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Source: *Journal of Mammalogy*, Vol. 61, No. 3 (Aug., 1980), pp. 395–413
Published by: American Society of Mammalogists
Stable URL: http://www.jstor.org/stable/1379834
Accessed: 16/07/2014 08:44

A NEW GENUS OF MURID RODENT FROM THE KOMODO ISLANDS IN NUSATENGGARA, INDONESIA

GUY G. MUSSER AND BOEADI

ABSTRACT.—A new genus is proposed for *rintjanus*, originally described as a species of *Rattus* (Sody, 1941). The rat is endemic to Rintja and Padar, two small islands between Flores and Komodo in Nusatenggara, Indonesia. Monsoon Forest covers parts of the islands; the external and cranial characteristics of *rintjanus* point to a ground dweller and reflect adaptations to dry or seasonally dry tropical forest where the structure of tall scrub and short, partly deciduous, trees provide dense cover above and sparse undercover at ground level. The new genus is not closely related to *Rattus*, and may be part of an old murid fauna known from Flores and some other islands to the east of the Sunda Shelf.

The small Indonesian islands of Komodo, Rintja, and Padar are famous for the Komodo Dragons (*Varanus komodoensis*) residing on them. There is also an endemic species of rat which lives on Rintja and Padar, but it, unlike the dragons, is neither famous nor even known to most mammalogists or biogeographers. Named *Rattus rintjanus* and first described by Sody in 1941, the species is one of the two living endemic murids that have been recorded from Nusatenggara (the Lesser Sunda Islands), those island stepping stones from Lombok to Timor which dot the sea south of Sulawesi. A giant rat, *Papagomys armandvillei*, is the other endemic. It lives on Flores and is also known by fragments from subfossil cave deposits (Hooijer, 1957). Other native rats have been obtained on both Flores and Timor, and all are represented only by subfossil or reputed Pleistocene specimens (Hooijer, 1957, 1967; Glover, 1970). Four species of *Rattus* and two of *Mus* also live in Nusatenggara, but they are likely not native to the islands; all of them are closely tied to habitats made by humans and all may have been introduced to Nusatenggara through human agency (Musser, 1972, 1973, 1977a).

Sody's (1941:310) description of *R. rintjanus* was based on an old adult male, the only specimen available to him. The animal had been preserved in alcohol, then later prepared as a study skin. Spots of pelage had sloughed away and the color was faded in places. The teeth were so worn that Sody could not discern their occlusal patterns. His description focused on color and texture of the pelage and the coarse scalation on the tail. Aside from a few cranial measurements, Sody did not provide a description of the skull. Nor did he contrast the features of *R. rintjanus* with other species in *Rattus*, especially those kinds that were already known to occur on the Lesser Sunda Islands. With such an incomplete description and inadequate diagnosis, there was no way to tell whether Sody's taxon represented a real species of *Rattus* which was endemic to Rintja, whether it had been described before under a name that applied to a native species of *Rattus* living elsewhere in the Indonesian Archipelago, whether it represented one of the commensal forms that now live in Nusatenggara, or whether it was even a member of the genus *Rattus*. In their list of mammals from New Guinea,

Celebes, and adjacent islands, Laurie and Hill (1954) listed *R. rintjanus* as *incertae sedis*, and the nature of the species has remained enigmatic until now.

During the 1950's and 1960's, other specimens of *R. rintjanus* were obtained by collectors from Rintja and from the smaller, adjacent island of Padar (Fig. 1). As a result, we have been able to study, in addition to the holotype, 16 other specimens of different ages and both sexes (Table 1). We find that *rintjanus* is not a species of *Rattus*, but instead belongs to a group of relicts that includes *Papagomys* and the indigenous genera on Flores and elsewhere in that region east of Bali and Borneo. The specimens of *rintjanus* are distinct not only from *Rattus* but from any other species of murid, and represent a species that must be placed in its own genus, which we name, diagnose, and define in the following pages.

INSTITUTIONS AND METHODS

Our results are based on specimens in collections of the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); and the American Museum of Natural History, New York (AMNH).

All measurements are in mm. Lengths of head and body, tail, and ear were made by collectors and are from labels attached to skins. We measured length of hindfoot (including claws) of all the skins. Cranial measurements (defined by Musser, 1970, 1979) were taken with Anderson's Craniometer attached to a Wild M5 stereomicroscope, or with dial calipers graduated to 0.1 mm.

Sixteen of the 17 specimens of *rintjanus* are covered by adult pelage, the other still retains portions of the juvenile coat. Among the adults, we distinguished three broad age categories based on body size (Table 1), conformations of the crania and mandibles, and degree of wear on occlusal surfaces of the molars: old adult (Fig. 2, left; Fig. 4A), adult (Fig. 2, center; Fig. 4B), and young adult (Fig. 2, right; Fig. 4C).

RESULTS AND DISCUSSION

Our View of Rattus

Because there is no stable definition and diagnosis of *Rattus* at the present time, we prelude our description of the new genus, and our comparisons, with the scope of *Rattus* as we use it in this report. Musser (1977*b*) discussed the limits of *Rattus* as they contracted from the 1940's and 1950's when Ellerman and his colleagues included many African, Indian, and Asian species in *Rattus*, to the late 1960's when Misonne (1969) outlined his limits of *Rattus*, boundaries that excluded species native to Africa and some native Indian and Asian species as well. Ellerman (1941), for example, incorporated 22 generic names that had been applied to rats in the Asian region into *Rattus*; Misonne retained 18 of these in his definition of the genus and deleted four: *Lenothrix, Apomys, Maxomys,* and *Diplothrix*. Misonne's treatment of the other 18 genera consisted of placing *Pullomys, Mollicomys, Geromys, Cironomys, Christomys, Octomys,* and *Arcuomys* as synonyms of *Rattus*; recognizing *Stenomys* and *Leopoldamys* as valid subgenera; and keeping *Bullimus* as a subgenus that included *Limnomys, Tarsomys, Tryphomys, Bunomys, Taeromys, Berylmys, Paruromys,* and *Frateromys* as synonyms.

Our view of *Rattus* is closer to Misonne's definition of the genus than to Ellerman's, but we would contract the limits of the genus even further. *Lenothrix, Diplothrix,* and *Apomys* are, as Misonne reported, good genera and should never have been placed in *Rattus*; they are neither morphologically nor even probably phylogenetically close to the core of species in *Rattus*. *Maxomys*, too, should be taken out of *Rattus*, but the species that belong in it, members of the *rajah-surifer* group, are not those placed in the genus by Misonne (Musser et al., 1979). We would also remove three additional groups that occur on Southeast Asia and the Sunda Shelf from *Rattus*. One of these is *Rattus niviventer* and its relatives, the assemblage Misonne had placed in *Maxomys*; another is the species in *Leopoldamys, R. edwardsi* and its allies;
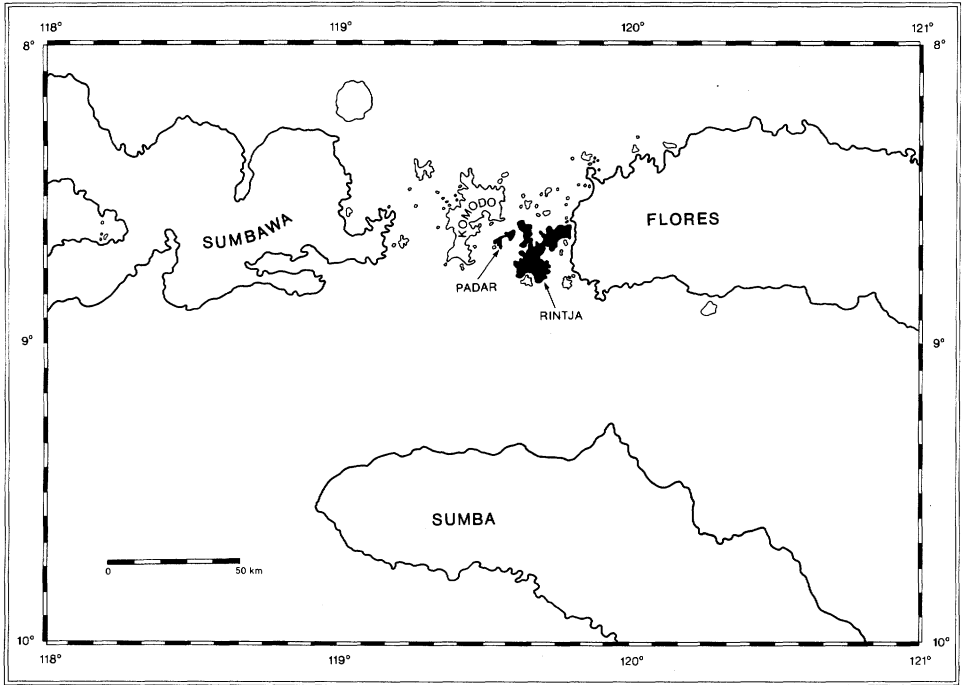
Fɪɢ. 1.   Map of the Komodo Islands in Nusatenggara, Indonesia.

and the third is the cluster of forms in *Berylmys*. Even with the removal of these groups of species, the limits of *Rattus* are fuzzy, primarily because there are particular groups on the Philippine Islands and on Sulawesi that are now included in that genus, but which do not belong there.

Features common to the species that we would include in *Rattus* are: 1) a basic configuration of the cranium and mandibles similar to those elements in *R. rattus* and *R. argentiventer* (Fig. 4); 2) long incisive foramina that end between the first molars; 3) a long palatal bridge terminating well behind the toothrows; 4) huge sphenopalatine vacuities, the anterior process of the basisphenoid and presphenoid appear suspended in air; 5) bullae that are of medium to large size relative to the cranium, rather than very small as in the *R. niviventer* or *Leopoldamys* groups; 6) orange pigment on the front of the incisors; 7) toothrows narrow relative to the palatal bridge; 8) each first upper molar with five roots; 9) occlusal patterns of the upper and lower molars as found in *R. argentiventer* and *R. rattus* (Fig. 4); 10) reduced third upper and lower molars relative to size of the other molars in each toothrow; 11) the extent to which the first upper molar overlaps the second and the second overlaps the third. This combination of features is common to typical *Rattus*, that core of species, for example, which Ellerman (1941, 1949) viewed as the subgenus *Rattus*. Although we would not restrict the limits of *Rattus* to that group, it is the assemblage we envision when we refer to *Rattus* below.

Komodomys, *new genus*

Type species.—*Rattus rintjanus* Sody (1941).
Included species.—The type species only.
Known distribution.—The islands of Rintja and Padar, which along with Komodo, are part of

TABLE 1.—Measurements (mm) of skins, skulls, and teeth of Komodomys rintjanus, Rattus argentiventer, and R. rattus. (Abbreviations: R, Rintja; P, Padar; M, male; F, female; OA, old adult; A, adult; YA, young adult; J-YA, molting from juvenile to adult pelage; LHB, length of head and body; LT, length of tail; SR/C, scale rows per cm on tail; LHF, length of hindfoot; LE, length of ear; GLS, greatest length of skull; ZB, zygomatic breadth; IB, interorbital breadth; BBR, breadth of braincase; HBR, height of braincase; LN, length of nasals; LR, length of rostrum; BR, breadth of rostrum; BZP, breadth of zygomatic plate; DZN, depth of zygomatic notch; BIT, breadth across incisor tips; LD, length of diastema; PTL, palatilar length; PL, palatal length; PPL, postpalatal length; LIF, length of incisive foramina; BIF, breadth across incisive foramina; LPB, length of palatal bridge; BPBM¹, breadth of palatal bridge at the first molar; BPBM³, breadth of palatal bridge at the third molar; BMF, breadth of mesopterygoid fossa; IFBM¹, incisive foramina beyond first molar; PBM³, palate beyond third molar; LB, length of bulla; HB, height of bulla; LM¹⁻³, alveolar length of maxillary toothrow).

	Komodomys rintjanus																	Rattus argentiventer†	Rattus rattus†
	2405*	7706	7709	7702	7710	7703	9014	9018	9017	9020	7707	9019	9015	7708	7704	9016	7711	Sumba	Sumba
Island	R	R	R	P	R	P	P	R	P	R	R	R	P	R	P	P	R		
Sex	M	M	M	F	F	F	M	M	M	M	M	M	F	M	M	M	M	M and F	M and F
Age	OA	OA	A	A	A	A	A	A	A	A	YA	YA	YA	YA	YA	YA	J-YA	Adults	Adults
LHB	200	187	187	166	167	164	180	170	175	163	159	130	145	131	135	125	106	198.3 (176–230), 15	202.6 (172–230), 9
LT	160	163	149	144		136	150	155	155	152	136	120	125	123	112	130	122	185.7 (172–201), 14	204.0 (176–237), 9
SR/C	8	8	8	8	8	8	9	8	9	9	11	10	10	9	10	10	10		
LHF	41	40	36	33	33	31	39	38	37	37	34	33	33	34	31	32	33	36.9 (35–40), 15	39.2 (35–43), 9
LE	24	22	21	21	20	19		20	20	19	20	20	20	16	15	20	17	21.8 (20–24), 14	24.1 (22–28), 9
GLS	45.9						41.5	39.2	38.7				35.3		34.2	34.0	33.9	43.4 (41.2–46.9), 14	43.4 (41.6–49.9), 8
ZB		19.5					19.9										16.4	20.8 (19.4–21.7), 10	21.1 (19.9–23.7), 7
IB	6.1	6.1	6.0	5.6	6.1	5.4	5.6	5.6	5.4	5.7		5.6	5.3	5.3	5.1	5.8	5.2	5.9 (5.5–6.3), 15	6.7 (6.3–7.1), 9
BBR	17.1	16.8					16.7	16.6					15.6		15.4	15.4	14.9	16.2 (15.9–16.8), 14	16.9 (15.9–17.6), 8
HBR	12.2	12.0					12.0	12.3							11.0	11.1	10.8	12.2 (11.4–12.7), 14	11.8 (10.5–13.3), 8
LN	18.4	15.8	15.9	15.3	14.2	15.2	15.7	14.7	14.8	14.4		13.8	13.3	12.0	12.5	11.8	12.3	15.5 (14.5–16.9), 15	16.7 (14.5–19.4), 9
LR	16.8	14.4	14.9	13.9	15.8	14.3	14.3	14.1	13.5	13.6		12.7	12.1	11.1	11.5	11.3	11.1	12.8 (11.6–14.2), 15	14.5 (12.8–16.9), 9
BR		7.7	8.1				6.9	6.8	6.7	6.8		6.1	6.0	5.5	6.0	5.6		8.0 (7.4–8.5), 14	8.1 (7.3–9.1), 7
BZP	6.0	4.2	5.0	4.4	4.7		4.8	4.6	4.4	4.5		4.5	3.8	3.1	3.4	3.8	3.6	5.2 (4.5–6.0), 15	5.3 (4.4–6.1), 9
DZN		2.6		3.6	3.0	2.9	3.1	3.7	2.9	3.4		3.9	2.7		2.9	2.5	2.4	3.0 (2.4–3.5), 15	
BIT	2.8	2.7			2.5	2.6	2.5	2.4	2.2	2.4		2.2	2.0	1.9		1.8	2.0	2.8 (2.5–3.1), 15	2.7 (2.1–3.3), 9
LD	12.0	11.1	11.2	10.4	10.8	9.9	10.3	9.8	9.5	10.1		9.0	8.7	8.3	8.4	7.8	8.2	11.6 (10.9–12.5), 15	11.9 (10.0–13.3), 9
PTL	20.8	19.8		18.6	18.8	18.1	18.8	17.9	17.6	17.7		16.6	16.4		15.7	15.2	15.4	20.8 (20.0–22.9), 14	21.9 (19.8–23.9), 9
PL	23.7	22.5		21.0	21.2	20.7	21.3	20.3	20.1	20.3		19.1	18.5		18.5	17.4	17.9	23.6 (22.7–25.8), 14	24.8 (22.1–27.0), 9
PPL		14.6					13.8	13.3	13.5						11.2	11.1	11.2	15.3 (14.2–17.4), 13	15.3 (13.0–17.5), 7
LIF	7.4	9.1		8.5	8.2	8.1	8.0	8.0	7.5	7.6		6.7	7.0	7.2	7.3	6.7	6.8	8.6 (7.4–9.3), 15	8.7 (7.3–9.7), 9
BIF	3.3	2.4		2.3	2.3	2.4	2.2	2.3	1.9	2.3		2.0	1.9	2.1	1.8	1.8	1.9	2.8 (2.4–3.0), 15	3.2 (2.5–4.0), 9
LPB	4.1	7.1		7.2	7.0	7.3	7.9	7.0	7.3	6.9		7.4	6.8		6.1	6.1	6.7	8.3 (7.9–9.4), 14	9.5 (8.6–10.6), 9
BPBM¹	2.8	3.1		2.8	3.4	3.0	2.8	2.5	2.6	2.8		2.4	2.3		2.3	2.2	2.4	3.5 (3.1–4.0), 15	4.0 (3.5–4.6), 9
BPBM³	4.1	4.0		4.1	3.7	4.0	3.5	3.2	3.4	3.3		3.2	2.9		3.3	3.1	3.1	4.6 (4.0–5.0), 15	4.9 (4.5–5.6), 9
BMF	2.8	2.1		2.5			2.1	2.3	2.0	2.3		2.0	2.1		2.2	2.0	2.2	2.6 (2.3–2.8), 13	2.9 (2.7–3.2), 7
IFBM¹	1.1	1.7	.8	1.2	1.1	1.1	.9	1.3	1.0	1.1		.9	1.2	1.5	1.2	1.5	1.2		
PBM³		.4		.4	.5	.4	.5	even	.2	.2		even	.1		.2	.2	even	even	
LB		7.8	8.4		7.6	7.9	7.7	7.3	7.1	7.6		6.7	7.1		5.5	6.9	6.7	8.4 (8.0–8.8), 14	7.7 (6.8–8.6), 9
HB		6.5			6.4	6.1	6.4	6.0	6.3	6.1		5.8			5.9	5.9	6.1		
LM¹⁻³	9.0	8.2	8.2	8.0	7.8	8.1	8.1	8.2	8.1	7.7	8.3	7.8	7.8	7.5	7.4	7.6	7.5	8.0 (7.6–8.5), 15	8.3 (8.0–8.5), 9

* Catalogue numbers for specimens of K. rintjanus; all in MZB.
† The mean, observed range (in parentheses), and size of the sample, respectively, are listed for each measurement.

the Komodo Islands clustered between the two large islands of Sumbawa on the west, and Flores on the east, in Nusatenggara (Fig. 1).

Etymology.—Komodo in this instance refers to the Komodo Islands; the Greek *mys* to mouse (or rat).

Diagnosis.—A genus of terrestrial murid that differs from all other murid genera in general and from *Rattus* in particular by the following combination of features: medium body size, tail much shorter than combined lengths of head and body; semi-spinous, sandy-colored fur on upperparts; gray underparts; hairy white feet; six plantar tubercles on hindfoot; 10 mammae, no pectoral pair; dorsal profile of cranium strongly arched from tip of nasals to occiput; long, narrow nasals and rostrum; top of skull nearly flat and wide between dorsal roots of zygoma, flat and wide at and behind interorbital area; weak ridges along dorsolateral margins of interorbital region and braincase; lacrimal bones large, angular, squarish; zygomatic plates wide, their anterior spines extending up to 4 mm forward of anterior dorsal zygomatic roots; leading edges of zygomatic spines usually slanting forward, rarely straight down; large, deep braincase; small interparietal; very long and narrow incisive foramina—from a narrow beginning they widen slightly about a third of the way back, then constrict into long slits, which terminate nearly 2 mm beyond the anterior margins of the first molars; short, very narrow palatal bridge, either extending past the posterior margins of the third molars by only 0.5 mm or terminating at the back edges of those teeth; narrow mesopterygoid fossa and deep ectopterygoid fossae; expansive sphenopalatine vacuities; large, deep bullae; high-coned, large (especially relative to palatal area), heavy teeth; cusps on M^1 slanting posteriorly so M^1 greatly overlaps M^2, which overlaps M^3; five roots on each M^1; laminae on M^1 and M^2 formed of high, separate cone-like cylindrical cusps, as in *Papagomys,* which remain discrete until young adulthood; labial cusp in second row on M^1 set apart and nearly isolated from adjacent medial cusp, both cusps connected by enamel and dentine ridge instead of appressed against each other as in *Rattus*; posterior lingual cusp (t7) and posterior cingulum not present on upper molars; M_2 much wider than M_1 or M_3; laminae on M_1 and M_2 formed by high narrow cusps meeting at sharp angle along their anteriomedial edges and forming scalloped patterns with wear, similar to the patterns of *Spelaeomys* and related genera; front row of cusps on M_1 forms lamina directed posteriolabially, joined to second row by thin enamel bridge; mandibles long, low, with weak coronoid processes.

Description and comparisons.—The specimens of *Komodomys rintjanus* represent medium-sized, short-tailed rats (Table 1). The dorsal pelage is thick, coarse and spinous. The fur is up to 12 mm long between the ears, up to 15 mm on the middle of the back, and 18 to 20 mm on the rump. Many guard hairs emerge from the coat and are most conspicuous, and longest, near the rump where they reach 40 to 50 mm. The guard hairs, along with fine underfur, coarse overhairs, and flexible flattened spines, form the dorsal coat. The underhairs and overhairs are gray for most of their lengths, then banded with pale brown and tipped with buff or straw-yellow, a pattern also found on the guard hairs. The spines are translucent and tipped with pale buff or straw-yellow. They are abundant throughout the dorsal pelage (usually spaced 0.5 to 1 mm apart where they emerge from the skin) and give the coat its coarse texture. The banding on the hairs and spines provide the basic color of the upperparts—straw-yellow or buff flecked with brown. The middle of the head and body, from nose to rump, is darker, suffused with more brown. The cheeks and sides of the head and body are paler, suffused with gray. The dark vibrissae emerging from the sides of the face extend up to 55 mm long. The eyelids are dark brown. There is a conspicuous triangle of bright buffy hairs behind each eye on those specimens which are intact and clean. The ears are tan and covered with fine, short hairs.

Composed of fine underhairs, short overhairs, and scattered soft spines, the ventral pelage is shorter (up to 8 mm long) and much softer than the dorsal coat. The hairs have pale gray or dark gray bases and white tips, the thin soft spines are white. The overall color of the ventral coat is white, moderately or densely suffused with pale or dark gray. The whitish-gray underparts of a few specimens are tinged with buff.

The hindfeet are long and narrow. The digits are long, as are the nails, which on the hindfeet are nearly straight. The dorsal surfaces of all four feet are densely covered by white hairs. The claws are cream in color and overladen with long white hairs. The palmar and plantar surfaces are naked, tan, and adorned with small oblong pads. There are five pads on each palmar surface (three interdigital and two palmar) and six pads on each of the plantar surfaces (four interdigital and two plantar).
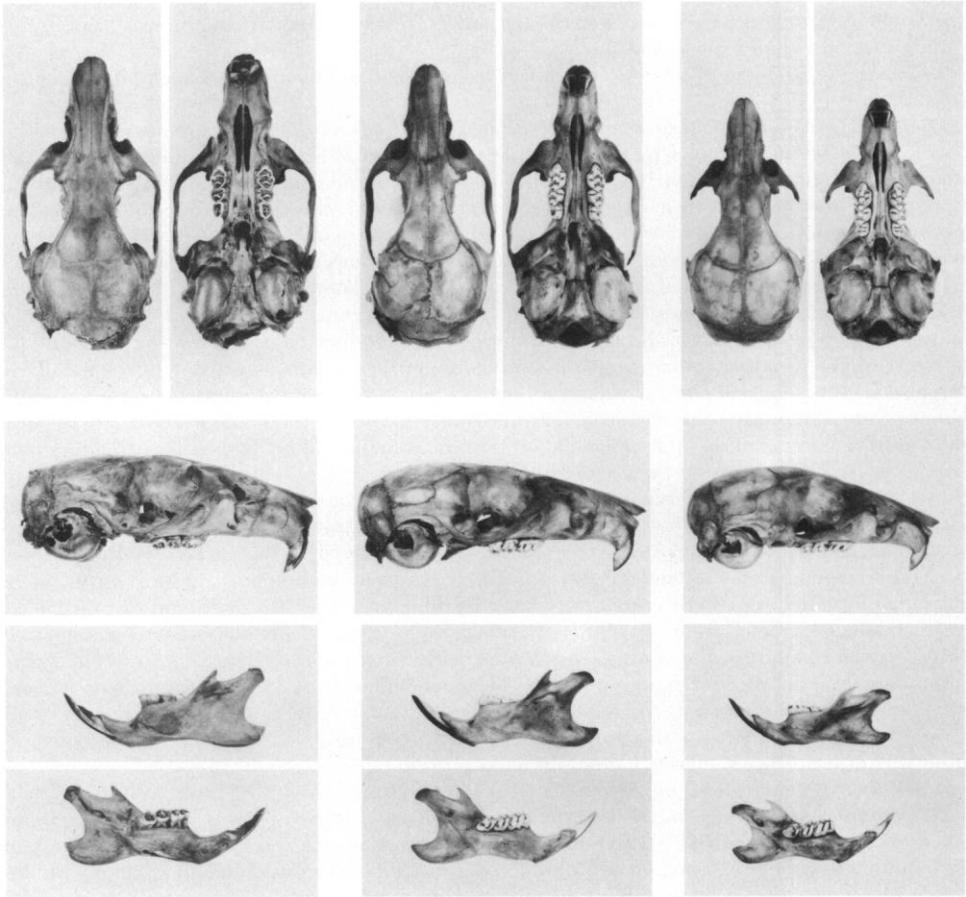
FIG. 2. Views of crania and mandibles of *Komodomys rintjanus*. Left, old adult (MZB 7706); center, adult (MZB 9015); and right, young adult (MZB 9016). All views are about natural size. These, and the views in Figs. 3 and 4 were taken by Robert E. Logan.

The tail is conspicuously shorter than the combined lengths of head and body, coarsely scaled, and covered with long silver hairs, giving it a hairier appearance than is usual on the tails of most species in *Rattus*. The dorsal surface and sides of the tails are dark brown, the ventral surface is paler, ranging from whitish-brown to tan; the proximal third is nearly unpigmented in some specimens.

The pelage of juveniles is colored much like the fur of adults described above, but is shorter and softer, with a finer, silky texture to the touch.

Females apparently have ten mammae—and no pectoral pair—but that count should be checked on freshly-caught rats. The few females we examined are poorly prepared; possibly some of the teats were removed or obscured when the specimens were prepared. We did locate two postaxillary pairs (one separated from the other by 13–15 mm), one abdominal pair, and two inguinal pairs. The pectoral areas of our specimens were intact so we feel confident we would have seen teats there had they been present.

Specimens of *K. rintjanus* can be distinguished from those of *R. argentiventer* and *R. rattus*— two kinds of rats that average larger than *K. rintjanus* in body size, that also occur on the island of Rintja, and that exemplify the characteristics of species in the core of *Rattus*—by features of the pelage and appendages. *R. argentiventer* has 12 mammae, including a pectoral pair; *R.*
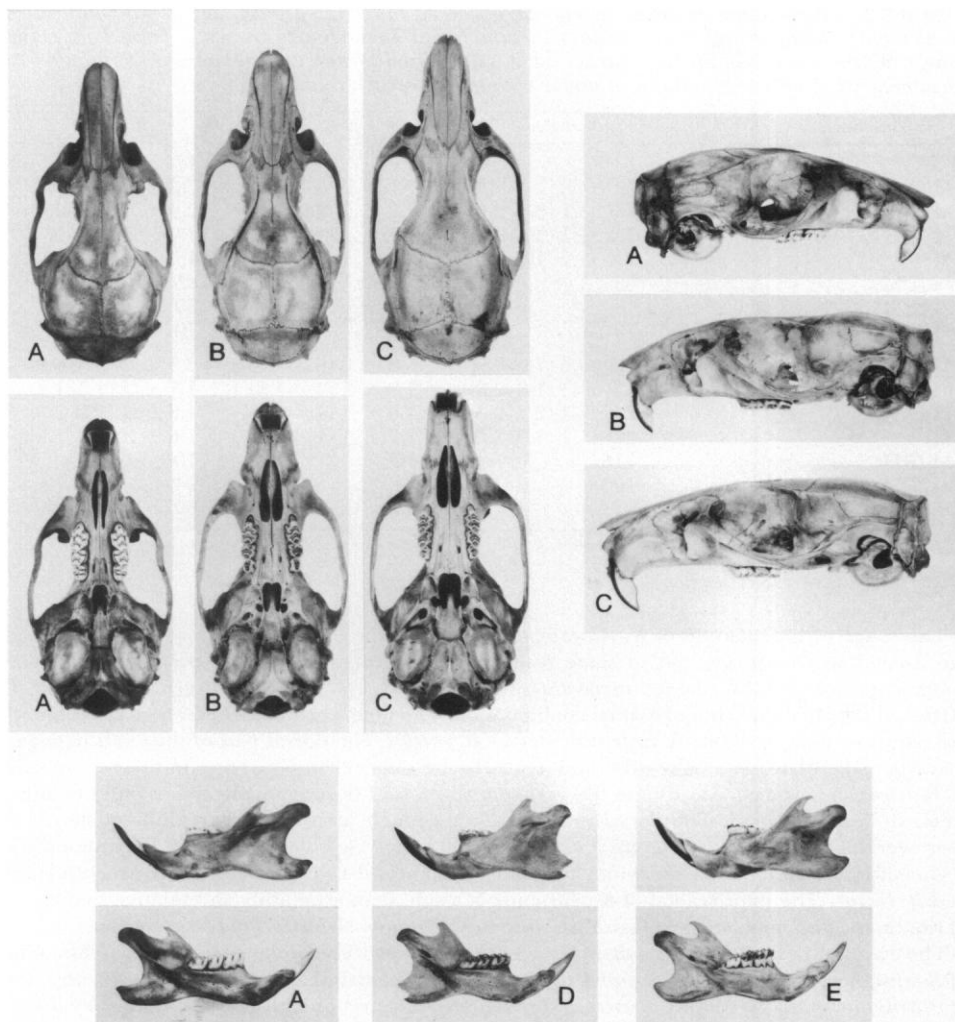
FIG. 3. Views of crania and mandibles. A, *Komodomys rintjanus* (MZB 9014); B, *Rattus argentiventer* from Bali (AMNH 107543); C, *R. rattus* from Sulawesi (AMNH 154004); D, *R. argentiventer* from Sulawesi (MZB 4879); and E, *R. rattus* from Sulawesi (AMNH 153000). All views are about natural size.

rattus has ten mammae, also with a distinct pectoral pair. The upperparts of *R. argentiventer* are darker and flecked with more black than in upperparts of *K. rintjanus*, the pelage is softer, the tail is dark brown all over and not as well haired, and the feet are whitish brown to brown and not hairy. Specimens of *R. rattus* have much softer pelage, dark brown upperparts, and underparts that range from cream to buffy grayish brown; its feet are colored like those of *R. argentiventer*. In all examples of *R. rattus*, the tail is dark brown everywhere, not hairy, and conspicuously much longer than the combined lengths of head and body.

Cranial measurements of *K. rintjanus* are listed in Table 1 and compared to values of adult *R. argentiventer* and *R. rattus*. The crania and mandibles of an old adult, an adult, and a very young adult *K. rintjanus* are contrasted in Fig. 2. In Fig. 3 we compare the cranium and mandibles of an adult *K. rintjanus* with the same elements from specimens of *R. argentiventer* and *R. rattus* that are slightly older.

TABLE 2.—*Measurements (mean ± one SD, observed range in parentheses; in mm) and ratios (in percent) of upper and lower molars in samples of* Komodomys rintjanus *from Padar and Rintja,* Rattus argentiventer *from Java, and* R. rattus *from Flores. (Abbreviations: N, number of specimens in sample; LM, length of molar row; BM, breadth of molar).*

Dimension	K. rintjanus	R. argentiventer	R. rattus
N	13	13	17
LM^{1-3} (alveolar)	7.9 ± .3 (7.4–8.2)	7.1 ± .2 (6.7–7.4)	7.2 ± .3 (6.7–7.8)
BM^1	2.5 ± .1 (2.3–2.6)	2.1 ± .1 (2.0–2.2)	2.0 ± .1 (1.8–2.1)
BM^2	2.4 ± .1 (2.2–2.5)	2.1 ± .1 (1.9–2.2)	1.9 ± .1 (1.7–2.0)
BM^3	1.9 ± .2 (1.8–2.0)	1.6 ± .1 (1.3–1.8)	1.5 ± .1 (1.3–1.6)
BM^2/BM^1	96	100	95
BM^3/BM^1	76	76	75
BM^3/BM^2	79	76	79
LM_{1-3} (edges of teeth)*	7.3 ± .2 (7.0–7.6)	6.5 ± .3 (6.2–7.0)	6.5 ± .2 (6.3–6.9)
BM_1	1.9 ± .1 (1.8–2.0)	1.8 ± .1 (1.7–1.9)	1.7 ± .1 (1.5–1.8)
BM_2	2.2 ± .1 (2.1–2.3)	1.9 ± .1 (1.8–2.1)	1.8 ± .1 (1.7–2.0)
BM_3	2.0 ± .1 (1.9–2.0)	1.7 ± .1 (1.3–1.9)	1.6 ± .1 (1.5–1.8)
BM_2/BM_1	116	106	106
BM_3/BM_1	105	94	94
BM_3/BM_2	91	90	89

* Limits of this measurement are from the anterior face of M_1 to the posterior margin of M_3.

The shape of the cranium of *K. rintjanus* recalls to us the cranial configuration of murids in the Australian *Conilurus*, and in some respects, the gerbils in *Tatera*; both of these genera contain species that are adapted to savanna woodlands. Specimens of *R. argentiventer* and *R. rattus* do not have this kind of cranial configuration. The long rostrum and nasals of *K. rintjanus* are narrower than in either *R. argentiventer* or *R. rattus*. The dorsal part of the skull between the zygomatic plates is much wider and is nearly flat rather than convex as in the two species of *Rattus*. The expansion is due to the wide dorsal roots of the zygomatic arches and the large, squarish lacrimal bones. The dorsal root of each zygomatic arch in the two kinds of *Rattus* is narrower than those of *K. rintjanus*, and the lacrimal bones are oblong and tiny. The interorbital region of *K. rintjanus* is flat and wide on top and not pinched as it is in skulls of *R. argentiventer* and *R. rattus*. The interparietal of *K. rintjanus* is small, both absolutely and relative to the size of the braincase, much smaller than that bone in specimens of *Rattus*.

The cranium of *K. rintjanus* is distinctive in ventral view. The long, narrow incisive foramina of *K. rintjanus* contrast strikingly with the broad incisive foramina of both *R. argentiventer* and *R. rattus*, foramina which are narrow at their front ends and quickly expand until they are as wide as the palatal bridge. The palatal bridges in both *R. argentiventer* and *R. rattus* are much wider than those of *K. rintjanus* and they extend well beyond the posterior margins of the third molars, a characteristic of most species of *Rattus*. The narrower mesopterygoid fossa in *K. rintjanus* as contrasted with the other two species also reflects its narrower palatal region. The ectopterygoid fossae are deep in specimens of *K. rintjanus*; much shallower in the examples of *Rattus*. A most prominent feature are the large auditory bullae of *K. rintjanus*, not only absolutely large, but also large relative to size of the braincase. *R. argentiventer* has moderately large bullae, but not like *K. rintjanus*; *R. rattus* has much smaller bullae. The molars of *K. rintjanus* have higher cusps, are absolutely longer and wider (Table 2), and are much larger relative to the palatal area than are the molars in the two species of *Rattus*.

In side view, the cranium of *K. rintjanus* is strongly convex along its dorsal profile, curving up from the occiput to a high point at the interorbital region, then descending in a long, flat and smooth curve to the tips of the nasals. The dorsal profiles of crania in both *R. argentiventer* and *R. rattus* are not so arched; instead, each is nearly flat from occiput to the back of the rostrum (between the dorsal roots of the zygomatic arches), which is well forward of the interorbital area, and only then descends to the nasal tips. The wide zygomatic plate with its jutting anterior spine is especially evident in the side view of *K. rintjanus*, as is the high braincase of that species. The height of the braincase above the squamosal root of each zygomatic arch is greater in *K. rintjanus* than in crania of either *R. argentiventer* or *R. rattus*.

FIG. 4.   Occlusal views of left toothrows. Upper row consists of upper and lower molars of *Komodomys rintjanus* shown in Fig. 2: A, old adult; B, adult; and C, young adult. Lower row is upper and lower molars of *K. rintjanus* (D, MZB 9014) contrasted with those of *Rattus argentiventer* (E, MZB 4879) and *R. rattus* (F, AMNH 153000). All views are approximately ×6.

The mandibles of *K. rintjanus* are similar in shape to those of the two kinds of *Rattus*, but there are small differences between them: in *K. rintjanus*, the coronoid processes are smaller and appear weaker; the angular processes are longer and more slender (narrower from dorsal to ventral surfaces), and each lower toothrow is longer and wider, both absolutely (Table 2) and relative to the length of the mandible.

The incisors of *K. rintjanus* are narrower than those in either *R. argentiventer* or *R. rattus*, but similar in shape. In each kind of rat the incisors curve back after they emerge from the rostrum. The enamel layers of both uppers and lowers are orange.

The shapes of the molars and the occlusal configurations formed by the cusps and cusplets in *K. rintjanus* are superficially similar to those configurations found in species of *Rattus*. Occlusal views of the upper and lower molars from an old adult, an adult, and a very young adult *K. rintjanus* are illustrated in Fig. 4, and compared there with molars from adults of *R. rattus* and *R. argentiventer*. The M^1 of *K. rintjanus* is the widest tooth, M^2 is as wide or only slightly narrower, and M^3 is narrower than either M^1 or M^2 (Table 2). The high cusps of M^1 and M^2 slant backwards so that M^1 overlaps part of M^2, and M^2 overlaps a bit of M^3. This interlocking among the teeth provides strength and is characteristic of species which do not have a posterior lingual cusp (t7) or a posterior cingulum on the molars, and is typical of species within *Rattus*, but is also found in some genera outside of *Rattus* (Misonne, 1969).

TABLE 3.—*Number of roots on* M^1; *and the presence* (+) *or absence* (−) *of cusp t3 on* M^{2-3}, *the anterior and posterior cusplets on* M_{1-3}, *the hypoconid on* M_3, *and the posterior cingulum on* M_3 *in samples of* Komodomys rintjanus *from Padar and Rintja,* Rattus argentiventer *from Java, and* R. rattus *from Flores. (Numbers of cusps or cusplets are expressed as percentages; N is in parentheses.)*

Character	K. rintjanus	R. argentiventer	R. rattus
Number of roots on M^1	5 (17)	5 (13)	5 (17)
Cusp t3 on M^2			
+	100 (13)	92 (12)	53 (9)
−		8 (1)	47 (8)
Cusp t3 on M^3			
+	90 (9)	39 (5)	6 (1)
−	10 (1)	61 (8)	94 (16)
Anterior cusplet on M_1			
+	10 (1)	23 (3)	23 (4)
−	90 (9)	77 (10)	77 (13)
Posterior cusplet on M_1			
+	100 (10)	100 (13)	100 (17)
−			
Anterior cusplet on M_2			
+	100 (10)	100 (13)	100 (17)
−			
Posterior cusplet on M_2			
+	100 (10)	100 (13)	100 (17)
−			
Anterior cusplet on M_3			
+	80 (8)	100 (13)	100 (17)
−	20 (2)		
Hypoconid on M_3			
+	80 (8)	100 (13)	100 (17)
−	20 (2)		
Posterior Cingulum on M_3			
+	69 (9)		
−	31 (4)	100 (13)	100 (17)

In specimens of *K. rintjanus*, there are three rows of cusps on each M^1. In slightly worn teeth (Fig. 4C) the labial and lingual cusps are high, narrow discrete cones flanking the sides of the larger middle cusps. With increase in wear, the dentine centers of the cusps merge and are outlined by the enamel in chevron-like shapes (Fig. 4B). Several features of M^1 are distinctive and unlike the occlusal patterns found in *R. rattus* and *R. argentiventer*. First, there is a small ridge-like cusplet (termed t1*bis* by Misonne, 1969) nestled between the lingual and medial cusps of the anterior row; such a cusplet is usually absent from the species of *Rattus*. Second, the labial cusp of the second row is separated from the medial cusp, and the two are connected only by a thin bridge of enamel and dentine (Fig. 4B); thus the labial cusp is nearly isolated from the central cone, and the configuration is retained even in very worn teeth (Fig. 4A). In species of *Rattus*, the labial cusp of the second row abuts tightly against the medial cusp (Fig. 4: E and F) and the two merge after only a little wear. Finally, the labial cusp of the third row is thin (compressed from side to side), small, and only its thin posterior edge meets the medial cusp so the two cusps seem to be barely attached; the medial cusp is smooth on its dorsal, lingual, and posterior faces. In *Rattus*, the labial cusp is larger, broader, and its lingual side joins more extensively with the central cusp; that cusp has a prominent enamel ridge defining its lingual edge.

Each M^2 of *K. rintjanus* has an occlusal surface formed by two anterior cusps, a large cylindrical lingual one, and a labial cusp (t3) that ranges from small to tiny but is present in all the specimens

FIG. 5.   Views of the habitats on the island of Rintja. These photographs and the one in Fig. 6 are from Hoogerwerf (1953–54).

we looked at (Table 3); a middle row of three cusps similar in configuration to the second row of M^1; and a back row of cusps which consists of a large central cone and a very small and slender labial one. A very low ridge defines the lingual edge of the central cusp. Cusp t3 is absent in a few specimens of *R. argentiventer* and from nearly half of the sample of *R. rattus* (Table 3); the labial cusp of the back row is always much larger, and the central cusp has a better developed ridge along its lingual edge, its prominence more like the ridge on the third medial cusp of the first molar.

Each M^3 in specimens of *K. rintjanus* is larger relative to the other upper molars than are the third molars of either *R. argentiventer* or *R. rattus*, and each has a simple occlusal topography which differs in details from those in *Rattus*. There is a large lingual cusp at the front of M^3 that does not impinge against the back part of the middle cusp on M^2; in the specimens of *Rattus*, the anterior lingual cusp abuts directly against the medial cusp of M^2, and the two cusps form part of the interlocking between the second and third molars. Opposite to the large lingual cusp is a small anterior labial cusp (t3), which occurs in 90% of our sample of *K. rintjanus*, in 39% of the sample of *R. argentiventer*, and in only 6% of the specimens of *R. rattus* (Table 3). The remaining occlusal surface on each M^3 of *K. rintjanus* consists of a nearly transverse comma-shaped lamina, and a cresent-like posterior lamina made up of a large central cusp and a sliver-like labial cusp which quickly becomes incorporated into the central cusp after only a little wear. The front lamina on M^3 of both kinds of *Rattus* is either strongly arcuate or nearly chevron-

FIG. 6.   View of the countryside on the island of Padar.

shaped, and the posterior lamina is elliptical and much narrower than its counterpart in *K. rintjanus.*

A small detail adds to the complexity of the upper molars in examples of *K. rintjanus.* There is a low, thin ridge flanking the backside of some of the labial and lingual cusps of M^1 and M^2. This sliver-like ridge is often most conspicuous on the labial cusp in the front row on M^1 but can also be seen on the anterior lingual cusp of M^2, and the lingual and labial cusps of the first lamina on that tooth.

The lower molars of *K. rintjanus* are distinctive in important ways. All the teeth are wide, compared with those of *R. argentiventer* and *R. rattus,* but M_2 is wider relative to M_1 than in the species of *Rattus,* and M_3 is wider than M_1, instead of narrower as it is in the two kinds of *Rattus* (Table 2). The occlusal surfaces on lower molars of *K. rintjanus* consist of three rows of cusps and a posterior single cusp (posterior cingulum) on M_1, two rows and a posterior cusp on M_2, and two rows of cusps on M_3. A posterior cingulum is absent from M_3 in *R. argentiventer,* *R. rattus,* and most other species of *Rattus,* but a cusp that we interpret to be the posterior cingulum (clearly seen in Fig. 4: B and C) is, although much smaller than its counterparts on M_1 and M_2, present on M_3 in most examples of *K. rintjanus* (Table 3). The second row of cusps on M_3 of *K. rintjanus* consists of a large cusp and in eight out of ten specimens a second, much smaller cusp (hypoconid); the hypoconid is present in all examples of the two kinds of *Rattus* (Table 3). There are also cusplets along the labial margins of each tooth: two on M_1, one (the anterior cusplet) at the anteriolabial margin of the second row of cusps, the other (the posterior cusplet) next to the third row of cusps; two on M_2; and an anterior cusplet at the anteriolabial margin of the first row of cusps on M_3. The occurrences of these cusplets in samples of *Komodomys* and *Rattus* are listed in Table 3. Finally, there is a small cusplet which occurs infrequently on the labial face of the front lamina of M_1. Out of 11 specimens of *K. rintjanus,* a cusplet was present on the right teeth of two individuals, and on both teeth of one other.

The shapes and relative positions of the cusps on slightly worn lower molars in *K. rintjanus* (Fig. 4C) are distinctive and reflect structural affinities with such genera as *Papagomys* and related forms rather than with species in *Rattus.* The cusps on M_1 and M_2 of *K. rintjanus* are high, cone-like cylinders, each compressed so that in cross-section they are nearly tear-drop in shape. In each row, the cones slant towards 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 M_1 and the two rows on M_2 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.

TABLE 4.—*Measurements (in mm) of the mean monthly and annual rainfall gathered from 1911 to 1940 near the Komodo Islands (Komodo, Padar, and Rintja) and in the wettest part of Central Sulawesi.**

Month	Komodo Islands	Central Sulawesi
Mean monthly rate		
January	no data	400–500
February	300–400	300–400
March	200–300	400–500
April	50–100	500–600
May	50–100	400–500
June	25–50	300–400
July	25–50	300–400
August	0–25	200–300
September	0–25	150–200
October	50–100	150–200
November	100–150	200–300
December	no data	300–400
Mean total	800–1,300 (10 months)	3,600–4,700 (12 months)

* Data were compiled from: Meteorological Note No. 9: Peta Hujan Indonesia; Vol. II: Sumatra, Kalimantan, Sulawesi, Nusatenggara, Maluku, Irian Jaya (1911–140); Departemen Perhubungan Lembaga Meteorologi dan Geofisika Republik Indonesia-Jakarta, 1973. During the period 1911–1940, apparently no meteorological stations were operated on the Komodo Islands and the rainfall measurements for those places are probably extensions of the information collected at stations on eastern Sumbawa, western Flores, and northern Sumba.

This scalloped configuration is similar to that in lower molars of *Spelaeomys florensis* (see Hooijer, 1957: pl. 14) and other genera that have similar cuspidation; it is not a pattern characteristic of *Rattus*—there the slightly worn cusps are shorter and meet at a broader angle to merge abruptly into laminae shaped like broad chevrons.

There are other significant differences between the lower molars of *K. rintjanus* and *Rattus*. One striking difference is the shape of the front row of cusps on M_1. In the teeth of *K. rintjanus*, the front row is formed by a large lingual cusp and a smaller labial one. As they become worn, 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. 4D). The two front cusps form part of a cloverleaf configuration in samples of the two kinds of *Rattus* and are not attached to the second lamina by an enamel ridge; the large lingual cusp is directed towards the front and the smaller labial cusp is situated at nearly a right angle to the lingual one (Fig. 4: E and F). The occlusal surface of each M_3 also differs among the species. The anterior lamina is thick and transverse on teeth of *K. rintjanus*, but shaped more like an hourglass in samples of the *Rattus*. The two lamina are also much wider than those on the teeth of the *Rattus*, a reflection of the wider third molars of *K. rintjanus*.

Habitat and Morphology

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 *Livistona* palms, 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. 5 and 6). Our information about the places where specimens of *K. rintjanus* were caught comes from Boeadi's recollections. He 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. He did not trap in the grass so we do not know if the rats occur there as well. We have no other information about the habitat, or even the habits, of *K. rintjanus*.

We do not know much about the grasslands and forests on either Padar or Rintja, except what we can glean from the photographs in Figs. 5 and 6, and the scanty

references in the literature of climates and forest formations. We do know that the Lesser Sunda Islands are included within the broad area over which tropical rain forests occur (Whitmore, 1975; Richards, 1976). The islands are seasonally very dry, an effect produced by the dry southern monsoon which blows off Australia during the middle months of the year. This seasonality is obvious in the mean monthly rainfall values listed in Table 4. The greatest rainfall near the Komodo Islands occurs from November through March, the lowest in August and September. In contrast, one of the wettest places in Central Sulawesi has a mean annual rainfall three to four times greater than that in the Komodo Islands, and rain falls regularly throughout the year with a slight decrease during September and October (Table 4). The area in Sulawesi is covered by tropical rain forests; that on most of the drier Lesser Sunda Islands by monsoon forest. According to Richards (1976:12), "In the eastern Sunda Islands from western Java to New Guinea the seasonal drought (due to the dry 'East Monsoon' from Australia) is too severe for the development of Rain forest, except as a post-climax in locally favourable situations." Whitmore (1975:160) stated that "In east Java and the Lesser Sunda Islands ever-wet climate and rain forest are in fact restricted to isolated patches on the south-facing sides of the mountains which receive rain from the on-shore winds."

Regretfully, "The seasonal (or Monsoon) forests of the eastern Sunda Islands are inadequately known and have for the most part been so much modified by fire and other biotic influences that their natural structure is hard to reconstruct" (Richards, 1976:328). The nature of the original forests on Padar and Rintja are just as inade-quately known, except that they apparently are monsoon forest. Whitmore (1975:159) uses that designation ". . . as a convenient general term for those forests of the tropical Far East where water is periodically seriously limiting to plants . . . . In general, monsoon forests are of lesser stature than rain forests, with a lower biomass, and are deciduous to a considerable degree. The boundary against rain forest is often sharp owing to the action of fire, rain forests often penetrating the monsoon Formations as narrow strips of 'gallery forest' along water courses." Botanists recognize several dis-tinct Formations within the category of monsoon forest, and the different Formations occur in habitats of increasing aridity. Monsoon forests, however are not necessarily a direct reflection of climatic influence, as Whitmore (1975:158) explains: ". . . there is a complex interaction between local variations in rainfall, water held available in the soil (which is dependent on the depth, structure, and texture of the soil), and nutrient status of the soil. The same Formation may occur over different rocks in places with different degrees of drought. It follows that in seasonally dry climates there is an intricate mosaic of forest Formations . . . which is made more complex by the great and greatly varying extent of alteration by man, resulting from the ready inflammability of these Formations in the dry season . . . . It is most probable that all tropical grasslands, with the obvious exception of those found on some more-or-less permanently swampy sites . . . are entirely derived from woodlands or forests as a result of long-continued burning by fires started by man or lightning and that there is no such thing as a tropical grassland climate . . . ." This view is shared by Richards (1976:316), who wrote that ". . . there is no such thing as a 'tropical grassland climate.' Evidence is accumulating in favour of the view that all lowland tropical grasslands and 'open' savannas are biotic climaxes usually due to fire, or edaphic climaxes due to soil conditions unfavourable to trees, or stages in a hydrosere. It is extremely doubt-ful whether any tropical grassland is in fact a true climatic climax."

If the grasslands on the islands of Padar and Rintja resulted from the conditions discussed above, then extensive grassland may not have been a part of the original vegetative cover on those islands and may not have been associated with the evolution of *K. rintjanus*. Instead, 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—those primary features that distinguish *K. rintjanus* from *R. argentiventer* and *R. rattus,* for example, 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.

Occurrence with Rattus *on Rintja and Padar*

Of the 17 specimens of *Komodomys rintjanus* available to us for study, seven were obtained on Padar and ten on Rintja (Table 1). We know of no other murids that have been taken on Padar, but specimens of both *R. argentiventer* and *R. rattus* are known from Rintja. During August of 1962, collectors (Boeadi among them) obtained small samples of those two kinds of *Rattus* and *K. rintjanus* from Loho Ginggo, a broad flat near the coast of Rintja: three *K. rintjanus* (MZB 9018–9020), one *R. argentiventer* (MZB 9003), and five *R. rattus* (MZB 9018–9020). If our examples of *K. rintjanus* reflect the real insular distribution of that species, then it is endemic to only Padar and Rintja. The ricefield rat, *R. argentiventer,* and the houserat, *R. rattus,* however, also occur elsewhere. Neither one is probably native to Rintja. They are two of the five species that, throughout the region bounded by the Philippines and Sulawesi on the west and New Guinea and Australia on the east, usually live only in habitats made and maintained by humans. They are absent from primary forests, and they also occur west of the Philippines and Sulawesi on the Sunda Shelf and mainland of Southeast Asia.

In the Lesser Sunda Islands, *R. argentiventer* occurs to the east of Rintja, where it has been found on Flores and Timor, to the south on Sumba, and to the west on Komodo, Sumbawa, and Lombok. The species has been recorded once from New Guinea, the only place east of Nusatenggara from which it has been collected. The ricefield rat has been taken north of Nusatenggara on Sulawesi and some of the Philippine islands, and to the west of those places it is known to occur on the Sunda Shelf (Bali, Java, Borneo, and Sumatra), and also on the Malay Peninsula north to Thailand and South Vietnam (Musser, 1973).

Rattus rattus lives on Rintja, and closely related populations also occur on the islands of Sumba, Flores, Lomblen, Alor, and Timor (Musser, 1972). Animals from these islands are related to Asian houserats that live on large and small islands throughout that broad area east of the Sunda Shelf, from the Philippines and Sulawesi in the west to parts of western New Guinea in the east.

Comparisons with Other Murids from Nusatenggara

As with *Komodomys rintjanus* and the two kinds of *Rattus* from Rintja, the rest of the murid fauna from the Lesser Sunda Islands consists of species that can be separated into those that were native elsewhere and brought to the Lesser Sunda Islands through human agency, and those indigenous to the islands. In addition to *R. argentiventer* and *R. rattus,* two other species of *Rattus,* both probably introduced, have been recorded from Nusatenggara—*R. norvegicus* and *R. exulans. R. norvegicus* has not been collected from either Padar or Rintja, but it is known from Flores (Sody, 1941), and has a spotty distribution throughout Nusatenggara where it is likely to be found in islands where large port cities provide suitable habitat. The Norway rat is probably an endemic of northeastern China (Johnson, 1962) and its occurrence in the Indo-Australian region in general and in Nusatenggara in particular is a result of

transport and introduction by humans. Examples of the species do not closely resemble specimens of *K. rintjanus* in external, cranial, or dental features.

The geographic range of *R. exulans* extends from southern Indochina to New Guinea and scattered groups of Pacific islands. We have examined examples of *R. exulans* from the islands of Sumba, Flores, and Timor, but none from Padar or Rintja. Laurie and Hill (1954) record the species from the islands of Lombok and Sumbawa and it probably occurs on many other small islands in Nusatenggara. *R. exulans* is more likely to occur on Padar and Rintja than is *R. norvegicus*, and if found on those places can easily be distinguished from examples of *K. rintjanus* by its small body size, brownish gray upperparts, whitish underparts, and eight mammae, two of which are distinctly pectoral in position. The size contrast between *K. rintjanus* and *R. exulans* is great. Means (in mm), for example, of lengths of head and body, tail, hind-foot, ear, skull, and maxillary toothrow for 41 adults from Tomado, a village in Central Sulawesi, are, respectively, 117.6, 131.6, 27.2, 18.2, 30.7, and 5.7. Specimens of *R. exulans* from Nusatenggara are similar to those from Sulawesi in body size, and in configuration of skulls and teeth. There is nothing associated with the morphological features of *R. exulans* that relates it closely to *K. rintjanus*.

Two members of *Mus*, both probably introduced by humans, round out the list of species not native to Nusatenggara. *M. caroli* occurs on Flores; the mouse has also been recorded from Java, Sumatra, Kedah State in West Malaysia, the Ryukyu Islands, and the mainland of Southeast Asia, from Thailand to China and Taiwan (Marshall, 1977). Marshall (1977) examined specimens of the house mouse, *M. musculus castaneus*, from the islands of Sumba and Komodo; the same form also occurs on the islands of Lombolen and Timor, according to Laurie and Hill (1954), and is spread throughout an extensive area on mainland Asia, and in the Malay Archipelago, the Philippine islands, Sulawesi, and the Moluccas. We know of no examples from Padar or Rintja, but house mice may live in villages on those islands, and are probably more widespread in Nusatenggara than is indicated either by specimens in museums or by published records.

In addition to Padar and Rintja, Flores and Timor are the only other islands where a native murid fauna has been found. The fauna on Flores consists of *Papagomys armandvillei*, which now lives on the island and is also known by subfossil fragments; *P. verhoeveni* and *Spelaeomys florensis*, two other giant rats described from subfossils; dental remains, reputed to be Pleistocene, of a rat related to *Papagomys*; and a species of *Rattus* consisting only of mandibular fragments (Hooijer, 1957, 1967). The endemic murid fauna from Timor is represented by subfossils, most of them obtained from prehisotric deposits in limestone caves excavated by Glover (1970). At least one species of *Rattus*, two kinds of *Melomys*, the giant rat *Coryphomys buehleri*, and three other kinds of large-bodied rats, each a different genus (yet unnamed and undescribed), are in Glover's material. These specimens from Timor are being studied by Mr. J. A. Mahoney at the University of Sydney. Musser has been working on the rats from Flores; through the kindness of Mr. Mahoney, Musser examined samples of the species from Timor. None of them contains examples of *Komodomys*.

CONCLUSIONS

Sody described *rintjanus* as a species of *Rattus*, but he suspected it might not be a member of that genus for in his description of the holotype he mentioned (1941:311), "As apparently, the inner cusps of m^2 and m^3, are not isolated, and the tail is very coarsely scaled it seems probable that a new genus shall have to be created for this species." Sody's supposition proved to be correct, but ironically neither of the features he thought were diagnostic can be used to exclude *rintjanus* from *Rattus*. The occlusal surfaces of the molars in the holotype are worn down to the level where the

original cusp pattern is nearly obliterated and the inner cusps are no longer discrete but have coalesced with the middle row of cusps. This is a common configuration in the worn molars of species not only in *Rattus*, but also of species in other genera as well. To Sody, the tail of *rintjanus* was covered with large scales. In our sample of 17 adult *rintjanus* the number of scales (per cm) range from 8 to 11, indicating wide scales but not exceptionally wide. The range of scales is 9 to 14 in 26 specimens of *R. rattus* that we studied from northern Sulawesi; most other species of *Rattus* have narrow scales, but some have wider.

The species *rintjanus* is not part of the morphological, ecological, and geographic radiation encompassed by *Rattus*, and it is not closely related to that genus, if the characters of *rintjanus* we studied are any guide to an estimate of its phylogenetic relationship. Instead, *Komodomys rintjanus* may be part of that old, relictual murid fauna known from the islands and continent to the east of the Sunda Shelf. Although set apart by its own very distinctive morphological features, *K. rintjanus* may tie in with the other endemic genera that occur on the Lesser Sunda Islands, especially those forms on Flores; in turn, those rats are allied to that large and diverse radiation of murids native to Australia, New Guinea, Sulawesi, and the Philippines. According to Misonne (1969), *Papagomys* and *Spelaeomys* of Flores cluster with such genera as *Crateromys* (Philippines), *Mallomys* (New Guinea), and *Coryphomys* (Timor) in an assemblage he calls the *Lenothrix* Group, which also contains *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.

The taxonomy of the murids from Flores will be reported elsewhere by Musser. The contrasts, as well as the possible connection, between *Komodomys* and the Floresian genera will be discussed in that paper. We only point out here that the dental patterns of *Papagomys armandvillei* are similar to the occlusal patterns in specimens of *K. rintjanus* (Fig. 7); this despite the fact that *P. armandvillei* is a giant rat and *K. rintjanus* a much smaller one and a species quite different in habitus. In both species the dental patterns are simple compared with such forms as *Spelaeomys, Lenomys, Pogonomys, Chiropodomys,* or *Hapalomys*, to name a few (see the illustrations in Misonne, 1969), and the occlusal patterns of each are *Rattus*-like; the cuspidation of both, however, differs from species of *Rattus* in significant details.

One of those distinctive differences, for example, concerns the height of the cusps. *K. rintjanus* and *P. armandvillei* have molars with very high cusps. In young adults, the cusps are still high; some of the lingual cones in the uppers of both species, and some labial ones in *K. rintjanus* remain discrete and have not yet merged with the large central cones. The cusps on M_1 and M_2 also remain separate, or the enamel edges are just beginning to merge when the rats are young adults or, often, adults. The cusps are much lower on molars in most species of *Rattus*, and most are discrete only shortly after the molars have erupted; the cusps quickly lose their identities and fuse into chevron-like laminae after a little wear, usually while the rats are late nestlings or juveniles, and always by the time they become young adults.

Komodomys rintjanus is an exceptional animal, not only because of its restricted insular distribution in Nusatenggara, but because of its body build, cranial structure, and dental form, a distinctive combination found nowhere else among species of Asian murids. By elucidating the features of *K. rintjanus*, we have documented another segment of the morphological divergence and adaptive radiation within the murid fauna from that vast region of islands and continent east of the Sunda Shelf. By defining the morphological limits of *K. rintjanus*, we point to a moderately large endemic murid fauna on the Lesser Sunda Islands, certainly a richer one than biogeographers had realized existed there. Furthermore, by bringing *K. rintjanus* out of the limbo of
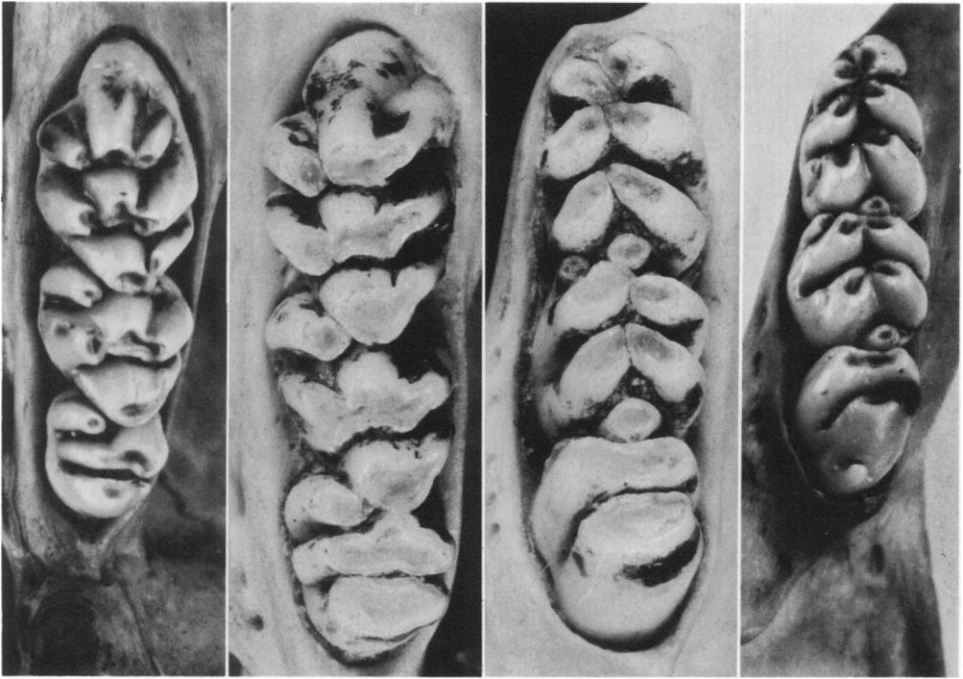
FIG. 7.   Occlusal views of left toothrows. The teeth of a young adult *Komodomys rintjanus* (MZB 9016) flank toothrows of *Papagomys armandvillei* (RMNH 18301), an older adult in which the cusps are worn down more than are those in MZB 9016. Views of *K. rintjanus* are × 8, those of *P. armandvillei* are × 5.

incertae sedis, we hope now to ask relevant questions about those unknown aspects of the species. Because of the incomplete biological exploration of Nusatenggara, we do not know if *K. rintjanus* is confined to the islands of Padar and Rintja or if it occurs elsewhere as well, on Komodo and Flores, for example. We have no details about the habitat of *K. rintjanus*, only a general impression that it may be tied to Monsoon forest. We know nothing of its habits or its general biology. We still do not have enough specimens to determine the extent of individual and secondary sexual variation in *K. rintjanus*, or whether there is significant insular variation in morphological or other characteristics.

Komodomys rintjanus is a rat of the Far East deserving of more study; the small islands between Sumbawa and Flores require fresh and intensive mammalogical and floristic exploration.

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