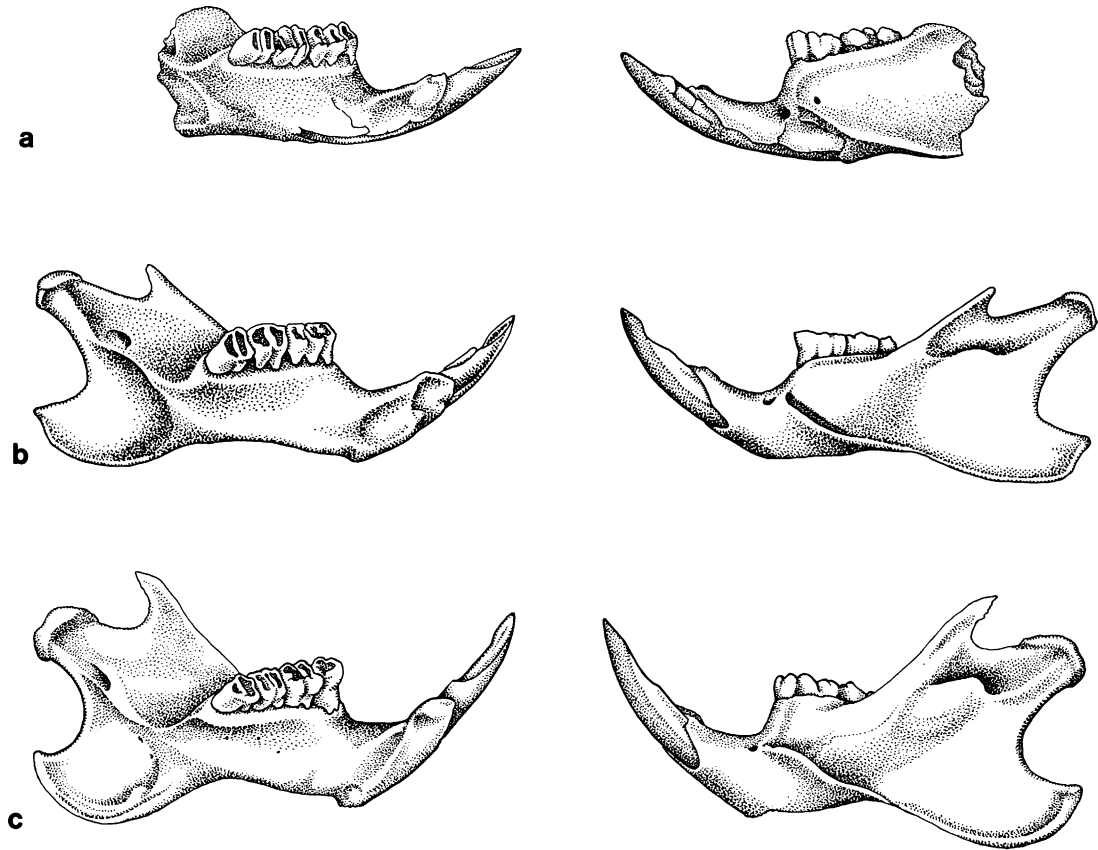


FIG. 22. A subfossil dentary fragment of an adult *Komodomys rintjanus* from Flores (a) compared with Recent adult examples of *K. rintjanus* (b) and *Rattus sordidus* (c). *Komodomys rintjanus*: a, specimen 5 from Liang Toge; b, Recent, from the Komodo Island of Rintja. *Rattus sordidus*: c, Recent, from Australia. Labial views are on the right side, lingual on the left side.

tary of *Rattus rattus* from Flores, which demonstrates the usual configuration of the dentary in front of the tooththrow in rats that are not long-nosed. In specimen 4, the distance between the base of the first molar and the place where the anterior tip of the dentary would have been is 8.6 mm. (measured after placing the mandible so the bases of the teeth were aligned along a horizontal plane). The incisors of all specimens are thin (the breadth of each in specimens 1 to 4, taken where the tooth emerges from the ramus, is respectively, 1.0, 1.2, 1.1, and 1.2 mm.) and have pale orange enamel surfaces.

In summary, each specimen of *F. naso* is characterized by slim incisors and small molars set in a large mandible in which the den-

tary anterior to each molar row is elongate. Such a configuration is common to murids with a long rostrum, and from these features I infer that *F. naso* was a long-nosed rat. Its characters, however, are not as derived or extremely specialized as are those peculiar to the shrew rats from the Philippines, *Chrotomys*, *Celaenomys*, and *Rhynchomys* (Thomas, 1898a); or to the shrew rats from Sulawesi, *Echiothrix*, *Melasmothrix*, and *Tateomys* (Musser, 1969). *Floresomys naso* is not related to those forms.

The occlusal configurations in *F. naso* are similar to those in the *chrysocomus*-group on Sulawesi, species usually included in *Rattus* but better placed in a different genus, *Bunomys*. *Bunomys chrysocomus* (*nigellus*,

TABLE 12  
Lengths and Breadths (in Millimeters) of Lower Molars from Adult *Floresomys*, *Bunomys*, *Komodomys*,  
and *Rattus*

		Breadths		
	Length of M <sub>1-3</sub>	M <sub>1-3</sub>	M <sub>2</sub>	M <sub>3</sub>
<i>Floresomys naso</i> , Liang Toge				
Specimen 1	7.6	2.0	2.1	1.9
Specimen 2	7.5	2.1	2.2	1.8
Specimen 3	—	2.0	2.2	—
Specimen 4	7.5	2.0	—	1.8
$\bar{X} \pm SD$ (N = 4)	7.5 $\pm$ .2	2.0 $\pm$ .1	2.2 $\pm$ .1	1.8 $\pm$ .1
<i>Bunomys</i>				
<i>B. fratorum</i> , N. Sulawesi				
$\bar{X} \pm SD$ (N = 20)	7.7 $\pm$ .2	2.1 $\pm$ .1	2.2 $\pm$ .1	1.8 $\pm$ .1
range	7.3–8.1	2.0–2.3	2.1–2.3	1.7–2.0
<i>Komodomys</i>				
<i>K. rintjanus</i> , Padar and Rintja				
$\bar{X} \pm SD$ (N = 13)	7.3 $\pm$ .2	1.9 $\pm$ .1	2.2 $\pm$ .1	2.0 $\pm$ .1
range	7.0–7.6	1.8–2.0	2.1–2.3	1.9–2.2
Specimen 5, Liang Toge	7.5	2.1	2.3	2.1
Australian <i>Rattus</i>				
<i>R. sordidus sordidus</i>				
$\bar{X} \pm SD$ (N = 34)	6.7 $\pm$ .3	2.0 $\pm$ .1	2.2 $\pm$ .1	1.8 $\pm$ .1
range	6.1–7.4	1.8–2.3	2.0–2.5	1.6–2.1
<i>R. sordidus villosissimus</i>				
$\bar{X} \pm SD$ (N = 27)	7.0 $\pm$ .2	2.0 $\pm$ .1	2.2 $\pm$ .1	1.8 $\pm$ .1
range	6.7–7.4	1.9–2.2	2.1–2.4	1.7–2.0
<i>R. sordidus gestroi</i>				
$\bar{X} \pm SD$ (N = 7)	6.7 $\pm$ .4	2.0 $\pm$ .1	2.2 $\pm$ .1	1.7 $\pm$ .1
range	6.2–7.2	1.8–2.2	2.0–2.4	1.5–1.9
<i>R. sordidus</i> , Fly River				
$\bar{X} \pm SD$ (N = 25)	6.8 $\pm$ .3	2.1 $\pm$ .1	2.3 $\pm$ .1	1.9 $\pm$ .1
range	6.3–7.4	1.8–2.3	2.0–2.5	1.6–2.1
<i>R. fuscipes</i> , W. Australia				
$\bar{X} \pm SD$ (N = 20)	6.8 $\pm$ .2	2.0 $\pm$ .1	2.1 $\pm$ .1	1.7 $\pm$ .1
range	6.5–7.1	1.7–2.1	1.8–2.2	1.6–1.8
<i>R. leucopus</i> , Papua				
$\bar{X} \pm SD$ (N = 20)	7.2 $\pm$ .2	1.9 $\pm$ .1	2.1 $\pm$ .1	1.8 $\pm$ .1
range	6.7–7.7	1.8–2.2	1.9–2.2	1.6–2.2
Commensal <i>Rattus</i>				
<i>R. rattus</i> , Flores				
$\bar{X} \pm SD$ (N = 17)	6.5 $\pm$ .2	1.7 $\pm$ .1	1.8 $\pm$ .1	1.6 $\pm$ .1
range	6.4–6.9	1.5–1.8	1.7–2.0	1.5–1.8
<i>R. argentiventer</i> , Java				
$\bar{X} \pm SD$ (N = 13)	6.5 $\pm$ .3	1.8 $\pm$ .1	1.9 $\pm$ .1	1.7 $\pm$ .1
range	6.2–7.0	1.7–1.9	1.8–2.1	1.3–1.9

TABLE 12—(Continued)

	Length of $M_{1-3}$	Breadths		
		$M_{1-3}$	$M_2$	$M_3$
<i>R. nitidus</i> , Burma				
$\bar{X} \pm SD$ (N = 20)	6.9 $\pm$ .3	1.8 $\pm$ .1	1.9 $\pm$ .1	1.7 $\pm$ .1
range	6.4–7.4	1.6–2.0	1.7–2.1	1.5–1.8
<i>R. norvegicus</i> , Java				
$\bar{X} \pm SD$ (N = 7)	7.2 $\pm$ .2	2.0 $\pm$ .1	2.2 $\pm$ .1	1.8 $\pm$ .1
range	7.0–7.6	1.9–2.2	2.1–2.4	1.7–2.1
<i>R. exulans</i> , C. Sulawesi				
$\bar{X} \pm SD$ (N = 20)	4.9 $\pm$ .2	1.3 $\pm$ .1	1.4 $\pm$ .1	1.2 $\pm$ .1
range	4.5–5.1	1.2–1.3	1.2–1.4	1.1–1.3

*rallus*, *brevimolaris*, *coelestis*, and *koka*) is a small-bodied rat occurring throughout Sulawesi at middle and high elevations. *Bunomys fratorum*, a larger animal, is known only from the northeastern peninsula where it lives in both lowland and mountain forests; *B. andrewsi* (*adspersus*, *inferior*, and *heinrichi*) is found in lowland forests throughout the island except on the northeastern peninsula; and *B. penitus* (*sericatus*), also a large-bodied rat, occurs in mountain forests in the central part and southwestern peninsula.

Lower molars of *B. fratorum*, *B. andrewsi*, and *B. penitus*, the three larger rats, are about the same size as, or slightly larger than, the teeth in *F. naso*. The occlusal configurations among all three are similar, but those of *B. fratorum* are most like those in *F. naso*, differing as follows: the teeth are slightly larger (table 12); the laminae are thicker and set closer, so they touch each other; anterior labial cusplets on the first molars and anterolabial cusps on the third molars are usually absent, as in *F. naso*, but anterolabial cusps are usually missing from the second molars as well, whereas they are present in *F. naso*; all the cusplets and anterolabial cusps in *B. fratorum* are low, small, and merge with the laminae at an early stage of wear to lose their definitions quickly, whereas the cusplets and anterolabial cusps remain discrete in *F. naso*; the anterolingual and anterolabial cusps forming the

anterior lamina of the first molar are dissimilar in size and after little wear coalesce into a high oblong surface that is narrower than the second lamina but flush with its anterior margin, a configuration unlike that in *F. naso*.

The two other large-bodied species, *B. andrewsi* and *B. penitus*, are like *B. fratorum* in their dental features. The smaller-bodied *B. chrysocomus* is also dentally similar to *B. fratorum* but has smaller teeth, and these differences: the laminae are set farther apart, there are anterolabial cusps on the third, sometimes anterior labial cusplets on the first molars, and the anterolingual cusp of each first molar is always larger than the anterolabial cusp.

Although the molars of species in the *chrysocomus*-group are superficially similar to molars of *F. naso*, the dentaries are dissimilar. The species of *Bunomys* have small slender dentaries, each with a low ramus and a short segment in front of the tooththrow. A large tooththrow set in a small dentary is the configuration, instead of small molars in a large dentary, as found in *F. naso*.

Because at one time I had determined specimens 1 to 4 to be examples of *Rattus*, I compared the specimens with all named forms in that genus, especially *R. rattus*, *R. argentiventer*, *R. norvegicus*, and *R. exulans*, the four kinds now found on Flores, and all the species of *Rattus* from the Philippines, Celebes, the Moluccas, New Guinea,

and Australia. The shapes of the first two laminae on the first molar, the absence of an anterolabial cusp from the third molar, the proportion of small molar size to large dentary, the elongated segment of the dentary in front of the toothrow, and the slim incisors is a combination of features not found in *Rattus*.

Specimen 5 also did not come from a species of *Rattus*. It represents the first documented Floresian example of *Komodomys rintjanus*, known previously only from the Komodo Islands of Rintja and Padar (Musser and Boead, 1980).

#### *Komodomys rintjanus*

Specimen 5 from Liang Toge, an adult, consists of a left mandibular fragment with an incisor and three molars (figs. 20 and 22). The segment of the dentary behind the toothrow is gone but the rest of the ramus is complete; the incisor is missing small chips from its base. The molars have been slightly separated from one another by thin wedges of matrix (which I accounted for in my measurements). All are intact except for small lost edges here and there and a fracture down the middle of the second molar. Dental measurements and proportions are listed in tables 12 and 13.

Judged from specimen 5, the mandible was large and robust. The masseteric ridges are prominent. The segment between the front of the toothrow and the tip of the dentary is short (6.1 mm., measured from the base of the first molar to the anterior tip of the dentary, with the ramus positioned so the base of the teeth were aligned along a horizontal plane). The lower incisor is sturdy, thick (1.4 mm. wide, measured where the incisor emerges from the ramus), and its enamel surfaces are deep orange. The lower molars are large and wide, both absolutely and relative to size of the mandible. The first molar is as wide as the third, and the second is conspicuously wider than either of those teeth.

The molars are moderately worn. Cusps are no longer distinct and now laminae comprise the occlusal surfaces. The first molar is much longer than wide in occlusal outline;

three laminae, spaced well apart from each other, form its surface. The first is erect, narrow, hemispheric in cross-section and slants obliquely to the left, parallel to the labial segment of the second lamina. The second and third laminae slant forward. The second one is arched into a low chevron with its lingual arm connected to the first lamina by an enamel and dentine ridge. The third lamina has a nearly straight anterior face, but an arcuate posterior wall, the configuration resulting when a gently arched lamina merges with an adjacent labial cusplet. The posterior cingulum is small, elliptical in cross-section and set at the back of the tooth so its labial side is closer to the back of the third lamina than is its lingual side. There is only one labial cusplet present on the first molar, located at the anterolabial margin of the third lamina where it has merged with the lamina. There is no evidence of a cusplet on the labial margin between the first and second laminae, or an anterocentral cusp on the anterior margin of the tooth.

The second molar is squarish in occlusal outline and consists mostly of two thin laminae that slant forward. The front one is nearly transverse, though its posterior wall is arcuate. The second lamina is thin, its lingual arm transverse, its labial arm bent back in an oblique curve to the left. The anterolabial margins of each lamina are formed by an anterolabial cusp and a posterior labial cusplet, respectively, which have merged with each lamina. The posterior cingulum is low, elliptical in cross-section, larger than its counterpart on the first molar, and joined along its labial edge to the back of the second lamina.

The third molar is large and chunky. Its surface is formed mostly from two thick, bulky, nearly transverse laminae that slant forward. The anterolabial corner of the front lamina is formed by an anterolabial cusp that has merged with the lamina to form part of the wear surface. There are no labial cusplets on the tooth.

The dentary and toothrow of specimen 5 is about the same size as each specimen of *Floresomys naso*, but with size the similarities end (figs. 21 and 22). The segment of the dentary in front of the toothrow is much

shorter in specimen 5 than in those of *F. naso* (6.1 mm. opposed to 8.6 mm.), the incisor is wider (1.4 mm. compared with a range of 1.0–1.2) and more robust, and the incisor is more strongly curved than the shallowly curved incisors of *F. naso*. The third molar of specimen 5 is wider than the third molars of *F. naso*, both absolutely and relative to either the first or second teeth (tables 12 and 13). The laminae of specimen 5 are thinner, not as closely packed together as are the thick and closely set laminae on toothrows of *F. naso*; the front lamina on the first molar is hemispheric in cross-section and set obliquely to the left, parallel to the labial arm of the second lamina, unlike each front lamina in *F. naso*, which is shaped like an inverted chevron; and the second lamina on the first molar in specimen 5 is arched, instead of nearly straight. The anterolabial cusps and cusplets on specimen 5 are shorter than those on the molars of *F. naso* and merge with the laminae after moderate wear instead of remaining discrete after much wear; and while there is an anterolabial cusp on the third molar of specimen 5, no such cusps exist on the third molars of *F. naso*.

I identified specimen 5 after I had sorted through lower jaws from species of *Rattus* known from the Asian mainland, the Sunda Shelf and nearby islands, the archipelagos east of the Shelf, Australia, and the New Guinea area; I also examined Pleistocene and subfossil records. These comparisons were necessary because the dental characteristics of specimen 5 resembled those in some species of *Rattus*. Most samples, however, were unlike specimen 5; only three groups of species had to be closely compared with the fragment from Liang Toge and require discussion here. One group consists of the five commensal species of *Rattus* that are found throughout that vast region east and north of Wallace's Line, four of which live on Flores. The species of *Rattus* found on Australia and their relatives in southern New Guinea comprise the second group. The species, *rintjanus*, from the Komodo Islands, and formerly placed in *Rattus*, forms the third group.

COMMENSAL SPECIES: *Rattus rattus*, *R.*

TABLE 13  
Ratios (in Percent) of Lower Molar Widths in  
*Floresomys*, *Bunomys*, *Komodomys*, and *Rattus*  
(Based on Samples Listed in Table 12)

	BM <sub>2</sub> BM <sub>1</sub>	BM <sub>3</sub> BM <sub>1</sub>	BM <sub>3</sub> BM <sub>2</sub>
<i>Floresomys</i>			
<i>F. naso</i> (N = 2)	105	91	87
<i>Bunomys</i>			
<i>B. fratorum</i> , N. Sulawesi	105	86	82
<i>Komodomys</i>			
<i>K. rintjanus</i> , Rintja and Padar	116	105	91
Specimen 5, Liang Toge	110	100	96
Australian <i>Rattus</i>			
<i>R. sordidus sordidus</i>	109	89	82
<i>R. sordidus villosissimus</i>	110	90	82
<i>R. sordidus gestroi</i>	110	85	77
<i>R. sordidus</i> , Fly River	110	91	83
<i>R. fuscipes</i> , W. Australia	105	85	81
<i>R. leucopus</i> , Papua	111	95	86
Commensal <i>Rattus</i>			
<i>R. rattus</i> , Flores	106	94	89
<i>R. argentiventer</i> , Java	106	94	90
<i>R. nitidus</i> , Burma	106	94	90
<i>R. norvegicus</i> , Java	110	90	82
<i>R. exulans</i> , C. Sulawesi	108	92	92

*argentiventer*, *R. exulans*, and *R. norvegicus* (fig. 23) now live on Flores; probably none of these is native to the island. They, and *R. nitidus* (fig. 23), are species that throughout the region bounded by the Philippines and Sulawesi on the west, and New Guinea and Australia on the east, live in habitats made and maintained by humans. They are absent from primary forests where the indigenous species of *Rattus* and other genera live, and they also occur west of Wallace's Line on the Sunda Shelf and Southeast Asia. None of the Wallacean endemics are found to the west of the Sunda Shelf; compared with those species, the five that are human associates seem to be an introduced element into the local native fauna on the Philippines, Sulawesi, the Moluccas, the Lesser Sunda Islands, New Guinea, and Australia (Musser, 1977). I compared examples of the five commensals with specimen 5 to determine

TABLE 14  
**Presence (+) or Absence (–) of the Anterior and Posterior Labial Cusplets on First Lower Molars in  
 Samples of *Komodomys* and *Rattus***  
 (Number of Cusplets is Expressed as Percentage; N is in Parentheses)

	Anterior cusplet		Posterior cusplet	
	+	–	+	–
<i>Komodomys</i>				
<i>K. rintjanus</i> , Padar and Rintja	—	100 (10)	100 (10)	—
Specimen 5, Liang Toge	—	100 (1)	100 (1)	—
Australian <i>Rattus</i>				
<i>R. sordidus sordidus</i>	5 (1)	95 (19)	100 (20)	—
<i>R. sordidus villosissimus</i>	—	100 (20)	100 (20)	—
<i>R. sordidus gestroi</i>	—	100 (6)	100 (6)	—
<i>R. sordidus</i> , Fly River	5 (1)	95 (19)	100 (20)	—
<i>R. fuscipes</i> , W. Australia	30 (6)	70 (14)	100 (20)	—
<i>R. leucopus</i> , Papua	80 (16)	20 (4)	100 (20)	—
Commensal <i>Rattus</i>				
<i>R. rattus</i> , Flores	23 (4)	77 (13)	100 (17)	—
<i>R. argentiventer</i> , Java	23 (3)	77 (10)	100 (13)	—
<i>R. nitidus</i> , Burma	30 (6)	70 (14)	100 (20)	—
<i>R. norvegicus</i> , Java		100 (7)	100 (7)	—
<i>R. exulans</i> , C. Sulawesi	85 (17)	15 (3)	100 (20)	—

whether it represented one of the species introduced onto Flores, or was instead a member of the fauna native to that island.

*Rattus rattus sumbae* is the name applied to house rats from Sumba (Musser, 1972), the island in Nusatenggara south of Flores. A similar kind of rat also occurs on the islands of Rintja, Flores, Timor, Lomblon, and Alor. In their coloration of pelage the animals on Flores are like those on Sumba but are smaller in size, judged by lengths of maxillary tooththrows. The mean and range is 8.3 mm. and 8.0–8.5 mm., respectively, in nine specimens of *R. rattus* from Sumba, 7.2 mm. and 6.7–7.8 mm. in 17 rats from Flores. In coloration and body size, house rats on the islands of Sumbawa and Lombok, to the west of Flores, are similar to *R. r. diardii* from Bali and the islands on the Sunda Shelf. The mean is 6.9 mm., the range 6.3–7.4 mm. in 61 specimens of *R. r. diardii* from the Greater Sunda Islands. In size at least, the rats from Flores fall between *R. r. diardii* and *R. r. sumbae*. So just what subspecific name should be applied to the population of

house rats on Flores is uncertain and will remain so until *R. rattus* from the Indo-Australian region is taxonomically revised. Here I shall refer to the Flores population as the *R. rattus* from Flores and restrict the name *sumbae* to the house rats from Sumba. The Flores house rats are related to the Asian forms of *R. rattus* and not to the European house rats, *R. r. rattus*. The two kinds differ in external features (Johnson, 1962; Jones and Johnson, 1965), chromosomes (Yosida, Tsuchiya and Moriwaki, 1971), other characteristics (Yosida et al., 1971), and geographic origins. It is the Asian form of *R. rattus* that is found throughout the Philippines, Sulawesi, the Moluccas, the Lesser Sunda Islands, and parts of New Guinea and nearby islands. The European house rat was introduced into parts of New Guinea and Australia and has been found in large port cities in the Philippines and Sulawesi (Barbehenn, Sumangil, and Libay, 1972–1973; Musser, 1977).

The ricefield rat, *R. argentiventer*, lives on Flores. The species has also been recorded

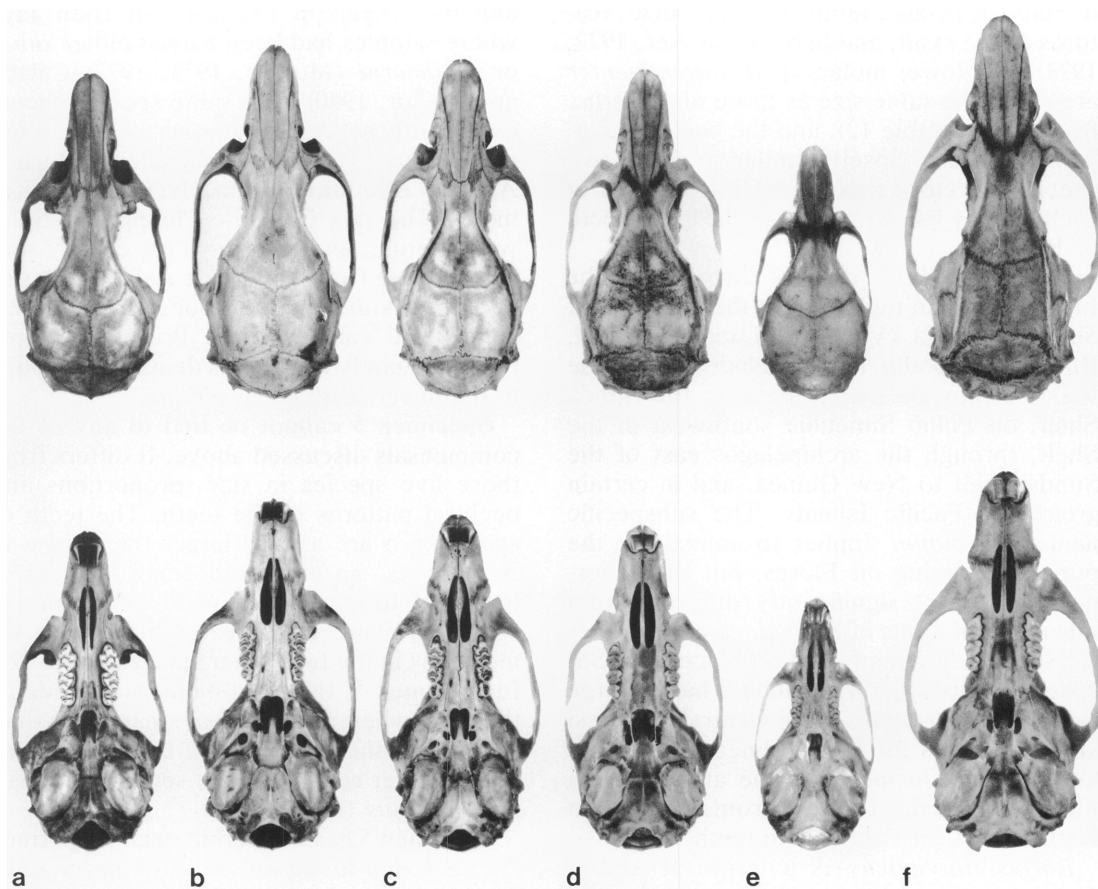


FIG. 23. Dorsal (top row) and ventral (bottom row) views of adult crania from Recent *Komodomys* and *Rattus*. *Komodomys rintjanus*: a, Padar Island (MZB 9014). *Rattus*: b, *R. rattus*, Celebes (AMNH 153004); c, *R. argentiventer*, Bali (AMNH 107543); d, *R. nitidus*, Philippines (FMNH 62431); e, *R. exulans*, Thailand (AMNH 215290); and f, *R. norvegicus*, Taiwan (AMNH 185196). All natural size. The specimens of *Rattus* portrayed here are examples of the species whose distributions in the area east of the Sunda Shelf is probably a result of inadvertent human transport and introduction. All but *R. nitidus* are found on Flores; *R. nitidus* occurs on the Philippines, Celebes, Ceram, and the Vogelkop of New Guinea.

from the mainland of Southeast Asia (Vietnam and Thailand); the Sunda Shelf (peninsular Thailand and Malaya, Sumatra, Borneo, Java, Kangean Island, and Bali); the Lesser Sunda Islands (Lombok, Sumbawa, Komodo, Rintja, Sumba, and Timor); Sulawesi; the islands of Luzon, Mindoro and Mindanao in the Philippines; and once from New Guinea (Musser, 1973; Barbehenn, Sumangil, and Libay, 1972–1973). The rats

from these places are morphologically similar to one another. Set against the pattern of morphological relationships shown by species of *Rattus* and other kinds of murids native to the area east of the Sunda Shelf, the occurrence of *R. argentiventer* in that region is best explained by the hypothesis that the species was introduced through human agency (Musser, 1973). *Rattus argentiventer* is similar to *R. rattus* in body size but differs

in color of pelage, number of mammae, features of the skull, and habitat (Musser, 1972, 1973). The lower molars of *R. argentiventer* are about the same size as those of *R. rattus* from Flores (table 12), and the occlusal configurations are closely similar in these two species, so close that separating samples of each kind by using features of the lower teeth is difficult.

*Rattus exulans* occurs throughout the Indo-Australian region, from the mainland of Southeast Asia (Vietnam, Laos, Thailand, Burma, Cambodia, and Bangladesh) onto the Malay Peninsula and islands on the Sunda Shelf, on Pulau Simeulue southwest of the Shelf, through the archipelagos east of the Sunda Shelf to New Guinea, and in certain groups of Pacific Islands. The subspecific name *wichmanni* applies to animals in the population living on Flores, but their morphology is not significantly different from rats in populations of *R. exulans* on the other Lesser Sunda Islands and on places like Sulawesi and its offshore islands. I have a large sample of *R. exulans* from Central Sulawesi and the values for measurements from that lot are listed in table 12; the animals from Flores are similar to those from Sulawesi in features of skins, skulls and teeth.

*Rattus norvegicus* is a large rat and is found in port cities on mainland Asia, the Malay Peninsula and larger islands on the Sunda Shelf, and in the region east and north of Wallace's Line to New Guinea and Australia. *Rattus norvegicus* is probably an endemic of northeastern China (Johnson, 1962) and its occurrence in the Indo-Australian region is a result of transport and introduction through human assistance.

*Rattus nitidus* is the fifth species that is associated with human habitats and was likely introduced into the archipelagos east of Wallace's Line. The species has not been documented from Flores, but it occurs in a spotty pattern throughout the region east of the Sunda Shelf and must be compared with specimen 5. *Rattus nitidus* has been found on Luzon in the Philippines; Sulawesi, where it was described as *R. hoffmanni subditivus*; Ceram, where it was named *R. manuselae*;

and the Vogelkop Peninsula of Irian Jaya where samples had been named either *ruber* or *vanheurni* (Musser, 1973, 1977; Calaby and Taylor, 1980). The same species occurs over Southeast Asia in southern China, Vietnam, Laos, Thailand, Bangladesh, Burma, Assam, Bhutan, Sikkim, Nepal, and Kamaon. The rats from the Philippines, Sulawesi, Ceram, and Irian Jaya are closely similar to those from Southeast Asia in features of skins, skulls and dentitions. In table 12 I have listed values from a Burmese sample that adequately represents dental dimensions in the lower teeth of *R. nitidus*.

Specimen 5 cannot be tied to any of the commensals discussed above. It differs from those five species in size, proportions and occlusal patterns of the teeth. The teeth of specimen 5 are a third larger than those in *R. exulans*, an animal of small body size; length of toothrow and width of molars in specimen 5 are also greater than those dimensions in the four other species (table 12). In specimen 5, the third molar is as wide as the first, whereas it is always narrower than the first in the five species; the third molar is also wider relative to the second one than in the *Rattus* (table 13).

Specimen 5 has a different occlusal pattern than is found in any of the other species. In *R. norvegicus*, for example, the front lamina is thick and chunky and its back edge is pressed against the anterior margin of the second lamina rather than being widely separated as in specimen 5. The occlusal configurations in *R. rattus*, *R. argentiventer*, and *R. nitidus* are closely similar. The laminae are chevron-shaped in all of them and not as straight or gently arcuate as they are in specimen 5. Finally, the teeth of *R. exulans* are not only smaller than those of specimen 5, but the laminae are chevron-shaped; the cusps comprising the front lamina on the first molar coalesce after little wear to form an extensive surface, an area produced at an earlier stage of wear than in any of the other *Rattus* from Flores; and there is usually an anterior labial cusplet on the first molar (found on 17 out of 20 specimens), but such a cusplet is absent from specimen 5.

It is significant that the occlusal configurations and not just size and proportions of the teeth in specimen 5 differ from those in the five commensal species. The differences indicate to me that specimen 5 does not represent just a large form of one of the *Rattus* now living on Flores, or of *R. nitidus*, the other commensal found in the region. Nothing, incidentally, like *R. rattus*, *R. argentiventer*, *R. norvegicus*, and *R. exulans*, or even *R. nitidus*, has yet been found as subfossils or in Pleistocene sediments on Flores.

**AUSTRALIAN *RATTUS* AND RELATIVES:** The characteristics of specimen 5 resemble those of some indigenous Australian *Rattus* and their relatives on New Guinea. Close comparison between that group and specimen 5 was necessary to determine whether the species represented by specimen 5 was a part of that Australian assemblage or whether it came from some other species, possibly something not even in *Rattus*. The taxonomy of the indigenous Australian *Rattus* has been revised by Taylor and Horner (1973). They delimited five species: *R. leucopus*, basically a species of New Guinea and found in Australia only in the eastern half of the Cape York Peninsula; *R. fuscipes*, *R. lutreolus*, *R. sordidus*, and *R. tunneyi*. Taylor and Horner considered *R. fuscipes* to be more closely related to *R. leucopus* than to the other Australian species of *Rattus*. In the opinion of Dennis and Menzies (1978), however, *R. fuscipes* is not closely allied to *R. leucopus* but to *R. lutreolus*, *R. sordidus*, and *R. tunneyi*.

*Rattus fuscipes* is of medium body size. It occurs in suitable habitats of coastal Australia and offshore islands in the east, southeast, and southwest. Taylor and Horner (1973) recognized four subspecies: *R. f. fuscipes* (*mondraineus* and *glauerti*), *R. f. greyii* (*murrayi*, *ravus*, *peccatus*, and *pelori*), *R. f. assimilis*, and *R. f. coraci* (*manicatus*).

*Rattus lutreolus*, about the same body size as *R. fuscipes*, has been recorded from Queensland, southeastern Australia and Tasmania. Three subspecies were accepted by



FIG. 24. Dorsal (top row) and ventral (bottom row) views of adult crania from recent *Komodomys* and *Rattus*. *Komodomys rintjanus*: a, Padar Island (MZB 9014). *Rattus*: b, *R. sordidus*, Australia (AMNH 194115); and c, *R. leucopus*, New Guinea (AMNH 157961). All natural size. *Rattus sordidus* represents the basic cranial conformation found in the species of *Rattus* indigenous to Australia. *Rattus leucopus* is a representative of the group of species indigenous to New Guinea and nearby archipelagos, which also overlaps onto Australia.

Taylor and Horner (1973): *R. l. lutreolus* (*lutreola*, *vellerosus*, *cambricus* and *imbil*), *R. l. velutinus* (*tasmaniensis*) and *R. l. lacus*.

*Rattus sordidus* (fig. 24) is a large-bodied rat and occurs in the eastern and part of the western half of Australia where the discontinuity of its geographic range combined with significant morphological distinctions led Taylor and Horner (1973) to recognize three

subspecies: *R. s. sordidus* (*contatus* and *youngi*), *R. s. villosissimus* (*longipilis* and *profusus*), and *R. s. colletti*. Closely related forms also occur in the southern part of mainland New Guinea where the names *gestroi*, *brachyrhinus*, *armia*, and *bunae* have been applied to samples that Laurie and Hill (1954) considered to be a single species, *R. sordidus*—the New Guinea counterpart of the Australian species—but that Dennis and Menzies (1978) regarded as two species, *R. gestroi* and *R. bunae*, both related to but distinct from *R. sordidus* of Australia.

*Rattus tunneyi* is a smaller rat than the other species in Australia. It occurs in eastern, northwestern, southwestern, central, and northcentral Australia. Taylor and Horner (1973) recognized *R. t. tunneyi* (*woodwardi*, *melvilleus* and *dispar*) and *R. t. culmorum* (*vallesius*, *austrinus*, *apex* and *australasicus*) as valid subspecies.

*Rattus leucopus* (fig. 24) is a forest rat that occurs on New Guinea and in the eastern half of the Cape York Peninsula of Australia. Taylor and Horner (1973) recognized two subspecies from Australia: *R. l. leucopus* (*personata*, *terra-reginae* and *mcilwraithi*) and *R. l. cooktownensis*.

Specimen 5 is easily distinguished from *R. leucopus* by features of the first molar. There is usually an anterior labial cusplet present on the first molar in *R. leucopus*, but such a cusplet is absent from specimen 5 (table 14). The front lamina on the first molar in *R. leucopus* is composed of a large oblong anterolingual cusp and a much smaller and round anterolabial cusp (the dissimilarity in size is striking); such a configuration is not found in specimen 5. The occlusal pattern on the first molars of *R. leucopus* are like those in *R. verecundus*, *R. richardsoni*, and *R. niobe*—all found on New Guinea (Laurie and Hill, 1954)—and unlike any of the Australian *Rattus*.

Samples of both *R. lutreolus* and *R. tunneyi* can be distinguished from specimen 5 by occlusal patterns. The teeth of *R. lutreolus* are large and chunky with laminae that are higher and straighter than those in specimen 5, and posterior cingula are absent from

the first and second molars in samples from the mainland of Australia (whereas they are large and a prominent feature of the teeth in specimen 5 and most species of *Rattus*), but present on the two molars in samples from Tasmania. The occlusal surfaces of *R. tunneyi* resemble those in *R. lutreolus*, but have very small and inconspicuous posterior cingula on the first and second molars, and laminae that are straighter and appear transverse—a striking contrast to the large posterior cingula and arcuate laminae in specimen 5.

Specimen 5 is more like *R. sordidus* and *R. fuscipes* than any of the other species, and of those two is more similar to *R. sordidus*. The lower molars of *R. sordidus* and *R. fuscipes* are similar in size (table 12) and occlusal patterns. They differ primarily in the shape of the front lamina on each first molar. In little worn teeth of *R. fuscipes*, the lamina is composed of discrete elongate anterolingual and anterolabial cusps separated by a deep and wide cleft. After more wear, the lamina becomes oblong, its anterior margin remains bifurcate, and its posterior margin is parallel to the front of the second lamina; the two lamina do not merge. Two large cusps also comprise the front lamina in *R. sordidus*, but they are larger and roundish rather than elongate, and they are separated by a shallow narrow cleft in slightly worn teeth. After more wear, the lamina becomes oblong, its anterior margin is either entire or only slightly indented in the center, its posterior margin is parallel to the front of the second lamina, and the two laminae are connected or nearly so by an enamel bridge on the lingual side. The latter configuration resembles that in Specimen 5.

Specimen 5 and samples of *R. sordidus* differ in molar size and proportions. The molars of specimen 5 are larger than those in samples of *R. sordidus*, whether from Australia or New Guinea (table 12). The breadth of the second molar relative to the first in specimen 5 is similar to that proportion in *R. sordidus*, but specimen 5 has a third molar that is as wide as the first, and wider relative to both the first and the second

molars than in *R. sordidus*; the third molar of the latter is narrower relative to the first and third (table 13).

Apparently no fossil *Rattus* from Australia ties in with specimen 5. All the subfossil and Pleistocene fragments of Australian *Rattus* that have been documented in the literature can be identified with, or are morphologically similar to one of the living species. Wakefield (1972), for example, identified material from Pyramids Cave in eastern Victoria as *R. fuscipes* and *R. lutreolus*, and reported *R. fuscipes* from the Broom Fauna of Wombeyan Caves in New South Wales. Marshall (1973) reported a single tooth of *Rattus*, which "shows a striking resemblance to *R. lutreolus*" from the Fisherman's Cliff fauna of southern New South Wales (either late Pliocene or early Pleistocene), but Archer and Bartholomai (1978) claimed, on the authority of P. Crabb, that the specimen did not come from that fauna. Marshall (1973) also identified fragments from the Lake Victoria Local Fauna (late Pleistocene-Holocene) as *R. lutreolus*, *R. cf. tunneyi*, and *R. cf. villosissimus*. Archer and Baynes (1972) recorded remains of both *R. fuscipes* and *R. tunneyi* from subfossil sediments (hair from one of the deposits was radiocarbon-dated  $430 \pm 160$  years B.P.) in two caves near Augusta, in the extreme southwest of Western Australia. Those authors also reviewed records of *R. fuscipes* from deposits in Devil's Lair (levels were dated between  $12,175 \pm 275$  and  $8500 \pm 160$  years B.P.) and Mammoth Cave ( $37,000$  or  $31,500$  years B.P.) in Western Australia; Baynes, Merrilees and Porter (1975) have elaborated on the fauna from Devil's Lair. Both *R. fuscipes* and *R. tunneyi* were collected from deposits in Skull Cave, Western Australia (Porter, 1979); remains of *R. fuscipes* were found throughout the intermediate level (radiocarbon-dated  $7875 \pm 100$  years B.P.) and the upper level ( $2900 \pm 80$  years B.P.); fragments of *R. tunneyi* were obtained only from the upper level. Finally, "*Rattus* sp., cf. *R. lutreolus* and *Rattus* sp., cf. *R. fuscipes*" were recorded by Archer (1978, p. 93) from what he determined to be Pleistocene sediments in

Russenden Cave, one of the two Texas Caves on Viator Hill in southeastern Queensland.

The morphological features characterizing specimen 5 resemble those associated with the mandibular tooththrows of *R. sordidus* more than they do any of the other Australian species. But specimen 5 has larger molars than most *R. sordidus*, and a third molar that is wider relative to the others in the tooththrow. These differences, as well as details of the cusp patterns, indicate that specimen 5 does not belong with *R. sordidus*, or with any other species in the Australian assemblage of native *Rattus*, including the known subfossil and Pleistocene samples.

THE IDENTITY OF SPECIMEN 5 WITH *KOMODOMYS*: Specimen 5 is an example of *rintjanus*, originally described by Sody in 1941 as a species of *Rattus*, but recently placed in its own genus, *Komodomys*, by Musser and Boeadi (1980), who, besides distinguishing *Komodomys* from *Rattus*, also provided descriptions of skins, skulls, and teeth, as well as information about habitat. *Komodomys rintjanus* is the only native murid recorded from Rintja and Padar, two small islands between Komodo and Flores, and is known from these two places by Recent specimens only.

*Komodomys rintjanus* is a rat of medium body size (ranges, in mm., from 16 old to young adults, are: length of head and body, 125–200; length of tail, 112–163; length of hind foot, 31–41; length of ear, 15–24; see table 1 in Musser and Boeadi, 1980) with a short tail, semi-spinous sandy-colored dorsal pelage, gray ventral fur, tan ears, hairy white feet, and 10 mammae (without a pectoral pair); figure 25.

The skull is of medium size (the range, in mm. for greatest length of skull from seven old to young adults is 34.0–45.9; see table 1 in Musser and Boeadi, 1980, for values from other cranial measurements) and distinctive in shape (fig. 26), recalling the skulls of the Australian *Conilurus* or the gerbils in *Tatera*, genera with species that are adapted to savanna woodlands. In *K. rintjanus*, the dorsal profile of the cranium is strongly convex;

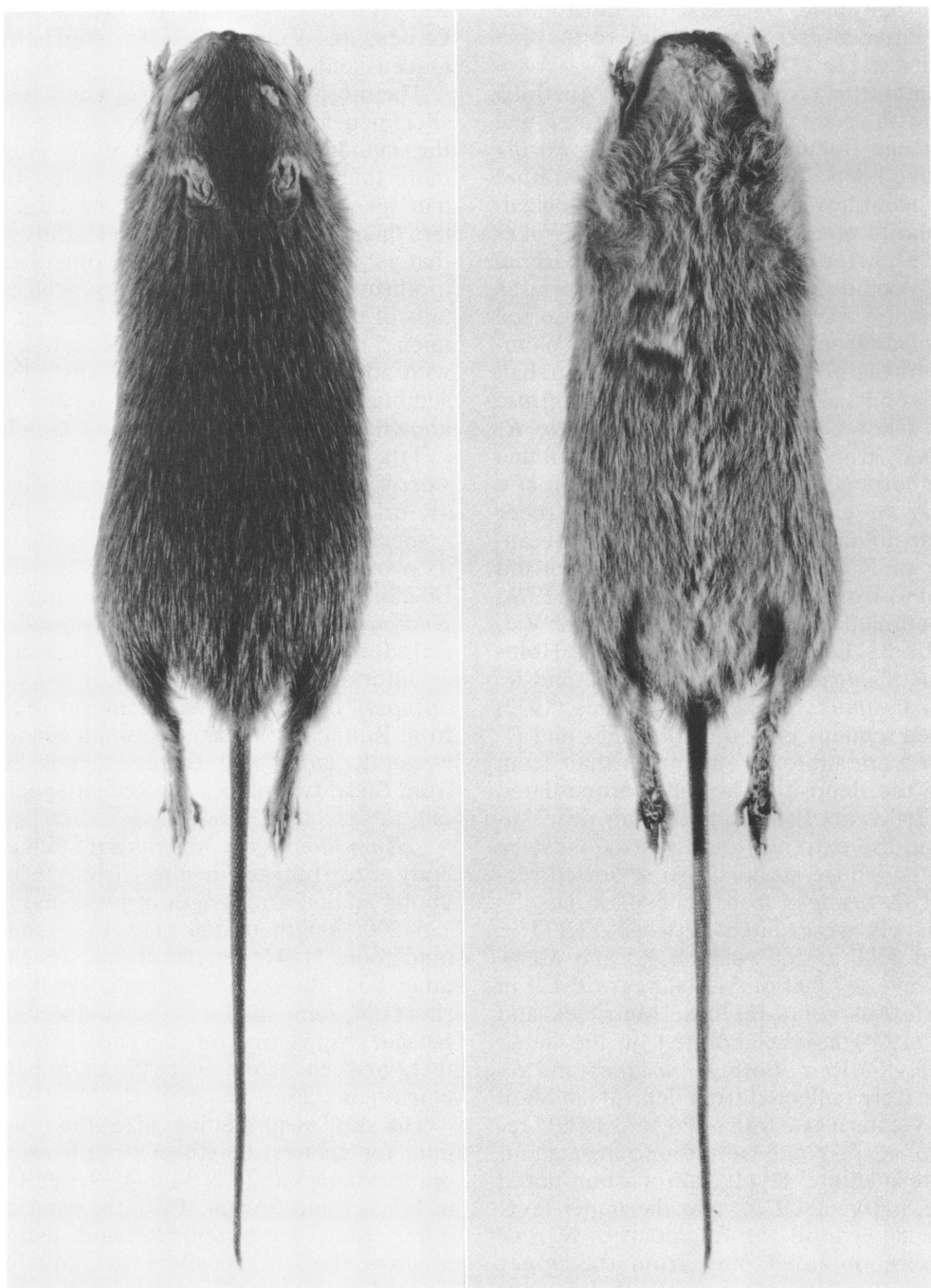


FIG. 25. Recent *Komodomys rintjanus* from Rintja Island. Dorsal (left side) and ventral (right side) views of skin (MZB 9020). Measurements in mm.: head and body, 163; length of tail, 152; length of hind foot, 36; and length of ear, 19.

the rostrum and nasals are long and slender; the top of the skull between zygomatic plates is very wide and nearly flat; the lacrimal bones are very large and squarish in dorsal outline; the tops of the dorsal maxillary roots of the zygoma are expansive; the zygomatic plates are wide, and the spine of each juts well anterior to the dorsal roots of the zygoma; the braincase is high, with most of that height above the squamosal roots of the zygoma; the interparietal is relatively small; the squamosal forming the braincase wall is intact above each bulla, not separated into two portions by the squamoso-mastoid foramen; the configuration of each alisphenoid region is like that in *Papagomys armandvillei* (fig. 7) in which the strut of alisphenoid bone is gone, as are the foramen ovale accessorius and the masticatory-buccinator foramina; the incisive foramina are long and narrow, constricted in their posterior fourth, and extend past the fronts of the first molars by 0.9–1.7 mm.; the palatal bridge is narrow and ends either even with the backs of the third molars or extends beyond them by 0.1–0.4 mm.; the mesopterygoid fossa is very narrow, its walls breached by huge sphenopalatine vacuities; the pterygoid fossae are deep, the floor of each is tilted toward the midline of the cranium, the anterior two-thirds is perforated by a small sphenopalatine canal, and the lateral margin is defined by a prominent ridge extending from back of the palatal bridge to the bulla, a configuration similar to that in *Papagomys armandvillei* (fig. 8); the bullae are very large, both absolutely and relative to size of the braincase, each is separated from the braincase by a wide postglenoid vacuity, and each bony eustachian tube is short and conspicuous; each coronoid process is small relative to size of the dentary.

*Komodomys rintjanus* has orange-enamelled upper and lower incisors; the uppers emerge from the rostrum and curve back (opisthodont in configuration).

The upper molars of *K. rintjanus* are large (the mean  $\pm$  one SD and the range, in mm., from 13 adults: alveolar length of maxillary toothrow,  $7.9 \pm .3$ , 7.4–8.2; breadth of first

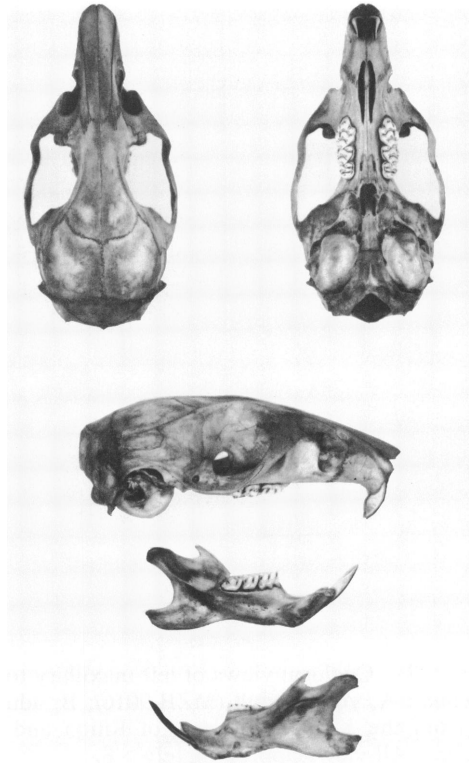


FIG. 26. Recent *Komodomys rintjanus*: dorsal, ventral, and side views of the cranium; lingual and labial views of the left dentary; an adult (MZB 9014) from Padar Island. All views natural size.

molar,  $2.5 \pm .1$ , 2.3–2.6; breadth of second molar,  $2.4 \pm .1$ , 2.2–2.5; and breadth of third molar,  $1.9 \pm .2$ , 1.8–2.0), both absolutely and relative to each palatal region and mandible (fig. 26), and have high conelike cylindrical cusps on the first and second molars that remain discrete until young adulthood. The first molar is the widest tooth, the second is as wide or only slightly narrower, and the third molar is narrower than either the first or second (table 7). The high cusps on the first and second molars slant back so that the first molar overlaps part of the second and the second part of the third in the same manner and to a similar extent as that in *Papagomys armandvillei* (table 6). Each first molar is anchored by five roots (anterior, di-

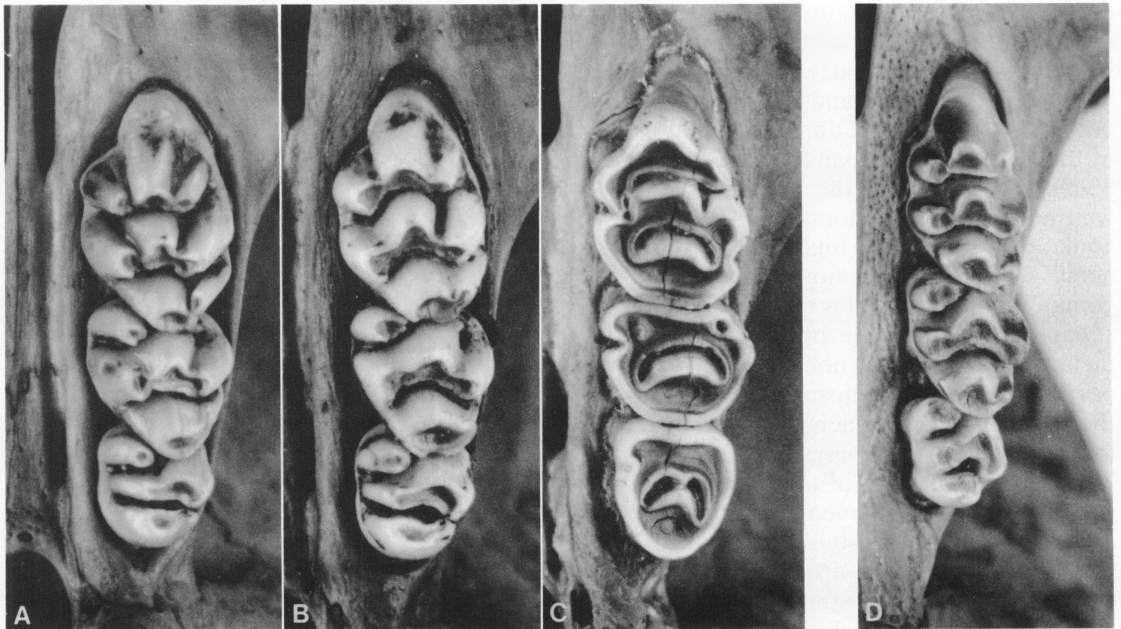


FIG. 27. Occlusal views of left maxillary toothrows in recent *Komodomys* and *Rattus*. *Komodomys rintjanus*: A, young adult (MZB 9016); B, adult (MZB 9014); and C, old adult (MZB 7706); specimens are from the Komodo Islands of Rintja and Padar. *Rattus rattus*: D, adult (AMNH 153000), from Celebes. All views approximately  $\times 8$ .

vided lingual, posterior, and small labial), each second molar has four roots (two anterior and two posterior), and three roots (two anterior and a single posterior) anchor each third molar.

The occlusal patterns on the upper molars, illustrated in figure 27, are similar to those patterns on the molars of *Papagomys armandvillei*. There are three rows of cusps on each upper molar, along with a small ridge-like t1bis; neither a cusp t7 nor posterior cingulum are present. Two distinctive features are the cusp t6 on the second row of cusps, which is nearly separated from the medial cusp, connected only by a thin bridge of enamel and dentine, a configuration retained even in worn teeth; and cusp t9 on the back row, which is compressed from side to side, small, and joined only by its thin posterior edge to the large medial cusp t8.

Each second upper molar has a large cylindrical cusp t1, a tiny cusp t3 that is present in all the specimens, a row of three cusps

similar in configuration to the second row on the first molar, and a back row formed from a large cusp t8 and very small and slender cusp t9. A cusp t7 and posterior cingulum are absent.

Each third upper molar has a large cusp t1, a minute cusp t3 that occurs in 90 percent of the sample, a nearly transverse comma-shaped lamina (formed of cusps t4, t5, and t6), and a crescent-like posterior lamina consisting of a large cusp t8 and a sliver-like cusp t9 that becomes incorporated into the central cusp after only a little wear. Cusp t7 and a posterior cingulum are absent.

The lower molars of *K. rintjanus* are illustrated in figure 28. The toothrows are long and the individual molars wide (table 12). The second molar is absolutely wider and relatively much wider than the first, and the third molar is as wide and usually wider than the first, both absolutely and relatively, a feature that is like *Papagomys* (table 7) and unlike *Rattus* or *Floresomys* (table 13). Each

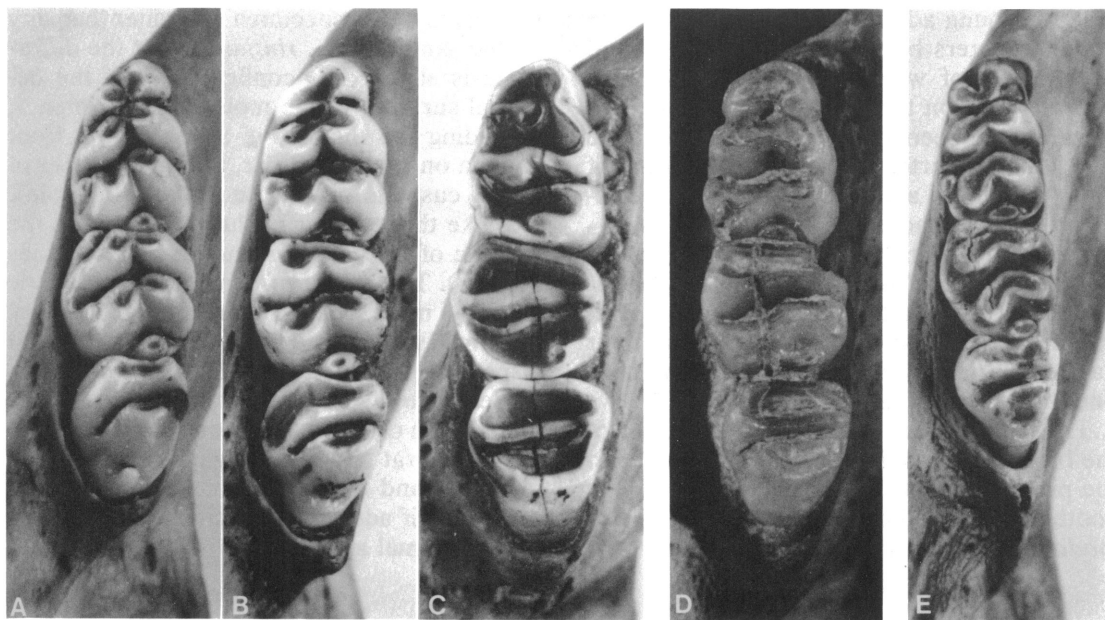


FIG. 28. Occlusal views of left mandibular toothrows in recent and subfossil *Komodomys*, and recent *Rattus*. A–C, young adult, adult, and old adult, respectively, from the same specimens shown in figure 27, all from the islands of Rintja and Padar; D, specimen 5, the subfossil from Liang Toge, Flores. *Rattus rattus*: E, an adult from the same example shown in figure 27, from Celebes. All views approximately  $\times 8$ .

first lower molar has four roots (large anterior and posterior, small labial and lingual), and three roots (two anterior and a single large posterior) anchor each second and each third molar.

The occlusal surfaces consist of three rows of primary cusps and a posterior cingulum on the first molar, two rows of cusps and a posterior cingulum on the second molar, and two rows of cusps on the third molar; there is a small tubercle on each third molar that is probably a posterior cingulum and present in nine out of the 12 specimens that are slightly to moderately worn (fig. 28A). There are also additional cusps and labial cusplets on each molar. The front row of each first molar is formed by a large anterolingual cusp and a smaller anterolabial one. As they wear down, the cusps join to form a lamina that slants back to the labial side, lies parallel to the anterior edge of the second lamina, and is connected to that second row of cusps by

a thin wall of enamel and dentine (fig. 28B). Infrequently attached to the front lamina on each first molar is an anterocentral cusp that, out of 11 specimens, is present on the right molars of two individuals, and on both right and left teeth of one other. An anterolabial cusp occurs on the second molar in all specimens, and is found on the third molar in eight out of 10 rats. In addition to these anterolabial cusps, there is a posterior labial cusplet on each first molar but no anterior labial cusplet (table 14), and a posterior labial cusplet on each second molar.

The shapes and relative positions of the cusps on slightly worn lower molars of *K. rintjanus* are high, conelike cylinders, each compressed so that they are nearly tear-drop in cross-section. In each row, the cones slant toward one another, the wide oval part at the outer margin, and join their thin inner edges at the midline of the tooth. The cusps are separate and remain discrete until the rat

reaches young adulthood, at which time the dentine centers begin to merge. At this and later stages of wear, the second and third row of cusps on the first molar, and the two rows on the second molar are in the shape of a broad inverted V in which the arms of the V are thick and oval, producing a scalloped back surface on each row of cusps—the effect resulting from cylinder-like cusps that are thick and round on one side and taper to a narrow edge on the opposite side, and are positioned so they meet along their narrow margins at a sharp angle in the midline of the tooth (fig. 28A and B).

The length of the toothrow in specimen 5, the breadths of its first and third molars, and the proportions of the molars relative to one another are like those in the sample of *Komodomys rintjanus* (tables 12 and 13). The

second molar in specimen 5 is wider than any in the sample of *K. rintjanus*, but the difference is slight. The configuration of the occlusal surfaces of the molars in specimen 5, including the distinctive shape of the front lamina on the first molar, and the number of labial cusplets on all the molars (table 14), are like those molar occlusal patterns in the sample of *K. rintjanus* and no other species (fig. 28). The dentary fragment appears to be slightly more robust than similar dentary portions in the sample of *K. rintjanus*; that aspect of specimen 5, along with its slightly wider second molar, may indicate that the population of *K. rintjanus* on Flores is a larger-bodied rat than those living on the islands of Padar and Rintja. This suggestion should be tested if additional specimens of the Floresian animal are found.

## POSSIBLE HABITS AND HABITATS OF THE FLORESIAN RATS

The morphological diversity among the six native rats on the Flores reflects not only phylogenetic relationships but also different food requirements and possibly habitats. Four of the six species represented by the fragments from cave deposits at Liang Toge may have been forest rats. Based on analogies from my firsthand experience with the endemic murids on Celebes, I speculate that *Floresomys naso* was likely terrestrial and could have included fungi, insects, snails, earthworms, and possibly some fruit in its diet (by analogy with species of *Bunomys*). *Spelaeomys florensis*, with its hypsodont molars and extensive occlusal surfaces, may have been partially arboreal and fed on leaves, buds, flowers, and insects such as moths and katydids (by analogy with *Lenomys*). *Papagomys armandvillei* is built like a terrestrial rat and may eat leaves, buds, fruit, and certain kinds of insects (by analogy with *Eropeplus*), a diet not inconsistent with its large hypsodont teeth (this presumption can be tested since *P. armandvillei* still lives on Flores). *Papagomys theodorverhoeveni*

may have fed on insects and fruit, possibly leaves, and probably exploited a different part of the habitat than *P. armandvillei*.

According to Musser and Boeadi (1980, p. 408), "Low terraces behind beaches that give way to rolling hills dissected by deep ravines and canyons comprise the countryside where specimens of *Komodomys rintjanus* were obtained. Grassland interrupted by isolated or clustered tall . . . palms [*Borassus flabellifer*], lone trees, thickets, and small patches of short forest seem to be the phytographic structure on the terraces and low hills. Tracts of gallery forest extend up through the ravines and canyons onto the hilltops [figs. 29 and 30]." Boeadi "trapped the rats on the ground under tall thickets and beneath the gallery forest along water courses. The ground is rocky and he thought that the spaces between the rocks and ground, and the crevices among the rocks, might have provided refuges for the rats." Musser and Boeadi (1980, pp. 408–409) also speculated that "the presence of a xerophilic, mostly deciduous forest in which the ground

beneath is relatively open or only thinly clumped with short grasses may have been the habitat in which an animal like *K. rintjanus* evolved. The sandy-colored upperparts, densely haired white feet, moderately large ears, and short hairy tail of *K. rintjanus* point to a ground dweller in dry scrub or forest. The specializations in the cranium and teeth . . . may reflect adaptations to a dry, or seasonally dry, tropical forest habitat where the structure of tall scrub and short, partly deciduous, forest provide dense cover above sparse undergrowth at ground level."

The Floresian *K. rintjanus* likely had habitat requirements that were similar to the populations on the islands of Rintja and Padar. If rain forest, or at least tall and extensive gallery forest, were necessary for the other four species represented by the fragments found at Liang Toge, then three to four thousand years ago, Flores may have been covered by monsoon forest or savanna woodland over the coastal plains and foothills, and tropical evergreen rain forest at higher elevations and in moist sheltered canyons at lower places. Such habitats would have been similar to the present natural cover on Flores before it was so drastically altered by humans (Whitmore, 1975; Richards, 1976).

The ecological significance of the morphological diversity among the five species represented in the sediments at Liang Toge could be better appreciated if there was information indicating that the five were contemporaneous; unfortunately, I do not have that kind of data. Hooijer (1957b, p. 300) related that certain specimens of *Papagomys*

*armandvillei*, *P. theodorverhoeveni*, and *Spelaeomys* were taken from the deepest layer in the cave; "The remainder of the collection was made without regard to the stratification of the cave deposit." Without careful stratigraphic information tied to the subfossils, it is difficult to reconstruct either the former habitats in the area or the species-diversity represented at any given time.

The possible habits and habitat of *Hooijeromys nusatenggara* are not readily apparent. The combination of wide zygomatic plates; long incisive foramina; first upper molars anchored by five large and strong roots; nearly transverse rows of cusps on the first and second molars, and the wide second molar are configurations similar to those found in *Bandicota indica*, the large tropical Asian bandicoot rat (see the illustrations in Marshall, 1977b). In my experience, *B. indica* lives in tall grass or cultivated fields of corn, dry rice, or sugar cane. The rat is terrestrial and nests underground in extensive burrows. Its food consists of large snails, crabs, and molluscs along with plant parts. Perhaps the habits and diet of *H. nusatenggara* were similar to those of *B. indica*.

The fragments of *Hooijeromys* were excavated (as Dr. Verhoeven explained to me) out of the same fossiliferous sandstone that yielded the pieces of *Stegodon*, sediments possibly of middle or late Pleistocene age (Hooijer, 1957a). Those beds, however, have yet to be dated. There is no way at present to know whether *H. nusatenggara* and the other native rats were contemporaneous or whether they were temporally isolated.

## THE OTHER MAMMALS FROM FLORES

The six indigenous rats are part of the 32 species of mammals now known from Flores: six other murids, the Javan porcupine, two stegodonts, one rusa, two pigs, the palm civet, the crab-eating macaque, nine bats, two shrews, and probably another (table 15). The two stegodonts and one native rat are known by fragments found in sediments

thought to be Pleistocene. Four native rats are represented only by material from deposits dated between 3000 and 4000 years old. The remaining 25 species are Recent; none are represented by Pleistocene samples but four are known by both subfossil and Recent specimens. Six out of the 32 species—one shrew and five rats—are

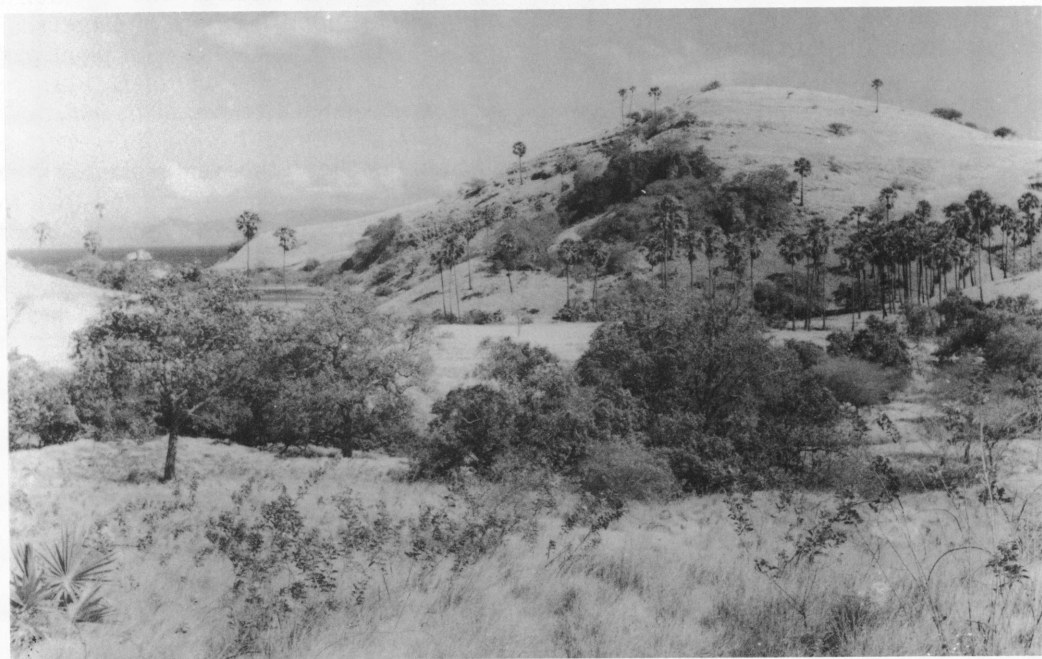
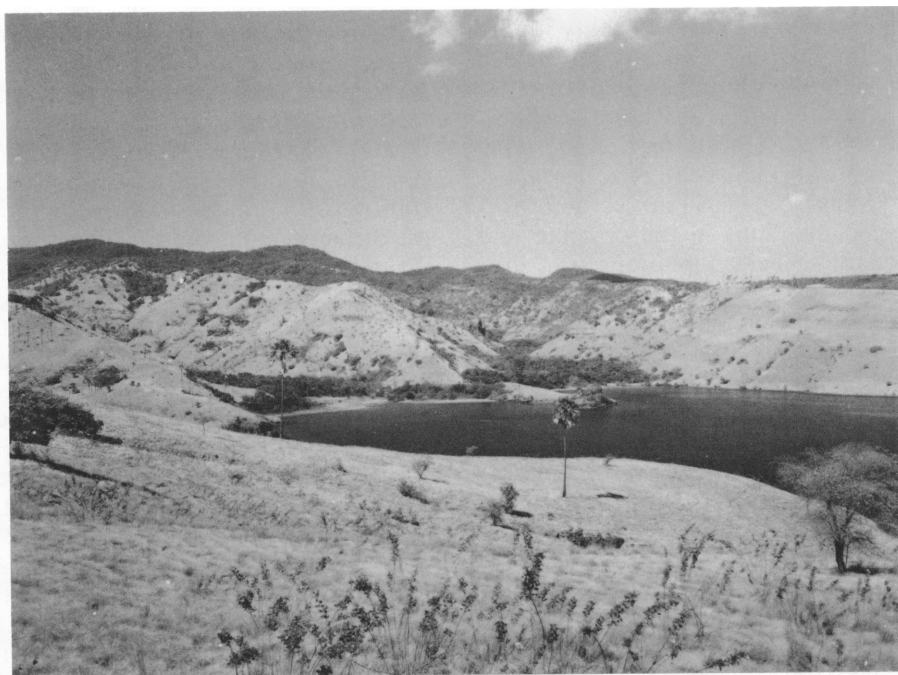


FIG. 29. Views of the habitats on the island of Rintja. These photographs and the one in figure 30 are from Hoogerwerf (1953–1954).

known only from Flores, 19 percent of the known fauna; four of these are presumed to

be extinct or at least have not yet been discovered living on the island. Two others,



FIG. 30. An example of gallery forest on the islands of Rintja and Padar.

*Suncus mertensi* and *Papagomys armandvillei*, are the only two out of the 25 species now living on the island that are known to occur only on Flores. One of the other shrews, a rat, and all the bats occur someplace else as well as on Flores. Thirteen of the species (52 percent) were likely introduced to Flores inadvertently or intentionally by humans: possibly one shrew, the crab-eating macaque, palm civet, two pigs, rusa, Javan porcupine, four rats, and two mice.

An explanation about the species that I consider to be introduced is necessary. That *Macaca fascicularis* (crab-eating macaque), *Paradoxurus hermaphroditus* (palm civet), *Sus scrofa* and *S. celebensis* (pigs), *Cervus timorensis* (rusa), and *Hystrix javanica* (Javan porcupine) were introduced onto Flores by humans is the hypothesis I am working with until it can be disproved. The present geographic distributions of these six species and the times of their occurrences as subfossils and in Pleistocene deposits on the Sunda Shelf and in the Lesser Sunda Islands comprise the basis for that hypothesis. All are

primarily components of the mammalian fauna indigenous to Southeast Asia, the Malay Peninsula and islands on the Sunda Shelf; remains of some of them have been found in Pleistocene sediments on the Shelf. None of the six have been discovered in Pleistocene deposits on Flores. Fragments of the crab-eating macaque, a pig, and Javan porcupine were found in cave deposits on Liang Toge (Hooijer, 1967b). The deposits there also contained remnants of five murids that are native to Flores and have not been found on any other island or continent to the east, west, or north of Wallace's Line, except for the Komodo Islands of Padar and Rintja. The macaque, however, also occurs on other islands in the Lesser Sunda Group (Laurie and Hill, 1954), the Philippines, on the Sunda Shelf (Fooden, 1964), and the mainland of Southeast Asia (Fooden, 1971). It has also been recorded from the Jetis and Trinil faunas (late Pliocene-early Pleistocene and middle Pleistocene, respectively) and Sampung Cave (early Holocene) of Java, and from sediments in the Niah Cave (late Pleistocene) of Sarawak (Medway, 1972). One of

TABLE 15  
Recent (R), Subfossil (S) and Pleistocene (P)  
Mammals of Flores<sup>a</sup>

Species	En- demic	Also else- where	In- tro- duced
<b>SHREWS</b>			
<i>Suncus mertensi</i>	R	—	—
<i>Suncus murinus</i> <sup>b</sup>	—	—	R
<i>Crociodura monticola</i>	—	R	—
<b>BATS</b>			
<i>Rousettus amplexicaudatus</i>	—	R	—
<i>Pteropus lombocensis</i>	—	R	—
<i>Acerodon mackloti</i>	—	R	—
<i>Dobsonia peronii</i>	—	R	—
<i>Taphozous longimanus</i>	—	R	—
<i>Myotis mystacinus</i>	—	R	—
<i>Scotophilus temmincki</i>	—	R	—
<i>Murina florium</i>	—	R	—
<i>Kerivoula hardwickei</i>	—	R	—
<b>PRIMATES</b>			
<i>Macaca fascicularis</i> <sup>c</sup>	—	—	R + S
<b>CARNIVORES</b>			
<i>Paradoxurus hermaphroditus</i>	—	—	R
<b>PIGS AND DEER</b>			
<i>Sus scrofa</i> <sup>d</sup>	—	—	R + S
<i>Sus celebensis</i>	—	—	R
<i>Cervus timorensis</i>	—	—	R
<b>STEGODONTS</b>			
<i>Stegodon trionocephalus</i>	—	P	—
<i>Stegodon sompoensis</i>	—	P	—
<b>RODENTS</b>			
<i>Hystrix javanica</i>	—	—	R + S
<i>Hooijeromys nusatenggara</i>	P	—	—
<i>Papagomys armandvillei</i>	R + S	—	—
<i>Papagomys theodorverhoeveni</i>	S	—	—
<i>Spelaeomys florensis</i>	S	—	—
<i>Floresomys naso</i>	S	—	—
<i>Komodomys rintjanus</i>	S	—	—
<i>Rattus rattus</i>	—	—	R
<i>Rattus argentiventer</i>	—	—	R
<i>Rattus exulans</i>	—	—	R
<i>Rattus norvegicus</i>	—	—	R
<i>Mus musculus</i>	—	—	R
<i>Mus caroli</i>	—	—	R

<sup>a</sup> The information is compiled from Mertens (1936), Sody (1941), Pohle (1950), Laurie and Hill (1954), Kock (1974), Hooijer (1967b, 1975), Marshall (1977), Groves (his letter to me), and my own files. I have excluded domestics such as goats, dogs, cats, kerbow, horses, and cattle.

the pigs, *Sus scrofa*, native to Europe and Asia, occurs throughout the archipelagos east of the Sunda Shelf and Laurie and Hill (1954, p. 86) speculated that "Pigs of the *scrofa* group, found throughout the Archipelago, appear to be the feral descendants of pigs carried from island to island by human agency. They are in some cases semi-domesticated." The other pig, *S. celebensis*, occurs on Sulawesi and other places east of the Sunda Shelf (listed as *S. verrucosus* in Laurie and Hill, 1954).<sup>1</sup> Finally, the Javan

<sup>1</sup> Dr. Colin P. Groves has been studying the taxonomy and geographic distribution of pigs found in the Far East and is now preparing a manuscript containing his results. He was generous enough to provide me with some information in a letter about the pigs on Flores: "There are two pigs on Flores, both introduced I'm sure. One is *Sus scrofa*: as witness the syntypes of *Sus floresianus*

<sup>b</sup> My sources for including *Suncus murinus* are Pohle's (1950) reference to its probable occurrence on Flores, as well as Lombok, Sumbawa and Sumba; and Laurie and Hill's (1954, p. 29) inclusion of the "Lesser Sunda Islands" within its range. The only specimens of a *Suncus* actually documented from Flores are those of *S. mertensi*, a species that Kock (1974), its describer, claims to be an inhabitant of forest and not a commensal.

<sup>c</sup> *Macaca fascicularis* is the oldest name for the macaque from Flores that has been recorded in the literature as *M. irus* (see Laurie and Hill, 1954, for example). Because of what he determined to be geographical intermediates between specimens of the rhesus (*Macaca mulatta*) and crab-eating (*M. fascicularis*) macaques, Fooden (1964) considered the two conspecific. Later, however, he (Fooden, 1971, p. 31) changed his mind: "The most reasonable interpretation of local morphological intergradation between *M. mulatta* and *M. fascicularis* now seems to be that the intergrade populations are hybrids that have resulted from secondary contact and occasional fertile breeding between two species that previously differentiated in geographic isolation . . ." Fooden is studying both kinds of macaques and until he completes those taxonomic revisions, I have used the name *M. fascicularis* for the crab-eating macaque, which reflects Fooden's latest interpretation of the specific relationship between populations of the rhesus and crab-eating macaques.

<sup>d</sup> The pig fragments from Liang Toge were originally identified as *Sus scrofa* (Hooijer, 1967b), but I considered that determination tentative until the pieces are compared with *S. celebensis*.

porcupine has also been recorded from Sumbawa, southern Sulawesi, Pulau Tanah Jampea, and Lombok off the Sunda Shelf; and Bali and Java on the Shelf (Laurie and Hill, 1954; van Weers, 1979). It too is known from the Pleistocene of Java in the Jetis and Trinil faunas and from subfossil deposits in Sampung Cave on Java (Medway, 1972, recorded it under the name *H. brachyurus*, apparently following Chasen, 1940, who listed the Javan porcupine as a subspecies of *H. brachyurus*. Chasen recorded it from Java and Bali and thought it also occurred on Borneo, Sumatra, and the Malay Peninsula; however, van Weers, 1979, has provided evidence for recognizing the form on Java and Bali as a distinct species).

Neither the rusa nor palm civet are known from fossil or subfossil deposits on Flores. Both now live on Java and their remains can be traced back to middle Pleistocene deposits on that island (Medway, 1972). The palm civet also occurs over the Sunda Shelf and on the mainland of Southeast Asia. Rusa are now found on many islands in the archipelagos east of Wallace's Line and Laurie and Hill (1954) have enumerated the times and places rusa were imported onto islands previously uninhabited by the species.

The crab-eating macaque, palm civet, a pig, and rusa also live on Timor nowadays. Their remains have not been found in Pleistocene sediments on that island, or in early prehistoric layers (dated from 6000 to 13,000 years B.P.) of the limestone caves excavated by Glover (1969, 1970). Specimens of all four species are present in sediments 4500 to 5500 years old, a time that Glover thinks agriculture may have been introduced into Timor. Glover (1971, p. 176) also speculated that

Jentink, 1905, from Maumeri. It was not stated, by Jentink or anyone else, whether these were wild or domestic; but if wild they are feral and rather unlike any other feral, domestic or wild pig so either long-established or else from a small founder population. The other is *Sus celebensis*: specimens from Ubwa and Bajawa in the Bogor Museum, and doubtless *Microsus floresianus* Heude, 1899 (of which I've seen the description and figures, but not of course the original specimen); these are again not specifically stated whether wild or domestic, but if wild then they must be feral."

"About this time [4500 to 5000 years ago] bones of four wild mammals first occur in the deposits—cuscus, civet cat, deer, and monkey; all probably were introduced to Timor through the agency of man."

I cannot yet discard the alternate hypothesis that the presence of the macaque, palm civet, rusa, and porcupine on islands in the Lesser Sundas represent post-Pleistocene natural dispersal to there from regions in the west—assuming that is where they were originally indigenous. Samples of the four species from Nusatenggara have been described as distinctive subspecies (Laurie and Hill, 1954), implying that populations have been isolated on a given island long enough for morphological differentiation to have taken place. Now, however, the significance of the described subspecies of the macaque, palm civet, and rusa on Flores and Timor cannot be evaluated because there are no careful studies of individual and geographic variation in any of the three from samples on the Sunda Shelf and Southeast Asia. The porcupine is an exception; van Weers (1979, p. 253), who reported on the taxonomy of Southeast Asian *Hystrix*, "could not perceive any significant difference neither in cranial nor in external characters . . ." between samples of the Javan porcupine from Nusatenggara and those from Java.

Finally, if these species got to Flores and Timor by non-human dispersal, why did not other kinds of mammals, those indigenous to Java and other islands on the Sunda Shelf, also get to islands in the Lesser Sundas? I think it significant that the macaque, civet, pigs, rusa, and porcupine are large in body size and the kind of animals that are even now kept by villagers and townspeople either for food or for the pleasures that pets provide. The same species were also probably kept by prehistoric agriculturists who may have brought them along during those early migrations from islands on the Sunda Shelf, such as Java and Bali, to places in Nusatenggara—Flores and Timor, for example.

The four rats (*Rattus rattus*, *R. argentiventer*, *R. exulans* and *R. norvegicus*) and two mice (*Mus musculus* and *M. caroli*), though probably the most common elements of the murid fauna now living on Flores, are

not native to that island but were likely brought there through human agency at different times in the long history of human occupation of Nusatenggara, possibly transported inadvertently in native prau or steamer. Samples of the six are known by Recent specimens only. All live in habitats closely associated with humans, such as houses in villages and towns, gardens, rice fields, plantations of coconut palms, and scrub. All of them are found elsewhere: on scattered islands to the east of the Sunda Shelf, on the Sunda Shelf itself, and north of there in Southeast Asia. All the species of rats and mice that are indigenous to islands and continent east of the Sunda Shelf do not occur on the Shelf or in Southeast Asia. Most of them are known only from a particular island, group of islands, or Australia. Their geographic ranges make sense set against what is known about the island geography, past and present. Compared with the zoogeographic patterns of endemism in native rats and mice east of the Sunda Shelf, the occurrence on Flores of six species that are also found on the Shelf and in Southeast Asia suggests that they were not originally native to the archipelagos east and north of

Wallace's Line. Of the *Rattus*, *R. norvegicus* has been spread around the world by shipping and Flores was just another spot where a population took hold. *Rattus argentiventer* may be associated with the spread of rice culture through the archipelagos. Rice fields are prime habitat for the rat. Its spotty distribution east of the Sunda Shelf is incomprehensible from any other viewpoint. *Rattus exulans*, according to Schwarz and Schwarz (1967), originated in Nusatenggara, probably Flores, but there is no evidence for that claim—the species was likely introduced. *Rattus rattus*, where it occurs on islands with endemic murids, is excluded from native environments and so closely tied to habitats made and maintained by humans and so widespread on the Asian mainland and throughout the archipelagos east of the Sunda Shelf that I view the species as an introduced element into the Flores fauna. Of the mice, *Mus musculus castaneus* lives in houses and very large buildings in cities of the Far Eastern tropics and was most likely distributed by shipping (Marshall, 1977a). *Mus caroli*, like *R. argentiventer*, inhabits rice fields and was likely unintentionally introduced on Flores along with rice culture.

## RELATIONSHIPS OF THE NATIVE FLORESIAN RATS

### NATIVES FROM EAST OF THE SUNDA SHELF

The living *Papagomys armandvillei* and the five murids represented by subfossil and fossil fragments comprise the bulk of the native mammal fauna on Flores. What the relationships of the Floresian rats are to murids outside of that island may be discerned by comparing them with samples of the genera occurring north and east of Wallace's Line, from Sulawesi and the Philippines to New Guinea and Australia (fig. 1). I introduce these genera by listing them below under the area each has been recorded from. An asterisk designates each genus containing some species indigenous to places on the Sunda Shelf and Southeast Asia.

### PHILIPPINE ISLANDS (excluding the Palawan and Calamian groups)

*Anonymomys*  
*Apomys*  
*Batomys* (includes *Mindanaomys*)  
*Bullimus*  
*Carpomys*  
*Celaenomys*  
*Chrotomys*  
*Crateromys*  
*Crunomys*  
*Limnomys*  
*Phloeomys*  
 \**Rattus*  
*Rhynchomys*  
*Tarsomys*  
*Tryphomys*

## SULAWESI

- Bunomys* (includes *Frateromys*)
- Crunomys*
- Echiothrix* (includes *Craurothrix*)
- Eropeplus*
- \**Haeromys*
- Lenomys*
- Margaretamys*
- \**Maxomys*
- Melasmothrix*
- Paruromys*
- \**Rattus* (includes *Mollicomys*)
- Taeromys* (includes *Arcuomys*)
- Tateomys*

## OBI AND TALAUD ISLANDS

- Melomys*

## SULA ISLANDS

- \**Rattus*

## MOROTAI ISLAND

- \**Rattus*

## CERAM

- Melomys*

- \**Rattus* (includes *Nesoromys*)

NEW GUINEA, BISMARCK ARCHIPELAGO,  
SOLOMON ISLANDS

- Anisomys*
- Chiruromys*
- Conilurus*
- Crossomys*
- Hydromys* (includes *Baiyankomys*)
- Hyomys*
- Leptomys*
- Lorentzimys*
- Macruromys*
- Mallomys* (includes *Dendrosminthus*)
- Mayermys*
- Melomys* (includes *Paramelomys*)
- Microhydromys*
- Neohydromys*
- Parahydromys* (includes *Drosomys* and *Limnomys*)
- Paraleptomys*
- Pogonomelomys*
- Pogonomys*
- Pseudohydromys*
- Pseudomys*
- \**Rattus* (includes *Stenomys* and *Geromys*)
- Solomys*
- Uromys* (includes *Cyromys*)
- Xenuromys*

## AUSTRALIA AND TASMANIA

- Conilurus* (includes *Hapalotis*)
- Hydromys*
- Leggadina*
- Leporillus*
- Mastacomys*

*Melomys**Mesembriomys* (includes *Ammomys*)*Notomys* (includes *Podanomalus*, *Ascopharynx*, and *Thylacomys*)*Pogonomys**Pseudomys* (includes *Paraleporillus*, *Gyomys*, and *Thetomys*)\**Rattus* (includes *Acanthomys*)*Uromys* (includes *Gymnomys*)*Xeromys**Zyzomys* (includes *Laomys*)

## TIMOR

*Coryphomys**Melomys**Pogonomelomys*

## Three other genera not yet named and described

## FLORES

*Floresomys**Hooijeromys**Komodomys**Papagomys**Spelaeomys*

## RINTJA AND PADAR (KOMODO ISLANDS)

*Komodomys*

Those genera from the Philippines, Ceram, New Guinea, Australia, Timor, and Flores do not occur to the west on either the Sunda Shelf or the Asian mainland. *Rattus* is the only genus extending across the eastern archipelagos from mainland Asia to Australia. Sulawesi is a special case. Aside from *Rattus*, nine of the genera from there are not found to the west, but two are: species of *Haeromys* also occur on Borneo (Medway, 1965), and *Maxomys* embraces many species on the Sunda Shelf and two in Southeast Asia (Musser, Marshall and Boeadi, 1979).

Most of the genera listed above are confined to either a certain island, a particular island group, New Guinea or Australia, but a few places share the same genera. *Crunomys* has been recorded from the islands of Luzon and Mindanao in the Philippines (Ellerman, 1941) and from Central Sulawesi as well (Musser, 1977). New Guinea shares *Melomys* with the islands of Ceram, Obi, Talaud, and Timor to the west, and *Pogonomelomys* with Timor (Tate, 1951; Laurie and Hill, 1954; Glover, 1970). *Uromys*, *Melomys*, *Pogonomys*, *Conilurus*, *Pseudomys*, and *Hydromys* are part of the fauna of both

New Guinea and Australia (Tate, 1951; Waithman, 1979; J. A. Mahoney, personal commun.).

The taxonomy of the genera has been based primarily on structure of the teeth, sometimes cranial features, and less so on characteristics of the skin. The viewpoints of interrelationships among the genera, and the prevalent picture of the evolutionary history implied from those relations can be summarized by discussing the treatments of first, Ellerman (1941), then Simpson (1945), and finally Misonne (1969).

Ellerman separated the genera from east of Wallace's Line into three subfamilies: the Hydromyinae, containing *Hydromys*, *Parahydromys*, *Crossomys*, *Leptomys*, *Xeromys*, *Pseudohydromys*, *Chrotomys*, and *Celaenomys*; the Rhynchomyinae, with *Rhynchomys*; and the Murinae, which he subdivided into the Group Anisomyes, containing *Anisomys*, and the Group Mures. The latter was broken into three sections by Ellerman (1941, p. 45): "those retaining the posterointernal cusp and having no extreme specialization of molars, i.e., those in which no reduction of the main cusps has started [*Pogonomys*, *Lenomys*, *Carpomys*, *Batomys*, *Crateromys*, *Hyomys*, *Mallomys*, *Conilurus*, *Laomys*, *Zyzomys*, and *Mesembriomys*]; those without the posterointernal cusp of the upper molars, and without other specializations, containing the majority of the subfamily, and centering round the genus *Rattus* [*Eropeplus*, *Gyomys*, *Leporillus*, *Pseudomys*, *Apomys*, *Melomys*, *Uromys*, *Leggadina*, *Macruromys*, *Nesoromys*, and *Crunomys*]; and a certain number of extremely specialized (or generalized) aberrant genera which appear to have no near relatives [*Mastacomys*, *Echiothrix*, and *Phloeomys*]." He had not seen examples of *Melasmothrix*, *Limnomys* or *Tarsomys*, but thought the last two to be close to, if not inseparable from, the genus *Rattus*.

In his classification, Simpson (1945) recognized the Hydromyinae and Rhynchomyinae, both embracing the same sets of genera which Ellerman (1941) had included in these subfamilies, but separated the other forms that Ellerman had put into one subfamily,

into two—the Phloeomyinae (*Lenomys*, *Pogonomys*, *Mallomys*, *Phloeomys*, and *Crateromys*) and the Murinae (*Carpomys*, *Batomys*, *Hyomys*, *Conilurus*, *Zyzomys*, *Laomys*, *Ammomys*, *Eropeplus*, *Gyomys*, *Leporillus*, *Pseudomys*, *Apomys*, *Melomys*, *Uromys*, *Leggadina*, *Nesoromys*, *Crunomys*, *Macruromys*, *Lorentzimys*, *Notomys*, *Mastacomys*, *Echiothrix*, and *Anisomys*). Simpson omitted *Melasmothrix* from his classification, and included *Limnomys* and *Tarsomys* within *Rattus*.

Misonne's arrangement of the genera native to places east of the Sunda Shelf was based on dental features. Most were placed in the *Lenothrix-Parapodemus* Division, a major group that Misonne considered to be (1969, p. 175) "A Division including the fossil and recent genera with both archaic and advanced molar characters [*Lenomys*, *Pogonomys*, *Crateromys*, *Mallomys*, *Papagomys*, *Spelaeomys*, *Coryphomys*, *Hyomys*, *Batomys*, *Carpomys*, *Eropeplus*, *Anisomys*, *Phloeomys*, *Mesembriomys*, *Conilurus*, *Leporillus*, *Zyzomys*, *Pseudomys*, *Notomys*, *Leggadina*, *Mastacomys*, and *Lorentzimys*]." Some genera were put into what Misonne termed the *Rattus* Division, "A Division including recent genera with all, or nearly all, characters more advanced, though not extreme [*Uromys*, *Solomys*, *Xenuromys*, *Melomys*, *Pogonomelomys*, *Apomys*, and *Nesoromys*]." Another main group, "A Division with basin-shaped molars" included both the Hydromyinae and the Rhynchomyinae of other authors in what Misonne (1969, p. 176) called "A peripheral subfamily, the Hydromyinae [*Chrotomys*, *Celaenomys*, *Leptomys*, *Paraleptomys*, *Xeromys*, *Hydromys*, *Pseudohydromys*, *Microhydromys*, *Neohydromys*, *Parahydromys*, *Crossomys*, *Mayermys*, and *Rhynchomys*]." Misonne placed *Macruromys*, *Echiothrix*, and *Crunomys* in the Murinae, but thought that what he had interpreted as their trends toward a basin-shaped molar suggested a position closer to the Hydromyinae. He considered *Melasmothrix* to be a Sulawesian relict and, like Simpson (1945), placed *Limnomys* and *Tarsomys* in *Rattus*.

Most other reports dealing with classifying

the Far Eastern genera contain groupings basically similar to those I summarized above. In 1936, for example, Tate, in a paper on some murids of the Indo-Australian region, sorted the genera into the Phloeomyinae (Muridae with complexly folded molars), the Murinae (Muridae with essentially *Rattus*-like molars), and the Hydromyinae (Muridae with basined molars); but in 1951 he placed the genera from New Guinea and Australia into either the Murinae or the Hydromyinae. Laurie and Hill (1954) did the same in their list of land mammals of New Guinea, Celebes, and adjacent islands. Simpson, when he wrote about historical zoogeography of Australian mammals in 1961, recognized the *Pseudomys* group from Australia as a distinct subfamily, the Pseudomyinae (which is antedated by the name Conilurinae, the term I shall use instead of Pseudomyinae throughout the following discussions).<sup>2</sup> He also argued that *Chrotomys* and *Celaenomys*, usually placed with the Hydromyinae, was convergent toward that group "and is of quite different ancestry within the Muridae." A tentative phylogeny of Australian rodents presented by Watts (1974, p. 110) provided a slightly different and personal view. In his analysis, "the vast majority of Australian rodents could have arisen from one early colonizer, a small, nondescript, *Rattus*-like animal."

That the native genera from east of Wallace's Line comprise at least two basic groups seems to be the consensus of most students who have studied the fauna. To these persons, the largest assemblage, the Murinae, is composed of a subgroup of gen-

era (including the Phloeomyinae and Conilurinae) that retain archaic features and are relictual in distribution, and a subgroup containing genera with more advanced states that cluster around *Rattus*. The other basic group, the Hydromyinae, consists of highly specialized rats, quite different in morphologies from those forms in the Murinae and possibly of "remote ancestry, necessarily near the base of the Muridae and possibly even in pre-murid cricetids . . .," as Simpson (1961, p. 435) put it.

Such a view has certain evolutionary implications and suggests a hypothesis explaining the past histories of migrations and adaptive radiations that have resulted in the pattern of diversity and distribution seen today in the East Indies and the Australian Region. That hypothesis is reflected in Simpson's (1961) analysis of the historical zoogeography of Australian mammals where, based mainly on data drawn from Tate's papers, he divided the Recent murids, from a historical point of view, into four primary groups. The first consisted of the "Local members of the very widespread genus *Rattus*," those introduced into the Australian area by human agency both before and after its discovery by Europeans, and those native to Australia and New Guinea. The "Old Papuan genera" comprised the second group: *Uromys*, *Melomys*, *Xenuromys*, and *Pogonomelomys* "all of which could well have been derived within New Guinea from a single ancestry near or in *Rattus*," were one subgroup; and *Mallomys*, *Hyomys*, *Anisomys*, *Pogonomys*, and *Macruromys* the other and a group Simpson thought must be older than the *Uromys* group "and may represent several different invasions through the East Indies." The 'Old Australians,' or Conilurinae formed the third group and included *Pseudomys*, *Leggadina*, *Zyzomys*, *Leporillus*, *Mastacomys*, *Notomys*, *Mesembriomys*, and *Conilurus*. The Hydromyinae constituted the fourth group.

To Simpson, the mainland of Asia was the ancestral home of the murids now living in New Guinea and Australia, and they got there by island-hopping down the East Indian archipelagos: "From some time in the

<sup>2</sup> Mr. J. A. Mahoney, at the University of Sydney, has written me that "Conilurinae Dahl, 1897 is an older, available subfamily name for the '*Pseudomys* group' than Pseudomyinae Simpson, 1961." The usage derives from the passages in Dahl's (1897, p. 196) report on mammals from northern Australia where he wrote about "*Conilurus hirsutus*," "*Conilurus penicillatus*" and "*Conilurus boweri*" and lamented: "It is said that the European *Muridae* in the southern parts of the continent are gradually extirpating and replacing the aboriginal representatives of the *Coniluridae*, and I shall not contradict the statement."

Miocene (perhaps but less probably even in late Oligocene) there was probably continual, intermittent drift of murids down that chain. There must have been marked attenuation, with fewer originally Asiatic lineages represented at increasing distances from the mainland." Simpson analyzed the migrations into three successive waves. The oldest was mostly Miocene and consisted of "up to seven but probably fewer different stocks already phylogenetically distinct before or while passing along the East Indies"; five of these included the Old Papuan genera *Mallomys*, *Hyomys*, *Anisomys*, *Pogonomys*, and *Macruromys*; another was the Hydromyinae radiation on New Guinea; and another the conilurine radiation, basically Australian. The second, intermediate wave, likely Pliocene, "involved the probably single stock that evolved into the *Uromys* group in New Guinea." And the third, late wave, Pleistocene or part of late Pliocene, "involved perhaps only one but probably two partly differentiated lineages of East Indian *Rattus*."

The results from the research by Baverstock and his colleagues into the karyology of Australian murids has provided a view of their relationships from a different perspective than was available from the viewpoint of data gathered from teeth, skulls, and skins. They studied chromosomal characteristics of the native species of Australian *Rattus* (Baverstock et al., 1977): the species in *Pseudomys*, *Conilurus*, *Mesembriomys*, *Leporillus*, *Mastacomys*, *Notomys*, and *Zyzomys*, all in the Conilurinae; the Australian forms of *Melomys* and *Uromys*; and the Australian hydromyines, *Hydromys* and *Xeromys* (Baverstock, Watts and Hogarth, 1977). Based on aspects of chromosome number and morphology, Baverstock and his associates formulated the working hypothesis that instead of the four primary groups of species suggested by Tate (1951) and Simpson (1961), only two major groups, possibly three, are involved in the evolutionary history of Australian murids. Members of the native Australian *Rattus* comprise one group; and the species in *Uromys*, *Melomys*, the Conilurinae, and the Hydromyinae com-

prise the other; *Zyzomys* may form a third group.

Study of spermatozoal morphology and male reproductive tracts of the native Australian murids have provided a view on relationships similar to that hypothesized from chromosomal data. Based on configurations of the spermatozoa, the species Breed and Sarafis (1979, p. 133) examined in the genera *Conilurus*, *Leporillus*, *Uromys*, *Hydromys*, *Zyzomys*, *Melomys*, and *Pseudomys* fell into one group; the species of *Notomys* formed another; and "The spermatozoa of *Rattus* spp. were very different from those of all other Australian rodents and similar to congeners occurring on other continents." Following with results from more detailed study of species in *Notomys* and *Pseudomys*, Breed (1980) surmised that the distinctive spermatozoal morphology of these species, compared with the other Australian rodents, represented recently derived features, and that the species are still part of the adaptive radiation in Australia that includes the native genera, but not *Rattus*. The data presented by Breed and Sarafis (1979) and Breed (1980), therefore, reinforce the contention that the indigenous Australian *Rattus* form one group that is very different, both morphologically and likely historically, from the native non-*Rattus* genera, which form another group.

A similar hypothesis was presented by Lidicker (1968) for the native murids of New Guinea. After studying morphology of the glandes penes in 19 genera (*Leptomys*, *Paraleptomys*, *Parahydromys*, *Hydromys*, *Crossomys*, *Pseudohydromys*, *Neohydromys*, *Mayermys*, *Anisomys*, *Pogonomys*, *Lorentzimys*, *Mallomys*, *Macruromys*, *Uromys*, *Melomys*, *Pogonomelomys*, *Hyomys*, *Mus*, and *Rattus*), Lidicker (1968, p. 639) concluded that the present murid fauna of New Guinea could have been a result of differentiation and adaptive radiation from two invasions. "The first invasion, probably occurring in the Miocene may have been composed of a single species of primitive murid resembling most closely the modern genus *Anisomys*. This form could have dif-

ferentiated into all of the extant New Guinea rodents except for *Rattus* and *Mus* . . . ." The second invasion for Lidicker "was that of a primitive form of *Rattus*, and probably occurred in the Pleistocene."

The work on chromosomes, spermatozoa, and male reproductive tracts is enticing because it allows a different approach to answering questions about the interrelationships among the species of murids native to places east of the Sunda Shelf. Does that entire fauna consist of two primary stocks, one composed of species in *Rattus*, the other formed by the hydromyine and non-hydromyine genera that are native to New Guinea, Timor, Flores, the Komodo Islands, Ceram, Sulawesi, and the Philippines? Or does the fauna consist of several stocks: one of *Rattus*; one containing species in *Melomys*, *Uromys*, and their relatives; one comprised of conilurines; one of hydromyines; one formed by other genera such as *Mallomys*, *Hyomys*, *Crateromys*, *Lenomys*, *Spelaeomys*, and *Coryphomys*, for example; and one consisting of species in such genera as *Taromys* and *Limnomys*, groups that may be phylogenetically closer to *Rattus* than to the others?

It is in the context of the questions posed above that morphological relationships not only among the native Floresian rats but between them and the other genera from the East Indies has to be studied. Data from such research are scanty, derived primarily from dentitions. According to Misonne (1969), for example, *Papagomys* and *Spelaeomys* cluster with *Crateromys*, *Mallomys*, and *Coryphomys* in an assemblage he calls the *Lenothrix* Group, which also contains, besides *Lenothrix*, *Pithecheir* from the Sunda Shelf, *Tokudaia* from the Ryukyu Islands, *Lenomys* and *Eropeplus* from Sulawesi, *Pogonomys* and *Hyomys* from New Guinea, and *Batomys* and *Carpomys* from the Philippines. Based on the patterns in cheek teeth, Misonne considered the *Lenothrix* Group to be a cluster of three primitive genera (*Lenothrix*, *Lenomys*, and *Pogonomys*) and nine that are more advanced (*Batomys*, *Coryphomys*, *Crateromys*, *Carpomys*, *Hy-*

*omys*, *Mallomys*, *Papagomys*, *Spelaeomys*, and *Tokudaia*). The *Lenothrix* group is the oldest type among the murids, in Misonne's view, and from his perspective the native rats from Flores could be relicts, perhaps descendants of the wave that Simpson speculated may have occurred during the Miocene. Where do the Floresian rats fit within the murid faunas east of the Sunda Shelf?

#### AFFINITIES OF *PAPAGOMYS*, *HOOIJEROMYS*, *FLORESOMYS*, AND *KOMODOMYS*

I hypothesize that the native murids on Flores consist of two groups: *Papagomys armandvillei*, *P. theodorverhoeveni*, *Hooijeromys nusatenggara*, *Floresomys naso*, and *Komodomys rintjanus* form the contents of one; *Spelaeomys florensis* comprises the other. I compared the six species in the two groups with examples of indigenous genera from continental Southeast Asia, the Sunda Shelf, and places east of the Shelf. *Papagomys*, *Hooijeromys*, *Komodomys*, and probably *Floresomys* morphologically cluster through derived dental features, and through shared cranial derivations between *Papagomys* and *Komodomys*; *Papagomys* has closer ties to native genera on Sulawesi and to *Komodomys* on the Komodo Islands than to those on Australia and New Guinea. *Spelaeomys* may have closer phylogenetic affinities with the murids of New Guinea and possibly Timor. I elaborate relationships of the first group of genera in this section, then follow it with discussions about affinities of *Spelaeomys*.

COMPARISONS AMONG THE FLORESIAN SPECIES: Certain features of the lower molars in *Floresomys* resemble those of species in *Bunomys* from Sulawesi, particularly *B. fratorum*, but the cusp patterns differ in important details, and the conformation of the dentaries in *Floresomys* is unlike anything in *Bunomys*. The phylogenetic affinities of *F. naso* are more likely to be with *Papagomys*, *Komodomys*, and *Hooijeromys*. The first upper molars of *Floresomys* probably had five roots, as do those in *Papagomys*, *Hooijer-*



FIG. 31. Occlusal views of right mandibular tooththrows in recent *Papagomys* and subfossil *Floresomys*. A, adult *P. armandvillei* (UF 9125). B, specimen 1, the adult holotype of *F. naso*. Both views approximately  $\times 8$ .

omys, and *Komodomys*. The occlusal patterns on the lower molars are simple and basically similar to those in *Papagomys* (fig. 31). This association between *Floresomys* and *Papagomys* is tentative and will have to be tested with comparative data from crania, upper molars, and less worn lower molars of *Floresomys*.

*Papagomys* and *Hooijeromys* are related by their dentitions. The occlusal patterns on the first and second upper molars of *Hooijeromys* consist of low cusps set in nearly transverse rows, a modified version of the basic cusp patterns in *Papagomys*. Both genera lack cusps t7 and posterior cingula; in both, cusp t3 is usually absent from each second molar; and both have five-rooted first upper molars, four-rooted second, and three-rooted third upper molars. If the three isolated lower molars that I associated with *Hooijeromys* actually are a sample of that genus, then they too are similar to *Papagomys* in cusp patterns, particularly the front two laminae on each of the first molars. How the cranial and mandibular features compare between *Papagomys* and *Hooijeromys* will not be known until crania from the latter are found.

Although *Papagomys armandvillei* is a giant rat and *Komodomys rintjanus* is one of the medium body size, and although the cranial conformation of *P. armandvillei* contrasts with that of *K. rintjanus* (compare the skull of *P. armandvillei* in fig. 4 with that of *K. rintjanus* in fig. 26), the two species are related through characteristics of their molars (fig. 32). Both are similar in the following: proportions of upper and lower molars relative to the cranium and dentaries, and relative to one another in each respective molar row; inclination of cusps, degree of overlap among the upper molars, and the interlocking configuration; number of roots on all the upper and lower molars; number, relative height, shape, and positions of the cusps on the upper molars, and of the primary cusps on the lowers, no posterior cingula or cusps t7; and either tiny or no cusps t3 on the second and third molars.

Many of the dental features common to *Papagomys*, *Hooijeromys*, *Komodomys*, and *Floresomys* are derived. All, for example, have five-rooted first upper molars (inferred in *Floresomys* because the lowers are four-rooted) and four-rooted first lower molars (inferred in *Hooijeromys* because the uppers are five-rooted). This number is derived from a three-rooted upper molar and two-rooted lower molar, a primitive config-

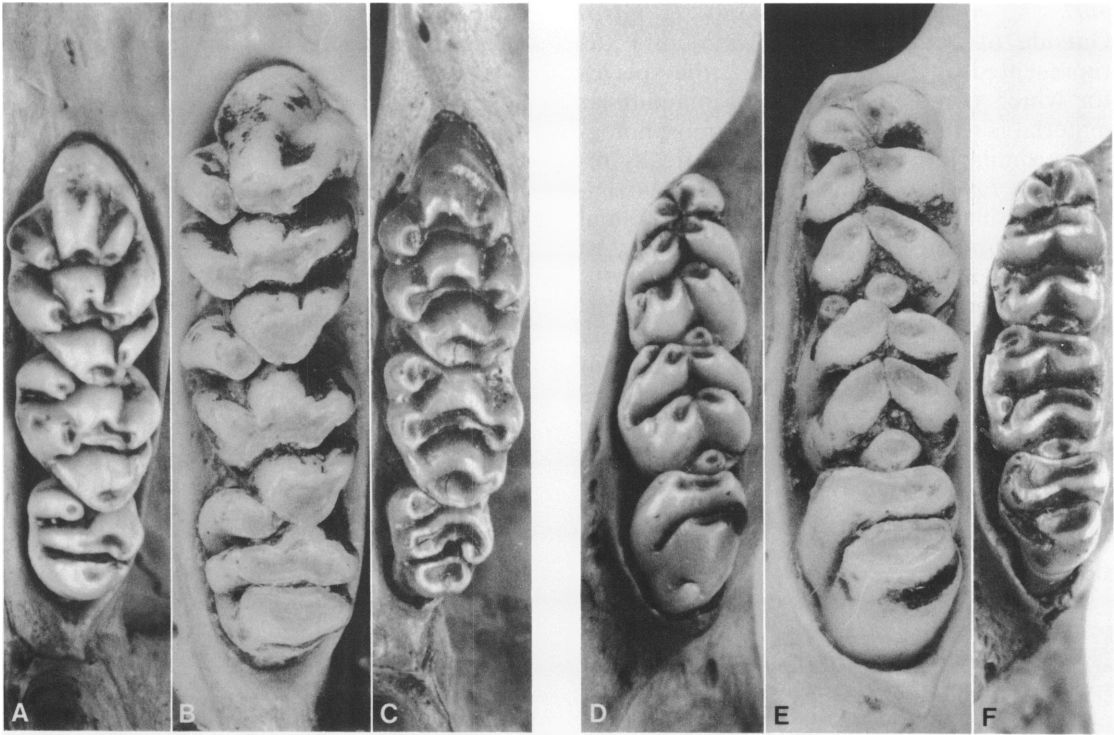


FIG. 32. Comparisons of occlusal views of left maxillary and mandibular tooththrows among recent *Komodomys*, *Papagomys*, and *Rattus*. Maxillary tooththrows: A, young adult *K. rintjanus* (MZB 9016); B, young adult *P. armandvillei* (RMNH 18301); and C, adult *R. argentiventer* (MZB 4879). Mandibular tooththrows: A, *K. rintjanus*; B, *P. armandvillei*; and C, *R. argentiventer*. Views of *Komodomys* and *Rattus*  $\times 8$ , those of *Papagomys*  $\times 5$ .

uration (Musser, 1981) found in some of the earliest murids from the Miocene (Jacobs, 1978), as well as many other groups of murid rodents. Lack of a posterior cingulum on the upper molars, and either no cusps t3 or minute ones on the second and third uppers are shared derivations uniting all the genera (except *Floresomys* and *P. theodorverhoeveni* for now because the uppers are unknown). The degree to which the rows of cusps on the upper molars slant, the extensive overlap and interlocking among the uppers, as seen in *Papagomys*, *Hooijeromys*, and *Komodomys*, is derived. A posterior cingulum is a primitive character (Misonne, 1969; Jacobs, 1978), as is the presence of cusp t3 (Misonne, 1969). Erect rows of cusps on molars that abut against one another with little or no overlap is also primitive.

**PAPAGOMYS COMPARED WITH LENOMYS AND EROPEPLUS:** *Papagomys armandvillei* has been phylogenetically linked to *Mallomys* of New Guinea (Thomas, 1898b; Mertens, 1936; Simpson, 1977) but it is unlike *Mallomys*, as I pointed out before. Many of the external, cranial, and dental features of *Papagomys* that contrast with those in *Mallomys* are derived, and *Papagomys* shares these derivations with genera other than *Mallomys*. The derivations found in *Mallomys* are either unique to the genus or shared with genera other than *Papagomys*, as I discuss later in this section.

*Papagomys*, at least in dental characteristics, seems more closely related to most of the other native rats on Flores, except *Speleomys*, and to the species on the Komodo Islands: *P. theodorverhoeveni*, *H. nusateng-*

*gara*, *K. rintjanus*, and possibly *F. naso*. Outside of Nusatenggara, *Papagomys* (as represented by *P. armandvillei*, the species for which complete cranial and mandibular material is available for study) is morphologically similar, and likely phylogenetically related to *Lenomys* and *Eropeplus*, two natives of Sulawesi (Musser, 1970b), in cranial and mandibular features, and particularly to *Eropeplus* in dental characteristics.

The crania of adult *Papagomys armandvillei*, *Lenomys meyeri*, and *Eropeplus canus* are contrasted in figures 33 and 34, the dentaries of those species are compared in figure 34, upper molar rows in figure 35, and lower molar rows in figure 36. *Lenomys* is smaller than *Papagomys* but both share the following features.

1. The rostrum is moderately long and slender.

2. The zygomatic arches are wide and appear robust.

3. The dorsal profile of the cranium of each species is similar.

4. The zygomatic plates are narrow, alike in shape, and with the same relative projection of the zygomatic spine anterior to the dorsal zygomatic roots.

5. The large lacrimals are triangular, in dorsal view.

6. High, shelflike ridges border the interorbital and postorbital margins and extend along the dorsolateral edges of the braincase.

7. The braincase is roughly rectangular (seen from a dorsal view), and the walls above the squamosal roots of the zygoma slope towards the midline of the cranium.

8. Squamosal roots of the zygomatic arches originate relatively high on sides of the braincase.

9. The posterior margin of each squamosal zygomatic root continues to the occiput as a low ridge.

10. The interparietal is squarish in dorsal outline, and most of it is nestled between the parietals, with only a slight posterior segment roofing the occipital region.

11. The squamosal above each bulla is complete, not divided into a dorsal segment and a ventral tympanic hook by the squamoso-mastoid foramen.

12. The configuration of the alisphenoid

region is similar in both species (no strut of alisphenoid bone, foramen ovale accessorius, or masticatory-buccinator foramina; the alisphenoid canal is open, exposing the foramen ovale and the opening of the canal into the sphenoidal fissure); a strut of alisphenoid bone is present in one out of the seven examples of *Lenomys*.

13. The configuration of each orbit, the position and relative sizes of the orbital foramina, and the shape of the maxilla forming the bottom of the orbit are closely similar in the two genera.

14. The incisive foramina are long and narrow, but end anterior to the front margins of the molar rows.

15. The large upper molar rows are set in a narrow palatal bridge that ends beyond or just in front of the posterior margins of the third molars; a pair of deep palatal grooves extend the length of the bridge.

16. The mesopterygoid fossa is wide and horseshoe-shaped in ventral view; its walls are breached by long and either moderately wide or spacious sphenopalatine vacuities.

17. The configuration of each pterygoid fossa is closely similar in the two genera; each fossa is deep, outlined by a prominent pterygoid ridge, and perforated by a conspicuous sphenopterygoid canal (or interpterygoid foramen).

18. The bullae of *Papagomys* and *Lenomys* are moderately large relative to the cranium, closely similar to each other in shape, and attached to the braincase in a similar manner.

19. The dentaries of the two genera are very similar to one another in overall shape and in proportions, though they differ in size.

20. Both have hypsodont molars that are large relative to size of the cranium and mandible.

21. Both genera have five-rooted first upper molars, four-rooted second uppers, and three-rooted third upper molars.

22. Each of the lower molars in *Papagomys* and *Lenomys* are anchored by more than two roots. In *Papagomys*, four-rooted first lower molars, and three-rooted second and third lowers are usual; in *Lenomys*, the first lower molars are five-rooted because the posterior root is divided, and the second low-

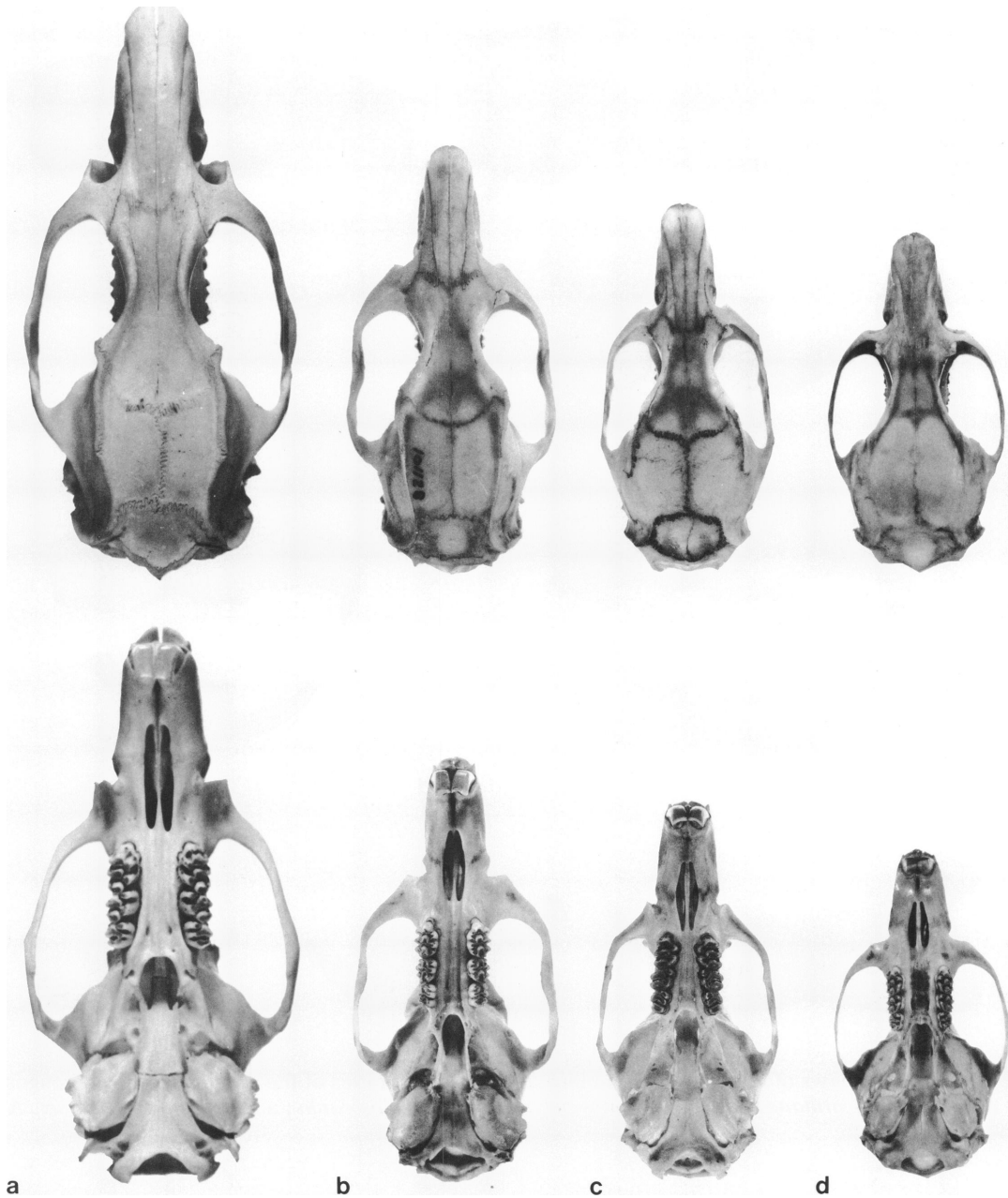


FIG. 33. Dorsal (top row) and ventral (bottom row) cranial views of adults: a, *Papagomys armandvillei* (MZB 2395) from Flores; b, *Lenomys meyeri* (AMNH 101128) from southwestern Sulawesi; c, *Eropeplus canus* (AMNH 223554) from central Sulawesi; and d, *Lenothrix canus* (AMNH 240358) from the Malay Peninsula. All views natural size.

er molars are four-rooted because of a divided root instead of a single one, as occurs in

*Papagomys*, and each third molar is three-rooted.

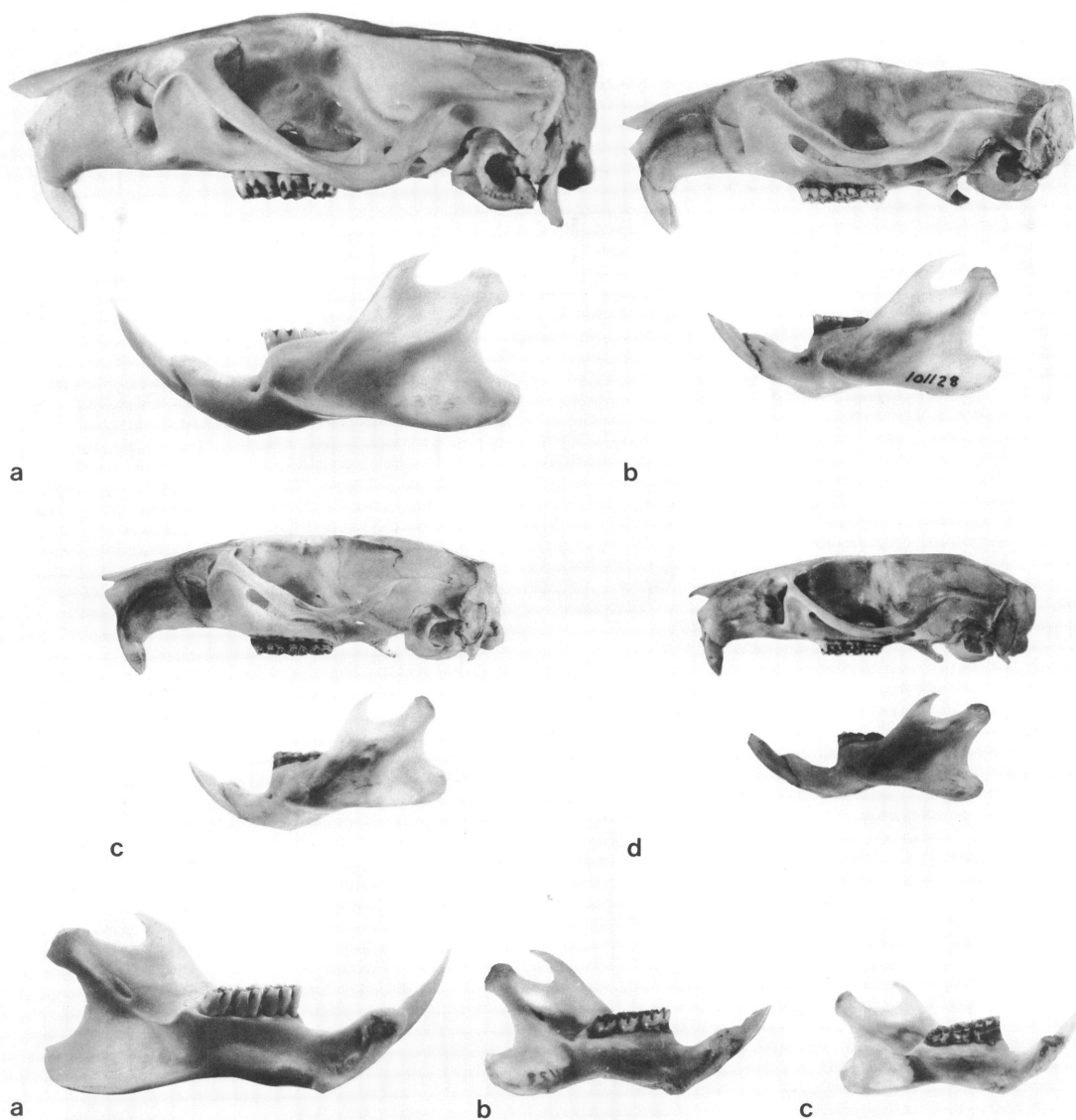


FIG. 34. Side views of crania, labial and lingual views of dentaries of the specimens shown in figure 33: a, *Papagomys armandvillei*; b, *Lenomys meyeri*; c, *Eropeplus canus*; and d, *Lenothrix canus*. All views natural size.

Although there are strong resemblances between *Lenomys* and *Papagomys*, there are conspicuous dissimilarities between the two genera in occlusal characteristics of the molars, and these should be noted here. The upper molar rows of *Lenomys* are nearly parallel, those in *Papagomys* diverge pos-

teriorly. In *Lenomys*, the upper molars abut against one another with only slight overlap, unlike the more extensive overlap among molars of *Papagomys*. The interlocking among the molars is formed by parts of cusps t7, t8, and the posterior cingulum of the molar in front pressing against parts of cusps t1,

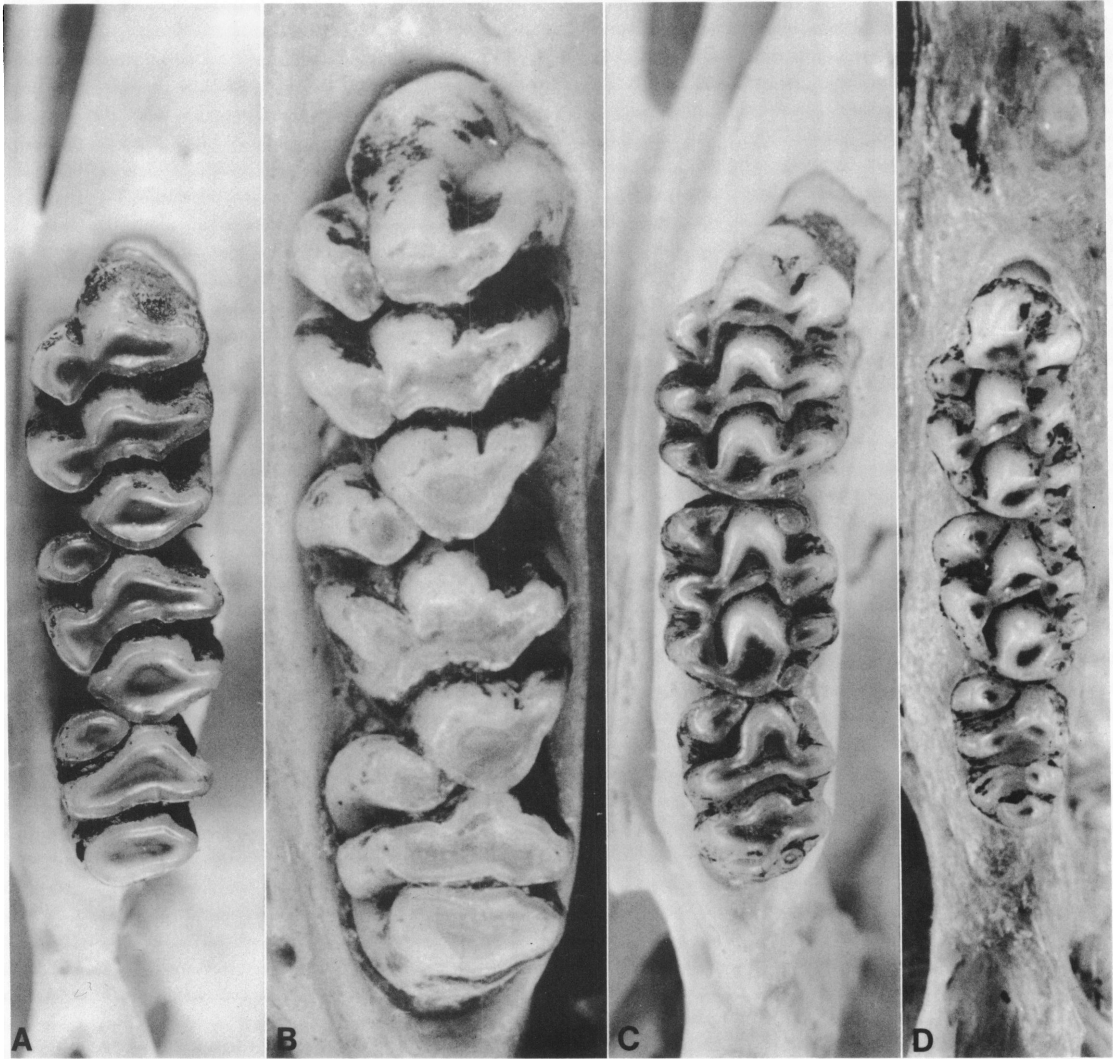


FIG. 35. Occlusal views of left maxillary tooththrows from adults. A, *Eropeplus canus* (AMNH 225121); B, *Papagomys armandvillei* (RMNH 18301); C, *Lenomys meyeri* (AMNH 101127); and D, *Lenothrix canus* (USNM 488914). All views approximately  $\times 8$ .

t5, and t3 of the molar behind; in *Papagomys*, the interlocking consists of cusp t8 of the molar in front pressing against cusp t1 and cusp t5 on the molar behind. The occlusal patterns on the upper molars of *Lenomys* are elaborate. Cusp t1bis occurs on the first molars of most specimens, cusp t7 and a posterior cingulum are present on each molar, cusp t3 is large and conspicuous on each sec-

ond and third molar, and there are ridges extending from one row of cusps posterior to the row behind (stephanodont crests, Misonne, 1969). All these elements, either missing or minute in *Papagomys*, provide elaborations to occlusal patterns that in conformation of the primary cusps are otherwise basically similar in configuration to those in *Papagomys*.

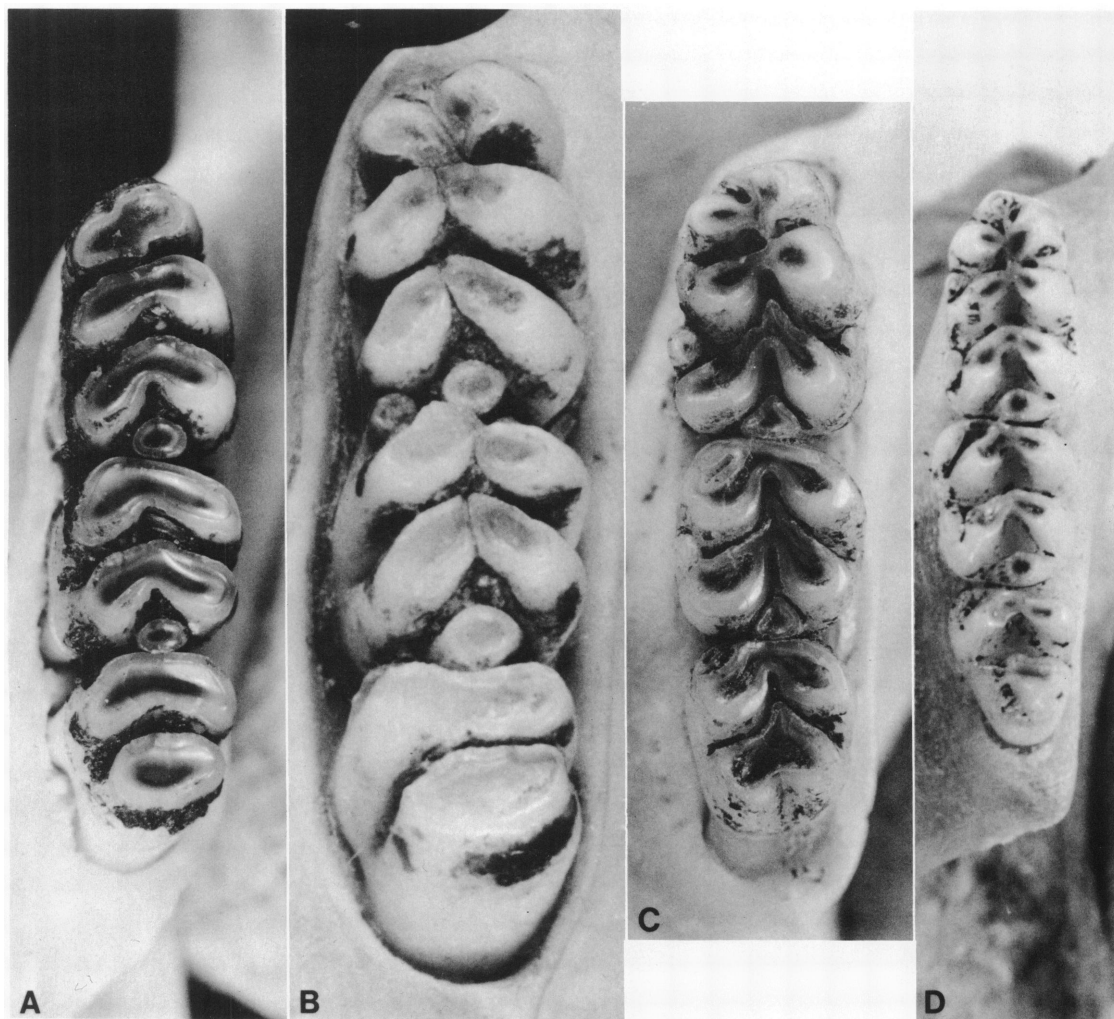


FIG. 36. Occlusal views of left mandibular toothrows from the specimens shown in figure 36. A, *Eropeplus canus*; B, *Papagomys armandvillei*; C, *Lenomys meyeri*; and D, *Lenothrix canus*. All views approximately  $\times 8$ .

Occlusal patterns of the lower molars of *Lenomys* are more elaborate than those in *Papagomys armandvillei*. The primary cusps are not as massive in *Lenomys* and form inverted V-shaped laminae on most molars. The anterolingual, anterolabial, and antero-central cusps form a front lamina on each first molar that resembles the shape of the front lamina in examples of *P. theodorverhoeveni* (compare fig. 15 with fig. 36). Large and prominent anterolabial cusps occur on

the second and third molars. Labial cusplets are present along the margins of the first and second molars; in their number, position, and size relative to the rows of primary cusps, these cusplets are much like the labial cusplets in *P. theodorverhoeveni*. The two laminae on each third molar are bent and cuspidate in *Lenomys* rather than either transverse or boomerang-shaped (the front lamina) or transverse (the posterior lamina), as in *Papagomys*. Finally, there is a small

cuspid on the backside of each third molar, which is likely a posterior cingulum, in four out of the seven specimens at hand; such a cusp is absent from my examples of *Papagomys*, but does occur on many examples of *Komodomys*.

*Eropeplus* resembles *Papagomys* and *Lenomys* in most cranial features. *Eropeplus* differs in being smaller, and having a rostrum that is wider relative to the rest of the cranium, upper molar rows that diverge strongly posteriorly (compared with *Lenomys*), a shorter bony palate that ends a few millimeters before the posterior margins of the third upper molars, and dentaries that are relatively higher and shorter—they appear squat compared with those in either *Papagomys* or *Lenomys*.

Shapes of the molars in *Eropeplus* are similar to those in *Papagomys*. The proportions of molar size relative to sizes of the cranium and mandible, degree of hypsodonty, number of roots anchoring each upper and lower molar, the posterior divergence of the molar rows, the degree of overlap among the molars and their interlocking, as well as the occlusal patterns of the uppers and the shapes of the cusps, closely resemble those in *Papagomys*. Furthermore, a cusp t7 and posterior cingulum are absent from all the molars in *Eropeplus*, and cusp t3 is either missing or very small on each second and third upper molar, all characteristics that are either missing or small in *Papagomys* as well.

The lower molars of *Eropeplus* and *Papagomys* bear even closer resemblance to each other in their occlusal patterns. As in *Papagomys*, *Eropeplus* does not have anterocentral cusps on the first molars, and usually lacks labial cusplets on all the molars (out of seven specimens, one has posterior labial cusplets on the first and second molars, one has posterior cusplets on the second molars only, and a third has a posterior labial cusplet on the right second molar only). *Eropeplus* does not have anterolabial cusps on the second and third molars, whereas *Papagomys* does; otherwise, the dentitions of the two genera are so alike that specimens of each with comparable wear

surfaces are sometimes difficult to distinguish except for size.

Structure of the molars in *Eropeplus* reflects derivations that are like those in *Papagomys*; *Eropeplus* may be slightly more derived because anterolabial cusps are absent from the second and third lower molars. *Lenomys*, on the other hand, compared with *Papagomys* and *Eropeplus*, has many primitive features such as posterior cingula on all the upper molars, prominent cusps t3 on the second and third uppers, slightly inclined rows of cusps with little overlap and weak interlocking among the upper molars, cuspidate lower molars, and prominent anterolabial cusps on the second and third lower molars. The derivations of *Lenomys* are a cusp t1bis on each first upper molar, cusp t7 on each upper molar, short crests where some labial and lingual cusps meet the central cusps on the first and second molars, and long third upper and lower molars relative to the other teeth in each molar row, specializations not found in either *Papagomys* or *Eropeplus*.

In summary, the cranial resemblances between *Papagomys* and *Lenomys* are striking. The latter looks much like a smaller version of the former; were it not for the distinguishing features associated with the skins (not mentioned here) and dentitions, the two species would be placed in the same genus if crania and dentaries were the only elements available for study. *Eropeplus* is much like *Lenomys* in cranial conformation; it too would either be included within *Lenomys* or regarded as being very closely related to that genus if not for the different dentitions; the molars of *Eropeplus* are similar to those in *Papagomys*.

COMPARISONS WITH INDIGENOUS NEW GUINEA AND AUSTRALIAN GENERA: It is evident from cranial and molar features that *Papagomys* on Flores is morphologically closer to the Sulawesi *Eropeplus* and *Lenomys* than to the indigenous murids on New Guinea and nearby archipelagos (*Melomys*, *Pogonomelomys*, *Solomys*, *Uromys*, *Xenuromys*, *Anisomys*, *Pogonomys*, *Chiruromys*, *Hyomys*, *Mallomys*, *Lorentzimys*, *Macrurumys*, *Leptomys*, *Paraleptomys*, *Parahydro-*

*mys*, *Hydromys*, *Crossomys*, *Pseudohydromys*, *Microhydromys*, *Neohydromys*, and *Mayermys*),<sup>3</sup> a few of which spill over into Australia (*Uromys*, *Melomys*, *Pogonomys*, and *Hydromys*), the Moluccas (*Melomys*), and Timor (*Melomys* and *Pogonomelomys*). The range of dental patterns among the genera of New Guinea is impressive (Rümmmler, 1938; Tate, 1936, 1951; Laurie and Hill, 1954; Misonne, 1969), extending from full molar rows with elaborate occlusal patterns such as those in *Pogonomys* and *Chiruromys* to the simple basined occlusal surfaces in hydromyines, where each molar row may be complete (as in *Leptomys*), or consist of two molars (as in most of the other hydromyines), or a single molar only (as in *Mayermys*). The crania, however, possess a set of basic conformations, and the first molars a primary number of roots, that are unlike either *Papagomys*, *Lenomys*, or *Eropeplus*.

These distinctive cranial configurations and dental features are outlined below. In addition, the cranial structures are portrayed in the illustrations of *Mallomys* (figs. 5–8), *Hyomys* (fig. 37), *Hydromys* (fig. 37), and *Uromys* (fig. 38); the last three are included here simply as representative genera. Similar structural characteristics can be clearly seen in the excellent views of *Anisomys* published in Ellerman (1941, p. 78), and in crania from most of the other indigenous New Guinea genera that are illustrated in Tate (1936), Rümmmler (1938), and Laurie and Hill (1954).

<sup>3</sup> *Melomys*, *Pogonomelomys*, *Solomys*, and *Uromys* are clusters of species that Ellerman (1949), Tate (1951), Simpson (1961), and Misonne (1969) would derive from an ancestry near *Rattus*, and would regard as modern elements in the New Guinea murid fauna, as opposed to the hydromyines and other old endemics. My studies of skins, skulls, and dentitions do not support their views but agree instead with the conclusions based on analyses of chromosomes (Baverstock, Watts and Hogarth, 1977), spermatozoal morphology (Breed and Sarafis, 1979), and penis structure (Lidicker, 1968): the *Uromys-Melomys* complex is an old one and belongs with the hydromyines, the other old native genera of New Guinea, and the conilurines. They seem to be part of an early murid radiation in the New Guinea area, and they have no close phylogenetic relationship to *Rattus*.

1. The interorbital and usually the postorbital margins are smooth or only slightly ridged (high, sometimes shelflike ridges bound the interorbital and postorbital margins in *Papagomys*, *Lenomys*, and *Eropeplus*).

2. The braincase is distinctive among murids indigenous to the New Guinea area. It is low, long, and usually smooth, either without temporal ridges or only indistinct ones, and usually lacking low horizontal ridges extending from the posterior margins of the squamosal zygomatic roots to the occiput (as opposed to a deeper braincase, high temporal ridges or shelves, and low horizontal ridges from the squamosal roots of the zygoma to the occiput).

3. Squamosal roots of the zygomatic arches originate high on sides of the braincase (instead of lower).

4. The squamosal above each bulla is usually separated into a dorsal part and a ventral process by a squamoso-mastoid foramen; the separation may be a shallow cleft as in *Uromys* (fig. 38), a deep notch, as in *Hyomys*, or a spacious vacuity as shown for *Peromyscus* by Klingener, 1968 (the squamosal is intact in *Papagomys*, *Lenomys*, and *Eropeplus*; the squamoso-mastoid foramen is small and hidden in the suture between the squamosal and occipital).

5. The configuration of the alisphenoid region that is common to the New Guinea genera is like that in *Mallomys* (fig. 7). There is a strut of alisphenoid bone, which may be wide but not as wide as in sciurids (Wahlert, 1974) or narrow as illustrated for *Peromyscus* (Klingener, 1968), concealing the alisphenoid canal, its opening into the sphenoidal fissure, and the foramen ovale. In side view, the strut of bone separates the foramen ovale accessorius posterior to the strut from the masticatory-buccinator foramina anterior to the strut; the latter two openings are often coalesced into a single foramen but are sometimes separate, as in examples of *Mallomys* (the contrasting configuration is shown in fig. 7, which illustrates the condition in *Papagomys*; the outer wall of the alisphenoid canal is absent so that in side view

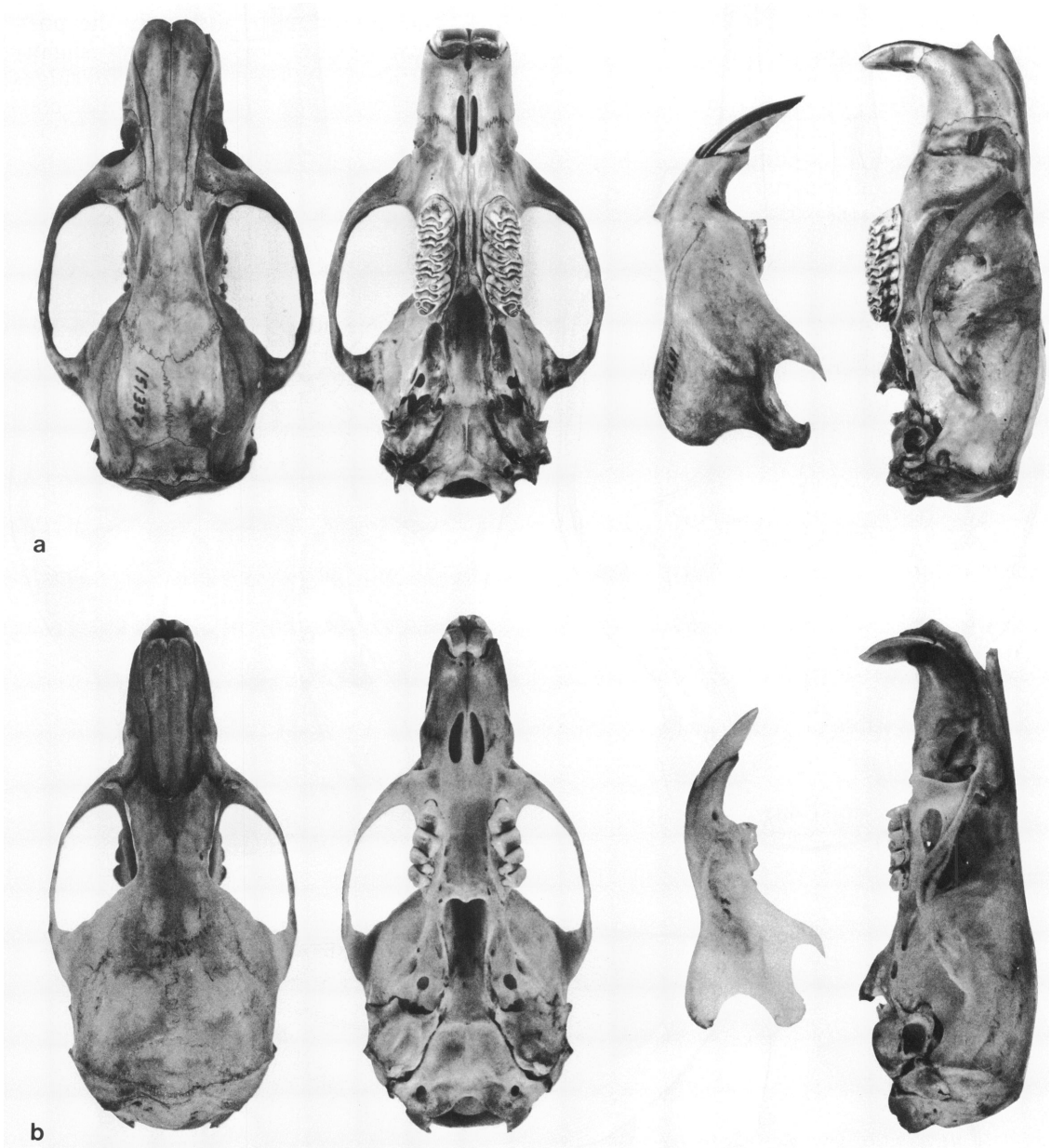


FIG. 37. Examples of *Hyomys* and *Hydromys*, old endemic genera from the New Guinea area: views of crania and dentaries. Top row (a): adult *Hyomys goliath dammermani* (AMNH 151337) from Irian Jaya; all views are natural size. Bottom row (b): adult *Hydromys chrysogaster* (AMNH 191432) from Papua; all views  $\times 1.5$ .

the foramen ovale can be seen, then an alisphenoid groove instead of a canal, and far-

ther anterior the opening of the canal into the sphenoidal fissure; there are no masticatory-

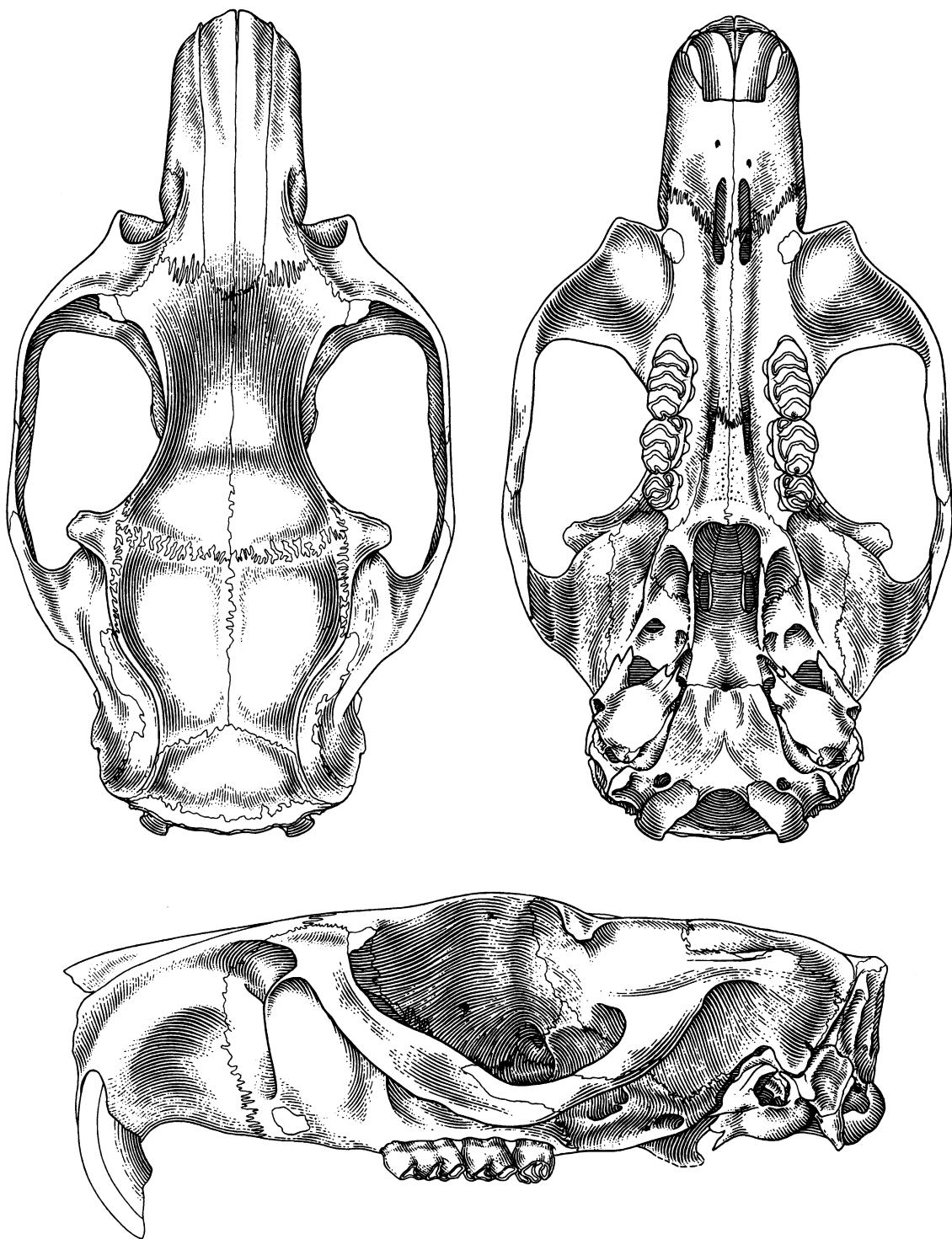


FIG. 38. Dorsal, ventral and side views of the cranium of *Uromys*, another old endemic genus from the New Guinea region. AMNH 99881, the holotype of *U. neobritannicus*, a young adult, from New Britain; the drawing was originally published in Tate (1936) in a different form.

buccinator foramina, and no foramen ovale accessorius).

6. The incisive foramina are short, often only small slits as they are in *Anisomys* (Ellerman, 1941, p. 78); *Mallomys* is an exception because the posterior portion is elongate and dilated (*Papagomys*, *Lenomys*, and *Eropeplus* have long and slender incisive foramina).

7. The palatal bridge is usually smooth, with only faint grooves or depressions for transmitting the palatine arteries, veins, and nerves. The grooves are deeper in some genera, but only in front of the posterior palatine foramina and not along the entire length of the bridge (as opposed to deep palatal grooves extending nearly the length of the palatal bridge, as seen in *Papagomys*, *Lenomys*, and *Eropeplus*).

8. The walls of the mesopterygoid fossa are either intact or perforated by small slit-like sphenopalatine vacuities (long and wide, even spacious vacuities in *Papagomys* and the other two genera).

9. The pterygoid fossae are shallow in most genera; in ventral view, the floor of each fossa is flat and its anterior two-thirds is intact, not perforated by a sphenopterygoid canal except in a few genera where tiny sphenopterygoid canals may be present; sometimes the fossa floor is perforated only by minute nutrient foramina (the pterygoid fossa are deep in *Papagomys*, *Lenomys*, and *Eropeplus*; the floors are inclined toward the midline of the cranium, and the sphenopterygoid canals are conspicuous and either moderate or large in size).

10. The bullae are very small, both absolutely and especially relative to the cranium; in some genera the bullae appear even tiny relative to skull size (the bullae are moderately large to large in *Papagomys* and its allies; the size of the bullae relative to the cranium is more like the proportions in species of *Rattus*).

11. Most species have three-rooted first upper molars and two-rooted first lowers. A few, such as in *Solomys*, *Pogonomys loriae*, many *Melomys*, and some hydromyines, have four-rooted upper molars, a configuration formed by a divided lingual root in ad-

dition to the main anterior and posterior roots; specimens of *Hyomys* and *Mallomys*, also have four-rooted uppers, but in their case the posterior root is divided. A few of the species with four roots anchoring each upper molar also have a small rootlet between the two primary roots on each first lower molar; *Mallomys* and *Hyomys* have three-rooted lowers because the posterior root is divided. (*Papagomys* and its allies has five-rooted upper molars and four-rooted lowers).

*Papagomys* and its allies on Flores are not more closely related to the indigenous Australian genera (*Mesembriomys*, *Conilurus*, *Notomys*, *Zyzomys*, *Pseudomys*, *Leggadina*, *Leporillus*, *Mastacomys*, and *Xeromys*), two of which (*Conilurus* and *Pseudomys*) also occur on New Guinea, than to either *Lenomys* or *Eropeplus*. The genera of Australia and New Guinea have several cranial and dental features in common: a smooth or slightly ridged conformation of the interorbital and postorbital margins, shape of the braincase, squamosal attachment of the zygomatic arches, low or no temporal ridging, a squamosal above each bulla that is divided into two processes by a squamoso-mastoid foramen, an alisphenoid configuration in which a strut of bone covers the lateral wall of each alisphenoid canal, nature of the palatal bridge, shape of the pterygoid fossae, and usually no sphenopterygoid canals, three-rooted first upper molars and two-rooted first lowers.

Several distinctive features, explained by Tate (1951), distinguish the Australian genera from those of New Guinea. These include long incisive foramina reaching to or usually beyond the anterior faces of the molar rows, spacious sphenopalatine vacuities, slightly larger bullae relative to size of the cranium, and a sigmoid-shaped anterior spine on each zygomatic plate.

Many of the characters common to the genera on New Guinea that contrast with those in *Papagomys* and its allies are primitive ones. The smooth or only slightly ridged interorbital and postorbital regions, the smooth and low braincase, high position of the squamosal roots of the zygoma, the con-

figuration of the alisphenoid region at the base of each side of the braincase, the short incisive foramina, the relatively smooth palatal bridge, the mesopterygoid fossa with walls that are either intact or perforated by only small vacuities, the conformation of the pterygoid fossa with the usual absence of sphenopterygoid canals, the very small bullae, and the small number of roots anchoring the first upper and lower molars (see Musser, 1981, for a discussion of the primitive and derived versions of these characters).

The derived counterparts of these cranial structures are found in *Papagomys*, in the sample of *Komodomys* from the islands of Rintja and Padar, and in *Eropeplus* and *Lenomys* from Sulawesi. Similar cranial derivations are found in species of *Rattus* (Musser, 1981), an observation that is critical to understanding the phylogenetic relationships among the murids native to places east of the Sunda Shelf. *Papagomys armandvillei* resembles a giant version of *Rattus* but with a shallow occiput, shorter incisive foramina, a shorter posterior part of the palatal bridge, and relatively larger hypsodont molars. *Komodomys*, its relative, is also *Rattus*-like and was even originally described as a species of *Rattus*.

The early association between *Mus armandvillei* and *Mallomys* was unfortunate because it implied that even if *armandvillei* was separated generically from *Mallomys*, the two kinds of rats were closely related (for example, as Simpson, 1977, treated them). The significance of the cranial and dental structures of *P. armandvillei* composed as they are of many derived configurations—compared with either *Mallomys* or any member of the indigenous New Guinea and Australian genera—and their resemblance to the derivations in *Rattus* has escaped most persons who have worked with Indo-Australian murid faunas. Tate became an exception. After first suggesting that *Mus armandvillei* and *Mallomys* might be related (Tate, 1936), he wrote in 1951 (p. 274) that “In the same paper I put forth the suggestion that *Mus armandvillei* Jentink of Flores might also be related to *Mallomys*. I now find that any close relationship is invalidated by the large

*Rattus*-like bullae of *armandvillei* and its very different temporal area. Relationship for *armandvillei* should be sought among the giant *Rattus* of Celebes.”

*Lenomys* and *Eropeplus* are *Rattus*-like in their cranial conformations. Ellerman (1941, pp. 83 and 140) even described *Lenomys* as having a “Skull like that of a specialized *Rattus*” and claimed *Eropeplus* to be “Very near *Rattus*, and doubtfully distinguishable from it.” For Ellerman, it was the structure of the molars that kept the two out of *Rattus*, particularly the dental patterns in *Lenomys*.

Neither *Papagomys* nor *Komodomys* are *Rattus*, nor are *Lenomys* and *Eropeplus*. Their crania, however, as well as some molar features, are characterized by many derivations that are also shared by *Rattus* (Musser, 1981). None of the old indigenous genera of either New Guinea or Australia are *Rattus*-like, even the *Uromys-Melomys* complex, which was once considered to be close to *Rattus*. In cranial and dental features, *Papagomys* and *Komodomys* from Nusantara, and *Lenomys* and *Eropeplus* from Sulawesi, do not fit with that group on New Guinea and Australia. And judged by their dental characteristics, *Hooijeromys* and *Floresomys* are more like *Papagomys* than anything on New Guinea or Australia.

COMPARISONS WITH THE SUNDANESE *LENOTHRIX*: Parts of the murid faunas from the Lesser Sunda Islands and from Sulawesi not only interconnect among themselves but to the fauna on the Sunda Shelf. The *Papagomys* cluster, along with *Lenomys* and *Eropeplus*, may tie, through dental characters, to *Lenothrix* (figs. 33 and 34) on the Sunda Shelf (known from the island of Tuanku off the northwest coast of Sumatra, Sarawak, and the Malay Peninsula; Musser, 1981). Misonne (1969) pointed out the close dental similarities between *Lenothrix* and *Lenomys*. The occlusal patterns in *Lenothrix* are slightly less elaborate than those in *Lenomys* (in *Lenothrix*, cusp t7 may be present or absent, cusp t3 is either missing from each third upper molar or minute, stephanodont crests are absent or poorly developed, cusp t6 is usually missing or incorporated into cusp t5 on each third molar, and cusp t9 is absent

from that molar as well) but the resemblance is striking otherwise (figs. 35 and 36).

Misonne (1969), but not Jacobs (1978), regarded *Lenothrix* as a primitive form, one possibly at the base of the murid radiation in Malaya and the Indo-Australian region. Compared with many of the genera indigenous to the Sunda Shelf and the mainland of Southeast Asia, as well as Sulawesi and Nusantaraenggara, *Lenothrix* is primitive, judged by the many primitive characters of its cranium and teeth (Musser, 1981). But whether *Lenothrix* is really an example of the basal primitive Malayan murid, or whether its features are derived from some Miocene form like *Antemus*, *Progonomys*, *Parapodemus*, or *Karnimata* (see the illustrations in Jacobs, 1978), for example, its dentition resembles that of *Lenomys*. The dental patterns of *Eropeplus*, *Komodomys*, *Papagomys*, *Hooijeromys* and even *Floresomys* can also be derived from a configuration similar to, but simpler than, that of *Lenothrix*.

#### AFFINITIES OF *SPELAEOMYS FLORENSIS*

*Spelaeomys florensis*, the other Floresian endemic, does not cluster with *Papagomys* and the other native rats on Flores. The conformation of the maxillae above the molars and shape of the zygomatic plates in *Spelaeomys* may have been similar to those structures in *Papagomys* and unlike that in *Hooijeromys*, but *Spelaeomys* is set apart from *Papagomys* and the other Floresian species by distinctive and diagnostic dental features, which are reviewed here: tall and separate cusps with different shapes on the upper molars, a large cylindrical cusp t1bis between cusps t1 and t2 on each first upper molar, a large and prominent cusp t7 on all three upper molars, posterior cingula on the first and second uppers, a large cusp t3 on each second and third, nearly upright cusps so there is only slight overlapping among the molars, an interlocking that involves three cusps (t7, t8, and the posterior cingulum) on the molar in front leaning against three cusps (t1, t5, and t3) on the molar behind, high and separate cusps that are shaped like elongate

tear drops on the lower molars, a large cylindrical antero-central cusp at the front of each lower molar row, a large anterolabial cusp on each second and third lower molar, numerous large and separate cylindrical labial cusplets along the lower molars, four-rooted first upper molars, and three-rooted first lower molars.

Although large molars and high cusps are common to both *Spelaeomys* and *Papagomys armandvillei* (figs. 39 and 40), the occlusal surfaces of the molars in *Papagomys* do not have cusps t1bis, t7, or posterior cingula. Cusps t3 are either absent from the second and third upper molars or minute on those teeth. The rows of cusps incline and the molars appreciably overlap one another with an interlocking among them involving cusp t8 of the molar in front leaning against cusps t1 and t5 of the molar behind. The lower molars lack antero-central cusps, anterolabial cusps are either small or missing from the second and third molars, labial cusplets are not present, and the primary cusps are not shaped like elongate tear drops. The first upper molars are anchored by five roots, the first lower molars by four.

Because the complex-cusped *Spelaeomys* is part of a murid fauna containing mostly simple-cusped species, I tested the hypothesis that the relationship between *Spelaeomys* and *Papagomys* might be analogous to that between *Papagomys* and *Lenomys*. The latter is closely similar to *Papagomys* in cranial conformation but has elaborate molar occlusal patterns compared to the simple patterns in *Papagomys*. *Spelaeomys* might be the Floresian counterpart of the Sulawesi *Lenomys*. In the absence of cranial material for *Spelaeomys*, any estimates of phylogenetic affinities among *Spelaeomys*, *Papagomys*, and *Lenomys* has to be based on structure of the molars. But *Spelaeomys* cannot be morphologically tied to *Lenomys*. It may be the ecological counterpart of *Lenomys* but it is not the Floresian phylogenetic counterpart. Superficial similarity of elaborate molar occlusal patterns is the only dental resemblance between the two genera. Many of the characters responsible for the complex chewing surfaces are the following

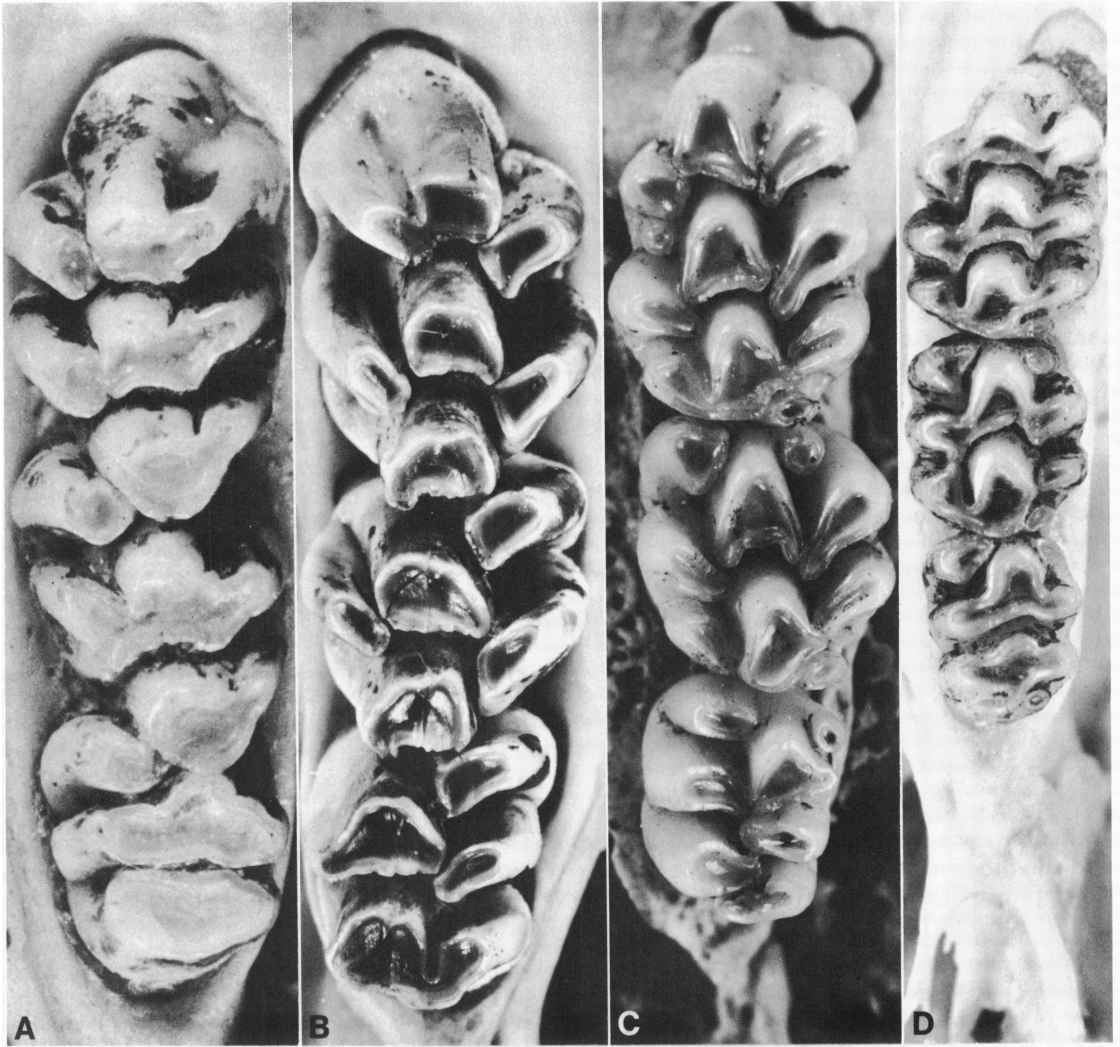


FIG. 39. Occlusal views contrasting maxillary tooththrows among *Papagomys*, *Mallomys*, *Spelaeomys*, and *Lenomys*. A, *P. armandvillei* (RMNH 18301); B, *M. rothschildi* (AMNH 194916); C, *S. florensis* (LT 205); and D, *Lenomys meyeri* (AMNH 101127). All views approximately  $\times 8$ .

primitive features that are shared by *Spelaeomys* and *Lenomys*: prominent, discrete cusps that are either separate in the rows or only weakly connected; rows of cusps that are nearly upright; upper molars abutting against one another with only slight overlap; cusp t1 that is positioned posterior to the central cusp t2, not even with it, on each first upper molar; posterior cingula on the second and third upper molars; a large and promi-

nent cusp t3 on each second and third upper molar; large anterolabial and anterolingual cusps on the first lower molars; and a large anterolabial cusp on each second and third lower molar.

The molars of *Spelaeomys* and *Lenomys* differ in significant details. The rows of primary cusps on both the upper and the lower molars in *Spelaeomys* are relatively higher than those in *Lenomys*. The cusps in *Spe-*

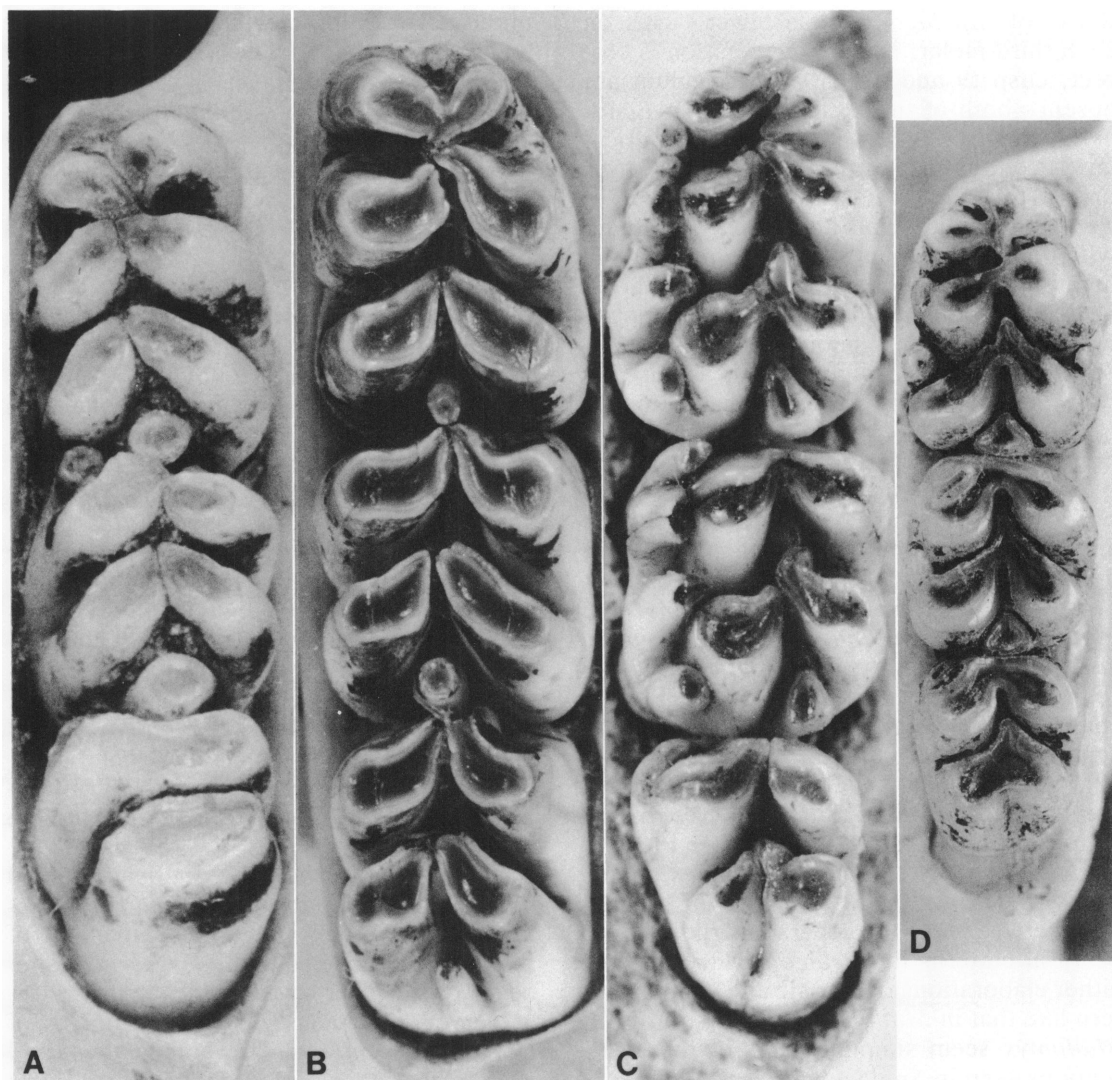


FIG. 40. Occlusal views contrasting mandibular tooththrows among *Papagomys*, *Mallomys*, *Spelaeomys*, and *Lenomys*. A, *P. armandvillei* (RMNH 18301); B, *M. rothschildi* (AMNH 194916); C, *S. florensis* (LT 85); and D, *Lenomys meyeri* (AMNH 101127). All views approximately  $\times 8$ .

*laeomys* are separate in the rows and merge together only after most of the chewing surfaces have worn away—even then the cusps are still only weakly connected (see the series of illustrations in Hooijer, 1957b); in *Lenomys*, the cusps in each row on both upper and lower molars are connected even in very young animals. All the cusps in *Spelaeomys* are shaped differently from those in

*Lenomys*, particularly the labial and lingual cusps on the upper molars, and all primary cusps on the lowers (figs. 39 and 40). *Spelaeomys* has a large cylindrical cusp t1bis on each first upper molar, whereas cusp t1bis is either missing or present in the form of a low and inconspicuous ridge in *Lenomys*. *Lenomys* has short or extensive stephanodont crests on the upper molars; *Spelaeomys*

does not. *Spelaeomys* has fewer cusps on each third molar; if my interpretation is correct, cusp t9 and a posterior cingulum are absent—both of these cusps occur in *Lenomys*. *Spelaeomys* has a large and cylindrical anterocentral cusp at the front of each lower molar row; such a cusp is either missing in *Lenomys*, or is small and partially merged with the anterolingual cusp. *Spelaeomys* has many more labial cusplets and all are large, prominent, and cylindrical; these contrast with the few inconspicuous small cusplets in *Lenomys* that are usually pressed against the rows of cusps or merged with them. Finally, *Spelaeomys* has fewer roots anchoring the first upper and lower molars.

Although the molar patterns differ between *Lenomys* and *Papagomys*, the shapes and positions of the primary cusps, and the number and pattern of the roots beneath the first upper and lower molars of *Lenomys* are more like those in *Papagomys*, and *Eropeplus*, than those in *Spelaeomys*. The cusps in *Spelaeomys* are, in their relative positions, shapes, and quality of being nearly erect and separate, like those in *Mallomys* (figs. 39 and 40). *Mallomys* has fewer cusps and no cusplets with a result that the molars have much simpler occlusal patterns than those in *Spelaeomys*, but the similarity in shapes of the cusps, particularly those on the lower molars, between the two genera is striking. The occlusal patterns in *Spelaeomys* seem to be either elaborations on a basic and simple pattern like that in *Mallomys*, or the patterns in *Mallomys* seem simplifications of the elaborations seen in *Spelaeomys*. Both *Spelaeomys* and *Mallomys* have the same number and pattern of roots beneath the first upper and lower molars.

The dentition of *Spelaeomys* is strikingly unlike that in *Papagomys*, *Hooijeromys*, *Floresomys*, and *Komodomys*. The differences reflect a suite of derived characters shared among the four genera but not with *Spelaeomys*, and derived features in *Spelaeomys* that are either unique or shared with genera other than those four. I interpret the significance of this strong contrast to indicate that *Spelaeomys* is not phylogenetically closely related to either *Papagomys* and the

other native Floresian murids on the one hand, or to the Sulawesi *Lenomys* and *Eropeplus* on the other. I hypothesize that *Spelaeomys* belongs with the old native genera of New Guinea, that it is a derivative of the ancestral stock common to the natives of New Guinea, possibly Australia, and likely Timor. Results from study of cranial material of *Spelaeomys* can either substantiate this contention or falsify the hypothesis.

What about Timor? There the endemic murid fauna is represented by subfossils only, most collected by Glover (1969, 1970) from excavations of prehistoric deposits in limestone caves. Remains of murids were abundant in the four main sites Glover excavated and included examples of three species preliminarily identified as *Rattus* (*R. exulans*, possibly *R. rattus*, and a third kind yet to be identified), one species of *Melomys* and one of *Pogonomelomys*, the giant rat *Coryphomys buehleri*, another giant rat morphologically similar to *Coryphomys* (an example is specimen 1 of the three Hooijer, 1965, had identified as *Coryphomys*), and two other kinds of large rats. Some specimens were found in deposits radiocarbon-dated as old as  $13,400 \pm 520$  years before present (Glover, 1969).

These prehistoric murids are being studied by J. A. Mahoney in the Department of Geology and Geophysics at the University of Sydney. Several years ago I was in Mahoney's office where we looked at the better preserved specimens. Excellent samples of *Coryphomys buehleri* are among them and each of the other three large rats represents a different genus in Mahoney's opinion, genera he will eventually name and characterize in publication. His conclusion is based on study of isolated teeth as well as complete molar rows and associated parts of crania, dentaries, and sometimes postcranial elements, all well preserved and some surprisingly complete for the type of material usually dug from prehistoric deposits. I agree with Mahoney's taxonomic evaluations. Furthermore, none of the four genera of giant rats seem to closely resemble any of the native murids on Flores—with the possible exception of *Spelaeomys*.

How the native Timor murids may relate to *Spelaeomys* on one hand and to those from New Guinea on the other can be determined after the Timor fauna has been described and the relationships of the species analyzed, and after the New Guinea murids have been carefully studied. The Timor *Melomys* and *Pogonomelomys* certainly belong with the fauna on New Guinea. At least three of the genera of giant rats have two-rooted or three-rooted first lower molars, which indicates that the first upper molars are probably three-rooted or four-rooted, and their occlusal patterns are more complex than those in *Papagomys*, *Hooijeromys*, *Floresomys*, or *Komodomys*. The upper molars of

*Coryphomys*, for example, have a large cusp t7 and a prominent wide posterior cingulum (some fragments from the giant rats are illustrated in Glover, 1970). Except for lack of labial cusplets, the configurations of the cusps on the lower molars and the antero-central cusp at the front of each molar row in *Coryphomys* is very much like shapes of those elements in *Spelaeomys*. What I have seen of the Timor fauna suggests to me that most if not all the species cluster with the New Guinea genera and *Spelaeomys* rather than *Papagomys* and its relatives. For further information we must await results from Mahoney's study of the Timor endemics.

## A HISTORICAL VIEW

*Papagomys*, *Hooijeromys*, *Komodomys*, and probably *Floresomys* cluster because of derived similarities in dental features; *Papagomys* and *Komodomys* share certain cranial derivations as well. These four genera appear to be phylogenetically more closely related to the Sulawesian *Eropeplus* and *Lenomys* than to *Spelaeomys* and the old native genera on Australia and New Guinea. This morphological and apparent phylogenetic link between Nusatenggara and Sulawesi implies a close faunal relationship between these islands early in the evolutionary history of the indigenous murids residing there. Furthermore, the connection between the Sulawesian *Lenomys* and the Sundanese *Lenothrix* suggests that the ancestor of at least a segment of the murid fauna on Sulawesi and of most of those on Flores may have originated on the Asian continent rather than the New Guinea area or Australian region.

The historical origins of the affinities between some of the murids on Sulawesi and Flores might be explained by considering the following two hypotheses. The first is that the Sulawesian *Lenomys* and *Eropeplus*, and the Floresian *Papagomys*, *Hooijeromys*, *Komodomys*, and *Floresomys* may have been derived from an older murid fauna that either migrated from the Sunda Shelf to Su-

lawesi by way of Kalimantan (Borneo) or Java, and to at least Flores from Java through the other Lesser Sunda Islands; or was at one time distributed over a continuous land area, part of which broke up into Sulawesi to the north and Nusatenggara to the south, thus isolating portions of the original stock, which differentiated into the native genera we know today.

The other hypothesis calls for direct interchange of an early murid stock over a land bridge between Sulawesi and Flores with subsequent isolation and differentiation into the modern genera.

The time that either migration or vicariant events may have occurred is hypothetical because fossil murids from sediments deposited earlier than Pleistocene times have yet to be discovered on the Sunda Shelf, Sulawesi, or any of the Lesser Sunda Islands. Fragments from a species of *Rattus*-like animal from the Middle Pleistocene of Trinil in East Java represent the earliest murid known from the Sunda Shelf; subfossil murids from Sulawesi have been found in Holocene cave deposits in parts of the southwest peninsula, and all of them represent species still living on the islands; finally, the fragments of *Hooijeromys*, if actually from middle or late Pleistocene sediments, are the oldest known fossils from Nusatenggara (the preceding

statements are based on my study of the material from Sulawesi and East Java, as well as Flores). If an early date can be tied to *Hooijeromys*, an early stock was either on Flores or migrated there before middle Pleistocene, guesses would be sometime in early Pleistocene, Pliocene, or possibly late Miocene times.

The extent of land surfaces in the area of Sulawesi, Kalimantan (Borneo), and Java during the Pliocene and Miocene is conjectural but two reconstructions possibly allow for faunal interchange between Sulawesi and Java, and between Sulawesi and Kalimantan. Groves (1976) has discussed the origin of the mammalian fauna of Sulawesi and in his view the larger Sulawesi endemics are representatives of an older faunal stratum and perhaps derivable from a Siwalik-like fauna that is represented in Central Java by Siva-Malayan fossils found in the Kali Glagah and Ci Julang deposits, which are Late Pliocene, according to Maglio (1973). How those larger endemics got to Sulawesi may have had something to do with the Pulau Laut Center of Diastrophism (Van Bemmelen, 1949), which to Groves (1976, p. 213), "would seem to be a large uplifted island, extending according to Van Bemmelen from the Mangkalihat peninsula southwards and across the Makassar Strait, curving around Pulau Laut to the southwest and ending near the Muriah volcano in Java. At the time of the existence of this island—Upper Pliocene according to Van Bemmelen—the present land areas of Southeastern Borneo and western Sulawesi were covered by sea, as was the northern part of East Java. It is in fact uncertain whether there was at any time a complete land bridge from Java or Borneo to Sulawesi; as the Ci Julang Faunal beds and other Pliocene sites in eastern Java are interbedded terrestrial and marine deposits it seems that there might from time to time have been a brief connection at least at the southern end between Java and the P. Laut Centre." Van Bemmelen dates the submergence of the Pulau Center of Diastrophism and accompanying uplift of the adjacent areas at the beginning of the Quaternary, but Groves would push it back to about Middle

Pliocene, and "To get the Siva-Malayan fauna into Sulawesi might require limited island-hopping or even no island-hopping at all . . . ."

Whether there was ever either a land connection or very narrow water gaps between Java and Sulawesi, eastern Kalimantan was at one time much closer to Sulawesi than it is now, probably even connected, if reconstructions by geologists reflect past reality (Audley-Charles, Carter and Milsom, 1972; Katili, 1978; and Hamilton, 1979). But there is disagreement as to when the Makassar Strait was closed. For Katili (1978), past movements of the Pacific plate gradually pushed Sulawesi against the Asian continent so that by late Pliocene the Makassar Strait had disappeared and the island was adjacent to Kalimantan, likely separated by a very narrow water gap; later, during the Quaternary, the Strait of Makassar opened by sea-floor spreading and Sulawesi gradually moved eastward to its present position, separated from the Sunda Shelf by deep waters. In the frame of Katili's postulation, migration of an early murid stock from the Sunda Shelf to Sulawesi could have occurred when the island was next to Kalimantan, possibly even before or just after that time when Sulawesi was being pushed toward Kalimantan or rifted away and the sea gap was not as narrow as in late Pliocene but narrower than it is now.

Hamilton (1979, pp. 185–187) portrays a different sequence of events: "Eastern and southeastern sections of Borneo share Cretaceous and early Paleogene features with Sulawesi suggestive that until middle Paleogene time Sulawesi was a part of Borneo, oceanic Makassar Strait having opened subsequently as Sulawesi drifted relatively southeastward away from Borneo. Southeastern Borneo, the shelf to the east of it, and the South Arm of Sulawesi all have basements of Cretaceous subduction complexes overlain by similar lower Paleogene shelf strata. In both Borneo and Sulawesi, quartzose Eocene clastic strata and coal are overlain by a thick sheet of limestone, of late Eocene, Oligocene, and early Miocene age, which gives way northward to mostly clastic

rocks. If Sulawesi has moved southeastward away from Borneo, the westward bulge of central Sulawesi having slid along the south-east-trending edge of the continental shelf off southeastern Borneo, then the limestone sheets and underlying continental strata on both islands were initially continuous. Rifting may have begun in Paleogene time." Subsequent to the rifting, Hamilton (1979, p. 188) explained that "From late Eocene into early Miocene time, the Java Sea-southeastern Borneo-western Sulawesi region was largely a shallow sea undergoing stable-shelf sedimentation." And according to Hamilton's reconstructions shown in a series of palinspastic maps (pp. 152-153), the Makassar Strait has remained open from the time of early Miocene, about 20 million years ago.

The extent of land surface between Java and Flores during the Pliocene is a conjectural subject. Apparently the northeastern part of Java did not emerge from the sea until late Pliocene-early Pleistocene, as indicated by the black clays of the Pujangan beds, which conformably overlay Pliocene marine sediments in the Kendeng Zone of East Java (Van Bemmelen, 1949; Ninkovich and Burckle, 1978). South of the Kendeng Zone, however, the Southern Mountains were lowlands, hardly above sea level, from the late Miocene through the early Pleistocene (Van Bemmelen, 1949). The islands to the east of Java from Bali to Romang (north of the eastern tip of Timor) are primarily volcanic in origin. The volcanism is Quaternary and much of the surface area of the islands result from differential uplift during the Quaternary lasting until the present (Van Bemmelen, 1949; Umbgrove, 1949). Furthermore, the present insular configuration of the chain between Romang and Komodo has apparently resulted from the uplift of a geanticlinal belt crested by volcanoes; the belt broke into isolated blocks separated by subsiding areas, thus producing the appearance of islands and straits, a Quaternary event (Van Bemmelen, 1949). It is not evident just how extensive the land areas of the islands were earlier than the Quaternary (for Auffenberg, 1980, part of Komodo has been a land area from Late

Mesozoic times), particularly during middle to late Pliocene, but possibly by at least Early Quaternary, an early murid stock may have been able to get to Flores from Java with little or no island hopping.

The Java-Flores passage is one of the routes postulated by Audley-Charles and Hooijer (1973) to get pygmy stegodonts, *Stegodon trigonocephalus* and *S. sompoensis*, from Java to Flores during the Pleistocene. The animals also occur on Timor and Sulawesi. Based on evidence from the Viqueque Formation in eastern Timor, those authors postulated a land connection between Timor and Flores via the island of Alor sometime in the early and middle Pleistocene allowing stegodonts to get from Flores to Timor. Subsequently, during the late Pleistocene and Holocene, downfaulting occurred involving about 3000 meters, which eliminated the land connection.

That faunal interchange occurred directly between Flores and Sulawesi infers dispersal by rafting over a water gap, island hopping or movement along a land bridge. A land bridge between Sulawesi and Flores is an old postulate (Sarasin and Sarasin, 1901; Barbour, 1912) that was buried by Mayr (1944) but resurrected recently by Audley-Charles and Hooijer (1973, p. 198) to move both species of pygmy stegodonts back and forth between Sulawesi and Flores: "At present south-west Sulawesi is connected to the northeast tip of Flores by a submarine ridge nearly 3,000 m deep that separates the Flores and Banda Seas . . . . The early and middle Pleistocene uplift, that we suggest affected Timor and the Flores-Wetar region, may have extended northwards to allow the pygmy stegodonts to wander back and forth between Flores and Sulawesi along the Kaloa-toa-Matjan ridge, then *via* Tanahjampea and Salajar ridge. This ridge system may also have been elevated above sea level by a regional uplift that followed the plate collision between eastern and western Sulawesi in the late Pliocene-early Pleistocene [Audley-Charles, Carter and Milsom, 1972]."

To Audley-Charles and Hooijer (1973, p. 198), "Another land connexion may have developed, as a result of glacial lowering of

sea level, across the Sunda Shelf (now 200 m deep) from Java *via* the Doangdoang shoals to Makassar in western Sulawesi. If these were the stegodont migration routes they imply late Pleistocene and Holocene down-faulting of the Flores Sea and southern Makassar Strait, analogous with the postulated recent down-faulting in the Savu Sea, Ombai and Wetar Straits, which followed the uplift that occurred after continental crust of the Australian plate collided with a subduction zone [Audley-Charles, Carter, and Milson, 1972]."

From a perspective of taxonomy and distribution of the Recent reptiles and amphibians on Komodo Island and adjacent areas, Auffenberg (1980) has provided an intriguing view of the historical zoogeography of the Lesser Sunda Islands. He presents (p. 137) new data "based on potassium-argon isotope dates obtained from igneous rock samples taken immediately below and above a fossil wood zone" indicating the history of Komodo to extend back into the Late Mesozoic. Samples from below the fossil wood zone were taken from "the top of the basaltic lacolithic dome of Gunung Insilung" ( $130 \pm 10$  million years), "the highest extruded sheet of basaltic rock on the flanks of Komodo" ( $134 \pm 19$  million years), and "a basalt porphyry from the larger of the two volcanic necks comprising Ntodo Klea, Komodo" ( $49.0 \pm 4.3$  million years). "The latter," writes Auffenberg, "is believed to represent the latest volcanic eruption on the island and obviously is much younger than the fossil wood zone. Invertebrate fossils from the raised coral reefs on the flanks of the Ntodo Klea complex range in age from early to middle Tertiary . . . . Thus the igneous activity responsible for the formation of the western half of Komodo occurred during the Jurassic. This land surface was later covered with a forest of large trees. Volcanism was again prevalent during the Eocene and created the Ntodo Klea complex on the eastern part of the island. At this time the eastern half of Komodo was significantly enlarged through the uplift of coralline strata, which continued throughout much of the Tertiary and was undoubtedly responsible

for the formation of Padar. Thus the land surface of Komodo was not formed in the Plio-Pleistocene, as is often assumed in zoogeographic studies . . . but in the late Mesozoic." "Rintja and extreme western Flores," continues Auffenberg (p. 138), "share a similar geologic history. In fact, Komodo, Rintja, and Flores may have been connected during the Eocene and Oligocene and again separated in the Mio-Pliocene by submergence resulting from volcanism on Flores."

For Auffenberg (p. 145), the Recent herpetofauna of Komodo contains endemics that "are all related to Celebes species, or to species from areas in which the Celebes may have been an important stepping stone to the Lesser Sundas, presumably across the Saleyer 'Bridge' . . . , first proposed by Sarasin and Sarasin (1901) as an actual land connection and thus largely disregarded since." Auffenberg notes (pp. 147-148) that "The presence in the Lesser Sundas of reptiles and amphibians with close relations to primitive Celebes species is probably best explained by an interchange having come about over the Saleyer 'bridge' area during the juxtaposition of the Celebes and the middle part of the Lesser Sunda chain in the Pliocene during compression of the arc after collision of the Sunda and Sahul shelves . . . . Thus the fauna probably evolved on the originally festooned island arc itself before diastrophism brought two originally more distant parts of the arc together, and part of the fauna was exchanged."

In his summary, Auffenberg (pp. 149-150) noted the lack of evidence that Komodo was ever completely submerged since Late Mesozoic times, and presented a hypothesis of how the herpetofauna on the Lesser Sunda Islands may have developed. By the Pliocene-Pleistocene interval, a land area that Auffenberg calls *protocelbes* "was folded westward in such a way that it was pushed close to Flores and Komodo, allowing movement of the ancient outer Lesser Sunda herpetofauna onto the base of the arc. The juxtaposition brought about by the crustal movement is undoubtedly the basis for the 'Saleyer Bridge' concept of Sarasin and Sar-

asin (1901), rather than the small Tukangbesi Islands between Celebes and Flores. Furthermore, the westward movement of the Celebes portion of the loop brought it close to Borneo, allowing for movement of a more modern herpetofauna onto the Celebes. Thus the westward movement of the loop allowed two very different faunas to move into the Komodo area (an ancient ultimately Asian-derived 'protocelebes' plus a more modern one from Sundaland across Borneo to Celebes and/or along the arc itself)."

Whether these postulated land connections between Sulawesi and Flores or between Sulawesi and Java have any bearing on the migration of an early murid fauna from which *Lenomys* and *Eropeplus* on one hand, and *Papagomys* with its Floresian relatives on the other, could have been derived is unknown at present. Because different genera are involved, any migrations or interchanges probably occurred early, possibly early Pleistocene, Pliocene, or maybe even late Miocene, with a subsequent period of isolation and differentiation. The stegodont migrations may have occurred later. If land bridges were involved, and if *Hooijeromys* was contemporaneous with at least one of the stegodonts, samples of that rat might turn up in Pleistocene sediments on Sulawesi, providing the habitat on Sulawesi at that time was similar to what it was on Flores.

The reconstruction of land bridges is based on the assumption that stegodonts could not swim long distances (Hooijer, 1972). But according to Sondaar (1977), the assumption underlying recent studies of unbalanced Pleistocene island faunas in the Mediterranean, the Japanese archipelago, the Philippines, and for him the Indonesian region, is that large animals such as elephants, deer, hippopotamus, and presumably stegodonts, were capable of swimming long distances (also, see Johnson, 1980, who discusses the swimming abilities of Recent elephants). If land connections did exist in the Indonesian area, more species besides stegodonts should be shared between Sulawesi and Flores; samples of *Elephas* and *Celebochoerus*, for example, might be expected in Pleistocene sediments on Flores. Better exploration

of Pleistocene beds on both islands is needed to elucidate the past faunal relationship between them.

No Recent indigenous species of murids are common to Sulawesi and Flores (at the levels of either genera or species). Thus, the close relationship between portions of the murid faunas on those two islands suggests that my first hypothesis may be the most reasonable. Sulawesi and Flores were probably not connected by a land bridge. The Sulawesi cluster and the Floresian assemblage may have been derived from a common murid fauna that migrated in one direction from the Sunda Shelf to Sulawesi, and in another direction to at least Flores in the Lesser Sunda chain, either over continuous land or islands; or the early stock may have been distributed over a continental land area, parts of which eventually separated from the continent and formed some of the present area of Sulawesi and of the Lesser Sundas. Either of the above events was followed by a period of isolation and presumably differentiation of the original murid stock. Some remnants or products of that ancestral stock might occur on the islands between Java and Flores. No Recent or fossil endemics are known from those places but none of the intervening islands have been carefully explored for recent or fossil murids.

In discussions and reconstructions of possible land areas during the past in the region of Sulawesi, the southeastern margin of the Sunda Shelf, and the Lesser Sunda Islands, it is important to note Batchelor's (1979) contention that sea levels during Pliocene to middle Pleistocene, although rising discontinuously, never were much higher than the break of the continental shelf, about 130 m. below present sea level, and during parts of the Pleistocene may have been more than 230 m. below present sea level.

The occurrence of *Spelaeomys* on Flores, if I have correctly estimated its phylogenetic affinities by linking it with the natives of New Guinea and possibly Timor, may reflect the early migration of an ancestral form from Timor to Flores and subsequent differentiation into that complex-toothed species that is now represented only by subfossil frag-

ments. A careful survey of the islands in Nusatenggara east of Flores might reveal murids that are related to *Spelaeomys* and to those on Timor.

There is some evidence, as I mentioned previously, that the native murids of Timor may be more closely related to the New Guinea fauna than to the Floresian *Papagomys*, *Hooijeromys*, *Komodomys*, and *Floresomys*. Access to Timor from New Guinea via Australia would have been possible in the Pliocene because Veevers (1969) postulated that during Pliocene time Timor was smaller and much closer to northwestern Australia than it is now or than it was during periods of lower sea levels during the late Pleistocene. Land with stepped surfaces extended from what is now the Australian coastline out nearly to Timor, separated by only a narrow water gap.

Possibly the murid fauna from Flores and the Komodo Islands of Padar and Rintja was spread over the other islands in Nusatenggara at one time. That no native rats have been found on the Lesser Sunda Islands either to the west of Padar and Rintja or to the east of Flores, except on Timor, is possibly real, but more likely simply reflects inadequate survey of those places.

Sometime during the Pleistocene, or even late Pliocene, eustatic drops in sea levels during the last few periods of glaciation were probably enough so that most or all the islands in Nusatenggara except Timor and Sumba were either joined or separated by very narrow water gaps (Van Andel et al., 1967; Jongsma, 1970; Batchelor, 1979; Geyh, Kudrass and Streif, 1979), allowing for faunal interchange between Flores and places to the west and east. In Auffenberg's (1980, pp. 140-141) view, "Komodo, Padar, Rintja, and western Flores were probably broadly connected to one another." And at high sea levels during the Pliocene-Pleistocene, Auffenberg notes that "it is reasonably clear that Komodo, Rintja, and western Flores were above sea level during these periods; though much or all of Padar may have been submerged. Ample evidence shows considerable

tectonic movements during the entire post-Tertiary in this area, so that the present and past separation of these islands may have resulted either from eustatic rise in sea level following glacial melting or from actual lowering of the sea bottom by tectonic activity—probably both." But for Auffenberg, not only were Timor and Sumba never connected to the other Lesser Sundas during this time, but there is no evidence "of past connection of Komodo to Sumbawa in the west or to Sumba southward, regardless of sea level or bottom depth changes."

That the islands may have once formed an elongate land mass does not mean that the habitats there were necessarily the same as those in which the species on Flores or the Komodo Islands evolved, and that the fauna of Flores would have spread out, or that *Komodomys* would have migrated westward. During insular isolation, the fauna on each island evolved along with particular environments and may have been ecologically isolated after insular isolation no longer existed.

Finally, the island of Sumba, neglected by mammalogical and paleontological exploration, may be important to understanding movement of land mammals between Flores and Timor for Sumba can now be included within the distribution of stegodonts. A group supervised by Dr. Sujono, representing the National Archeological Institute in Jakarta and the Institute of Technology at Bandung, excavated what appears to be a stegodont from Pleistocene calcareous gravel deposits on Sumba, according to a report in the Indonesian Nature and Science News Letter of October, 1978. Was the route of stegodont movement between Flores and Timor through Sumba rather than via Alor, as was postulated by Audley-Charles and Hooijer (1973)? Or is Sumba simply another island that stegodonts reached by swimming? It is now important to determine what fragments of other kinds of mammals, if any, are imbedded in those Pleistocene gravels on Sumba.

## CONCLUSIONS AND SUGGESTIONS

Of the 12 murid species now known from Flores, four also occur elsewhere in the region from Australia and New Guinea to mainland Asia: *Rattus rattus*, *R. argentiventer*, *R. exulans*, and *Mus caroli*. Two others have worldwide distributions: *Rattus norvegicus* and *Mus musculus*. The present geographic ranges of these six species, the nature of geographic variation within the populations over such large areas, and their close association with habitats made and maintained by humans suggest that their distributions east of the Sunda Shelf, and their occurrence on Flores in particular, are results of dispersal through human agency.

Six of the 12 species are native to Flores: *Papagomys armandvillei*, *P. theodorverhoeveni*, *Hooijeromys nusatenggara*, *Floresomys naso*, *Komodomys rintjanus*, and *Spelaeomys florensis*. *Papagomys* still lives on Flores and is also known from subfossil fragments. *Hooijeromys* is represented by reputed Pleistocene specimens, the others consist of subfossil specimens only. *Komodomys rintjanus* still lives on the islands of Rintja and Padar west of Flores.

The native rats can be separated into two primary groups. Dental characters of *Spelaeomys* may link it to the native murids on New Guinea and adjacent islands, Australia, and probably Timor. These species seem to comprise an old assemblage, derived from one or more ancient ancestral stocks. Dental characteristics of *Hooijeromys*, *Komodomys*, and possibly *Floresomys* indicate their closer phylogenetic relationship to *Papagomys*; cranial characters of *Papagomys* are much like those crania of *Lenomys* and *Eropeplus* on Sulawesi; molar structure also ties *Papagomys* to *Eropeplus*, less so to *Lenomys*; all these Floresian and Sulawesi genera may represent derivations from an ancestral stock present in the Sulawesi-Nusatenggara region at a later time than the earlier period during which the New Guinea-Australian fauna originated.

The striking similarities in derived cranial

characters between *Lenomys* and *Eropeplus* on one hand and between those two and *Papagomys* on the other, as well as the derived resemblances in molar structure between *Eropeplus* and *Papagomys* and in some dental features between *Lenomys* and *Papagomys*, along with the dental link between *Lenomys* and the Sundanese *Lenothrix*, suggest that the Sulawesi genera and *Papagomys* with its Floresian allies were derived from a common ancestral stock that once occurred on the Sunda Shelf, Sulawesi, and Flores at a time when these areas were either once continuous or separated only by narrow water gaps. Two species of stegodonts once lived on Sulawesi and Flores (whether they were contemporaneous or each lived at a different time is unknown; Hooijer, 1975), as well as Timor, which stimulated Hooijer (1975, p. 54) to write that "For the present we may consider Celebes, Flores and Timor to have been one, the homeland of the pygmy stegodonts, which may be called Stegoland . . . . Situated between Sundaland and Sahulland, Stegoland is a zoogeographic subunit of the area intermediate between the Indo-Malayan and Papuan-Australian faunal regions." The similarity between Sulawesi and Flores of portions of their murid faunas suggests that the postulate of Stegoland may be more than just a charming fancy.

Phylogenetic relationships among the genera native to the islands and continent east of the Sunda Shelf are poorly known. Some assemblages, still incomplete in content and imprecise in outline, are beginning to emerge from my studies. These provisional broad groupings are listed in table 16. In the Moluccas, the New Guinea area, Australia, and probably Timor, there appear to be two major groups of rats and mice. The non-*Rattus* genera, diverse in morphological structure and in habitus, form one group. Included here are the genera usually thought of as comprising a very old faunal stratum, a cluster I refer to as Group I, the old endemics; examples are the hydromyines, conilurines,

and the *Uromys-Melomys* complex. The genera retain many primitive features and a few derived, sometimes highly specialized structures. The phylogenetic relationships among most of the species are obscure, and likely complex. The other major group in the New Guinea and Australian region contains the native species that have been regarded as members of *Rattus* (Group III).

In the Philippine Islands (excluding the Palawan and Calamian groups), there are three major groups of native murids. Genera that are likely part of a very old faunal stratum comprise one assemblage (Group I). These genera (*Crateromys*, *Phloeomys*, and the shrew rats *Chrotomys*, *Celaenomys*, and *Rhychomys* are some examples) are comparable to the old endemic genera in the New Guinea and Australian areas and may be more closely related to that cluster than to any known from the Asian mainland, a scheme of relationships that I am currently testing. The second group (which I refer to as Group II, the assemblage with *Rattus*-like derivations) consists of genera characterized by a combination of mostly derived along with some primitive cranial and dental features. Many of these derivations, particularly the ones associated with the crania and number of roots beneath the molars, are similar to those found in *Rattus*. It was thought that the species were so much like *Rattus* in cranial conformation and dental patterns that they were either originally named and described as species of *Rattus* or described as species in genera that were later incorporated into *Rattus*. The Philippine *Tryphomys* is an example of this group. Counterparts of the genera in Group II include *Lenomys*, *Eropeplus*, and a few others on Sulawesi. This Philippine group that is characterized by derived features, as compared with the many primitive characters retained among the old endemics, has no counterpart in the New Guinea and Australian region. The third major group in the Philippines consists of species in *Rattus* (Group III).

The murids native to Sulawesi are a mixed lot. One genus, *Crunomys*, is part of the old endemic Philippine assemblage. Six other genera are also old endemics but their phy-

logenetic affinities appear to be with the fauna on the Sunda Shelf (*Maxomys*, *Haeromys*, and *Margaretamys* are some examples; Musser, 1981) and not with the old endemics of the Philippines or with the genera from the New Guinea and Australian region. A second large and roughly defined group on Sulawesi is formed from genera characterized by a combination of many derived and some primitive cranial and dental characters. The derivations, particularly those in the crania, resemble those in *Rattus*. This assemblage (Group II) contains *Lenomys*, *Eropeplus*, and other genera, and is comparable to the one on the Philippines that includes *Tryphomys*. Native *Rattus* (Group III) forms the third primary assemblage on Sulawesi.

Only two major groups are now known from the Lesser Sunda Islands. If my interpretation of its characters is correct, *Speleomys* is the only member of one group, and constitutes the Floresian representative of the old endemic genera (Group I) of the New Guinea and Australian areas. *Papagomys*, *Hooijeromys*, *Komodomys*, and *Floresomys* comprise the other major group, a cluster of genera with cranial and dental features that are mostly derived, similar to those in *Rattus*. This cluster (Group II) is comparable with the assemblage on Sulawesi that contains *Eropeplus* and *Lenomys*. To date, no native species of *Rattus* (Group III) have been found in Nusatenggara, unless one of the species that I have hypothesized as being commensal—*R. argentiventer* or *R. exulans*, for example—is really native to the Lesser Sunda Islands.

It may prove to be significant that only two primary groups of native murids are found in the New Guinea and Australian area, the region farthest from the Asian mainland. By contrast, on the Philippines and Sulawesi, islands closer to continental Asia, there are in addition to a group of old endemics and one of *Rattus*, an intermediate group, one that is not represented in the New Guinea and Australian region. And on Sulawesi itself, a land area even closer to the Sunda Shelf, nearly all the old endemics may be phylogenetically closer to the murids that are native to the Sunda Shelf and mainland of

TABLE 16  
A Hypothesis of Generic Groupings of Native Murids from East of the Sunda Shelf

	New Guinea, Australia, Timor, Moluccas	Philippines (excluding Palawan) and Calamian islands)	Sulawesi	Lesser Sunda Islands
GROUP I: OLD ENDEMICS				
New Guinea-Australian- Philippine subgroup	Anisomys, Chiruromys, Conilurus, Coryphomys, Crossomys, Hydromys, Hyomys, Leggadina, Leporillus, Leptomys, Lorentzimys, Macruromys, Mallomys, Mastacomys, Mayermys, Melomys, Mesembriomys, Microhydromys, Neohydromys, Notomys, Parahydromys, Paraleptomys, Pogonomelomys, Pogonomys, Pseudohydromys, Pseudomys, Solomys, Uromys, Xenuromys, Xeromys, Zyzomys	Anonymomys, Apomys, Batomys, Carpomys, Celaenomys, Chrotomys, Crateromys, Crunomys, Phloeomys, Rhynchomys	Crunomys	Spelaomys
Asian mainland subgroup			Echiothrix, Haeromys, Margaretamys, Maxomys, Melasmothrix, Tateomys	
GROUP II: RATTUS-LIKE		Bullinus, Limnomys, Tarsomys, Tryphomys	Bunomys, Eroleplus, Lenomys, Paruromys, Taeromys	Floresomys, Hooijeromys, Komodomys, Papagomys
GROUP III: RATTUS	Rattus	Rattus	Rattus	

Asia than to those in the Philippines and the New Guinea and Australian region.

Species of native *Rattus* seem to be present on all the archipelagos and the continent east of the Sunda Shelf except for the Lesser Sunda Islands. Whether this pattern is real or whether it simply reflects insufficient biological exploration on Nusatenggara is important to determine in order to reveal the source of the native *Rattus* in the Moluccas, the New Guinea area, and the Australian region. Species of *Rattus* form a small part of the murids that are native to Australia and New Guinea; the bulk of the rat and mouse fauna consists of genera not phylogenetically closely related to *Rattus*. In the Moluccas, the opposite proportions exist. Except for records of *Melomys* from Ceram, Pulau Obi, and the Talaud Islands (Laurie and Hill, 1954), and the Ceramese *Nesoromys*, which is closely related to the *Rattus niobe* group on New Guinea if not actually part of that assemblage (Rümmler, 1938; Misonne, 1969), as I have treated it (table 16), the known native rat fauna on the Moluccas consists entirely of species in *Rattus*. *Rattus elaphinus* (Sody, 1941) occurs on Pulau Taliabu in the Sula Islands, *R. morotaiensis* (Kellogg, 1945) on Pulau Morotai north of Halmahera, and *R. felicius* (Thomas, 1920) on Ceram. In addition, there are two new species from Pulau Taliabu yet to be named and described. Features of the skins, skulls, and teeth of some of these Moluccan species of *Rattus* may ally them with species of *Rattus* that occur on New Guinea and offshore islands, the Solomon Islands, and the Bismarck Archipelago.

Set against the distributional patterns of *Rattus* and the other murid genera that occur east of the Sunda Shelf, the following questions come to mind. Are there two primary clusters of *Rattus* occurring east and south of Sulawesi, one consisting of species native to New Guinea with some relatives scattered through the Moluccas, the other formed of species indigenous to Australia? Based on chromosomal evidence, Dennis and Menzies (1978) suggest the core of New Guinea *Rattus* to be a different group from the Australian species, a dichotomy recognized earlier

by Schodde and Calaby (1972, p. 269) who noted that the "two groups of *Rattus* appear to have little in common." Does this relationship mean that New Guinea was populated by *Rattus* migrating through the Moluccas or does the distribution reflect a back-migration from New Guinea to the Moluccas?

And if the *Rattus* on Australia are really such a different group from those on New Guinea, where did they come from? If we assume that the ancestral Australian *Rattus* came from the Asian mainland then the Lesser Sunda Islands is a place to look for possible *Rattus* that may be related to those on Australia. It is for this reason that I originally compared the small subfossil *Rattus*-like fragments from Liang Toge with samples of the native Australian species of *Rattus*, testing the hypothesis that the fragments represented true *Rattus* and that they might tie to the Australian fauna. But the subfossils do not represent *Rattus* although they are *Rattus*-like. The presence on Flores of true *Rattus*, related to either the Australian cluster or to the species on continental Asia, remains to be demonstrated.

There is another side to the problem of *Rattus* occurring east of Wallace's Line. The pervading past and current dogma is that the native *Rattus* on New Guinea and Australia are related to species of *Rattus* on continental Asia and the Sunda Shelf, and that they represent migration of one or several ancestral stocks from the continent to the New Guinea and Australian region at a time (Pleistocene is the interval usually summoned up) much later than that period during which the older native species were evolving on New Guinea (beginning in the Miocene is the conventional guess) and Australia (present by the Pliocene). There is no hard evidence to substantiate this assertion. Part of the data required to test the statement is unavailable because the genus *Rattus* has never been adequately diagnosed or defined, or the species taxonomically revised. The relationships of the native *Rattus* on New Guinea and Australia to those occurring on islands to the west and to those on the Asian continent can only be ascertained after the

monophyly of *Rattus* is established, a task yet to be completed but one already started (for example, Misonne, 1969; Musser, 1981).

Until *Rattus* is defined and diagnosed, students of the group should also be trying to test an alternate assumption. Possibly the *Rattus*-like features characterizing the species in the New Guinea and Australian region are independently derived from those that define the groups of *Rattus* on the Asian mainland. It is plausible that the species now on New Guinea and Australia evolved from a *Rattus*-like ancestral stock that was characterized by a suite of derived cranial and dental features similar to those found in some of the *Rattus*-like genera on Flores. If this speculation proves to be a better interpretation, then perhaps native species of *Rattus* will not be found in the Lesser Sunda Islands. Furthermore, the native murids in the New Guinea and Australian region would then consist of a group of old endemics and a group of *Rattus*-like species, a dichotomy similar to that now characterizing the native murid fauna of Flores and the Komodo Islands.

Because so few places east of the Sunda Shelf have been sampled for fossils and because most of the fossils that are available come from young deposits, it is difficult now to discern past species-relationships and patterns of either dispersal or vicariant events that may help to explain present distributions of the Recent murids. And trying to unravel past histories of the rodents within the framework of tectonics that shaped the Indo-Australian region into its present configuration is exasperating. The area is geologically and tectonically extremely complex. It is difficult to reconstruct palaeogeography during the Tertiary and Quaternary from the data presented either in classical studies (Van Bemmelen, 1949; Umbgrove, 1949) or that derived from modern inquiries set in the context of plate tectonics (Griffiths, 1971; Ridd, 1971; Audley-Charles, Carter and Milsom, 1972; Raven and Axelrod, 1972; Audley-Charles, 1975; Norton and Molnar, 1977; Katili, 1975, 1978; Haile, 1978; Silver and Moore, 1978; Brunn and Burollet, 1979; Van Bemmelen, 1979; Hamilton, 1979; Katili and

Hartono, 1979; Weissel, Anderson and Geller, 1980). At the present time, the best approach to understanding murid zoogeography in that vast region east of Borneo and Bali is to analyze the phylogenetic relationships among living and extinct species as carefully as possible and let the patterns that emerge from those studies provide clues to the palaeogeography and past tectonic events.

My analysis of the native Floresian murids is a small part of that broader zoogeographic inquiry. Some relationships among the species on Flores seem real enough to allow the formulation of hypotheses regarding affinities of the fauna on that island to those on islands elsewhere in the Far Eastern archipelagos. The conclusions I present in this report will have to be tested against results from studies of interrelations among the endemics of Australia, New Guinea, the Philippines, Timor, and Sulawesi. Much more work also needs to be done on Flores itself. Very little is known about its Recent fauna; we need to know whether *Papagomys armandvillei* is really the only surviving native or if there are other rats living in the native habitats still left on the island, environments which have never been carefully sampled for mammals. More collecting in subfossil and Pleistocene deposits on Flores is also required to determine if the samples that were available to me represent the entire indigenous assemblage of murids or if the group was once more diverse.

Flores is not the only place where palaeontological exploration is required to discover antecedents of the endemic murids east and north of Wallace's Line. The Philippines, Sulawesi, the Moluccas, New Guinea, Australia, and the other islands in addition to Flores and Timor in the Lesser Sundas must be explored. The kind of careful excavations made by Glover on Timor, for example, revealed not only what the ancient murids of that island were like but also when that fauna died out (assuming no examples still live in forests of Timor that have yet to be sampled by mammalogists) and a new fauna appeared associated with humans and probably introduced to the island through human agency.

The threads of careful and detailed palaeontological, archaeological, and recent biological explorations; of data from study of karyotypes, biochemistry, reproductive tracts, and other non-conventional sources; and of careful re-examination of skins,

skulls, and teeth may eventually be woven together into a tapestry portraying the real pattern of evolutionary relationships and past distributions among murids native to the archipelagos and continent east of Borneo and Bali.

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