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Species-limits of *Rattus brahma*, a Murid Rodent of Northeastern India and Northern Burma

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Rattus brahma is a rodent with long, thick fur, orange brown upper parts, whitish underparts, and a long tail densely covered with hair and tipped with a short brush. Its external features superficially resemble those of species in the Neotropical genus *Rhipidomys* on one hand, or species of *Pogonomelomys*, long-tailed rodents endemic to New Guinea, on the other. It occurs in cool, moist, and temperate forests in the highlands of northeastern India and northern Burma. *Rattus brahma* was first described and named in 1914 by Oldfield Thomas on the basis of one specimen. Since that time knowledge of the geographic distribution and ecology of populations of *R. brahma*, and its relationships to other species of *Rattus* has remained obscure for three main reasons: there are still only a few specimens in museum collections; some of these specimens were originally misidentified in the literature (Anthony, 1941) and their significance unrecognized; and since Thomas' original description the taxon has been consistently and incorrectly allocated to another species, *R. fulvescens* (Ellerman, 1949, 1961; Ellerman and Morrison-Scott, 1951). In the present paper I document information on the taxonomic status of *R. brahma*, its relationships to other species of *Rattus*, and present other biological data to supplement the information thus far recorded.

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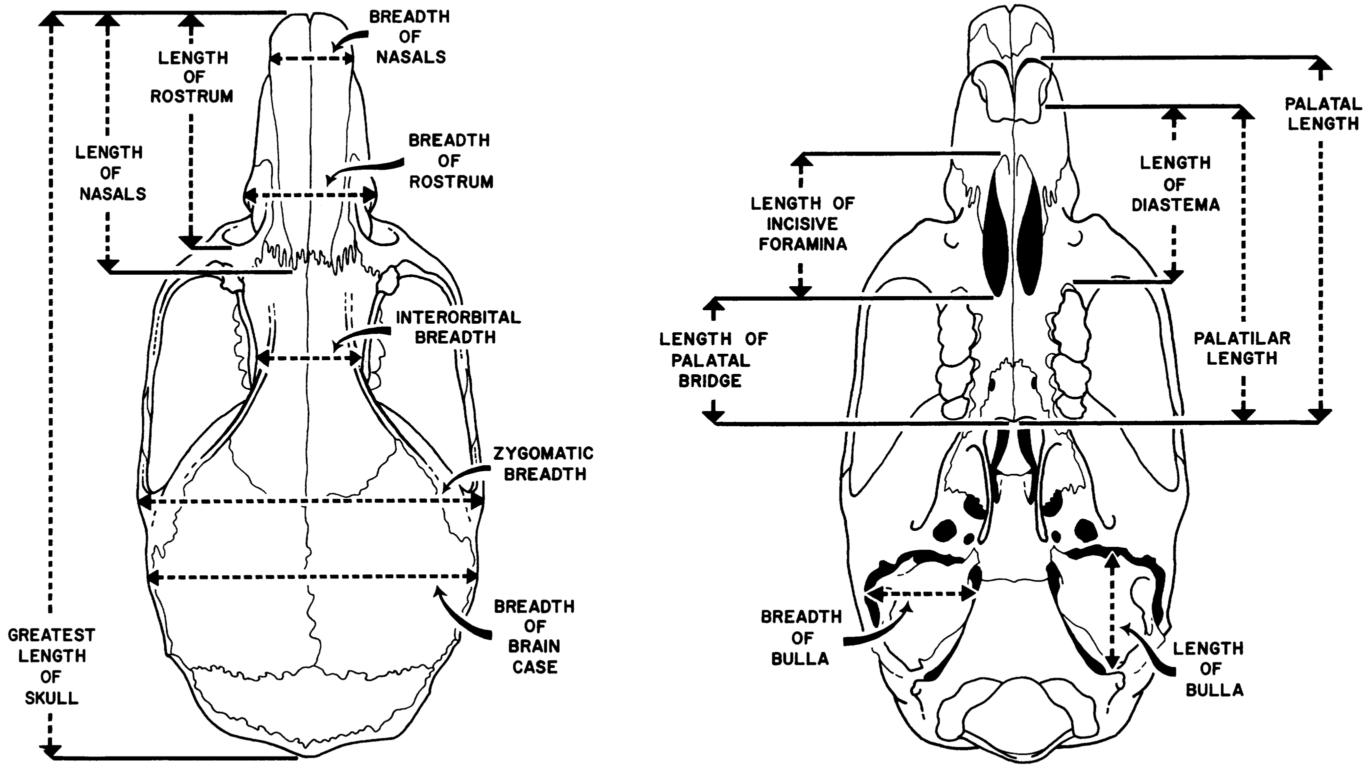

FIG. 1. Dorsal (left) and ventral (right) views of skull of an adult *Rattus eha* showing limits of cranial measurements.

METHODS

Data were obtained from dry study skins with skulls that are housed either in the British Museum (Nat. Hist.) (B.M.) or in the American Museum of Natural History (A.M.N.H.). Total length, length of tail vertebrae, and length of hind foot (including claws) are those of the collectors and were taken from skin labels. Length of the head and body was computed as total length minus length of tail. To measure the ears, I relaxed all specimens in a humid chamber until the ears became soft and pliable, probably as soft as they were in life. I measured the length of the ear from the notch. Most cranial measurements were taken with Anderson's (1968) craniometer attached to a Wild M5 stereomicroscope; a few were taken with dial calipers graduated in tenths of millimeters. Because I have used some of the same measurements in past reports and will use them again in future, I have illustrated the limits of those cranial measurements in figures 1 and 2.

Cranial Measurements

To take all measurements of length, except length of the nasals, the the skull was oriented on the mechanical stage so that its longitudinal axis was parallel to the forward-backward axis of movement of the stage, and so that the palatal region of the skull was parallel to the surface of the stage. Each of these measurements is actually the distance between two planes passing through the specified points that are perpendicular to the longitudinal axis of the skull.

Greatest Length of Skull (Occipitonasal Length): The distance from the tip of the nasals to the posterior margin of the occiput, as noted in figure 1.

Greatest Length of Nasals: The distance from the anterior tip of the nasal bones to the most posterior suture between the nasal and frontal bones (fig. 1), measured parallel to the surface of the nasal bones.

Breadth of Nasals: The greatest breadth across both nasal bones (fig. 1).

Length of Rostrum: From the tip of the nasal bones to the posterior margin of the zygomatic notch (or the anterior edge of the dorsal maxillary root of the zygomatic plate) (fig. 1).

Breadth of Rostrum: The greatest breadth across the rostrum, including the bony capsules enclosing the nasolacrimal canals (fig. 1).

Interorbital Breadth: The least distance, as viewed dorsally, across the frontal bones between the orbital fossae (fig. 1).

Zygomatic Breadth: The greatest breadth across the zygomatic arches, taken across the zygomatic processes of the squamosal bones (fig. 1).

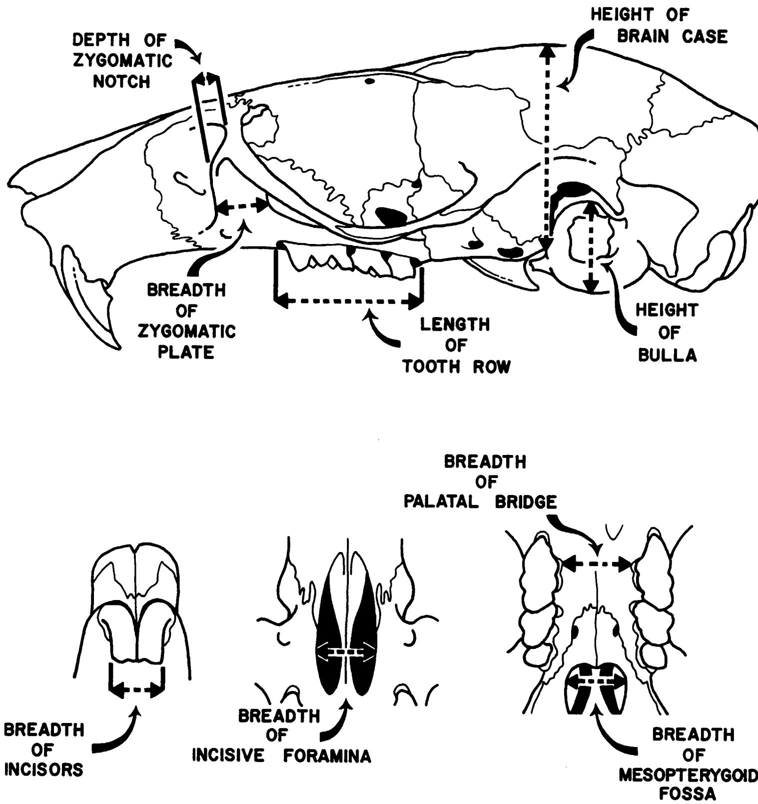

FIG. 2. Lateral (top) and additional ventral (bottom) views of skull of an adult *Rattus eha* showing limits of cranial measurements.

Greatest Breadth of Brain Case: Measured just behind and slightly above the squamosal roots of each zygomatic arch (fig. 1).

Height of Brain Case: From the top of the brain case to the ventral surface of the basisphenoid bone (fig. 2).

Breadth of Zygomatic Plate: The least distance between the anterior and posterior edges of the zygomatic plate (fig. 2).

Depth of Zygomatic Notch: From the anterior edge of the zygomatic plate to the anterior edge of the dorsal maxillary root of the zygomatic plate, and parallel to the long axis of the skull (fig. 2).

Greatest Length of Diastema: The distance from the posterior alveolar margins of the incisors to the anterior alveolar margins of the first molars (fig. 1).

Greatest Palatilar Length: The distance from the posterior alveolar margins of the incisors to the posterior edge of the palatal bridge (fig. 1). In two other reports (Musser, 1969a, 1969b), I have called this measurement "Palatal Length."

Greatest Palatal Length: The distance from the anterior alveolar margins of the incisors to the posterior edge of the palatal bridge (fig. 1).

Length of Incisive Foramina: From the anterior edge of one of the foramina to its posterior edge (fig. 1). I usually measured the right foramen.

Breadth Across Incisive Foramina: The greatest distance across both foramina (fig. 2).

Greatest Length of Palatal Bridge: The distance from the posterior edge of the incisive foramina to the posterior margin of the bony palate (fig. 1).

Breadth of Palatal Bridge: The least distance between the lingual edge of the alveolus of the first molar and the lingual edge of the alveolus of the opposite molar (fig. 2).

Greatest Breadth of Mesopterygoid Fossa: The distance from one edge of the mesopterygoid fossa to the other (fig. 2).

Greatest Length of Bulla: The length of the bulla, excluding the bony eustachian tube (fig. 1). This measurement and the next two were usually taken on the right bulla.

Breadth of Bulla: From the dorsolateral edge of the internal auditory meatus directly across to the point where the bulla touches the basioccipital bone (fig. 1).

Height of Bulla: From the dorsal surface of the bulla to its ventral surface (fig. 2).

Greatest Breadth of Incisor Tips: The distance across the tips of the incisors (fig. 2).

Greatest Alveolar Length of Maxillary Tooth Row: The distance from the anterior edge of the alveolus of the first molar to the posterior edge of the alveolus of the third molar (fig. 2).

COMPARISONS BETWEEN SPECIMENS OF *RATTUS BRAHMA*, *R. FULVESCENS*, AND *R. EHA*

In 1939, Arthur S. Vernay and C. Suydam Cutting sponsored an expedition to northeastern Burma to collect mammals, birds, and botanical specimens. The mammals obtained during that expedition were deposited in the American Museum of Natural History and subsequently identified and reported by Harold E. Anthony in 1941. Among the several species of *Rattus* recorded by Anthony was a series of 23 specimens from Hpimaw Road, Imaw Bum, the road to Chimeli Pass, and Nyetmaw River, all of which he (1941, p. 107) identified as *R. eha ninus.* This series actually represents two species, not one as Anthony thought. The 20 specimens from Hpimaw Road, Imaw Bum, and the road to Chimeli Pass are examples of *R. eha.* All have a short head and body, long tail, thick and soft pelage, brownish orange upper parts, and gray underparts. In color of pelage and size of external dimensions, these specimens answer Thomas' (1922, p. 404) original description of *R. eha ninus* and they also fit (1940, p. 1035) the more detailed description of that animal that Allen gave based on the seven original examples in the British Museum that were obtained from Yunnan Province, China.

I have also compared the crania of the 20 specimens of *R. eha* in the American Museum of Natural History with measurements and photographic prints of the holotype of *R. e. ninus.* The prints and cranial measurements, which are in the files of the Department of Mammalogy of the American Museum, were obtained by George H. H. Tate when he visited the British Museum in 1937. The configuration and available measurements (table 2) of the skull of the holotype of *ninus* fall within the ranges of variations seen in cranial features of specimens of comparable age in the American Museum.

The three specimens from Nyetmaw River are not examples of *R. eha,* but they represent *R. brahma,* a species originally described and named by Oldfield Thomas (1914, p. 231) on the basis of an adult female (B.M. No. 14.6.24.2) taken at an elevation of 6000 feet from the Anzong Valley in the Mishmi Hills of northern Assam, India. Pelage features of the three specimens from Nyetmaw River are closely similar to Thomas' description of *R. brahma.* The three examples also agree with that taxon in cranial features, as judged by me from a photographic print of the holotype. As a final check of my identification I sent the oldest specimen of the three from Nyetmaw River (A.M.N.H. No. 115216) to John Edwards Hill at the British Museum and asked him to compare it with the holotype of *R. brahma.* He wrote: "I have compared your example of *Rattus* with the type specimen of *R. brahma* with which it is in good agreement excepting only that the ventral surface is slightly whiter, the flanks a little more ochraceous and the rostrum slightly broader. The small difference in the colour of the flanks may, of course, be due to slight fading of the type specimen."

The relationships of *R. brahma* to other species of *Rattus* has been unclear. In his original description, Thomas compared *R. brahma* with *R. fulvescens,* indicating that *R. brahma* was morphologically most like that

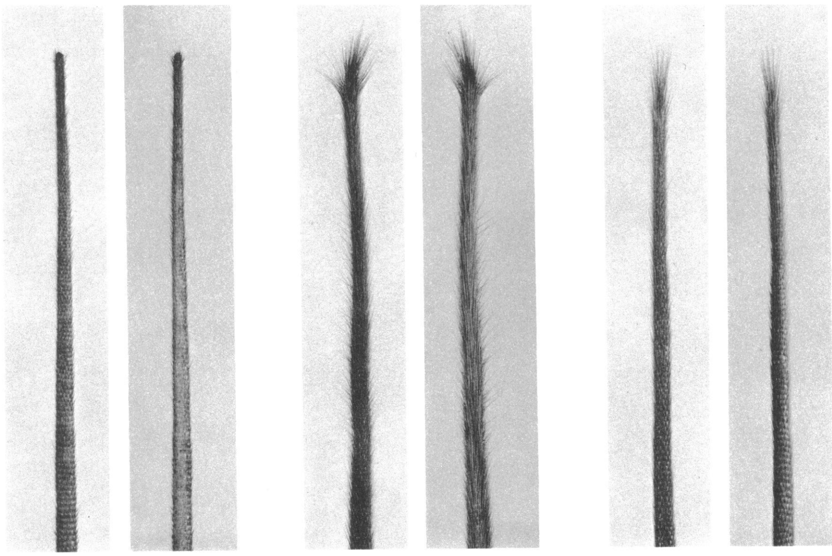

FIG. 3. Dorsal (left member of each pair) and ventral (right member of each pair) views showing the distal third of the tail in three species of *Rattus*. From left to right: *Rattus fulvescens* (A.M.N.H. No. 43300, adult male), Namting River, western China; *R. brahma* (A.M.N.H. No. 115216, adult male), Nyetmaw River, northern Burma; and *R. eha* (A.M.N.H. No. 115214, adult male), Imaw Bum, northern Burma. Natural size.

species, but specifically distinct from it. Subsequently, however, Ellerman (1949, 1961) and Ellerman and Morrison-Scott (1951) listed *brahma* as a subspecies of *R. fulvescens.* Their material of *brahma* consisted of the holotype and five males from the Adung Valley in northern Burma.

My study reinforces Thomas' original estimate of the specific distinctness of *R. brahma.* The three specimens from the Nyetmaw River and the holotype from northern Assam (I have not examined the five specimens from the Adung Valley) represent a population of *Rattus* that is morphologically and specifically distinct from populations of *R. fulvescens. Rattus brahma,* however, is not especially closely related to *R. fulvescens* as Thomas thought, but is morphologically and possibly phyletically closer to other species that are currently placed in the "*niviventer* Group" and the "*eha* Group" of *Rattus.* Among the species that Ellerman (1949) listed in those groups, *R. brahma* needs closest comparisons with samples of *R. fulvescens* and *R. eha.* These three species are contrasted in tables 1 and 2, and in figures 3 to 6; the comparisons are based on the following specimens.

TABLE 1

DIFFERENTIAL EXTERNAL FEATURES OF *Rattus brahma* AS COMPARED WITH *R. eha* AND *R. fulvescens*

Feature	*R. brahma*	*R. eha*	*R. fulvescens*
Upper parts	Bright, orange brown to yellow brown; pelage long (*ca.* 15 mm.), dense and soft; without spines	Paler, with more brownish hues; pelage also long, dense, and soft; without spines	Bright, orange brown; pelage shorter (*ca.* 10 mm.), thinner, and relatively harsh; many soft and semi-rigid spines
Face	Each eye surrounded by blackish brown ring (*ca.* 2 mm. wide), connected across muzzle by narrow (2–3 mm.) blackish brown band producing a narrow mask across face; nose blackish brown	Eye rings similar in color and size, blackish bands extend only to bases of vibrissae, not across muzzle; nose blackish brown	Eye rings blackish brown, but narrower (*ca.* 1 mm. wide), no mask; nose brown to brownish orange
Ears	Dark brown; outer and inner surfaces moderately haired; without brownish tuft at base of each ear	Color similar; outer and inner surfaces densely covered with long hairs; brownish black tuft of hairs at base of each ear	Color similar; outer and inner surfaces moderately haired; without tuft at base of each ear
Underparts	White, lightly suffused with gray; basal half of each hair gray, distal half white; pelage long (8–10 mm.), dense, and soft	Grayish white (smoky); basal three-fourths of each hair gray, distal one-fourth white; pelage slightly shorter (7–9 mm.), but also dense and soft	White to pale yellow; each hair white or pale yellow from base to tip; pelage shorter (*ca.* 5 mm.), thinner, relatively harsh; many soft, thin spines

TABLE 1—(*Continued*)

Feature	*R. brahma*	*R. eha*	*R. fulvescens*
Hind feet	Dorsal surface of metatarsal area brownish gray; edges of foot and toes silver gray	Coloration closely similar	Lighter, silver gray with pale brown or pale orange highlights; some individuals with pale brown streak on metatarsal area
Tail	Pigmented above and below; dorsal surface brownish black, ventral surface brownish gray; densely haired; hairs gradually increase in length towards tip of tail where they form brush 6–8 mm. long extending beyond tip (fig. 3); 15–17 (M = 15.7, S.D. = 1.16, *n* = 3) scale rows per cm.	Coloration of dorsal surface similar, ventral surface gray instead of brownish gray; also well haired with brush extending beyond tip, but hairs much shorter (fig. 3); 11–14 (M. = 12.0, S.D. = .82, *n* = 16) scale rows per cm.	Dorsal surface and all around tip pale brown, ventral surface unpigmented; thinly covered with short hairs, no brush at tip (fig. 3); 10–15 (M = 12.4, S.D. = 1.24, *n* = 15) scale rows per cm.
Mammae	Three pair, one post-axillary, one abdominal, and one inguinal[a]	Three pair, distributed on the body as in *R. brahma*	Four pair, one pectoral, one post-axillary, one abdominal, and one inguinal

[a] Thomas, 1914, p. 231.

Rattus fulvescens fulvescens (18 specimens)

NORTHERN BURMA: Ngawchang River, altitude 1800 feet, one male (A.M. N.H. No. 115257); Gangfang (or Kangfang), altitude 5200 feet, three males (A.M.N.H. Nos. 115254-115256); Dalu, elevation 626 feet, one male (A.M.N.H. No. 113048); Tasu Bum, altitude 4200 feet, one male (A.M.N.H. No. 113047); Pumsin, altitude 3900 feet, one male (A.M.N.H. No. 113046); Gora, altitude 2600 feet, two males (A.M.N.H. Nos. 113044 and 113045); Mansum, elevation 3200 feet, two males (A.M.N.H. Nos. 113041 and 113061) and two females (A.M.N.H. Nos. 113042 and 113043). The Burmese specimens from Lonkin (A.M.N.H. No. 113056), Tawmaw (A.M.N.H. No. 113060), Lahkow (A.M.N.H. No. 113065) and one (A.M.N.H. No. 113062) of the five obtained at Mansum that were identified by Carter (1943, p. 113) as *R. fulvescens* are actually examples of *R. niviventer.*

WESTERN CHINA, YUNNAN PROVINCE: Namting River, Burma border, altitude 1700 feet, three males (A.M.N.H. Nos. 43297, 43298, and 43300); Hsiao-ke-la, Mekong River, elevation 8000 feet, one male (A.M.N.H. No. 43302); Yang-pi River, elevation 5000 feet, one male (A.M.N.H. No. 43301).

Rattus eha ninus (20 specimens)

NORTHERN BURMA: Hpimaw Road, elevation 9000 feet, one male (A.M.N.H. No. 115230) and one female (A.M.N.H. No. 115231); Imaw Bum, elevation 9000 feet, five males (A.M.N.H. Nos. 115211–115215) and two females (A.M. N.H. Nos. 115209 and 115210); road to Chimeli Pass, elevation 10,000 feet, 11 males (A.M.N.H. Nos. 115219–115229).

Rattus brahma (3 specimens)

NORTHERN BURMA: Nyetmaw River, elevation 8600 feet, three males (A.M.-N.H. Nos. 115216–115218).

EXTERNAL FEATURES: The pelage and other external traits of *Rattus brahma* were adequately described by Thomas (1914); external features of *R. eha* and *R. fulvescens* were enumerated by Allen (1940). The reader is referred to those two sources for detailed descriptions of pelage and other external features of the three species. In table 1, I have listed primarily the qualitative external characteristics that contrast samples of *brahma, eha,* and *fulvescens.*

In absolute size, specimens of *Rattus brahma* have shorter lengths of head and body than do those in the sample of *R. fulvescens,* and their hind feet average longer; the differences between the two samples are not significant (at the .05 level of statistical significance). The specimens of *R. brahma,* however, differ significantly from those in the sample of *R. fulvescens* in that they have longer tails and longer ears (table 2; fig. 4).

Available specimens of *R. eha* are significantly smaller than specimens

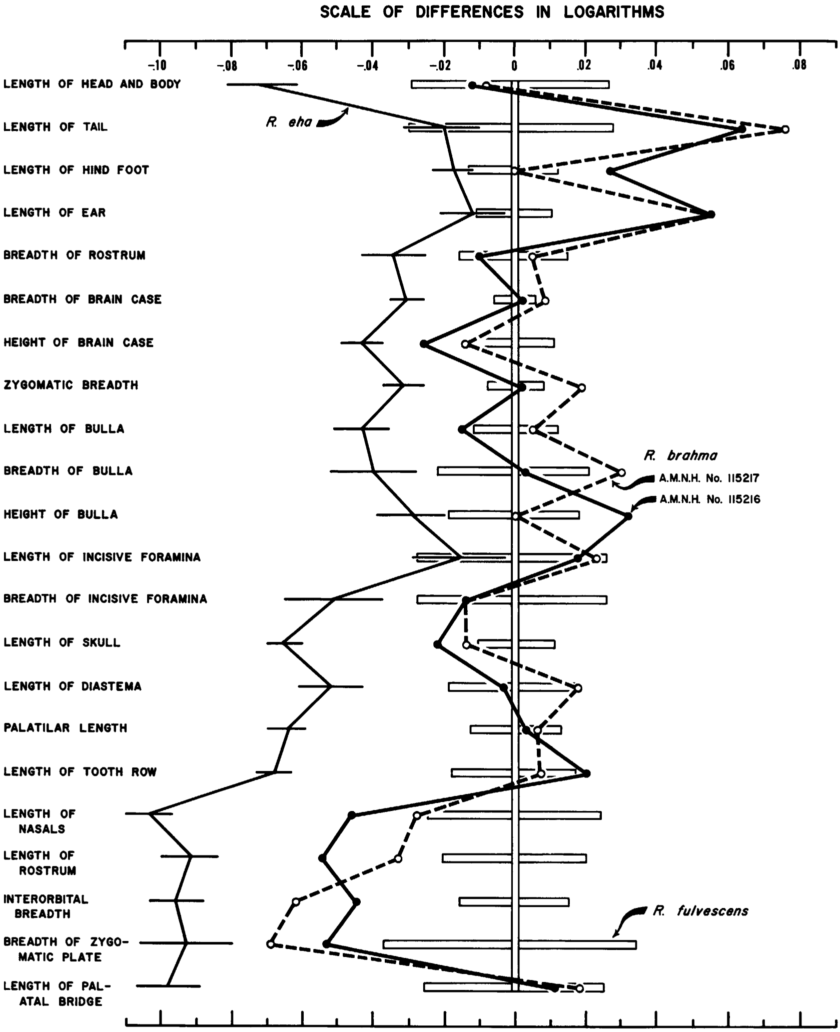

FIG. 4. Ratio diagram. Twenty-two dimensions are compared in samples of *Rattus fulvescens* (the standard), *R. brahma,* and *R. eha* from northern Burma.

of *R. brahma* in all of the external measurements that were taken. Specimens of *R. eha* are also significantly smaller than those in the sample of *R. fulvescens* in length of head and body and length of hind foot, but examples of these two species are closely similar in length of tail and length of ear.

TABLE 2

Measurements (in Millimeters) from Samples of *Rattus fulvescens*, *R. eha*, and *R. brahma*.

(The mean and standard deviation, plus and minus two times the standard error of the mean, extremes [in parentheses], coefficient of variation, and size of sample are listed, in that order, for each dimension.)

	R. f. fulvescens	*R. eha ninus*		*R, brahma*			
	Northern Burma (adult males)	Northern Burma (adult males)	Yunnan, China (holotype, B.M. No. 22.9.1.107, adult female)[a]	Northern Burma (A.M.N.H. No. 115217, adult male)	(A.M.N.H. No. 115216, adult male)	(A.M.N.H. No. 115218, subadult male)	Assam, India (holotype, B.M. No. 14.6.24.2, adult female)[b]
Length of head and body	139.7±11.1	118.7±5.4	127	137	136	136	145
	130.7–148.7	116.1–121.3	—	—	—	—	—
	(128–160)	(112–130)	—	—	—	—	—
	7.9	4.5	—	—	—	—	—
	6	16	—	—	—	—	—
Length of tail	188.8±14.0	180.2±8.1	—	225	219	201	218
	176.2–201.4	176.0–184.4	—	—	—	—	—
	(176–210)	(165–195)	—	—	—	—	—
	7.5	4.5	—	—	—	—	—
	5	14	—	—	—	—	—
Length of hind foot	31.0±1.1	29.8±.8	27	31	33	32	28
	30.1–31.9	29.4–30.2	—	—	—	—	—
	(29–32)	(28–31)	—	—	—	—	—
	3.5	2.7	—	—	—	—	—
	6	16	—	—	—	—	—

TABLE 2—(*Continued*)

	R. f. fulvescens	*R. eha ninus*		*R, brahma*			
	Northern Burma (adult males)	Northern Burma (adult males)	Yunnan, China (holotype, B.M. No. 22.9.1.107, adult female)[a]	Northern Burma (A.M.N.H. No. 115217, adult male)	(A.M.N.H. No. 115216, adult male)	(A.M.N.H. No. 115218, subadult male)	Assam, India (holotype, B.M. No. 14.6.24.2, adult female)[b]
Length of ear	18.5±0.6	18.0±0.7	20	21	21	20	25
	18.1–18.9	17.64–18.36	—	—	—	—	—
	(18–19)	(17–19)	—	—	—	—	—
	3.2	3.9	—	—	—	—	—
	6	16	—	—	—	—	—
Greatest length of skull	36.33±.89	31.30±.67	32.1	35.2	34.5	34.1	35.8
	35.45–37.21	30.96–31.64	—	—	—	—	—
	(35.0–36.9)	(30.2–32.6)	—	—	—	—	—
	2.45	2.14	—	—	—	—	—
	4	15	—	—	—	—	—
Length of nasals	13.33±.93	10.51±.32	11.0	12.5	12.0	11.2	11.7
	12.57–14.09	10.35–10.67	—	—	—	—	—
	(12.0–14.4)	(9.9–11.2)	—	—	—	—	—
	6.98	3.04	—	—	—	—	—
	6	16	—	—	—	—	—
Length of rostrum	11.65±.66	9.43±,33	—	10.8	10.3	9.6	—
	11.11–12.19	9.27–9.59	—	—	—	—	—
	(10.6–12.3)	(8.7–9.9)	—	—	—	—	—
	5.67	3.50	—	—	—	—	—
	6	16	—	—	—	—	—

TABLE 2—(*Continued*)

	R. f. fulvescens	*R. eha ninus*		*R, brahma*			
	Northern Burma (adult males)	Northern Burma (adult males)	Yunnan, China (holotype, B.M. No. 22.9.1.107, adult female)[a]	Northern Burma (A.M.N.H. No. 115217, adult male)	(A.M.N.H. No. 115216, adult male)	(A.M.N.H. No. 115218, subadult male)	Assam, India (holotype, B.M. No. 14.6.24.2, adult female)[b]
Breadth of rostrum	6.03±.27	5.58±.24	—	6.1	5.9	5.8	—
	5.81–6.25	5.46–5.70	—	—	—	—	—
	(5.7–6.3)	(5.3–6.2)	—	—	—	—	—
	4.48	4.30	—	—	—	—	—
	6	16	—	—	—	—	—
Interorbital breadth	5.77±.25	4.63±.16	4.3	5.0	5.2	5.0	5.0
	5.57–5.97	4.55–4.71	—	—	—	—	—
	(5.4–6.0)	(4.4–4.9)	—	—	—	—	—
	4.33	3.46	—	—	—	—	—
	6	16	—	—	—	—	—
Zygomatic breadth	16.28±.29	15.13±.39	14.5	17.0	16.3	16.3	16.6
	16.00–16.56	14.95–15.31	—	—	—	—	—
	(15.9–16.6)	(14.6–16.0)	—	—	—	—	—
	1.78	2.58	—	—	—	—	—
	4	16	—	—	—	—	—
Depth of zygomatic notch	1.30±.29	.61±.19	—	.6	.7	.6	—
	1.06–1.54	.53–.69	—	—	—	—	—
	(.9–1.6)	(0.3–0.9)	—	—	—	—	—
	22.30	31.15	—	—	—	—	—
	6	16	—	—	—	—	—

TABLE 2—(*Continued*)

	R. f. fulvescens	*R. eha ninus*		*R, brahma*			
	Northern Burma (adult males)	Northern Burma (adult males)	Yunnan, China (holotype, B.M. No. 22.9.1.107, adult female)[a]	Northern Burma (A.M.N.H. No. 115217, adult male)	(A.M.N.H. No. 115216, adult male)	(A.M.N.H. No. 115218, subadult male)	Assam, India (holotype, B.M. No. 14.6.24.2, adult female)[b]
Breadth of zygomatic plate	3.17±.31	2.56±.15	2.4	2.7	2.8	2.7	2.7
	2.91–3.43	2.48–2.64	—	—	—	—	—
	(2.7–3.6)	(2.3–2.8)	—	—	—	—	—
	9.78	5.86	—	—	—	—	—
	6	16	—	—	—	—	—
Breadth of brain case	14.73±.19	13.72±.28	—	15.0	14.8	15.1	15.3
	14.55–14.91	13.58–13.86	—	—	—	—	—
	(14.6–15.0)	(13.4–14.5)	—	—	—	—	—
	1.29	2.04	—	—	—	—	—
	4	16	—	—	—	—	—
Height of brain case	10.30±.27	9.36±.24	—	10.0	9.7	9.9	—
	10.02–10.58	9.24–9.48	—	—	—	—	—
	(10.1–10.7)	(9.0–9.6)	—	—	—	—	—
	2.62	2.56	—	—	—	—	—
	4	14	—	—	—	—	—
Length of diastema	8.73±.45	7.75±.32	8.4	9.1	8.7	8.4	9.4
	8.37–9.09	7.59–7.91	—	—	—	—	—
	(8.0–9.2)	(7.3–8.5)	—	—	—	—	—
	5.15	4.12	—	—	—	—	—
	6	16	—	—	—	—	—

TABLE 2—(*Continued*)

	R. f. fulvescens	*R. eha ninus*		*R, brahma*			
	Northern Burma (adult males)	Northern Burma (adult males)	Yunnan, China (holotype, B.M. No. 22.9.1.107, adult female)[a]	Northern Burma (A.M.N.H. No. 115217, adult male)	(A.M.N.H. No. 115216, adult male)	(A.M.N.H. No. 115218, subadult male)	Assam, India (holotype, B.M. No. 14.6.24.2, adult female)[b]
Length of incisive foramina	6.05±.46	5.84±.34	6.5	6.4	6.3	6.7	6.6
	5.67–6.43	5.66–6.02	—	—	—	—	—
	(5.6–6.8)	(5.4–6.4)	—	—	—	—	—
	7.60	5.82	—	—	—	—	—
	6	16	—	—	—	—	—
Breadth of incisive foramina	2.68±.20	2.39±.15	2.2	2.6	2.6	2.4	2.7
	2.52–2.84	2.31–2.47	—	—	—	—	—
	(2.4–2.9)	(2.1–2.6)	—	—	—	—	—
	7.46	6.28	—	—	—	—	—
	6	16	—	—	—	—	—
Palatilar length	15.12±.56	13.04±.33	—	15.3	15.2	15.0	—
	14.66–15.58	12.88–13.20	—	—	—	—	—
	(14.2–15.9)	(12.6–13.9)	—	—	—	—	—
	3.70	2.53	—	—	—	—	—
	6	16	—	—	—	—	—
Length of palatal bridge	6.33±.45	5.06±.22	—	6.6	6.5	6.3	—
	5.95–6.71	4.96–5.16	—	—	—	—	—
	(5.8–6.8)	(4.7–5.4)	—	—	—	—	—
	7.14	4.35	—	—	—	—	—
	6	16	—	—	—	—	—

TABLE 2—(*Continued*)

	R. f. fulvescens	*R. eha ninus*		*R, brahma*			
	Northern Burma (adult males)	Northern Burma (adult males)	Yunnan, China (holotype, B.M. No. 22.9.1.107, adult female)[a]	Northern Burma (A.M.N.H. No. 115217, adult male)	(A.M.N.H. No. 115216, adult male)	(A.M.N.H. No. 115218, subadult male)	Assam, India (holotype, B.M. No. 14.6.24.2, adult female)[b]
Length of tooth row	6.30±.32	5.39±.14	5.0	6.4	6.6	7.0	6.5
	6.04–6.56	5.33–5.45	—	—	—	—	—
	(5.9–6.6)	(5.1–5.6)	—	—	—	—	—
	5.08	2.59	—	—	—	—	—
	6	16	—	—	—	—	—
Length of bulla	4.65±.13	4.21±.15	4.2	4.7	4.5	4.6	4.6
	4.53–4.77	4.13–4.29	—	—	—	—	—
	(4.5–4.8)	(4.0–4.5)	—	—	—	—	—
	2.80	3.56	—	—	—	—	—
	4	15	—	—	—	—	—
Breadth of bulla	4.58±.22	4.17±.23	—	4.9	4.6	4.6	—
	4.36–4.80	4.05–4.29	—	—	—	—	—
	(4.3–4.8)	(3.8–4.6)	—	—	—	—	—
	4.80	5.52	—	—	—	—	—
	4	15	—	—	—	—	—
Height of bulla	3.90±.16	3.65±.15	—	3.9	4.2	4.1	—
	3.74–4.06	3.67–3.73	—	—	—	—	—
	(3.7–4.1)	(3.4–4.0)	—	—	—	—	—
	4.10	4.11	—	—	—	—	—
	4	15	—	—	—	—	—

[a] External measurements are from Thomas (1922) and cranial measurements are from Tate's manuscript notes.

[b] External measurements are from Thomas (1914) and cranial measurements are from Tate's manuscript notes.

Proportional relationships between the samples of *R. fulvescens*, *R. brahma*, and *R. eha* in external features are graphically illustrated in the form of a ratio diagram in figure 4. Simpson (1941) has described the method for constructing such a diagram, but figure 4 requires a brief explanation. For each external and cranial measurement, the absolute value of the mean (or the absolute value of a single measurement) and the absolute values of plus and minus two standard errors of the mean were converted to logarithms. The sample of *R. fulvescens* from northern Burma was chosen as the standard. For each dimension the logarithm of the mean of the standard was subtracted from the logarithm of the mean, and from the logarithms of plus and minus two standard errors of the mean, of the sample of *R. eha*. The values for *R. brahma* were obtained by subtracting the logarithm of the mean of *R. fulvescens* from the logarithms of each specimen of *R. brahma*. Measurements larger than the standard are represented on the diagram by positive values, those smaller than the standard are represented by negative values. In the samples of *R. fulvescens* and *R. eha*, the lines connect the means of each measurement, the horizontal bars and rectangles represent plus and minus two standard errors of the mean. Values for the two specimens of *R. brahma* are plotted separately and the lines connect individual values for each measurement. A sample, or specimen, with the same proportions as the standard will be represented by means or single values on a line parallel to that of the standard, regardless of absolute size. Also, if values for the samples being compared with the standard are similar in absolute size they will be close together on the diagram. And, if proportions between any of the measured dimensions are similar, the relative positions of their points to each other on the horizontal scale will be similar.

Absolute single values, values of the mean, and plus and minus two times the standard error of the mean, for each dimension in each sample, and size of each sample are listed in table 2. All the points in the ratio diagram were derived from males.

The two specimens of *R. brahma* are proportionally unlike the sample of *R. fulvescens* in most of the measured external dimensions. With respect to the standard (*R. fulvescens*), each of the two specimens of *R. brahma* has a much longer tail relative to its length of head and body, length of hind foot, and length of ears than do the specimens of *R. fulvescens;* a shorter hind foot relative to its length of tail or length of ear; and longer ears relative to its length of head and body or length of hind foot.

With respect to the standard, the sample of *R. eha* resembles the two specimens of *R. brahma* in relative length of tail; each species has a conspicuously longer tail relative to its length of head and body, than does *R. fulvescens.* But, length of tail in *R. eha,* relative to length of head and body, is similar to length of hind foot and length of ear, and all three of these dimensions are proportionally like those of *R. fulvescens* and unlike those of *R. brahma.*

Cranial Features: Similarities and differences in configurations and sizes of the crania of *Rattus fulvescens, R. brahma,* and *R. eha* can be seen in figures 5 and 6 and in table 2. In absolute size, the specimens of *R. brahma* are more similar to those of *R. fulvescens* than to those of *R. eha.* The available examples of *R. brahma* are larger than the examples of *R. fulvescens* of comparable age in breadth of brain case, zygomatic breadth, breadth and height of bullae, length of incisive foramina, palatilar length, length of tooth row, and length of palatal bridge, but they are smaller in length of bullae and breadth of incisive foramina; these differences between samples of the two species are average and not significant at the .05 level of statistical significance. On the other hand, samples of the two species differ significantly and conspicuously in seven of the measured dimensions: *R. brahma* has a shallower brain case, longer skull, shorter nasals and rostrum, narrower interorbital breadth, narrower zygomatic plates, and shallower zygomatic notches (a reflection of the narrow zygomatic plates) than those of *R. fulvescens.*

Rattus eha and *R. brahma* are closely similar in the over-all shape of their skulls, but specimens of *R. eha* are significantly smaller than those of *R. brahma* in all the cranial measurements that were taken. Examples of *R. eha* are also significantly smaller than those in the sample of *R. fulvescens* in all measured cranial dimensions except length of incisive foramina, a feature in which specimens of the two species are alike.

Rattus brahma, R. eha, and *R. fulvescens* are proportionally similar in several of the measured cranial dimensions (fig. 4). For example, with respect to the standard, breadth of the brain case and the zygomatic breadth are similar, relative to breadth of rostrum, in samples of all three species. The breadth and height of the bullae are similar, relative to their length, in the samples of *R. brahma, R. eha,* and *R. fulvescens.*

In most other cranial proportions, however, the two specimens of *Rattus brahma* are proportionally similar to the sample of *R. eha,* and both species are unlike the sample of *R. fulvescens.* Here are some of the conspicuous proportional contrasts between *R. fulvescens* and the other two species. With respect to the standard, the two specimens of *R. brahma* and the sample of *R. eha* have shallower brain cases relative to their breadths, than does the sample of *R. fulvescens;* wider zygomatic breadths

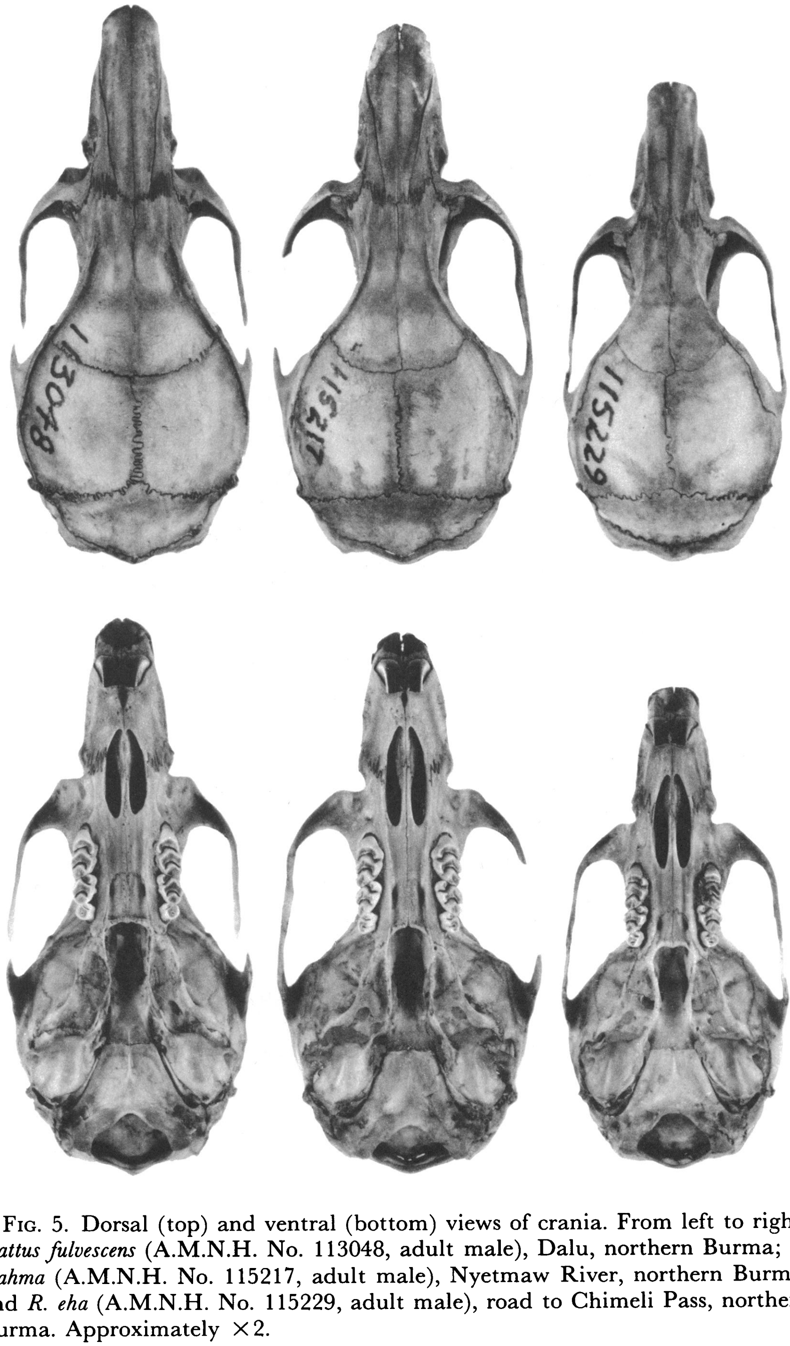

FIG. 5. Dorsal (top) and ventral (bottom) views of crania. From left to right: *Rattus fulvescens* (A.M.N.H. No. 113048, adult male), Dalu, northern Burma; *R. brahma* (A.M.N.H. No. 115217, adult male), Nyetmaw River, northern Burma; and *R. eha* (A.M.N.H. No. 115229, adult male), road to Chimeli Pass, northern Burma. Approximately ×2.

relative to their height of brain cases; longer incisive foramina relative to their breadths, although absolute size of this dimension is similar in all three species; shorter skulls relative to lengths of their incisive foramina, but lengths of the skulls are proportionally similar to breadths of incisive foramina; shorter nasals and rostra, narrower interorbital breadths,

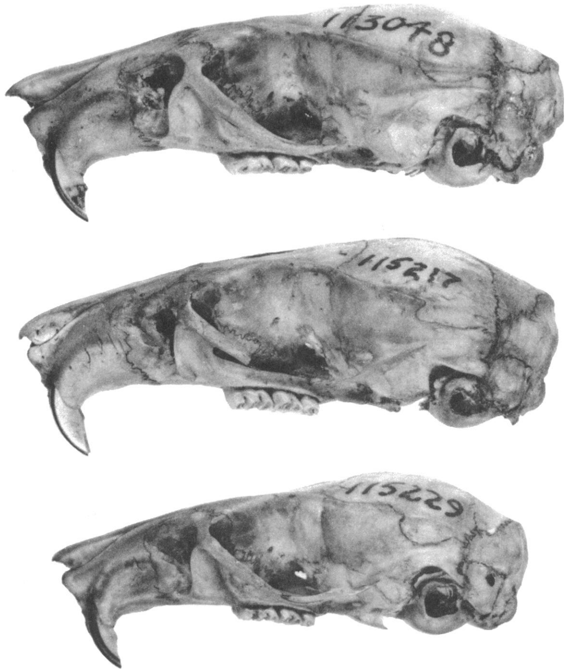

FIG. 6. Lateral views of crania of the specimens in figure 5. From top to bottom: *Rattus fulvescens,* Dalu; *R. brahma,* Nyetmaw River; and *R. eha,* road to Chimeli Pass. Approximately ×2.

and narrower zygomatic plates relative to any other measured cranial dimension; and much shallower zygomatic notches relative to any other measured external or cranial dimension (this measurement is not illustrated on the ratio diagram). For example, the logarithmic difference between the mean of the sample of *R. eha* and that of the sample of *R. fulvescens* is —.406; the logarithmic differences between the two specimens of *R. brahma* and the mean of the sample of *R. fulvescens* are —.269 (A.M.N.H. No. 115216) and —.336 (A.M.N.H. No. 115217).

Although samples of *R. brahma* and *R. eha* are proportionally alike in most cranial dimensions, they differ in a few. For example, with respect to the standard, the sample of *R. eha* has a shorter palatal bridge relative to its length of tooth row than does either specimen of *R. brahma,* in which length of palatal bridge and length of tooth row are proportionally similar. Other similarities and differences in proportions of the dimensions that were measured in the samples of *R. brahma, R. eha,* and *R. fulvescens* are evident in the ratio diagram.

The maxillary and mandibular teeth of the three species are closely similar in shape and topography of crowns but differ in size. The teeth of *R. brahma* average larger and heavier than those of *R. fulvescens;* the teeth of *R. eha* are smaller versions of those of the other two species.

HABITAT

I do not have firsthand knowledge of the habitat of *R. brahma.* The most complete information comes from Anthony's published description of the area in which he obtained the specimens of *R. brahma* that are in the American Museum of Natural History, and the scanty information recorded in his field notes (on file in the Department of Mammalogy, the American Museum of Natural History). Anthony obtained all three specimens of *R. brahma* on the upper reaches of the Nyetmaw River, about 8500 feet in elevation, a camp he worked out of during the period, January 24 to 31. Nyetmaw River dissects the steep, eastern flanks of Imaw Bum, one of the highest mountainous regions in northeastern Burma. During his stay at this camp, Anthony recorded daily temperatures (taken in the sun) that fluctuated from 27° F. to 91° F. His description (1941, p. 52) of the forest follows:

"The Nyetmaw River at this point is a small mountain brook, easily crossed without wetting one's feet, and the hills rise steeply back from the river. Splendid climax forest extends in an unbroken stand for here the natives have not yet brought fire. The common trees include oaks (several species, deciduous and evergreen), *Rhododendron magnificum* (a large tree reaching a height of fifty feet and a diameter of a foot or more), a red-barked birch, a *Heptapleurum,* and a number of broad-leaf evergreen trees. Up on the ridges hemlock occurs and everywhere bamboo springs up where a fallen tree provides an opening. The undergrowth is not especially heavy but there is an abundance of ground cover. Shrubs include a number of species of *Rhododendron,* a *Berberis, Gaultheria, Vaccinium,* and other plants with palearctic affinities. In occasional openings where sunshine could strike through, a primrose, *Primula whitei,* was in bloom. Ample evidence of spring was to be seen although the calendar told us that it was midwinter.

"Everywhere the ground was damp; moss and ferns grew along the watercourses and about fallen logs and stones. In most places the forest canopy kept the ground well shaded and only where the bare limbs of deciduous trees predominated could one see much sky."

In his published report, Anthony (1941, p. 108) indicated that the three specimens of *brahma* (which he reported as *R. eha*) were taken from, "Traps set on logs, well above the ground." Data from his field notes, however, conflict with that statement. From those notes it is clear that only one of the three specimens was taken above the ground on logs; the other two were trapped on the ground, one from a well-worn runway along a bank. Besides the three specimens of *R. brahma*, Anthony took two specimens of *R. andersoni* (A.M.N.H. Nos. 115182 and 115183) at the Nyetmaw River camp, the only other species of *Rattus* taken from that locality.

The habitat and habits of *Rattus eha* are also poorly known, but available information suggests that populations of this species occur at higher elevations than do those of *R. brahma*. Commenting on specimens of *R. eha* from western China, Allen (1940, p. 1037) recorded that: "The collector's notes tell that three of the specimens were taken amongst alpine rocks at altitudes between 8,000 and 11,000 feet, one in scrub at 8,000 feet and one in forest at 11,000 feet. No doubt it is to some extent a tree climber, but the long slender feet indicate a preference for ground living." Anthony (1941, p. 108) took specimens of *R. eha* only in dark, wet, temperate forest at elevations of 9000 and 10,000 feet. He indicated that, "specimens were caught along the banks of streams, about rocky outcroppings, and, in some instances, in well-marked runways on the forest floor." Thus, populations of *R. brahma* and *R. eha* are apparently restricted to high elevations in cool, damp, temperate forests. Members of both species, as judged from trapping records, are predominantly terrestrial, although *R. brahma* may be semi-arboreal.

In contrast to the highland distributions of *Rattus brahma* and *R. eha*, populations of *R. fulvescens* occur mainly at lower elevations and in rain forest. In Burma samples of *R. fulvescens* that I studied were obtained from elevations of 626 feet (Dalu) to 5200 feet (Gangfang). Anthony (1941, p. 106) collected specimens in open, shrubby habitat along the Ngawchang River and at Gangfang. Farther west, specimens of *R. fulvescens* were obtained from Mansum, Gora, Pumsin, Tasu Bum, and Dalu in dense rain forest broken up by patches of bamboo or paddy fields (Carter, 1943). Specimens I have examined from western China are from elevations of 1700, 5000, and 8000 feet. More specific information regarding habits and habitat of *R. fulvescens* is unavailable to me.

DISCUSSION

Within the genus *Rattus* as it is currently defined (Ellerman, 1949), *Rattus brahma* is morphologically most closely allied to species in the "*niviventer* Group" and the "*eha* Group," two of the five groups assembled by Ellerman and listed under the subgenus *Maxomys*. Ellerman's concept of the *niviventer* group of species consisted of *R. coxingi* (with three subspecies), *R. niviventer* (with 20 subspecies), *R. huang* (monotypic), *R. fulvescens* (with 11 subspecies), *R. cremoriventer* (with 12 subspecies), and *R. beccari* (monotypic). Not all of the taxa, listed either as valid species and subspecies or as synonyms, associated with this group belong in it. Ellerman himself questioned the placement of several forms, such as associating the name, *moi*, with *Rattus coxingi*, for example. He also pointed out in a footnote (1949, p. 72) that another name, *osimensis*, questionably allocated in his list to a subspecies of *Rattus fulvescens*, had nothing to do with that species, and belonged in a different genus. The taxon is now correctly listed as the only species within the genus *Tokudaia* (Ellerman and Morrison-Scott, 1951, p. 558). My own research indicates that several other names, some now listed as synonyms, will eventually be reallocated, either to other species within the *niviventer* group or to forms outside that group. *Rattus brahma*, originally listed in the *niviventer* group as a subspecies of *R. fulvescens*, is one of these forms.

In my opinion, the name *brahma* cannot be associated with any names currently listed, either as valid taxa or as synonyms, in the *niviventer* group of species. Ellerman (1949, p. 85) suggested that *brahma* was very similar to *R. fulvescens lepturus*, a form indigenous to western Java. This estimate of affinity was based primarily on large teeth, soft pelage, and long tails, features common to specimens of both *brahma* and *lepturus*. I have examined series of *R. f. lepturus* and the two closely related forms, *R. f. maculipectus* of western Java and *R. fulvescens fraturnus* of southwestern Sumatra. The morphological affinities of these series are with *R. fulvescens* and not with *R. brahma*. Whether *lepturus* and the other forms that Ellerman listed as subspecies of *R. fulvescens* actually represent well-differentiated populations of *R. fulvescens* or whether they are species closely related to *R. fulvescens* is another question and one that will only be answered by a thorough systematic revision of that species.

My analysis of available data, primarily that obtained from skins and skulls, indicates that *Rattus brahma* is a valid species and that it is morphologically more closely related to *R. eha*, the sole occupant of Ellerman's "*eha* Group," than to any of the other species currently placed in the subgenus *Maxomys*, or to my knowledge, to any other known species of *Rattus*. Although *R. brahma* and *R. eha* differ conspicuously in size and in proportions of some external and cranial dimensions, the many morphological similarities between the two species suggest close affinity. Both have long, dense, soft, and spineless pelage; brownish orange or brownish yellow upper parts; whitish gray underparts; long, hairy, and penicillate tails; and three pairs of mammae. The two species differ conspicuously in size of skull and in a few cranial proportions, but they are closely similar in over-all configuration of the skull and in most proportions of the cranial dimensions that were measured. In fact, in the majority of its cranial features, the skull of *R. brahma* is a larger version of the skull of *R. eha*.

The geographic distribution and habitat of populations of *R. brahma* and *R. eha* are poorly known, but there is nothing in the available, meager data which negates close relationship between the two. For example, both occur in the high, rugged mountains of northeastern India and northern Burma. *Rattus eha* is known from farther west in the mountains of western China, but I would look for *R. brahma* in the same region. Furthermore, specimens of both species have been taken only from cool, moist, dense, temperate forests. Unfortunately there are insufficient data on other aspects of their ecology and habitus which can be used to evaluate relationships between *R. brahma* and *R. eha*.

Ellerman (1949) has recognized five groups of species within the subgenus *Maxomys:* the "*chrysocomus* Group," the "*niviventer* Group," the "*eha* Group," the "*bartelsi* Group," and the "*inflatus* Group." The available data on morphology and habitat of *R. brahma* suggest that within Ellerman's framework of clusters, *brahma* should be placed with *R. eha* in the "*eha* Group." This placement best expresses the morphological and probable phyletic affinities of *R. brahma*, according to my interpretation of available data. With this allocation I do not imply agreement with Ellerman's groupings of forms within the subgenus *Maxomys*. Taxa now listed in that subgenus are in need of critical systematic revision and Ellerman's groupings need to be tested with more data than was available to him.

At the present time, however, sorting taxa into assemblages within *Maxomys*, or within any of the other currently recognized subgenera of *Rattus* is not the primary focus in studying members of this large genus. The main question is: What are the species-boundaries of populations within *Rattus?* Answers to this question will provide a solid core of information that can be used to answer inquiries of broader scope. How many species of *Rattus* are there? What is the geographic, ecologic, morphologic, physiological, and genetic diversity of those species? And, what are the zoogeographic and possible phyletic relationships among them?

The species-limits of populations of *Rattus,* particularly those within the subgenus *Maxomys,* can be estimated by study of material now housed in museum collections. The data derive primarily from study of skins and skulls, and habitat and habits noted by collectors. As such, any conclusions as to their affinities will have to be tested with additional kinds of data when they become available. In the present paper I suggest that *R. brahma* is closely allied with *R. eha* rather than with any other species in the subgenus *Maxomys.* This suggestion should be tested with data obtained from study of other aspects of their biology, data from such sources as ecology, behavior, reproductive anatomy, serology, and karyology.

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