

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 170

**Systematics of
Oriental Pygmy Squirrels
of the Genera *Exilisciurus*
and *Nannosciurus*
(Mammalia: Sciuridae)**

by

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and Division of Biological Sciences
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Ann Arbor
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
December 17, 1985

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ABSTRACT

Heaney, Lawrence R. 1985. *Systematics of Oriental pygmy squirrels of the genera Exilisciurus and Nannosciurus (Mammalia: Sciuridae)*. Misc. Publ. Mus. Zool. Univ. Michigan, 170:1-58, figs. 1-16.—Multivariate analysis of cranial morphology does not support the current recognition of four previously described species of pygmy squirrels in the Philippines; all four are here considered to represent a single species, *Exilisciurus concinnus*. There is little geographic variation within the species, and no subspecies are recognized. *Exilisciurus concinnus* occurs only on islands separated from Mindanao by waters less than 120 m deep, which was the level to which sea level dropped during the late Pleistocene.

Analysis of qualitative characters indicates that the genus *Exilisciurus* is monophyletic, and contains three species, *E. concinnus*, *E. exilis*, and *E. whiteheadi*; its sister-group is *Nannosciurus melanotis*. Contrary to the set of relationships proposed by Moore (1959), these two genera constitute a monophyletic group. The genera *Sundasciurus* and *Prosciurillus* are closely related, but evidence indicates that *Sundasciurus* may be paraphyletic. The subtribe Hyosciurini should be discarded because it lacks defining characters. All Southeast Asian pygmy squirrels are members of the tribe Callosciurini.

Convergence in pygmy squirrels of qualitative characters due to the allometric constraints of dwarfing is considered to be likely; such convergence could lead to incorrect conclusions about phylogenetic relationships. To identify such convergence in the data set, a method is developed in which 1) an ecologically similar, same-sized reference species is selected, 2) characters shared by the reference and study species are examined and those correlated with and likely to result from allometric trends are removed, and 3) the amount of variation in the remaining characters due to allometry is estimated.

Key words: *Rodentia*, *Sciuridae*, *Southeast Asia*, *Philippines*, *zoogeography*, *allometry*.

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INTRODUCTION

The sciurid fauna of the island archipelago of Southeast Asia is the most diverse of any in the world, with well over 50 species recognized. Among the most distinctive in this assemblage are the pygmy squirrels of the genera *Nannosciurus* and *Exilisciurus*. Adult least pygmy squirrels (*Exilisciurus exilis*) from Borneo and adjacent small islands weigh only 15 g, making this the smallest species of squirrel in the world as measured by weight and second smallest by length of head and body (Medway, 1977; Emmons, 1979). A second species, the tufted pygmy squirrel (*E. whiteheadi*), is confined to montane forest above 1000 m on Borneo. The third species in the genus, the Philippine pygmy squirrel (*E. concinnus*), as defined below, is found in the southern Philippine islands. The black-eared pygmy squirrel (*Nannosciurus melanotis*), noteworthy for its striking black and white facial stripes, is widespread in the Malaysian subregion, with recognized subspecies on Borneo, Sumatra, Java, and several adjacent small islands.

The presence of *E. concinnus* in the Philippines is of zoogeographic interest because there are few sciurids found there, in spite of the high diversity of squirrels on the adjacent island of Borneo. In addition to *E. concinnus*, there are three species-groups (or perhaps three species) of diurnal squirrels of the genus *Sundasciurus* in the Philippines (Heaney, 1979). Two species-groups occur in the Palawan chain, and one group on Bohol, Leyte, Mindanao, Samar, and nearby smaller islands. Flying squirrels are represented by three species: *Hylopetes nigripes*, confined to the Palawan chain; *H. mindanensis*, apparently confined to Mindanao; and *Petinomys crinitus*, found on Mindanao and several adjacent islands (Taylor, 1934; Rabor, 1939; Heaney and Rabor, 1982). This depauperate sciurid fauna probably represents invasions of the Philippines by a few species since the mid-Pleistocene, and it therefore presents the opportunity for unravelling part of the complex history of the Philippine mammalian fauna through analysis of the relationships of populations and the geographic barriers that isolate them.

This paper is concerned with three closely related problems. First, the limits of species of *Exilisciurus* and *Nannosciurus* will be defined, with special attention given to the poorly understood Philippine taxa. Second, patterns of relationships of Philippine populations will be compared with the hypothesized late Pleistocene geographic history of the Philippines, in an attempt to elucidate the factors affecting the zoogeography and speciation of mammals in the Philippines. Third, the relationship of the two genera of pygmy squirrels to each other and to other genera of Oriental squirrels will be considered, to determine if they represent a monophyletic or polyphyletic group.

METHODS AND MATERIALS

Specimens referred to below are housed in the American Museum of Natural History (AMNH), British Museum (Natural History) (BM(NH)), Delaware Museum of Natural

History (DMNH), Field Museum of Natural History (FMNH), Museum of Comparative Zoology, Harvard University (MCZ), Rijkmuseum van Natuurlijke Historie (RMNH), University of Illinois Museum of Natural History (UIMNH), University of Michigan Museum of Zoology (UMMZ), and United States National Museum of Natural History (USNM). External measurements were taken from the collectors' specimen labels. I took cranial measurements with dial calipers graduated to 0.05 mm. Most measurements are adapted from DeBlase and Martin (1974), are shown in Fig. 1, and are defined as follows:

Condylbasal length (A in Fig. 1): anteriormost edge of premaxillae to posteriormost projection of occipital condyles.

Interorbital breadth (B): least distance dorsally between the orbits, anterior to the postorbital process.

Zygomatic breadth (C): greatest distance between the outer margins of the zygomatic arches.

Mastoid breadth (D): greatest width of skull including mastoids.

Nasal length (E): anteriormost point of nasal bones to posteriormost point, taken along midline of skull.

Anterior nasal breadth (F): greatest width across the nasals, usually at the anteriormost lateral margins.

Rostral length (G): from anteriormost point of nasal bones at midline to anteriormost point of orbit.

Rostral depth (H): from ventral point of maxillary-premaxillary suture at midline to closest point on dorsal surface at midline.

Orbital length (I): from anteriormost point in orbit to posteriormost point in orbit.

Maxillary toothrow (J): alveolar length of maxillary toothrow, including P³ when present.

Palatal breadth (K): breadth taken at labial alveolar margins of P¹.

Diastema (L): posterior margin of alveolus of incisors to point at midline medial to anterior alveolar margins of first upper cheek teeth.

Unless stated otherwise, all descriptions refer to adults, defined as those individuals having all permanent teeth in place and exhibiting some wear. Specimens of *E. concinnus* were grouped into ten operational taxonomic units (OTUs). Each OTU consisted of all specimens from a given island, except those from Mindanao, which were divided into four groups comprising the following provinces: Misamis Occidental + Zamboanga del Norte + Zamboanga del Sur; Bukidnon + Lanao del Norte + Lanao del Sur; Cotabato + Cotabato del Sur + Davao City; and Davao Oriental. Numbered OTUs in Table 1 and Figs. 5 and 6 refer to these groupings. Sexual dimorphism in crania of adults was tested for by Student's t-tests on each measurement for all males and females of *E. concinnus* from Mindanao. Only one measurement (rostral length) showed significant dimorphism, and that at the .043 level. Given the small observed difference between means for males and females (less than 1.5% in all cases), it was decided that such a result could not be taken as convincing evidence of dimorphism. Thus, the sexes were lumped for all analyses.

Univariate and multivariate analyses were carried out using programs in the University of Michigan Interactive Data Analysis System (MIDAS). The principal components analyses of log-transformed measurements were based on covariance matrices. The Wagner Tree was generated using Wagner 78, described by Kluge (1976) and Carleton (1980). The program was run repeatedly with taxa entered in different order to determine the shortest tree.

The 120 m bathymetric line in Fig. 13 was estimated from hydrographic charts in the 90,000 Series from the United States Defense Mapping Agency, Washington, D. C. The scale of the maps varies from 1:20,000 to 1 to 402,000; most are 1:100,000.

SYSTEMATIC ACCOUNTS

Exilisciurus Moore, 1958

1958. *Exilisciurus* Moore, Amer. Mus. Novitates 1914:4-5. Type species: *Sciurus exilis* Müller, 1838.

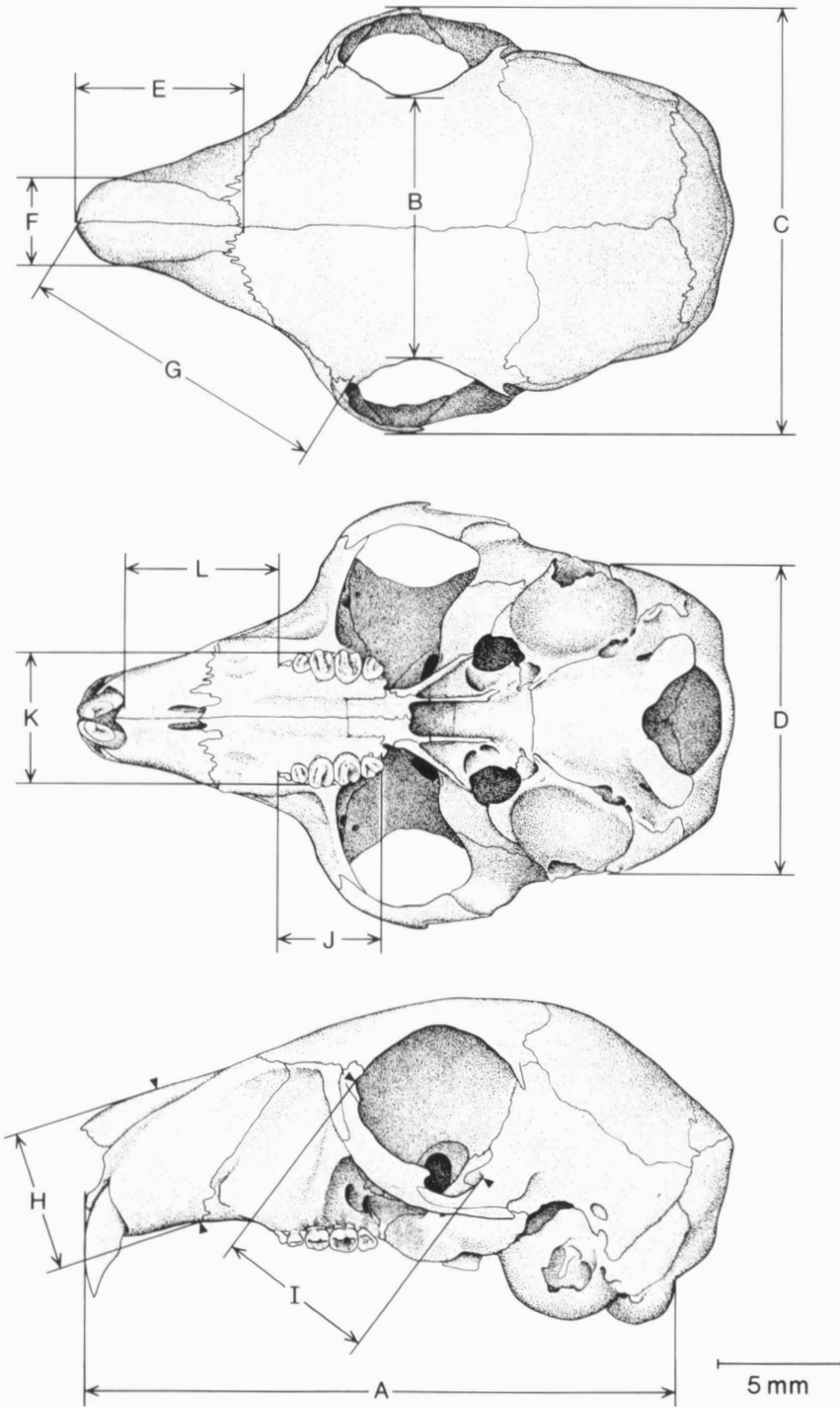


FIG. 1. Skull of *Exilisciurus concinnus* (DMNH 4539 from Dinagat) showing the measurements used in this study; for measurement names and definitions, see Methods and Materials.

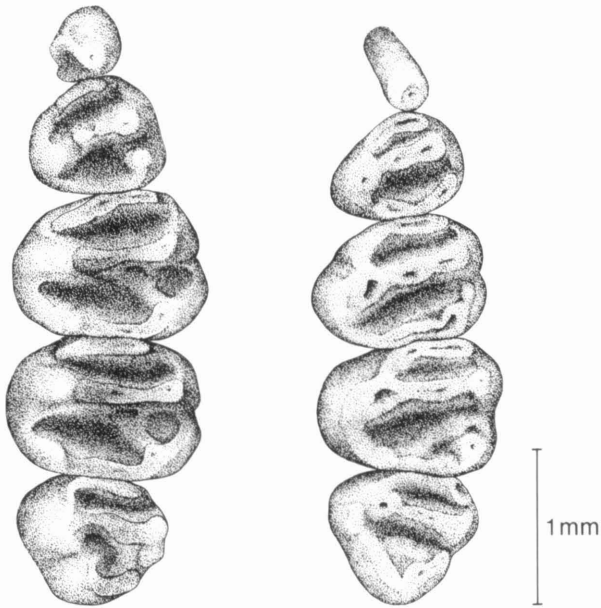


FIG. 2. Left maxillary toothrow of *Nannosciurus melanotis* (at left; USNM 121496 from Java) and *Exilisciurus exilis* (at right; USNM 196629 from Borneo). Occlusal surface at horizontal.

DISTRIBUTION.—BORNEO, Java, Sumatra, Banggi, Bangka, and Sinkep, and the southern Philippines, including Basilan, Biliran, Bohol, Dinagat, Leyte, Mindanao, Samar, and Siargao islands.

DIAGNOSIS.—Size small (Tables 1 and 2). Pelage plain, with no facial stripes; ear tufts present in one species (*E. whiteheadi*). Skull with proportionately globose brain case, and relatively long, narrow rostrum. Anterior opening of infraorbital canal with solid base, i.e., not opening ventrally as well as anteriorly. Postorbital process reduced. Orbital notch absent. Palate extending posterior to M^3 . Maxillary toothrows converging posteriorly. P^4 smaller than M^3 (Fig. 2). Ectopterygoid ridge well developed. Hypothenar pad on hind foot absent. Transbullar septa usually absent. Anterior half of baculum sharply upcurved, at about a 70° angle. Blade of baculum with dorsal edge serrated.

COMPARISONS.—*Exilisciurus* differs from *Nannosciurus* in that 1) all species lack facial stripes, 2) in two species the anterior opening of the infraorbital canal has a solid base, rather than having a short cleft into the base, 3) the postorbital processes are relatively reduced and the orbital notch absent, 4) the palate does not extend as far beyond M^3 , 5) P^4 is smaller than M^3 , rather than equal, 6) the maxillary toothrows converge posteriorly, rather than being nearly parallel, 7) the maxillary-premaxillary suture does not touch the top of the infraorbital foramen, 8) the outer plantar pad on the hind foot is absent, rather than present but reduced, 9) the dorsal surface of the bacular blade is serrated rather than even, and 10) transbullar septa are absent, rather than usually present. In addition to the great difference

TABLE 1
CRANIAL MEASUREMENTS OF *EXILISCIURUS*, *NANNOSCIURUS*, *PROSCIURILLUS*,
AND *SUNDASCIURUS* (MEAN \pm STANDARD DEVIATION)

	N	Condylolbasal length	Interorbital breadth	Zygomatic breadth	Mastoid breadth	Nasal length	Nasal breadth	Rostral depth	Rostral length	Orbital length	Maxillary toothrow length	Palatal breadth	Diaema length
<i>E. concinnus</i>													
1. Basilan	5	23.7 \pm 0.44	10.3 \pm 0.25	16.8 \pm 0.34	11.9 \pm 0.31	7.9 \pm 0.50	3.6 \pm 0.19	5.3 \pm 0.24	13.1 \pm 0.35	6.3 \pm 0.16	3.6 \pm 0.16	4.9 \pm 0.17	6.3 \pm 0.17
2. Zamboanga	11	24.7 \pm 0.38	10.5 \pm 0.30	17.5 \pm 0.30	12.4 \pm 0.19	8.3 \pm 0.48	3.5 \pm 0.28	5.9 \pm 0.18	13.8 \pm 0.32	6.4 \pm 0.18	3.7 \pm 0.17	5.1 \pm 0.25	6.7 \pm 0.21
3. Lanao	16	24.8 \pm 0.38	10.6 \pm 0.25	17.3 \pm 0.37	12.3 \pm 0.30	8.2 \pm 0.33	3.6 \pm 0.18	5.9 \pm 0.20	13.8 \pm 0.39	6.3 \pm 0.12	3.7 \pm 0.09	4.9 \pm 0.18	6.9 \pm 0.22
4. Catabato	24	24.1 \pm 0.64	10.5 \pm 0.37	17.1 \pm 0.55	12.4 \pm 0.39	8.0 \pm 0.42	3.6 \pm 0.19	5.7 \pm 0.21	13.6 \pm 0.57	6.2 \pm 0.20	3.7 \pm 0.21	4.9 \pm 0.19	6.5 \pm 0.26
5. Davao Oriental	6	24.5 \pm 0.35	10.3 \pm 0.36	16.8 \pm 0.37	12.3 \pm 0.13	8.2 \pm 0.41	3.8 \pm 0.47	5.6 \pm 0.12	13.1 \pm 0.51	6.2 \pm 0.18	3.6 \pm 0.05	4.8 \pm 0.18	6.5 \pm 0.39
6. Siargao	3	23.0	10.3	16.7	12.4	8.0	3.8	5.2	12.2	6.2	3.4	4.7	6.0
7. Dinagat	10	23.6 \pm 0.38	10.5 \pm 0.34	16.8 \pm 0.48	12.1 \pm 0.18	7.9 \pm 0.32	3.6 \pm 0.15	5.6 \pm 0.31	12.7 \pm 0.16	6.3 \pm 0.18	3.6 \pm 0.16	4.8 \pm 0.16	6.4 \pm 0.21
8. Bohol	2	24.8	11.3	17.7	12.5	7.4	3.5	5.8	13.3	6.4	3.6	5.0	6.3
9. Leyte	3	22.9	10.8	--	11.9	7.7	3.4	5.4	12.9	6.1	3.4	4.8	5.9
10. Samar	2	22.7	10.7	16.3	12.0	6.9	3.4	5.9	12.8	6.4	3.5	4.8	5.9
<i>E. exilis</i>	18	20.2 \pm 0.52	9.6 \pm 0.31	14.5 \pm 0.52	11.05 \pm 0.33	6.8 \pm 0.46	2.9 \pm 0.25	4.9 \pm 0.25	12.0 \pm 0.55	5.3 \pm 0.20	3.2 \pm 0.11	4.2 \pm 0.11	5.4 \pm 0.32
<i>E. whiteheadi</i>	28	23.2 \pm 0.67	11.4 \pm 0.34	17.5 \pm 0.57	11.7 \pm 0.28	7.5 \pm 0.51	3.2 \pm 0.18	5.6 \pm 0.25	14.4 \pm 0.49	5.8 \pm 0.19	3.6 \pm 0.14	4.6 \pm 0.14	6.3 \pm 0.30
<i>N. melanotis bancanus</i>	11	21.4 \pm 0.34	10.0 \pm 0.20	16.0 \pm 0.25	11.7 \pm 0.24	7.6 \pm 0.52	3.3 \pm 0.13	5.7 \pm 0.14	11.9 \pm 0.21	6.2 \pm 0.12	3.1 \pm 0.08	4.5 \pm 0.12	5.2 \pm 0.15
<i>N. melanotis borneanus</i>	13	21.8 \pm 0.53	10.3 \pm 0.38	16.3 \pm 0.46	11.9 \pm 0.29	7.5 \pm 0.40	3.3 \pm 0.20	5.5 \pm 0.21	12.3 \pm 0.49	6.1 \pm 0.11	3.1 \pm 0.16	4.5 \pm 0.15	5.5 \pm 0.21
<i>N. melanotis melanotis</i>	3	21.7 \pm 0.31	9.8 \pm 0.25	16.3 \pm 0.32	12.0 \pm 0.58	7.7 \pm 0.40	3.2 \pm 0.15	5.3 \pm 0.17	11.7 \pm 0.40	6.1 \pm 0.10	3.3 \pm 0.58	4.5 \pm 0.15	5.4 \pm 0.12
<i>P. leucomis</i>	12	40.8 \pm 0.88	17.5 \pm 0.59	27.6 \pm 0.54	19.1 \pm 0.46	12.8 \pm 0.45	6.7 \pm 0.33	10.3 \pm 0.32	20.2 \pm 0.57	12.7 \pm 0.37	7.6 \pm 0.31	9.7 \pm 0.32	9.5 \pm 0.53
<i>S. jentucki</i>	21	31.8 \pm 0.99	12.1 \pm 0.54	21.3 \pm 0.56	15.6 \pm 0.30	10.9 \pm 0.43	4.8 \pm 0.27	7.0 \pm 0.23	14.4 \pm 0.53	11.6 \pm 0.35	6.1 \pm 0.20	7.6 \pm 0.30	7.9 \pm 0.45
<i>S. temis</i>	7	33.6 \pm 0.60	12.7 \pm 0.6	22.0 \pm 0.51	16.3 \pm 0.31	11.1 \pm 0.72	5.2 \pm 0.39	7.6 \pm 0.29	15.0 \pm 0.67	12.1 \pm 0.42	6.2 \pm 0.20	8.0 \pm 0.21	8.6 \pm 0.41

TABLE 2
EXTERNAL MEASUREMENTS AND WEIGHTS OF SOUTHEAST ASIAN PYGMY SQUIRRELS
(\pm STANDARD DEVIATION)

	N	Total	Tail	Hind Foot	Ear	Weight (N)
<i>E. concinnus</i>						
1. Basilan	6	159.8 \pm 9.0	71.8 \pm 7.3	26.2 \pm 1.9	10.2 \pm 1.2	-
2. Zamboanga	8	160.9 \pm 7.3	69.5 \pm 8.6	25.1 \pm 2.0	10.5 \pm 0.8	31.4 \pm 2.9 (4)
3. Lanao	14	160.9 \pm 4.2	71.7 \pm 3.5	26.5 \pm 1.2	11.4 \pm 0.6	-
4. Cotabato	25	161.6 \pm 10.1	70.2 \pm 9.4	25.0 \pm 1.8	10.5 \pm 1.1	34.8 (1)
5. Davao Oriental	5	153.0 \pm 8.9	60.5 \pm 5.4	25.8 \pm 1.6	11.0 \pm 1.0	-
6. Siargao	3	142.5	59.5	25.3	11.0	25.0 (2)
7. Dinagat	10	153.1 \pm 5.0	66.3 \pm 3.9	25.5 \pm 1.2	11.2 \pm 0.6	25.5 (1)
8. Bohol	0	-	-	-	-	-
9. Leyte	3	159.5	70.0	25.7	11.3	-
10. Samar	2	150.0	69.0	24.0	11.0	29.7 (1)
<i>E. exilis</i>	14	122.4 \pm 9.2	52.3 \pm 8.4	23.1 \pm 1.2	9.0	15 (2)
<i>E. whiteheadi</i>	23	149.7 \pm 8.1	65.4 \pm 7.4	24.1 \pm 2.4	12.6 \pm 1.9	22.1 \pm 4.6 (6)
<i>N. melanotis bancanus</i>	11	149.3 \pm 3.8	66.3 \pm 3.4	22.4 \pm 1.3	-	-
<i>N. melanotis borneanus</i>	13	147.1 \pm 5.1	65.3 \pm 5.0	23.3 \pm 0.9	-	-
<i>N. melanotis melanotis</i>	0	-	-	-	-	-

in size, *Exilisciurus* and *Nannosciurus* both differ from *Sundasciurus* and *Prosciurillus* in the following ways: 1) the rostrum is long relative to the brain case, 2) the basicranial flexion is greater, 3) the palate extends well past M^3 , rather than ending at or anterior to the posterior edge of M^3 , 4) the coronoid process of the mandible is low, almost absent, 5) the orbit is nearly as wide as long, rather than much longer than wide, 6) the zygomatic plate lies at an angle of 85° to 90° to the plane of the maxillary tooththrow alveoli, rather than about 75° , and 7) the metatarsal pads on the hind feet are reduced. For comparisons with other genera, see Moore (1959).

Exilisciurus concinnus (Thomas, 1888)
Philippine Pygmy Squirrel

1888. *Sciurus concinnus* Thomas, Ann. Mag. Nat. Hist., ser. 6, 6:407.
 1897. *Nannosciurus samaricus* Thomas, Minutes Zool. Soc. London, 15 June, p. 1. Redescribed 1898, Trans. Zool. Soc. London 14:389, pl. 30, fig. 2. Type from Samar, Philippines.
 1913. *Nannosciurus surrutilus* Hollister, Proc. U. S. Nat. Mus. 46:313. Type from Mt. Bliss, Mindanao, Philippines.
 1934. *Nannosciurus luncefordi* Taylor, Philippine Bur. Sci. Monogr. 30:373. Type from Saub, Cotabato Prov., Mindanao, Philippines.

HOLOTYPE: Adult female, BM(NH) No. 76.10.4.7, obtained at Isabela, Basilan Island, Philippines, by J. B. Steere. Skin in good condition, skull with right zygoma and rear of braincase damaged. Measurements of the holotype given (in mm) in the description are: head and body, 85; tail without hairs, 59; hind foot, 25.5; heel to front of last foot-pad, 11.4; heel to front of anterior digital pad, 18.4; ear (contracted), 4.8. Skull: basal length, 19.6; greatest breadth, 15; length of nasals, 7.1; breadth of nasals, 3.9; diastema, 6.3; length of tooth-series (P^4 to M^3), 3.8. Not examined; condition of specimen verified by P. D. Jenkins.

DISTRIBUTION.—Recorded throughout Mindanao, mostly at elevations ranging from 700 to 2000 m but also at scattered localities down to sea level; taken at elevations above 500 m on Bohol, Leyte, and Samar; found from 100 to 400 m on Basilan, Dinagat, and Siargao (Fig. 3); sighted at 700 to 920 m on Biliran (see "Ecology").

DIAGNOSIS AND COMPARISONS.—Largest member of genus (Tables 1 and 2), total length averaging 160 mm, condylobasal length 24.5 mm. Pelage plain, without facial stripes or ear tufts. Maxillary tooththrows parallel; suprabullar vacuity open (Fig. 4A). Differs from *E. exilis* in its larger size, shallower rostrum, large, open suprabullar vacuity (vs. closed), and bacular blade with serrations along entire length. Differs from *E. whiteheadi* in its larger size, relatively shorter and shallower rostrum, lack of ear tufts, and in having the bacular blade serrated along its entire length.

DESCRIPTION.—Fur dense and soft, generally dark brown with slight reddish tint. Dorsal fur with guard hairs and underfur distinct. The longest guard hairs are black for entire length; these are scattered at moderate frequency on dorsal surface, less common on sides, and rare on

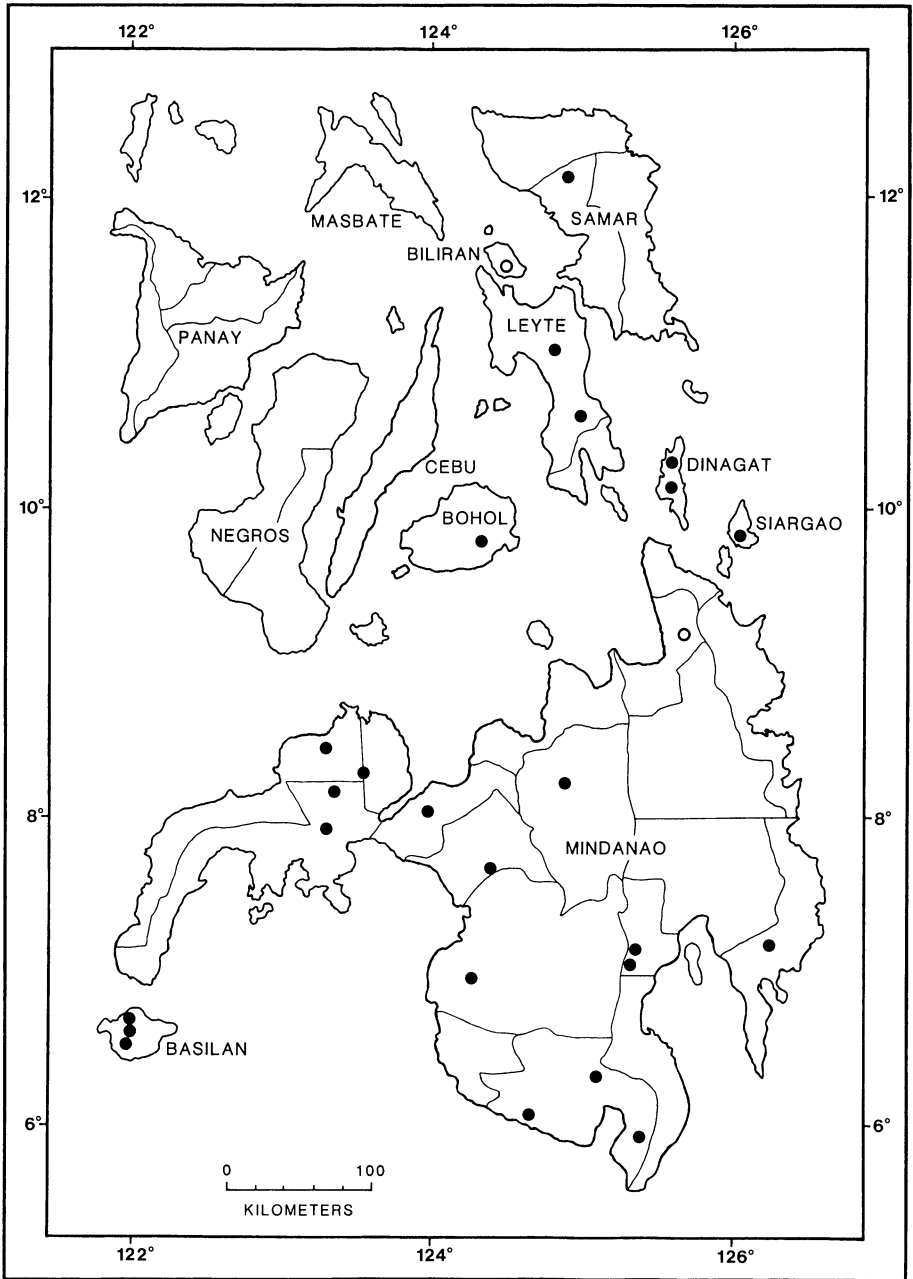


FIG. 3. Distribution of *Exilisciurus concinnus*. Solid dots = specimens examined; open circles = other records.

ventral surface. Most guard hairs agouti, straight, 6 to 8 mm long; tip of hairs black (distal ca. one-eighth to one-fourth of hair), with orange-brown band below (ca. one-eighth of hair), and a black base. Hairs on ventral surface with orangish band larger, somewhat paler, making the ventral surface appreciably paler than dorsal surface. Guard hairs normally covering underfur completely. Underfur hairs thinner than guard hairs, curly, usually entirely dark gray or black but sometimes with small orange-brown band near tip. Both guard hairs and underfur more sparse on ventrum, but covering surface of skin entirely except near eyes and mouth.

Mystacial vibrissae stiff, coarse, 10 to 27 mm long, usually black but some small vibrissae dark brown. Supraorbital and suborbital vibrissae present, but small (5 to 10 mm), few in number, and inconspicuous. Two small ulnar-carpal vibrissae on forelimbs, ca. 5 mm.

Eyes without any encircling band of bare skin or light hairs; surrounding hairs all typical (but short) agouti guard hairs. Pinnae covered with fine, short hairs, except for the concha and crus, which are naked.

Forefeet well-furred dorsally, hairs short, agouti. Forefeet bare of fur on palmar surface; interdigital and metacarpal pads large, morphology typical of "*Callosciurus* type" of Pocock (1923a), except that pollex is absent (Long and Captain, 1974). Dorsal surface of hind feet heavily furred, ventral surface well furred proximal to metatarsal pads (see detailed description below). Distal to metatarsal pad, hair on ventral surface restricted to fringe of short, stiff hairs along edge of foot. Claws stout, sharp, strongly curved and compressed, apparently pigmented lightly.

Tail heavily furred, slightly bushy. Guard hairs vary from ca. 12 mm long at base to 40 mm at tip, with up to six alternating bands of black and orange color zones, always black at tip. Most hairs at tip of tail entirely black.

Cranium (Fig. 4A) large for genus (Table 1), bone fairly thick. Rostrum elongate, about 58% of condylobasal length. Premaxillae with slight lateral swelling at about one-third of the way anterior of posterior edge of nasals, so that preorbital width is about twice breadth of tip of nasals in dorsal view. Zygomatic arches strong, widest at point where jugal flares dorso-laterally to form a sharp process that lies dorsal to the anterior root of the squamosal. Postero-ventral portion of jugal usually forming a sharply pointed process that lies ventral to the squamosal portion of the zygoma. Squamosal portion of zygoma short, curving from cranium ventrally and laterally in a smooth arc. Interorbital region broad, lateral edge forming smooth arc along orbit. Postorbital process short (about 1 mm), closely appressed to braincase. Braincase globose, arching smoothly from naso-frontal suture to parietal-interparietal suture, then curving less strongly ventrally. Temporal ridges not evident. Most sutures on braincase prominent in all age classes.

In lateral view, dorsal surface of rostrum straight from naso-frontal suture to anterior tip. Orbit nearly round, orbital notch not evident. Zygomatic plate inclined at ca. 90° angle to plane of maxillary toothrow alveoli, with ventral margin reaching to base of maxillary toothrow above

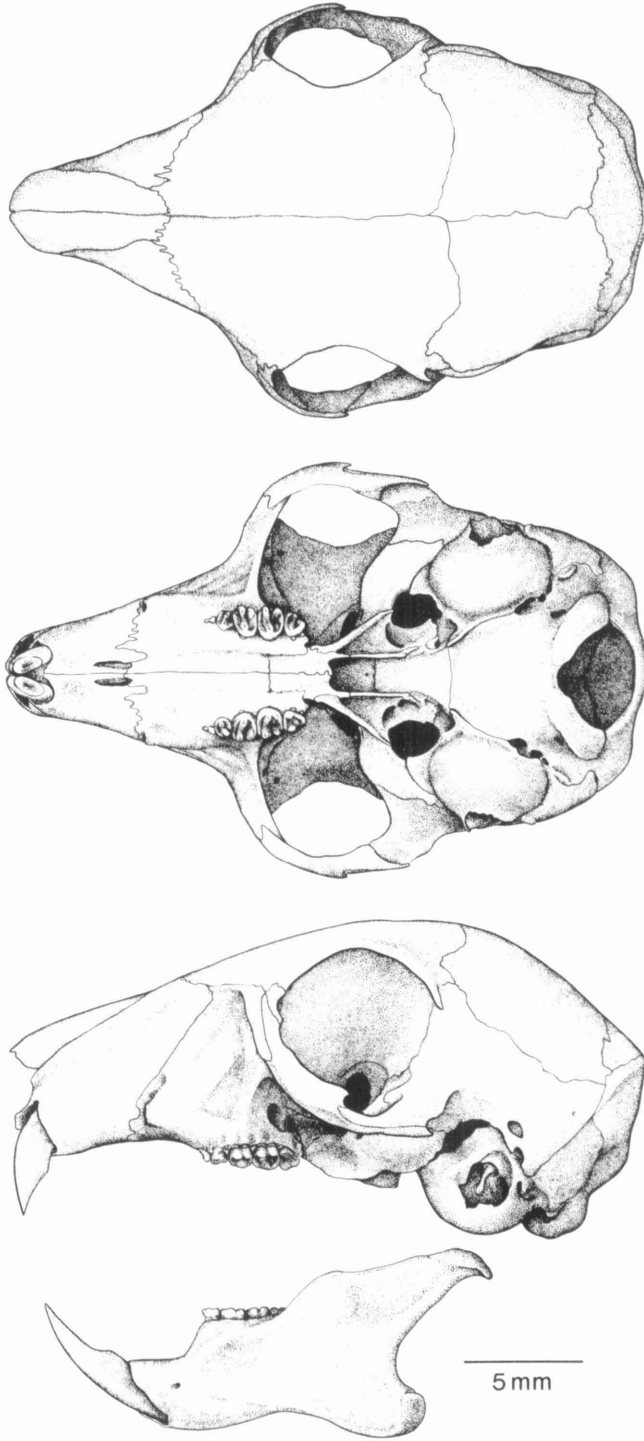


FIG. 4A. Dorsal, ventral, and lateral view of the skull and lateral view of the mandible of *Exilisciurus concinnus* from Dinagat (DMNH 4539). Approximately $\times 3$.

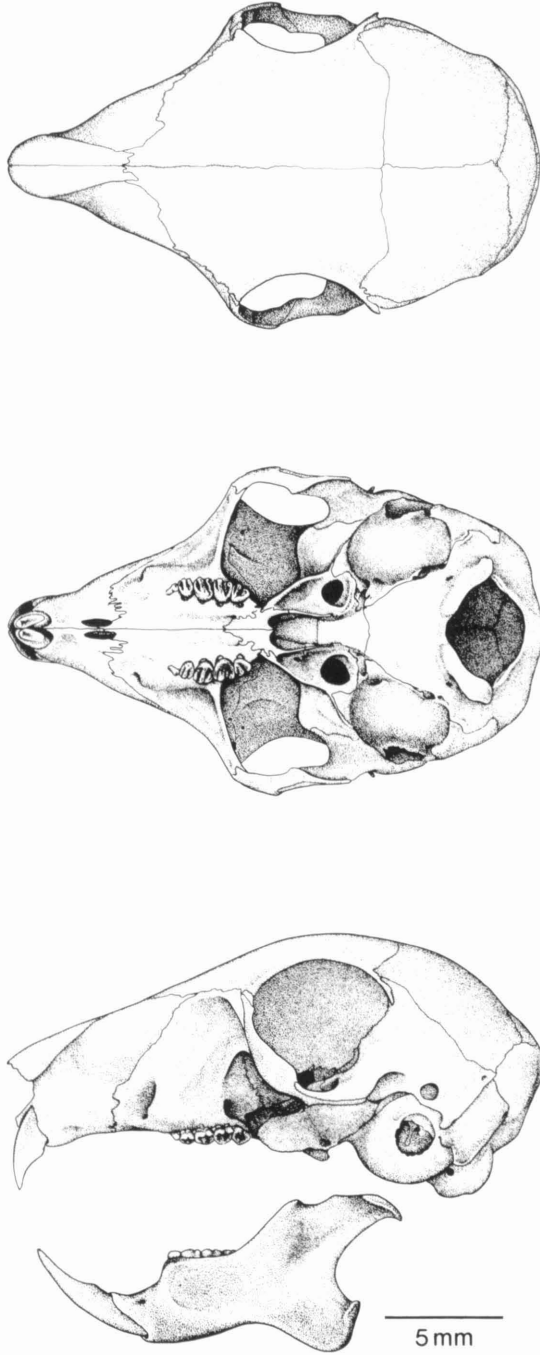


FIG. 4B. Dorsal, ventral, and lateral view of the skull and lateral view of the mandible of *Exilisciurus exilis* from Borneo (USNM 196629). Approximately $\times 3$.

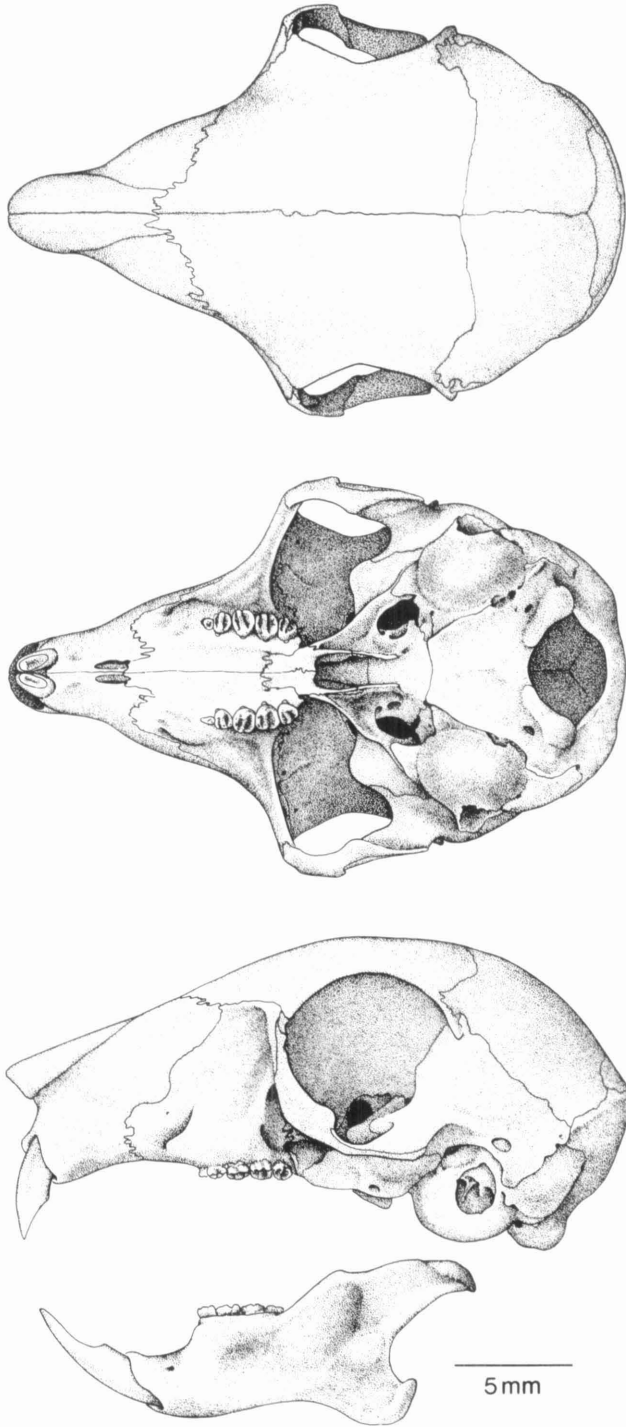


FIG. 4C. Dorsal, ventral, and lateral view of the skull and lateral view of the mandible of *Exilisciurus whiteheadi* from Sabah (USNM 292646). Approximately $\times 3$.

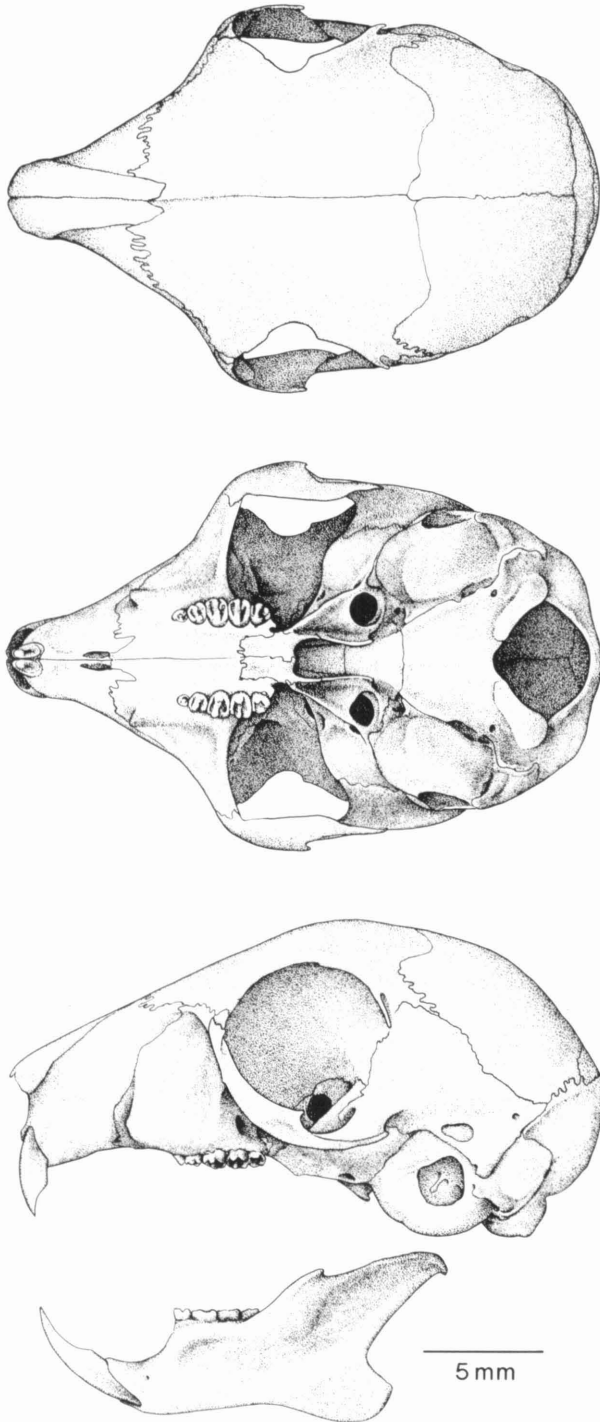


FIG. 4D. Dorsal, ventral, and lateral view of the skull and lateral view of the mandible of *Nannosciurus melanotis* from Java (USNM 121496). Approximately $\times 3$.

M¹. Masseteric tubercle much reduced, represented mostly by roughened area on surface of maxillary above infraorbital canal. Suprabullar vacuity large. Auditory bullae small but globose, compressed laterally in anteroposterior plane.

Nasolacrimal foramen minute. Posterior end of infraorbital canal very low, dorsal to M², slightly posterior to ventral base of zygomatic plate. Sphenopalatine foramen small, lying above M³, just posterior to infraorbital canal, separated by ca. 0.5 mm strut of bone. Optic foramen fused with sphenopalatine foramen, large, ovoid with long axis dorsoventral. Sphenoidal fissure large, ovoid with long axis dorsoventral, obscured in lateral view by alisphenoid capsule. Foramen ovale circular, large (slightly less than half diameter of bulla).

Incisors strongly procumbent, with distal tip nearly as far forward as anterior tip of nasals. Anterior surface smooth, yellow. Maxillary toothrow short, teeth small. P³ very small, unicuspid, diameter one-third that of P⁴. P⁴ with single transverse ridge, oriented with labial end of ridge axis ca. 15% forward of lateral plane. Molars typical of callosciurines, but very low-crowned. M² largest molar, slightly larger than M¹, diameter one-third greater than M³. Occlusal surface of maxillary toothrow oriented at ca. 20° angle to horizontal. This angle increases slightly from anterior to posterior.

DISCUSSION.—Philippine pygmy squirrels previously have been considered to belong to four distinct species. The diagnostic features for three of these taxa (*concinus*, *samaricus*, and *surrutilus*) were cited as variations in coat color, cranial size, and the presence or absence of P³. The fourth species (*luncefordi*), which is represented by a single specimen, was diagnosed on more substantial grounds, and is discussed below. With the exception of *luncefordi* (which overlaps with *surrutilus*), the three nominal taxa are allopatric: *concinus* was described from Basilan, *samaricus* from Samar, and *surrutilus* from Mindanao.

Thomas's (1888) description of "*Sciurus*" *concinus* emphasized that, relative to *E. exilis*, *concinus* is larger, has different foot-pad morphology, has a relatively shorter and broader rostrum, lacks P³, and has darker pelage. With the exception of P³, these characters are valid for the samples examined, and are discussed elsewhere. Thomas (1898) later noted that the holotype has a deciduous P⁴, and suggested that two permanent premolars may be typical. As noted below, P³ is absent in 29% of the skulls of *E. exilis* examined, whereas P³ or its alveolus is present in all adults of Philippine pygmy squirrels examined. Lawrence (1939) noted that all of the adults she obtained on Basilan possessed the P³, as did the one specimen obtained by Taylor (1934).

Thomas's (1897, 1898) description of "*Nannosciurus*" *samaricus* distinguished the new species from the holotype of *concinus* on the basis of "its longer fur, much more rufous coloration, and rounder molars." He noted that it "is perhaps merely the representative of *N. concinus* in Samar." I am unable to see any difference in average molar shape, and the pelage differences are minor, as he suggests; pelage variation is discussed below.

Hollister (1913) diagnosed "*Nannosciurus*" *surrutilus* as having darker, less reddish pelage and a longer, more slender skull than *concinus* of Basilan, especially having "the nasals and rostrum narrower and the braincase more elongate, (and) the audital bullae slightly larger." He noted that "this new form apparently needs no special comparison with *N. samaricus*, as the coloration is widely different from that described of the Samar animal." Contrary to Hollister's description, specimens from the area of the type locality of *surrutilus* have longer, broader nasals and rostra than specimens from Basilan (Table 1), and I detect no difference in braincase shape or bulla size. The principal components analysis of mean cranial measurements (discussed below) shows only that Basilan specimens are slightly smaller in mean size than those from Mindanao. Furthermore, as is discussed below, the pelage characteristics do not differ significantly from other populations of pygmy squirrels in the Philippines. Thus, there are no trenchant differences unique to this taxon.

Taylor (1934) described "*Nannosciurus*" *luncefordi* on the basis of a single specimen from about sea level in Saub, Cotabato (del Sur) Province, Mindanao. No specimens have been referred to this species subsequently. The holotype (UIMNH 33398) consists of the skull and skin of a young adult male; my estimate of its age is based on the unfused basisphenoid-basioccipital suture, and molar teeth that show very little wear. The animal apparently was shot; a small hole pierces the left frontal, a larger hole is anterior to the left bulla, and the left bulla is shredded. The left zygomatic arch and right occipital condyle are also broken, and mostly missing.

Taylor listed the following as the primary diagnostic features of *luncefordi*, relative to *concinus*: 1) ear larger and more flattened; 2) tail distinctly less bushy, fur softer; 3) vibrissae shorter; 4) nasals distinctly broader; 5) bullae larger; and 6) molar teeth larger, with deep groove on labial side between the two major cusps. I am unable to see any difference between the holotype of *luncefordi* and a series of *E. concinns* in ear size or shape or vibrissae length. The tail of *luncefordi* is missing its tip; it is perhaps less bushy than average, but not substantially so. The nasals are damaged at the anterior tip, with a small notch missing and a small crack penetrating a short distance. This gives the nasals the appearance of being unusually broad, but my measurement of the anterior nasal breadth (3.8 mm) is well within the range of *E. concinns* (Table 1). The single remaining bulla is not appreciably different from those of a series of *E. concinns*.

The teeth of the *luncefordi* holotype show little wear. As a result, the tops of the cusps and transverse ridges stand in high relief above the basins between. This feature is typical of unworn teeth; as the teeth wear down, the basins become less prominent, and eventually disappear as the occlusal surface approaches the base of the tooth. The teeth of *luncefordi* are identical in configuration to those of young *E. concinns*.

My examination of the molars of *luncefordi* indicates that they are unusually large, as noted by Taylor, although the length of the total molar toothrow (3.8) is within the range of *E. concinns* (Table 1); thus, it is the breadth of the teeth that can be considered as potentially diagnostic.

Comparison with a series of seven *E. concinnus* suggests that the molars of *luncefordi* are at the upper end of the distribution of molar sizes. For example, the breadth of M¹ of *luncefordi* is 1.35 mm; the mean of M¹ breadth of seven *E. concinnus* is 1.19, with a range of 1.10 to 1.30 mm.

Thus, the only feature of *luncefordi* that is different from *E. concinnus* is molar breadth, and that feature appears to be simply at the large end of the range of normal variation. On the basis of these observations, it is likely that the lowland pygmy squirrels seen by Taylor and represented by the holotype of *luncefordi* are part of the same genetic population that is widespread at higher elevations. Accordingly, I list *luncefordi* as a junior synonym of *E. concinnus*.

Pelage variation in Philippine pygmy squirrels is relatively slight; it is, for example, much less conspicuous than that seen in the subspecies of *Nannosciurus melanotis*. The most conspicuous difference is the paler pelage exhibited by specimens from Basilan; however, this is apparent only on the average, since some specimens from Mindanao are as pale. The trend from palest to darkest dorsal pelage is Basilan; Mindanao and Siargao; Dinagat; and Leyte and Samar. Dinagat specimens are slightly more reddish than the others. Ventral pelage variation shows the same trend in darkness. Some Dinagat specimens show a wash of reddish-rusty orange color, especially on the throat, in contrast to a more generally grayish throat in other populations. Specimens from Leyte and Samar appear to have shorter dorsal pelage than those from elsewhere. However, some specimens from moderate to low elevations on Mindanao show the same condition, so it is not unique. I conclude that differences in pelage between populations of *E. concinnus* are slight and variable, and that specimens cannot be correctly assigned to their natal population on the basis of pelage.

The results of a principal components analysis (PCA) on cranial measurements (described more fully below; Table 3, Fig. 5) indicated that Philippine pygmy squirrels are consistently distinguishable from the species on the Sunda Shelf. The few specimens available from Basilan, Dinagat, and Samar are scattered in an apparently random pattern among those from Mindanao. There is greater variation within the Philippine squirrels than within any other species, but this appears to be at least partly an artifact of sample size. Two specimens from Siargao have higher loadings on the second axis than other *E. concinnus*, but are close to average on other axes.

The principal components analysis of group means (Fig. 6, Table 4) produced similar results. All populations of Philippine pygmy squirrels (including those from Siargao) cluster together on the first two axes; the four populations from Mindanao fall at one edge of the cluster, and those from other islands lie near them, with Siargao most distant. Again there is less variation within the Philippine populations than there is between other species, indicating the general similarity of Philippine pygmy squirrels.

The data presented here all indicate that the Philippine pygmy squirrels, regardless of geographic origin, form a cluster of similar populations that

is distinct from other species of pygmy squirrels. Because no consistent qualitative or quantitative differences were found between populations of Philippine squirrels, the hypothesis that they form more than one species cannot be accepted. I therefore regard populations previously referred to *E. concinnus*, *E. luncefordi*, *E. samarensis*, and *E. surrutilus* as a single species, *E. concinnus*.

Subspecies often are designated in widespread insular species. In this case, it would be possible to designate each island as having a distinct subspecies, with such differences as the slightly smaller size of the Siargao squirrels as a diagnostic feature. However, several arguments can be offered against this. 1) The same information could be conveyed simply by referring to the island of origin as would be carried by the subspecies name. 2) Individuals from any given population are not identifiable on the basis of color, size, or cranial proportions as belonging with certainty to a particular island population, and thus definition of the subspecies would be arbitrary. 3) Principal components analysis of group means (Fig. 5) indicates that there is little geographic pattern to cranial variation; for example, the Dinagat population is more similar to the Basilan than to the Siargao population. Thus, I choose not to recognize subspecies within *E. concinnus*.

ECOLOGY.—Lawrence (1939:67) found *E. concinnus* to be “rather common and not shy” on Basilan, where “their habit of running along fallen logs and whisking in and out of holes (was) reminiscent of chipmunks”. Hoogstraal (1951:43) stated that on Mt. McKinley, Mindanao, *E. concinnus* “inhabits older second growth and original forest (near 3000 ft.), and extends into the mossy forest to at least 6,400 feet”; at both places they frequently were heard chirping. At 1500 ft (460 m) near Burungkot, Cotabato Prov., Hoogstraal (1951:65) found pygmy squirrels to be abundant in forest where some cutting was taking place. Rabor (1977:244) stated that in western Mindanao they are often seen during daylight hours inside dense virgin forest where they climb on the trunks of large forest trees, and on the underside of smaller branches. When startled, they often were seen to run head-first down tree trunks and disappear among the root buttresses.

In early May 1984, I and another member of my field team each saw an *E. concinnus* on Biliran Island, at elevations of 700 m and 920 m, in recently logged primary dipterocarp forest, 3½ km south, 5½ km west of Caibiran. One animal was in a partially cleared area where logs were being sawed, at 06:15. It ran up then down a ca. 2 m high stump, ran across the ground for several meters, and then leapt a short distance into a pile of dead branches and disappeared. It produced a brief, high-pitched vocalization several times. Its movements were similar to those of a chipmunk (e.g., *Eutamias minimus*), but it appeared to hold its limbs out laterally further than chipmunks do. The second individual was seen during early-morning hours in similar, recently disturbed forest near a small clearing. It was seen only briefly as it climbed in a tangle of small vines at the edge of a ca. 15 m tree, about 8 m above ground.

SPECIMENS EXAMINED.—Total 126. PHILIPPINES: BASILAN: Abung Abung, 25 km S Isabela (1 AMNH); 15 km NE Malusa (= Maluso) (6 MCZ, 1 FMNH); near Isabela (3 USNM). BOHOL: Cantaub, Sierra Bullones (8 FMNH). DINAGAT: Surigao del Norte Prov.: Plaridel, Albor (1 DMNH); Balitbiton, Loreto (6 DMNH, 1 USNM); Kambinlio, Loreto (3 DMNH); Paragua, Esperanza, Loreto (1 DMNH). LEYTE: Leyte Prov.: Bulog Peak, Mt. Kabalanti-an, Mahaplog (1 DMNH); Ma-alugon, Buri, Mt. Lobi Range, Buraue (3 DMNH). MINDANAO: Bukidnon Prov.: Mt. Katanglad, Malaybalay, 4200 ft (1280 m) elev. (1 DMNH), 5800-6200 ft (1770-1890 m) elev. (3 FMNH); Cotabato del Sur Prov.: Mt. Tudut, Tugal, Glan, 1100-2100 ft (340-640 m) elev. (2 DMNH); Mt. Matutum, Balisong, Kablon, Tupi, 2700-5000 ft (820-1520 m) elev. (18 DMNH, 4 AMNH); Saub (1 UIMNH); Cotabato Prov.: Burungkot, Upi, 1500 ft. (460 m) elev. (5 AMNH); Davao City Prov.: east slope Mt. McKinley, 3020-5800 ft (920-1770 m) elev. (3 FMNH); Mt. Apo, east slope, Baclayan, 5400 ft (1650 m) elev. (1 FMNH); Davao Oriental Prov.: Mt. Mayo, Limot, Mati, 500-4000 ft (150-1220 m) elev. (7 DMNH); Lanao del Norte Prov.: Balintad, Munai (1 DMNH); Lanao del Sur Prov.: Piagayungan Mt., 300 Line Siwagat, Lumba Bayabao, 4000-5000 ft (1220-1520 m) elev. (9 DMNH); Piagayungan Mts., Saronayan, Lumba-Bayabao, 3500-4000 ft (1070-1220 m) (15 DMNH); Zamboanga del Norte Prov.: Mt. Malindang, Masawan, Mutia, 4400-7000 ft. (1340-2130 m) elev. (6 DMNH, 3 FMNH); Mt. Malindang, Gandawan, 5000 ft. (1520 m) elev. (1 FMNH); Mt. Malindang, Daapitan Peak, 6250 ft. (1900 m) elev. (1 FMNH); Gubat, Katipunan, 2500 ft (760 m) elev. (4 FMNH); Zamboanga del Sur Prov.: Mt. Sugarloaf, Tandasag Hill, Mid-salip, 1500-3000 ft (460-910 m) (8 DMNH); summit of Mt. Bliss, 5720 ft. (1740 m) (1 USNM). SAMAR: Western Samar Prov.: Mt. Capoto-an (1 FMNH); Matuguinao (1 FMNH). SIARGAO: Surigao del Norte Prov.: Osmeña, Dapa (3 DMNH).

ADDITIONAL RECORDS.—BILIRAN: Leyte Prov.: 3½ km S, 5½ km W Caibiran, 11° 32'N, 124° 32'E, elev. 700-920 m (sightings by Heaney, described above). MINDANAO: Agusan del Norte Prov.: Mt. Hilong-Hilong, 1350 m (Sanborn, 1953).

Exilisciurus exilis (Müller, 1838)

Least Pygmy Squirrel

1838. *Sciurus exilis* Müller, Tijdschr. Natuurl. Geschied. Physiol. 5 (1):148.
 1910. *Nannosciurus exilis relictus* Thomas, Ann. Mag. Nat. Hist., ser. 8, 5:387. Type from Banguey Island, Northeast Borneo.
 1928. *Nannosciurus exilis sordidus* Chasen and Kloss, Jour. Malay. Branch Royal Asiatic Soc. 6:44. Type from Long Temelan, Telen River, Middle East Borneo.

LECTOTYPE: The original description is based on two specimens; no lectotype has been designated. The first specimen reportedly was from Mount Singalang, Sumatra; it has been assigned RMNH no. 13318 (C. Smeenk, pers. comm.). It consists of a mounted skin and a cleaned skull,

was the specimen depicted by Müller and Schlegel in the 1841 plate, and was designated specimen "b" in Jentink's (1887) catalog of the RMNH collection. The second specimen, with the locality given as "In de bergachtige streken der laaut-landen op Borneo", interpreted by Medway (1977:99) to mean Tanah Laut (= Pleihari) district, South Kalimantan, Borneo has been assigned RMNH no. 13319. This specimen was designated "c" by Jentink (1888); the damaged, incomplete skull was extracted subsequent to the catalog by Jentink, but prior to 1951 (C. Smeenk, pers. comm.). An additional specimen listed by Jentink (1888), "d", as a cotype came from the Schwaner collection, not from the original type series, and so is unavailable for designation as a lectotype. Because 13318 is a member of the original series and is in better condition than 13319, I designate 13318 as the lectotype. As noted by Chasen and Kloss (1928) and Chasen (1940), no specimens have been taken on Sumatra and the locality is probably erroneous. I therefore follow Medway (1977) in considering Tanah Laut, South Kalimantan, to be the type locality.

DISTRIBUTION.—Stated by Medway (1977:99) to occur in nearly all parts of Borneo, chiefly at low elevations, although there are a few records in Sarawak from 750 to 1700 m, and possibly higher on Gunong Dulit. Also reported from Banggi Island, off the northeastern tip of Borneo (Chasen and Kloss, 1932). Early reports from Malacca and Sumatra are probably in error (Chasen and Kloss, 1928).

DIAGNOSIS AND COMPARISONS.—Smallest member of the genus, total length averaging 122 mm, condylobasal length 20.2 mm. Pelage plain, without facial stripes or ear tufts. Maxillary toothrows converging posteriorly; masseteric tubercle at anterior edge of infraorbital foramen with slight lateral projection; rostrum very deep at base; suprabullar vacuity closed; bacular blade not serrated along entire dorsal edge. Differs from *E. concinnus* in its smaller size, more strongly developed masseteric tubercle, relatively deeper rostrum, absence of suprabullar vacuity, and bacular blade serrated along only a portion of its length. Differs from *E. whiteheadi* in its smaller size, relatively shorter rostrum, closed suprabullar vacuity, and lack of ear tufts.

DESCRIPTION.—Smallest member of genus (Tables 1 and 2). Fur dense and soft, dorsally a medium brown with strongly rusty tint, venter paler, less rusty. Most guard hairs agouti, straight, 4 to 5 mm long, with short black tip, reddish-orange band (ca. one-eighth length of hair) near tip, black base. Longest guard hairs 8 to 10 mm, all black, scattered evenly over dorsal and lateral portions of body. Dorsal underfur slate gray, wavy, ca. 5 mm long, thinner than guard hairs, covered entirely by guard hairs when fur in normal position. Guard hairs on ventral surface thinner than on dorsum, pale yellowish-orange. Underfur as on dorsum, but guard hairs are sparser, so grayish tone evident on venter.

Mystacial vibrissae stiff, coarse, black or dark brown, 6 to 22 mm long. Supraorbital and suborbital vibrissae apparently present, but barely distinguishable from long guard hairs. Two to four small ulnar-carpal vibrissae present on some specimens, apparently absent on others.

Eyes with narrow encircling band of darkly pigmented bare skin, surrounded by band of very short, pale rust hairs. Pinnae covered with fine, short, rusty colored hairs, except concha and crus, which are naked. Forefeet and hindfeet as in *E. concinnus* (see also discussion of foot pads, below).

Tail heavily furred, but less bushy than other species in genus. Guard hairs shortest at base (ca. 9 mm), increasing in length gradually to tip (up to 24 mm long). Hairs at tip with up to nine alternating bands of black and orange, always black at tip. Tail much redder ventrally than dorsally.

Cranium (Fig. 4B) small for genus (Table 1), bone generally rather thin. Rostrum moderately long, about 58% of condylobasal length. Tip of rostrum narrow. Base of rostrum unusually deep. Premaxillae with prominent dorsolateral swelling, so that preorbital width is about three times that of anterior nasal breadth in dorsal view. Zygomatic arches moderately strong, widest where jugal flares laterally and dorsally to form a rounded process that lies dorsal to anterior terminus of squamosal. Posteroventral portion of jugal forming a small projection that lies ventral to squamosal portion of zygoma. Squamosal portion of zygoma very short. Interorbital region broad. Postorbital process minute, barely separated from braincase at tip. Braincase globose, similar to *E. concinnus*. Posterior margins of nasals in slight depression on dorsal surface of skull, due to swelling of premaxillae.

Zygomatic plate inclined at over 90° angle to plane of maxillary tooththrow alveoli, with ventral root terminating well above alveolar line of maxillary tooththrow, above anterior edge of M². Masseteric tubercle absent, roughened area for attachment of muscle barely apparent. Orbit nearly round in lateral view, orbital notch absent. Suprabullar vacuity walled by dorsal projection of bulla. Auditory bullae proportionately smaller and less globose than in congeners.

Palatal foramina short, slightly broader posteriorly than anteriorly. Nasolacrimal foramen minute. Posterior end of infraorbital canal low, dorsal to M² and ventral to ventral root of zygomatic plate. Sphenopalatine foramen, optic foramen, and sphenoidal fissure as in *E. concinnus*, but latter two separated by a narrower strut of bone. Foramen ovale small, ca. one-tenth diameter of bullae.

Incisors strongly procumbent, with distal tip slightly anterior to tip of nasals when skull rests on incisors and bullae; anterior surface smooth, yellow. Maxillary tooththrow short, converging posteriorly, teeth small. P³ minute, unicuspid, diameter less than one-fourth that of P⁴ (Fig. 2). P⁴ with single transverse ridge, which is oriented perpendicular to long axis of skull. M² largest tooth, slightly larger than M¹, diameter ca. one-third greater than M³. Occlusal surface of maxillary tooththrow oriented at 25° to 30° angle to horizontal, high on labial side, with angle increasing from anterior to posterior.

DISCUSSION.—Three subspecies have been recognized in the past: the nominate form from western Borneo, *sordidus* from eastern Borneo, and *retectus* from Banguey (= Banggi) Island, which lies off the northern coast

of Borneo. Medway (1977:99) considered *sordidus* to be a synonym of the nominate form on the basis of lack of consistency in having "the upperparts duller and more olive in tone and the cinnamon-rufous tinge (of the dorsum) much reduced" (Chasen and Kloss, 1928) relative to specimens from other parts of Borneo. Chasen and Kloss (1932:29) noted that *retractus* "is a shade less richly colored above and has the underparts rather more creamy in color." Their measurements (p. 62) indicate that *retractus* averages slightly larger than Bornean individuals (condylobasal length of adults 19.2 and 18.7, respectively). These differences seem slight to me, but I do not synonymize the two subspecies here because I have not seen specimens of *retractus*.

Contrary to the statement by Thomas (1888) that *E. exilis* typically possesses P³, I found P³ to be absent in four of fourteen (29%) adult skulls examined.

ECOLOGY.—Davis (1962:82) "found this squirrel to be quite common in both primary and old logged forest. It was most often seen in the lower story, but was also observed in the middle story, 40 feet or more above ground. Individuals were usually on the trunks of the smaller trees forming the middle story, less often on vines or the buttresses of large trees . . . Stomach contents of four individuals . . . taken in old logged forest . . . contained very finely divided plant tissue . . . Three of the four stomachs also contained minute ants, ranging from a few individuals . . . to about 40 per cent of the total food bulk . . . Of seven females collected between May 22 and August 10, two were pregnant . . . each (with) two young".

Conaway (1968) presented evidence of post-partum estrus in *E. exilis* on the basis of observations made at Quoin Coco Research Station, Quin Hill, near Tawau, Sabah. In July 1964 an adult female was "taken in a small globular nest located about 3 ft above the ground in the roots of a fallen tree. There were also three hairless young in the nest." The female was lactating, and had three recently implanted embryos measuring 2mm each. In December 1964 a second lactating female, who had three well-developed embryos, was captured in a nest. Two fully haired young squirrels were captured in the same nest. No other sciurids are known to have a post-partum estrus.

SPECIMENS EXAMINED.—Total 38. (All are from Borneo.) INDONESIA: KALIMANTAN: Batu Mt. (2 USNM); Birang River (3 USNM); Karangan River (1 USNM); Karong Mumus River (2 USNM); Laham (7 USNM); Mahakam River (1 USNM); Menganne River (3 USNM); Merah River (1 USNM); Ritan River (1 USNM); Sanggau (1 USNM); Segah River (9 USNM); Tandjong (= Cape Seglu) (1 USNM). MALAYSIA: SABAH: Kampong Lasing (1 USNM); Paring, elev. 1600 ft (490 m) (2 USNM); Ranau (2 USNM); 1 mi. (1.6 km) N Ranau (1 USNM).

ADDITIONAL RECORDS.—INDONESIA: KALIMANTAN: Mandurao; Camp 4 (between the Kayan River and Gunong Sandang); Long Pangian, Boelongean (on the Kayan River); Pipoh, Boelongean (on the Kayan River); Kampong Maroewe (on the Barito River) (Gyldenstolpe, 1920).

MALAYSIA: SARAWAK: Anyut, Sarebas (Hill, 1960); Bukar, Samarahan (Hill 1960); Kubaan, upper Tutoh River, elev. 2500 ft (760 m) (Tan, 1966); Gunong Pueh, elev. 5600 ft (1700 m) (Medway, 1977); Sula Balu, Gunong Dulit (Medway, 1977); Paku, Sarebas (Hill, 1960).

Exilisciurus whiteheadi (Thomas, 1887)
Tufted Pygmy Squirrel

1887. *Sciurus whiteheadi* Thomas, Ann. Mag. Nat. Hist., ser. 5, 20:127.

HOLOTYPE: BM(NH) No. 95.10.4.18. Type locality Mount Kina-Balu, North Borneo. Skin in good condition, skull with damaged nasals and rear of braincase missing. Measurements of the type given in the description as (in mm): head and body, 90; tail, without hairs, 53, with hairs, 87; hind foot, without claws, 24.5; ears, without hairs 7, with hairs 28; tip of nasals to center of fronto-parietal suture, 20; length of nasals, 7.5; interorbital breadth, 12; palatal length, 12; length of upper toothrow, 4.1. Not examined; condition of specimen verified by P. D. Jenkins.

DISTRIBUTION.—Recorded above 1000 m throughout northwestern Borneo, including Mt. Kinabalu, Trus Madi, and the hills southwest of Tenom at 4,000 ft (1220 m) in Sabah; the Merapok Hills, Gunong Mulu, Bukit Batu Song, Gunong Murud, the Kelabit uplands, Gunong Dulit, the Usun Apau, Gunong Penrisen, and Gunong Pueh in Sarawak; and Gunong Liang Kubang, Sungai Mandai, upper Sungai Kapuas, in West Kalimantan (Medway, 1977:99; see also "Specimens examined").

DIAGNOSIS AND COMPARISONS.—Moderate size for genus, total length averaging 149.2 mm, condylobasal length 23.2 mm; ears with long tufts of black and white hair; maxillary toothrows show slight convergence posteriorly; rostrum very long; supra-bullar vacuity large; anterior edge of infraorbital foramen not forming a laterally curving projection (Fig. 4C). Differs from *E. exilis* in its larger size, longer rostrum, large suprabullar vacuity (vs. closed), bacular blade with proportionately more serrations, and possession of ear tufts. Differ from *E. concinnus* in its smaller size, relatively longer and deeper rostrum, bacular blade with serrations absent from anterior portion of blade, and possession of ear tufts.

DESCRIPTION.—Size moderate for genus (Tables 1 and 2). Fur dense and soft, relatively long, dark brown dorsally, paler ventrally. Most guard hairs straight, 5 to 6 mm long, with short black tip, reddish-orange band (ca. one-eighth length of hair) near tip, and black base. Longest guard hairs ca. 15 mm long, all black, scattered evenly over dorsal and lateral surfaces of body. Dorsal underfur wavy, 6 to 7 mm long, usually slate gray but sometimes with narrow orange band near tip, covered entirely by guard hairs when fur in normal position. Guard hairs on ventral surface thinner than on dorsum, pale yellow or orange. Underfur on venter slate-gray, showing through guard hairs to give venter a grayish tone.

Mystacial vibrissae black, coarse, stiff, 5 to 33 mm long. Supraorbital and suborbital vibrissae present but inconspicuous. Twelve to 15 ulnar-carpal

vibrissae on ulnar surface of forearm, most black but some with white tip comprising up to one-half of four to five mm length.

Eyes with encircling narrow band of pigmented skin, surrounded by band of very short pale rusty hairs. Inner portion of pinna with sparse, very short hairs. All outer portions of pinna with long dense hair. Hair on rim of pinna black, usually ca. two mm long, but some hairs on dorsal rim of pinna 15 to 20 mm long. Back of pinna covered by white hair, usually two to three mm long, but some white hairs 15 to 25 mm long. The elongate hairs form a tuft that lies back onto body of museum study skins.

Forefeet and hindfeet as in *E. concinnus* (see also discussion of foot pads, below).

Tail heavily furred, moderately bushy. Color the same dorsally and ventrally. Guard hairs shortest at base of tail (ca. 15 mm), increasing in length to tip (ca. 30 mm). Hairs at tip black. Hairs on rest of tail with up to 5 alternating bands of black and orange, always black at tip.

Cranium (Fig. 4C) of moderate size for genus (Table 1), bone of moderate thickness. Rostrum long, ca. 63% of condylobasal length. Tip of rostrum moderately narrow. Premaxillae with dorsolateral swelling, but not as swollen as in *E. exilis*, so that preorbital width is about two and one-half times anterior nasal width. Zygomatic arches moderately strong, widest where jugal flares dorsolaterally to form rounded process that lies dorsal to anterior terminus of squamosal. Posteroventral portion of jugal forming a small projection that lies ventral to squamosal portion of zygoma. Squamosal portion of zygoma short. Interorbital region broad. Postorbital process very small, less than 1.5 mm long, barely separated from braincase at tip. Braincase globose, dome somewhat higher than in congeners. Temporal ridges not evident.

Zygomatic plate and orbit as in *E. exilis*. Masseteric tubercle greatly reduced, but roughened area for muscle attachment evident. Suprabullar vacuity open. Auditory bullae of moderate size and inflation, similar to *E. concinnus*.

Palatal foramina very short, widest at mid-length. Nasolacrimal foramen minute. Posterior end of infraorbital canal as in *E. exilis*. Sphenopalatine foramen, optic foramen, and sphenoidal fissure as in congeners. Foramen ovale moderately large, about one-third diameter of bullae.

Incisors strongly procumbent, with distal tip about even with tip of nasals when skull rests on incisors and bullae; anterior surface smooth, yellow. Maxillary toothrow short, converging slightly posteriorly, teeth small. P³ minute, unicuspid, diameter less than one-fourth that of P⁴. P⁴ with single transverse ridge, oriented with labial end of ridge axis ca. 10% forward of lateral plane. M¹ and M² about equal in width, M² longer. M³ about two-thirds diameter of M². Occlusal surface of maxillary toothrow oriented at ca. 20° angle to horizontal, high on labial side, with angle increasing slightly from anterior to posterior.

GEOGRAPHIC VARIATION.—There appears to be none.

ECOLOGY.—*E. whiteheadi* is an endemic species of montane forest in northern Borneo, with specimens known from 3,000 ft (915 m) to 9,800 ft

(3000 m) on Mt. Kinabalu. Davis (1958) reported collector's labels with the following notations: "In high jungle", "Big tree. One only, going up"; "tall virgin jungle". Thomas (1889) noted that this species is often seen running up and down the trunks of trees, apparently gnawing at their bark.

COMMENTS.—As noted by Davis (1958), P^3 is present in most individuals but is reduced in some and absent in others. My observations indicate that the tooth is absent in about 5% of 35 specimens.

SPECIMENS EXAMINED.—Total 39. MALAYSIA: SABAH: Kalawat Rest House, elev. 3600 ft (1100 m) (1 USNM); Kamborangah (1 USNM); Mt. Kinabalu, Bundu Tuhan, elev. 4200 ft (1280 m) (3 FMNH, 8 USNM); Mt. Kinabalu, Kiau, elev. 3100 ft (940 m) (1 MCZ, 1 USNM); Mt. Kinabalu, Lumu Lumu, elev. 5500 ft (1780 m) (6 MCZ, 2 USNM); Mt. Kinabalu, Tenompak, elev. 4500 ft (1370 m) (5 USNM); Mt. Kinabalu, no specific locality (1 AMNH, 1 FMNH, 3 USNM); Mt. Tibang (1 MCZ). SARAWAK: Fourth Division, Buya (1 FMNH); Kelabit Plateau, elev. 5000 ft (1520 m) (1 FMNH); Ula Kubaan, Ula Tutoh, elev. 3800 ft (1160 m) (1 FMNH); Ula Selio, elev. 3500 ft. (1070 m) (3 FMNH).

ADDITIONAL RECORDS.—MALAYSIA: SARAWAK: Mount Dulit, Baram, 3400-3500 ft (1040-1070 m) (Hill, 1960).

Nannosciurus Trouessart, 1880

1880. *Nannosciurus* Trouessart, le Naturaliste, p. 292. Type species: *Sciurus melanotis* Müller and Schlegel, 1841.

DISTRIBUTION.—Java, Sumatra, Borneo, and two small islands near Sumatra (Sinkep and Bangka), at elevations below 1,000 m.

DIAGNOSIS.—Size small. Pelage plain agouti, except for four prominent facial stripes and two postauricular patches. Rostrum with narrow (1 mm) bands of black hairs running from anterior dorsal tip of nares to corner of eye; a wider (2 mm) cream-colored band immediately below that extends beneath eye and expands behind eye into prominent light cream patch. Narrow (1 mm) black band immediately below, (but above mystacial vibrissae) with cream patch below, extending 5 mm to mouth. Back of ear (except leading edge) black, with black patch extending ca. 6 mm behind ear. Cream-colored fur at base of ear extending beneath black fur for equal distance. One transbullar septum usually present (Moore, 1959). Anterior ventral edge of infraorbital foramen with slight laterally bending projection, with small notch in base. Lateral lip of infraorbital foramen in contact with maxillo-premaxillary suture. Maxillary tooththrows parallel, teeth higher-crowned than in *Exilisciurus* (Fig. 2). P^4 and M^3 equal in size. Suprabullar vacuity very small or absent. Rostral length proportionately great. Postorbital process long. Palate extending past M^3 a distance equal to 1.5 times the diameter of M^3 . Orbit length approximately equal to width. Coronoid process of the mandible reduced. Plane of zygomatic plate about 85° to plane of maxillary tooththrow alveoli. Ectopterygoid ridge well developed. Plantar pads of hind foot reduced, with a small subsidiary pad

often present. Anterior half of bacular shaft curved sharply upward at about 70° angle. Bacular blade with even (non-serrated) dorsal surface.

COMPARISONS.—Differs from *Exilisciurus*, *Prosciurillus*, and *Sundasciurus* as noted above.

Nannosciurus melanotis Müller and Schlegel, 1841
Black-eared Pygmy Squirrel

1841. *Sciurus melanotis* Müller and Schlegel, in Temminck, Verh. nat. ges. Ned. overz. bezitt., Zool. (Mamm), pp. 87, 88 and 98, pl. 14, fig. 4, 5.

1838. *Sciurus soricinus* Waterhouse, Cat. Mamm. Zool. Soc., p. 46. *Nomen nudum, non vid.*, Anderson, Zool. Res. Exp. Yunnan, 1878:265.

LECTOTYPE: The correct citation for this species is Müller and Schlegel 1841, rather than Müller 1844, as has been done on occasion, because the plate in the 1841 publication contained a caption that designated the species as new, provided a suitable Latin epithet, contained locality data, and provided reference to specific specimens as a type series. The ten specimens were designated “a” through “j” by Jentink (1888); although he omitted reference to “a” and “c” as cotypes, Smeenk (pers. comm.) asserts that these were in the collection at the time that the description was written, and so should be considered part of the type series. Lyon (1906) referred to “a” (from Padang, western Sumatra), “c” (from Borneo), and “g” and “h” (from Java) as cotypes, and restricted the type locality to Java. I designate “h”, an adult female, now cataloged as RMNH 13338, as lectotype, because it was figured in the original description and accords with Lyon’s (1906) restrictions.

DISTRIBUTION.—As noted for genus.

DIAGNOSIS AND COMPARISONS.—As noted for genus.

DESCRIPTION.—Size moderate among Southeast Asian pygmy squirrels (Tables 1 and 2). The following description refers to the nominate subspecies; other subspecies are less reddish and slightly darker (see Lyon, 1906). Fur dense and soft, dorsally a reddish brown, ventrally pale orange-brown. Most guard hairs straight, 6 to 7 mm long, agouti, with black tip (ca. one-tenth length), orange band below (ca. one-eighth length); black band often continues to base, but on some hairs is broken by another small orange band. Longest guard hairs are black, 10 to 11 mm long, scattered evenly over dorsal and lateral surfaces of body, absent from venter. Dorsal underfur pale slate-gray, wavy, 5 to 6 mm long, often with pale orange band, ca. one-eighth length, below gray tip. Ventral hairs intermediate between dorsal guard hairs and underfur in thickness and waviness, ca. 6 mm long. Tip of hairs very pale orange-brown for ca. one-sixth length, pale slate gray at base. Gradation between ventral and dorsal/lateral fur types gradual.

Mystacial vibrissae stiff, coarse, black, 4 to 32 mm. Supraorbital vibrissae black, 10 mm, usually two; suborbital vibrissae 15 mm, usually three. Three white ulnar-carpal vibrissae usually present, 6 to 7 mm.

Prominent black and white facial stripes and postauricular patches present, described in generic diagnosis, above. Inner portion of pinna covered with soft, fine, medium-brown hairs, except concha, which is naked.

Forefeet as in *E. concinnus*. Hindfeet with metacarpal pads much reduced in relative size, hypothenar extremely small. Fur on limbs shorter than elsewhere, but otherwise similar.

Tail heavily furred, but only slightly bushy. Guard hairs shortest at base, 7 to 8 mm, increasing gradually to tip (up to 24 mm). Hairs at tip with up to seven alternating bands of black and pale orange-brown, always black at tip and base, often with only three bands. Hairs along most of tail with prominent pale band below black tip, giving tail prominent "frosted" appearance. Tail color slightly paler ventrally than dorsally.

Cranium (Fig. 4D) of moderate size for Southeast Asian pygmy squirrels, bone rather thin. Rostrum moderately long, about 57% of condylobasal length. Tip of rostrum moderately narrow. Premaxillae with slight dorso-lateral swelling, so that preorbital width is about twice that of anterior nasal breadth in dorsal view. Zygomatic arches moderately strong, as in *E. whiteheadi*. Interorbital region broad, with orbital notch large and conspicuous. Postorbital process reduced but not rudimentary, length one to two mm, sharply pointed. Braincase globose, frontals with dorsal swelling, highest point on skull just posterior to line between orbital notches.

Zygomatic plate inclined at about 85° angle to plane of maxillary toothrow alveoli, with ventral root extending nearly to alveolus of maxillary toothrow, anterior to posterior end of infraorbital canal. Masseteric tubercle moderately strong, projecting at ca. 30° angle to midline, with narrow cleft in base extending posteriorly. Lateral lip of the infraorbital foramen in contact with the maxillo-premaxillary suture. Orbit nearly round in lateral view. Suprabullar vacuity absent. Auditory bullae small but proportionately larger than in *Exilisciurus*, globose; a single septum usually present, with medial origin at level of basioccipital suture.

Palatal foramina short. Nasolacrimal foramen minute. Posterior end of infraorbital canal very low, dorsal to M², posterior to ventral root of zygomatic plate. Sphenopalatine and optic foramina and sphenoidal fissure as in *E. whiteheadi*. Foramen ovale of moderate size, about one-fourth diameter of bullae.

Incisors procumbent, but less so than in *Exilisciurus*. Anterior surface smooth, yellow. Maxillary toothrows short, approximately parallel. Teeth small, higher-crowned than in *Exilisciurus* (Fig. 2). P³ small, about one-third diameter of P⁴, with small antero-labial cusp and postero-lingual basin surrounded by continuous circumferential ridge. P⁴ molariform, about three-fourths diameter of M¹. M¹ and M² of equal width, but M¹ with greater antero-posterior breadth. M³ about three-fourths size of M¹, equal to P⁴. Occlusal surface of maxillary toothrow oriented at 15° to 20° angle to horizontal, with angle increasing from anterior to posterior.

ECOLOGY.—Virtually nothing is known of the ecology of this species. Lyon (1906) cited field notes by W. L. Abbott stating that it is locally abundant at times.

DISCUSSION.—Lyon (1906) described and provided a key to five of the six taxa now recognized as subspecies of *N. melanotis*. No attempt was made here to extend Lyon's observations (and Chasen and Kloss's description of an additional subspecies) because few additional specimens were available to me. The following subspecies are recognized currently:

- N. m. melanotis* Müller and Schlegel. Type locality: Java.
N. m. bancanus Lyon, 1906. Proc. Biol. Soc. Washington 19:55. Type locality: Klabat Bay, Banka Island.
N. m. borneanus Lyon, 1906. Proc. Biol. Soc. Washington 19:54. Type locality: Sanggau, West Borneo.
N. m. pallidus Chasen and Kloss, 1928. Jour. Malay Branch Roy. Asiatic Soc. 6:43. Type locality: Long Poehoes (= Putus), Middle-East Borneo.
N. m. pulcher Miller, 1902. Proc. Acad. Nat. Sci. Philadelphia 1902:153. Type locality: Singkep Island, Lingga Archipelago.
N. m. sumatranus Lyon, 1906. Proc. Biol. Soc. Washington 19:53. Type locality: Tarussan Bay, West Sumatra.

The distributions of the two subspecies on Borneo were discussed by Medway (1977:98).

SPECIMENS EXAMINED.—Total 41. *N. m. bancanus*. INDONESIA: BANGKA ID.: Klabat Bay (10 USNM); Tanjong Tedong (1 USNM). *N. m. borneanus*. INDONESIA: BORNEO: KALIMANTAN: Boentok, Barito River (1 MCZ); Kapuas River (1 USNM); Kapuas River, Pulo Saporu (1 USNM); Kapuas River, below Tyan (1 USNM); Karangan River (1 MCZ); Kendawangan River (1 USNM); Klumpang Bay (1 USNM); Landak River (5 USNM); Matan River (3 USNM); Pang Kallahan River (1 USNM); Sanggau (2 USNM); Sama River (1 USNM); Saratok River (1 USNM); Sempang River (2 USNM). *N. m. melanotis*. INDONESIA: JAVA: Tanjong Priok (near Batavia) (3 USNM). *N. m. pallidus*. INDONESIA: BORNEO: Karangan River (1 USNM). *N. m. pulcher*. INDONESIA: SINGKEP ID.: no specific locality (3 USNM). *N. m. sumatranus*. INDONESIA: SUMATRA: Tarussan Bay (1 USNM).

ADDITIONAL RECORDS.—MALAYSIA: SARAWAK: Mount Dulit, Baram; Ulu Paku, Sarebas; Gunong Sidong, Samarahan; Entawa, Samarahan (Hill, 1960).

ANALYSES

PRINCIPAL COMPONENTS ANALYSIS OF CRANIAL VARIATION IN *Exilisciurus* and *Nannosciurus*

A principal components analysis (PCA) of *Exilisciurus* and *Nannosciurus* cranial measurements was conducted to provide 1) a generalized, quantitative description of cranial variation in these genera, 2) an estimate of the distinctiveness of the populations of *Exilisciurus concinnus*, and 3) a quantitative description of the cranial differences between the species. In this analysis, all individuals having complete sets of measurements were in-

cluded. All measurements were converted to natural logarithms for the analysis.

GENERAL RESULTS.—Most variation (67%) was explained by the first axis (Table 3; Fig. 5). This axis shows moderate loadings for all twelve measurements; thus, axis I appears to be primarily a size axis.

The second axis, which accounts for an additional 13% of the total variation, primarily contrasts individuals with long orbits, long and wide nasal bones, and short diastemas, rostra, and molar toothrows, with those that have the converse. A plot of individuals on the second axis shows that it is *E. whiteheadi* and to a lesser extent *E. exilis* that are distinguished on this axis by low scores (Fig. 5).

The third axis accounts for an additional 6% of the variation. It contrasts individuals with broad interorbital regions and short nasals, maxillary toothrows, and diastemas with those with the converse; a plot of individuals on the axis indicates that it is *E. exilis* that has especially low scores on axis three.

DISTINCTIVENESS OF THE POPULATIONS OF *E. CONCINNUS*.—As shown in Fig. 5, there is substantial overlap among populations of *E. concinnus*. On the first axis, there is no discernable geographic pattern to individual scores. On axis 2 the two specimens from Siargao have high loadings, but all others again fall into a single cluster. If all of the populations from Mindanao are considered together, they encompass the range shown by nearly all other individuals. Thus, there is little evidence for significant geographic variation in this analysis.

DISTINCTIVENESS OF THE SPECIES.—As noted above, much of the total variation described by the analysis appears to be between, rather than within species (Fig. 5). Much of the variation on the first axis, which primarily indicates size differences, is between *E. exilis* and the other species, although specimens of *N. melanotis* have lower loadings than all but one *E. concinnus* and two *E. whiteheadi*. The second axis primarily distinguishes *E. whiteheadi*; its relatively long diastema and rostrum and moderately narrow nasal bones are conspicuous diagnostic characters. The third axis (not shown) tends to separate out *E. exilis*, but overlap between all species is substantial, and the variation within *E. concinnus* is especially great. Other axes add little additional discrimination.

The two species least distinguishable by these cranial measurements are *N. melanotis* and *E. concinnus*. The only consistent difference between them was on the first axis, i.e., size.

COMPARISON WITH *PROSCIURILLUS* AND *SUNDASCIURUS*.—In order to investigate the variation in skull shape that is associated with dwarfing in these pygmy squirrels, I conducted a second PCA of group mean measurements of pygmy squirrels, along with the same measurements of reference populations of *Prosciurillus leucomus*, *Sundasciurus jentinki*, and *S. tenuis*. Moore (1959) considered these two genera to be closely related to Southeast Asian pygmy squirrels, as is discussed below. I was interested in answering the questions, 1) what are the primary differences among the tree squirrels and pygmy squirrels in skull morphology, and 2) to what extent are these differences associated with size differences?

TABLE 3
RESULTS OF A PRINCIPAL COMPONENTS ANALYSIS¹
OF CRANIAL MEASUREMENTS (LOG-TRANSFORMED) OF 77 ADULT
EXILISCIURUS AND *NANNOSCIURUS*

Character	Axis			
	1	2	3	4
Condylobasal length	.33	-.04	-.10	-.07
Interorbital breadth	.20	-.26	.60	.05
Zygomatic breadth	.27	-.01	.24	.07
Mastoid breadth	.17	.12	.01	-.03
Nasal length	.27	.32	-.35	.65
Anterior nasal breadth	.33	.54	.26	-.51
Rostral depth	.26	.04	.24	.39
Rostral length	.31	-.42	.22	.18
Orbital length	.21	.37	.10	.12
Maxillary tooththrow length	.28	-.30	-.30	-.16
Palatal breadth	.27	.17	-.20	-.14
Diastema length	.46	-.31	-.36	-.23
Cumulative % variance	66.7	79.8	85.8	90.3
Significance level	.01	.01	.01	.01

¹A test of sphericity showed that there is significant variation (test statistic = 1700; 17 degrees of freedom; $p < .01$)

TABLE 4
RESULTS OF A PRINCIPAL COMPONENTS ANALYSIS¹
OF MEAN CRANIAL MEASUREMENTS (LOG-TRANSFORMED) OF 17 GROUPS
OF TREE AND PYGMY SQUIRRELS (DATA FROM TABLE 1)

Character	Axis		
	1	2	3
Condylobasal length	.28	.11	-.16
Interorbital breadth	.20	.43	.33
Zygomatic breadth	.23	-.14	.10
Mastoid breadth	.22	-.03	.15
Nasal length	.26	-.15	-.17
Anterior nasal breadth	.31	.02	.01
Rostral depth	.26	.28	.47
Rostral length	.17	.54	-.09
Orbital length	.41	-.57	.23
Maxillary tooththrow length	.40	-.11	-.24
Palatal breadth	.36	-.13	.06
Diastema length	.24	.18	-.68
Cumulative % variance	95.1	97.6	98.6
Significance level	.01	.01	.01

¹A test of sphericity showed that there is significant variation (test statistic = 851; 77 degrees of freedom; $p < .001$).

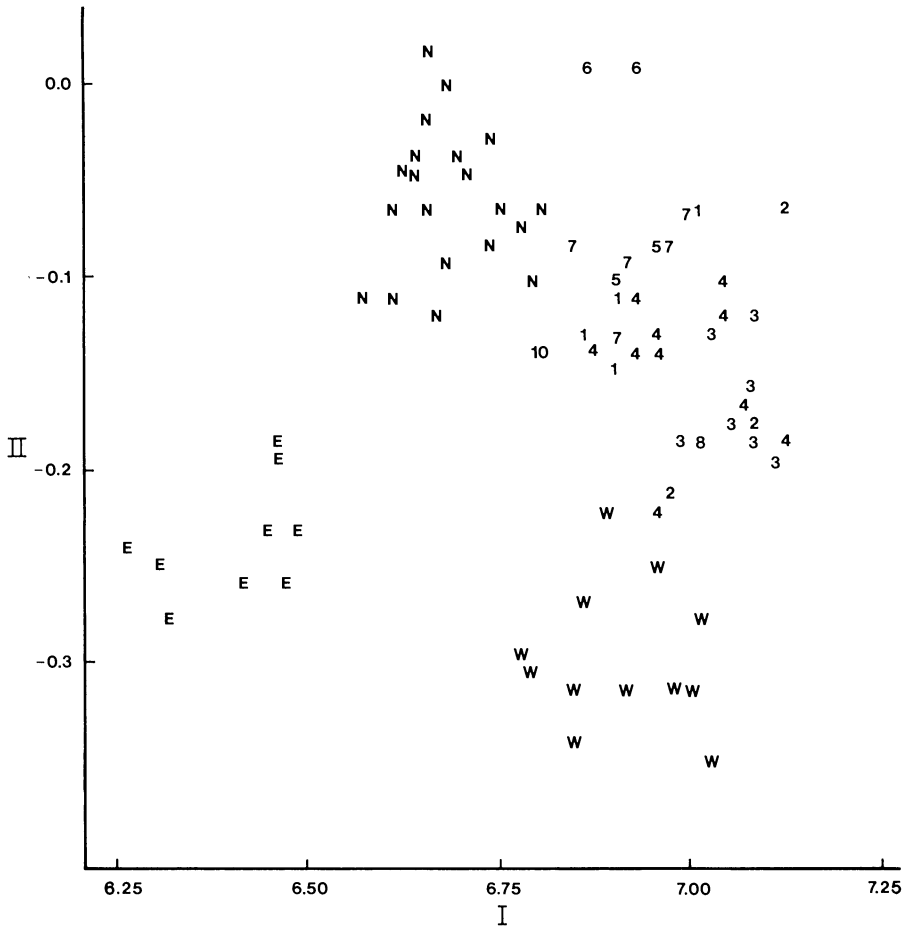


FIG. 5. Results of principal components analysis of cranial measurements of pygmy squirrels; each symbol represents the score of an individual on axes I and II (see text). N = *N. melanotis*; E = *E. exilus*, W = *E. whiteheadi*; 1 through 10 = *E. concinnus* (OTU numbers as in Table 1).

Results of the analysis (Table 4) indicate that 95% of the total variation exists along a single axis. All variables had similar, moderate to low loadings, indicating that this is a general, size-related axis. The second axis accounted for an additional 2.4%, and two subsequent axes added only an additional 1.75%.

Figure 6 shows that *P. leucomus*, *S. jentinki*, and *S. tenuis* had high scores on the first axis; this clearly is primarily a size axis. On no other axes do the tree squirrels differ consistently from the pygmy squirrels. The second axis describes another significant source of variation that contrasts the two species of *Sundasciurus* against *P. leucomus* and *E. whiteheadi*, with the other species being intermediate (Fig. 6). Loadings of variables on this axis (Table 4) indicate that the *Sundasciurus* have relatively long orbits, short rostra,

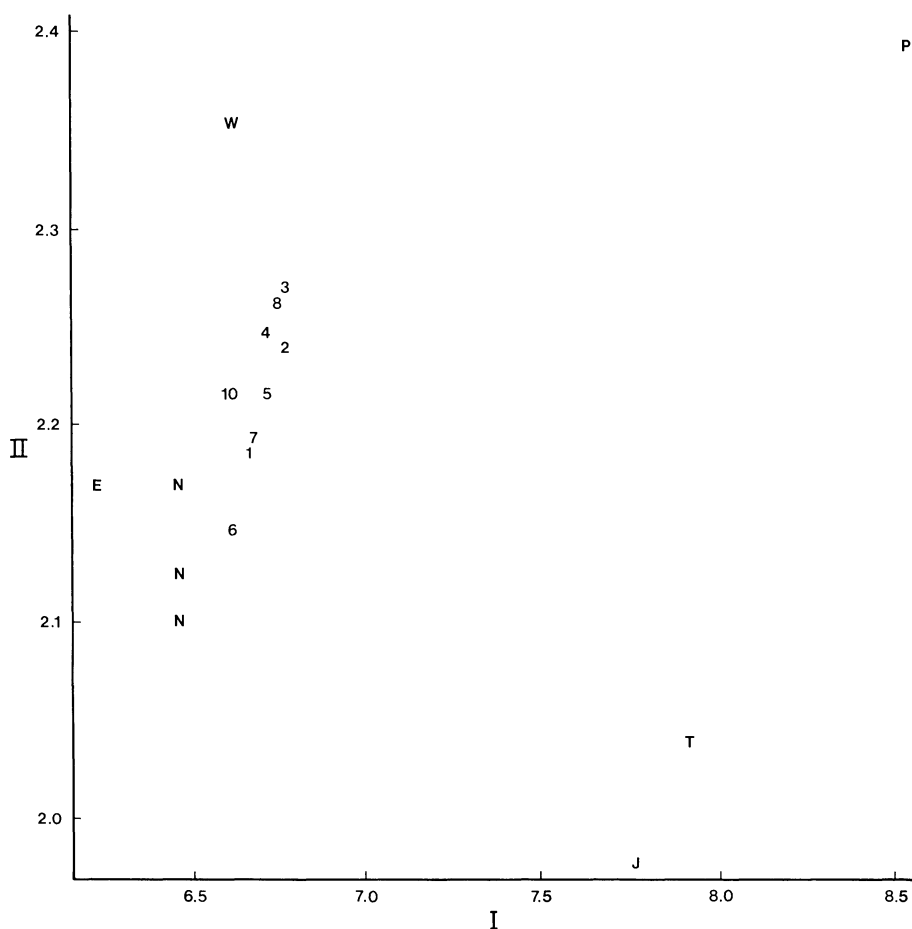


FIG. 6. Results of principal components analysis of cranial measurements of species means of pygmy and tree squirrels; each symbol represents the score of axes I and II (see text). Symbols as in Fig. 5, plus: P = *Prosciurillus leucomus*; J = *Sundasciurus jentinki*; T = *S. tenuis*.

and narrow interorbital regions; *P. leucomus* and *E. whiteheadi* have the converse. Obviously, these characters are not size-related.

RELATIONSHIPS OF THE SOUTHEAST ASIAN PYGMY SQUIRRELS

In his review of the classification of the diurnal squirrels (Sciurinae), Moore (1959) presented evidence for convergence in a variety of cranial characters in Oriental, African, and Neotropical pygmy squirrels. His conclusion that the pygmy squirrels from the three continents are not closely related is supported by a variety of data (Anthony and Tate, 1935; Hill, 1959; Long and Captain, 1974; Pocock, 1923a, 1923b), and is not disputed here. I also accept without reservation Hill's (1959) detailed

assessment of the close relationship of the one additional Southeast Asian pygmy squirrel, *Glyphotes*, with the *notatus* group of *Callosciurus*, rather than with *Nannosciurus* or *Exilisciurus*.

Moore (1959) suggested that *Nannosciurus* and *Exilisciurus* belong in separate subtribes within the tribe Callosciurini. He placed *Nannosciurus* in the subtribe Callosciurina, which included *Callosciurus*, *Sundasciurus*, *Glyphotes*, *Dremomys*, and several other genera, all of which occur on the Sunda Shelf or Southeast Asian mainland. He placed *Exilisciurus* in the subtribe Hyosciurina, which also includes *Hyosciurus*, *Prosciurillus*, and *Rubrisciurus*, all of which occur on Celebes. This taxonomic relationship seems in need of reconsideration because of the heavy weighting he placed on a single character, the number of transbullar septa. If his suggested phylogeny is correct, it implies that *Exilisciurus* most likely represents an invasion of the Sunda Shelf from Celebes, since it has mostly derived characters relative to the Celebes species (see Moore, 1959, and discussion below). Such a pattern of repeated colonization across the Makassar Strait, which defines the edge of the Asian continental shelf, would be of considerable interest to zoogeographers. I have investigated the relationships of these taxa by multivariate analysis of cranial morphology, and qualitative assessment of cranial, foot pad, and bacular morphology. In these analyses, two species of *Sundasciurus* and one of *Prosciurillus* were included as outgroups for comparison with the pygmy squirrels. These genera have both been postulated as possible ancestors of these pygmy squirrels (Hill, 1959; Moore, 1959).

The following discussion deals first with cranial characters, and second with non-cranial characters (foot morphology, bacula, and pelage); all qualitative characters are then combined for multivariate analyses.

SURVEY OF CRANIAL CHARACTERS.—In his review of pygmy squirrel relationships, Moore (1958, 1959) mentioned 14 characters that he believed to be useful in their classification. Hill (1959) considered 22 characters in his discussion of the relationships of *Glyphotes*, many of them the same as the ones utilized by Moore. Some characters are appropriate only for discussion of genera not considered here, and so are not listed, but most do pertain to *Exilisciurus* and *Nannosciurus*. These are described and discussed below, along with additional characters found to be useful.

All pygmy squirrels, regardless of taxonomic relationships, are likely to share some cranial characters due to convergent allometric effects of their small size. Inclusion of these characters in the analysis could falsely indicate relatedness between the pygmy squirrels. In order to identify such characters, I compared *Nannosciurus* and *Exilisciurus* with *Myosciurus*, the African pygmy squirrel. As stated above, evidence has been presented by numerous authors that *Myosciurus* is related to other African tree squirrels, and not to Asian squirrels. Any character shared by all species of these three genera is excluded because of the strong possibility of convergence due to common allometric trends associated with dwarfing. Some true synapomorphies may be missed using this technique, but this is preferable to including misleading data. Characters shared by only some pygmy

squirrels are assumed not to result from convergence, and are considered to be useful.

The following six characters were not included in analyses for the reasons stated. *Largest molar*: Moore (1958) stated that in *Exilisciurus* the second upper molar has the largest occlusal surface of the maxillary cheek teeth, whereas in *Nannosciurus*, the first molar is largest. I found this to be a very minor difference at best, and probably not accurate for *E. exilis* and some *Nannosciurus melanotis*. *Ventral aspect of premaxillary-maxillary suture*: Moore (1958:4) stated that "in *Nannosciurus* a finger of the premaxillary bone projects posteriorly into the maxillary on each side of the incisive foramina for a distance exceeding or approximating the length of the incisive foramen; in *Exilisciurus* such projections are only incipient". *E. concinnus* seems to have a longer projection than *N. melanotis*; however, the character is quite variable and difficult to assess. *Length of orbit*: Hill (1959) and Moore (1959) documented that in contrast to other squirrels, all pygmy squirrels have an orbit that is approximately as long as wide; this appears to result from convergence. I am unable to distinguish any difference between the orbital configuration of *Myosciurus*, *Nannosciurus*, and *Exilisciurus*, and so disregard it here as an indicator of phyletic affinity. *Interparietal outlined by sutures*. Moore pointed out that the Southeast Asian pygmy squirrels have a well-defined suture around the interparietal, even in adults. Because *Myosciurus* also has a well-defined suture, I consider the character to be unreliable. *Zygomatic plate*: In all pygmy squirrels, the plane of the zygomatic plate lies at nearly a right angle to the vertical plane of the rostrum. Because many genera share this character as a result of convergence (Hill, 1959), it is excluded from analysis. *Basiscranial flexion*: In the Southeast Asian and African pygmy squirrels, the occipital condyles lie at an 80° to 85° angle to the horizontal plane of the skull, whereas in most medium to large tree squirrels, the angle is close to 45°. This is presumed to be convergent, and is not included.

The following is a list of characters used in analyses of relationships, including descriptions of character states and reasons for polarity assignments.

Character 1. Transbullar septa.

(0) One septum.

(1) No septa.

Moore (1959:188) pointed out that *Exilisciurus* and *Prosciurillus* usually lack transbullar septa, whereas *Nannosciurus* and *Sundasciurus* typically have one septum. *Myosciurus* has two. This coding presumes that possession of septa is primitive for callosciurines. It is unquestionably the most common state (Moore, 1959:163).

Character 2. Anterior infraorbital foramen.

(0) Lateral projection present, cleft at base.

(1) No lateral projection, base solid.

In some species the lateral wall of the infraorbital foramen projects at a 20° to 30° angle to the midline; this projection, which is also referred to as the masseteric tubercle, has a narrow cleft at the base, leaving the anterior

base of the infraorbital foramen open for a short distance. Other species have no masseteric tubercle, with only a roughening on the side of the maxillary for muscle attachment; these have a solid base to the infraorbital canal. Lateral projections are present in nearly all sciurids, and are likely to be a primitive trait for callosciurines.

Character 3. Posterior infraorbital canal.

(0) Posterior margin with strong lateral lip.

(1) Posterior margin thin, ventral to root of zygomatic plate.

In *Exilisciurus exilis* and *E. whiteheadi*, the posterior end of the infraorbital canal has a very thin lateral wall, and the posterior margin lies directly below the ventral root of the zygomatic plate. In all of the other species examined, the ventral root of the zygomatic plate, which is a ridge projecting laterally along the side of the maxillary, extends nearly to the alveolus of the molars. The latter condition is widespread among sciurids, and is here considered the primitive state for callosciurines.

Character 4. Orbital notch.

(0) Orbital notch present.

(1) Orbital notch absent.

All three species of *Exilisciurus* lack an indentation on the medial dorsal edge of the orbit. All other species of sciurids have this notch.

Character 5. Maxillary tooththrow angle.

(0) Tooththrows parallel.

(1) Tooththrows converging posteriorly.

The maxillary tooththrows are either parallel, or converge posteriorly at about a 15° angle. Parallel tooththrows are present in all *Sundasciurus* and *Prosciurillus*, and most callosciurines. Although *Myoscurus* has converging tooththrows, *Nannosciurus* does not, which indicates that convergence on this state by pygmy squirrels may not be assumed.

Character 6. Size of P⁴ relative to M³.

(0) P⁴ is smaller than M³.

(1) P⁴ equals M³.

The last premolar is either smaller than or equal to the last molar in size. All species of *Callosciurus*, *Sundasciurus*, *Dremomys*, and *Prosciurillus* examined have P⁴ slightly smaller than M³; in *Menetes*, *Lariscus*, and *Glyphotes* they are equal. Since *Sundasciurus* and *Prosciurillus* are presumed to be close to the ancestry of the pygmy squirrels, "P⁴ smaller than M³" is coded as primitive.

Character 7. Position of maxillary-premaxillary suture.

(0) Lateral lip of infraorbital foramen not connected with maxillary-premaxillary suture.

(1) Lateral lip of infraorbital foramen connects with maxillary-premaxillary suture.

Moore (1959:176) observed that in *Exilisciurus*, "the lateral lip of the infraorbital foramen does not connect at the top with the maxillo-premaxillary suture", whereas it does in *Nannosciurus*. No callosciurine examined other than *Nannosciurus* has character state (1); I consider it to be uniquely derived.

Character 8. Suprabullar vacuity.

- (0) Suprabullar vacuity closed.
- (1) Suprabullar vacuity open.

In two species of *Exilisciurus* and in *Myosciurus* there is a vacuity anterior and dorsal to the auditory bulla, just anterior to the postglenoid foramen. In *Nannosciurus* the vacuity is closed by a swelling of the bulla. In *Sundasciurus* and *Prosciurillus* it is closed, though without noticeable swelling of the bulla. Because the open vacuity occurs only in *Exilisciurus* among the callosciurines I have examined, I regard it as derived.

Character 9. Rostral length.

- (0) Rostrum short, 30 to 35% of condylobasal length.
- (1) Rostrum intermediate, 55 to 59% of condylobasal length.
- (2) Rostrum long, 62 to 64% of condylobasal length.

The rostrum of pygmy squirrels is long relative to length of the post-rostral region, but the extent is variable, and at least one small species (*Glyphotes simus*) has a short rostrum (Hill, 1959). A short rostrum is characteristic of nearly all tree squirrels.

Character 10. Rostral depth.

- (0) Rostrum of moderate depth.
- (1) Rostrum deep.

The rostrum of callosciurines is typically robust; the thickness gradually increases from a point just posterior to the incisors to the anterior edge of the zygomatic plate. In *Exilisciurus exilis* and *E. whiteheadi* (Fig. 4), the rostrum is unusually deep at its posterior terminus so that the lateral wall of the rostrum is extraordinarily broad. The rostra of *E. concinnus* and *Nannosciurus* are narrower (Fig. 4), and of *Prosciurillus*, *Sundasciurus*, and *Myosciurus* much narrower. The two *Exilisciurus* are the only callosciurines to exhibit state (1), and this state is rare among other sciurids; it is considered to be derived.

Character 11. Postorbital process.

- (0) Postorbital process well developed.
- (1) Postorbital process reduced.

A well-developed postorbital process is characteristic of sciurids. *Exilisciurus* and *Myosciurus* (but not *Nannosciurus*) are unusual in having greatly reduced processes (see Hill (1959) for discussion of the position of the postorbital process).

Character 12. Palatal length.

- (0) Edge of palate at middle of M^3 .
- (1) Edge of palate midway between posterior edge of M^3 and junction of pterygoid and ectopterygoid ridges.
- (2) Edge of palate between junction of pterygoid and ectopterygoid ridges.

The posterior edge of the hard palate lies between M^3 in some species, and as far back as the junction of the pterygoid and ectopterygoid ridge in others, with several intermediate lengths. Polarity is provisional, and is based on commonness of states (0) and (1) among *Sundasciurus* and *Callosciurus*. Since *Myosciurus* shares state (2) with *Nannosciurus* and *Exilisciurus*, convergence due to allometry is possible.

Character 13. Coronoid process of the mandible.

(0) Coronoid process long and slender.

(1) Coronoid process greatly reduced.

The coronoid processes of the pygmy and tree squirrels examined fall into two types: either long and slender, reaching a height greater than the articular process, or atrophied, consisting of a very low, slightly pointed process much shorter than the articular process. Nearly all sciurids have a long, slender coronoid process, and it is a common feature in other rodents (Hill, 1959); it is assumed to be primitive for sciurids. The atrophied condition of the African pygmy squirrel appears to be convergent, since the morphology of the mandible is otherwise quite different from that of the Southeast Asian pygmy squirrels. For example, in *Myosciurus* there is a deeply concave fossa for attachment of the internal pterygoid muscle, whereas in *Exilisciurus* and *Nannosciurus* it is a shallow, open fossa; additionally, in *Myosciurus* the condylar process is weak and slender, whereas in *Exilisciurus* and *Nannosciurus* it is stronger and broader.

ANALYSIS OF CRANIAL CHARACTERS.—Character states for the crania of pygmy squirrels and outgroups are summarized in Table 5; the apparent synapomorphies were used to construct the phylogenetic tree shown in Fig. 7. The genus *Exilisciurus* appears to be a monophyletic group defined by five synapomorphies: absence of transbullar septa, shape of the anterior portion of the infraorbital foramen, absence of an orbital notch, angle of the maxillary toothrows, and reduced postorbital processes. Within *Exilisciurus*, two characters (position of the infraorbital canal and rostral depth) are shared by *E. exilis* and *E. whiteheadi*, and a single character (presence of a supra-bullar vacuity) is shared by *E. concinnus* and *E. whiteheadi*. Although the relationships within *Exilisciurus* are in need of further investigation, the cranial data clearly indicate that *Nannosciurus* and *Exilisciurus* represent a monophyletic group. *Nannosciurus* and *Exilisciurus* share three synapomorphies: an elongate rostrum, a long palate, and reduced mandibular coronoid processes. *Nannosciurus* has two unique features: the relative size of P⁴ and M³, and the position of the maxillo-premaxillary suture. There is only one derived character state that is not shared by *Prosciurillus leucomus* and *Sundasciurus*: palatal length. For this single character, it appears that *Sundasciurus* is more similar to the pygmy squirrels than is *Prosciurillus*.

The one character which does not support this analysis is the number of transbullar septa. As Moore (1959) correctly noted, *Prosciurillus* and *Exilisciurus* normally have no septa, whereas *Sundasciurus* and *Nannosciurus* have one septum. However, the number in all four taxa shows substantial variation (Moore, 1959:163), casting some doubt on the usefulness of the character. If the tree shown in Fig. 7 were to be reconstructed assuming that the absence of transbullar septa is a synapomorphy for *Prosciurillus* and *Exilisciurus*, it would require the assumption that seven other characters are convergent. Considering the far greater complexity of the other characters and the detail of their similarity, such convergence seems unlikely. Thus, the one character used by Moore (1959) to allocate *Nanno-*

TABLE 5
CRANIAL CHARACTER STATES OF PYGMY SQUIRRELS AND REFERENCE SPECIES¹

Character	<i>N. melanois</i>	<i>E. concinnus</i>	<i>E. exilis</i>	<i>E. whiteheadi</i>	<i>S. jentinki</i>	<i>S. tenuis</i>	<i>P. leucomus</i>	<i>M. pumilio</i>
1. Transbullar septa	0	1	1	1	0	0	1	2
2. Anterior infraorbital foramen	0	1	1	1	0	0	0	1
3. Posterior infraorbital canal	0	0	1	1	0	0	0	0
4. Orbital notch	0	1	1	1	0	0	0	0
5. Maxillary tooththrow angle	0	1	1	1	0	0	0	1
6. Size of P ⁴ .M ³	1	0	0	0	0	0	0	0
7. Maxillo-premaxillary suture	1	0	0	0	0	0	0	0
8. Suprabullar vacuity	0	1	0	1	0	0	0	1
9. Rostral length	1	1	1	2	0	0	0	1
10. Rostral depth	0	0	1	1	0	0	0	0
11. Postorbital process	0	1	1	1	0	0	0	1
12. Palatal length	2	2	2	2	1	1	0	2 ¹
13. Coronoid process	1	1	1	1	0	0	0	1 ¹

¹Characters shared by *Myosciurus* with *Nannosciurus* and *Exilisciurus* by superficial convergence only; see text.

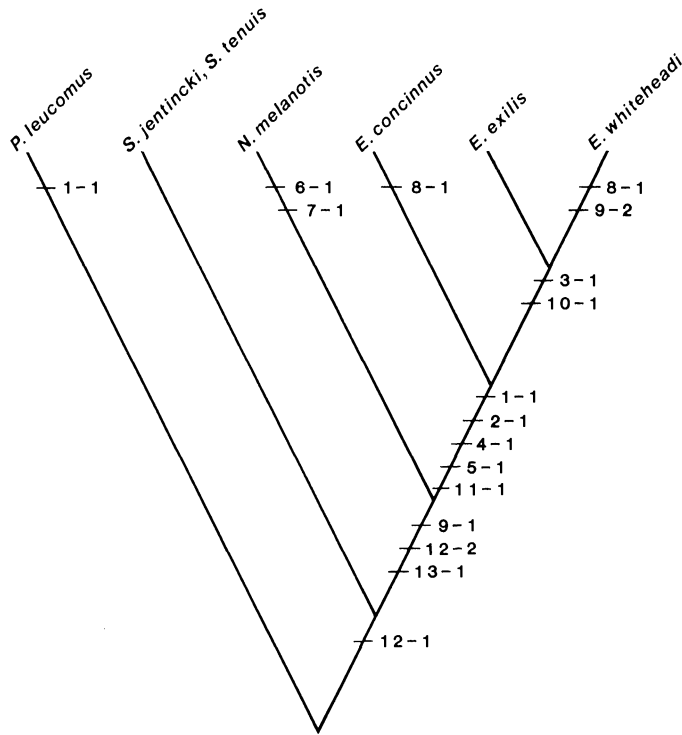


FIG. 7. Cladogram of cranial characters for *Exilisciurus*, *Nannosciurus*, *Prosciurillus*, and *Sundasciurus*. Bars indicate synapomorphies; numbers adjacent to the bars correspond to character numbers and states given in Table 5.

sciurus and *Exilisciurus* to different subtribes probably results from convergence.

As discussed earlier, one of the most dramatic characters shared by *Exilisciurus* and *Nannosciurus* is their small size. I consider it likely that some consistent changes in cranial morphology are likely to have taken place in all dwarfed sciurids due to allometric scaling. In order to detect such allometric convergence, *Myosciurus pumilio*, an African funambuline pygmy tree squirrel (Moore, 1959), was compared with the Southeast Asian callosciurine pygmy tree squirrels. Only three of the characters examined are shared by *Myosciurus*, all *Exilisciurus*, and *Nannosciurus*: one (rostral length) is sufficiently similar in all three genera that I cannot be certain that it is a true synapomorphy for *Exilisciurus* and *Nannosciurus*, and it is excluded from further analyses. The other two apparent convergences (palatal length and coronoid process shape) are sufficiently different between *Myosciurus* and the callosciurine pygmy squirrels that I feel confident that they are true synapomorphies.

Three additional characters (shape of the infraorbital foramen, maxillary toothrow angle, and length of the postorbital process) are shared by all *Exilisciurus* and *Myosciurus*; because *Nannosciurus* lacks these characters,

they are retained as probable autapomorphies for the genus *Exilisciurus*, but it should be noted that they are probably unreliable in comparisons between tribes of sciurids. Likewise, the presence of a supra-bullar vacuity is shared by *Myosciurus* and two species of *Exilisciurus*, and should be regarded as a character possibly influenced by allometry.

Removal of the one character (rostral length) that is thus considered to result from probable convergence does not require any changes in the topology of the tree shown in Fig. 7.

SURVEY OF NON-CRANIAL CHARACTERS.—Pocock (1923a) demonstrated that the morphology of the feet, and in particular that the interdigital and metatarsal pads of the hind feet, is a useful character in discerning relationships among sciurids. However, Pocock had no fluid-preserved pygmy squirrels available to him, and in general was able to make few statements about their relationships (Pocock, 1923a, 1923b).

The forefeet of the *Sundasciurus*, *Prosciurillus*, *Nannosciurus*, and *Exilisciurus* that I examined showed no consistent difference from those of the *Callosciurus* type illustrated by Pocock (1923a:1184), except that *Nannosciurus* and *Exilisciurus* lack external evidence of a pollex (Long and Captain, 1974; *Myosciurus* also lacks a pollex (Emmons, 1979; discussed below). The hind feet exhibited substantial differences in pad morphology (Fig. 8). Terminology follows that of Brown and Yalden (1973).

Sundasciurus tenuis has interdigital and metatarsal pads much like those of *Callosciurus prevostii* (Pocock, 1923a). There are two metatarsal pads: a large, elongate inner (thenar) pad and a smaller elliptical outer pad (hypothelar). There are four interdigital pads; the innermost (at the base of the pollex) is the largest, with a slight cleft dividing the pad into a small inner and a large outer portion. The next two pads are oblong, and of approximately equal size. The outer pad (below digit V) is about the same size as the preceding two, but is divided by a cleft into a larger inner portion and smaller outer portion. *Sundasciurus jentinki* is very similar, except that the innermost pad has no conspicuous cleft, and the outermost has the appearance of two distinct pads.

The footpads of *Prosciurillus leucomus* are much like those of the species of *Sundasciurus*. It differs in that all of the pads are larger in proportion to the foot, especially the hypothelar. The outer interdigital pad is partially divided, as in *S. tenuis*. Digit I has a prominent digital pad that has much the same appearance as the interdigital pads.

Nannosciurus melanotis shows only one significant modification from the *Sundasciurus* type of hind foot: both metatarsal pads are much reduced relative to foot size. The thenar is an oval pad near the location of the distal portion of the pad in *Sundasciurus*. The hypothelar pad is a circular speck, proximal to the third plantar pad. In three of four specimens there is also a very small pad next to the thenar pad on the outer edge; this pad was not seen in any other species.

In *Exilisciurus*, the hypothelar pad has been lost entirely, and the thenar is further reduced in relative size. Three of four *E. whiteheadi* have retained the very small "accessory pad" on the outer edge of the fourth interdigital pad, but in all of four *E. exilis* this small pad is absent. The hind foot of

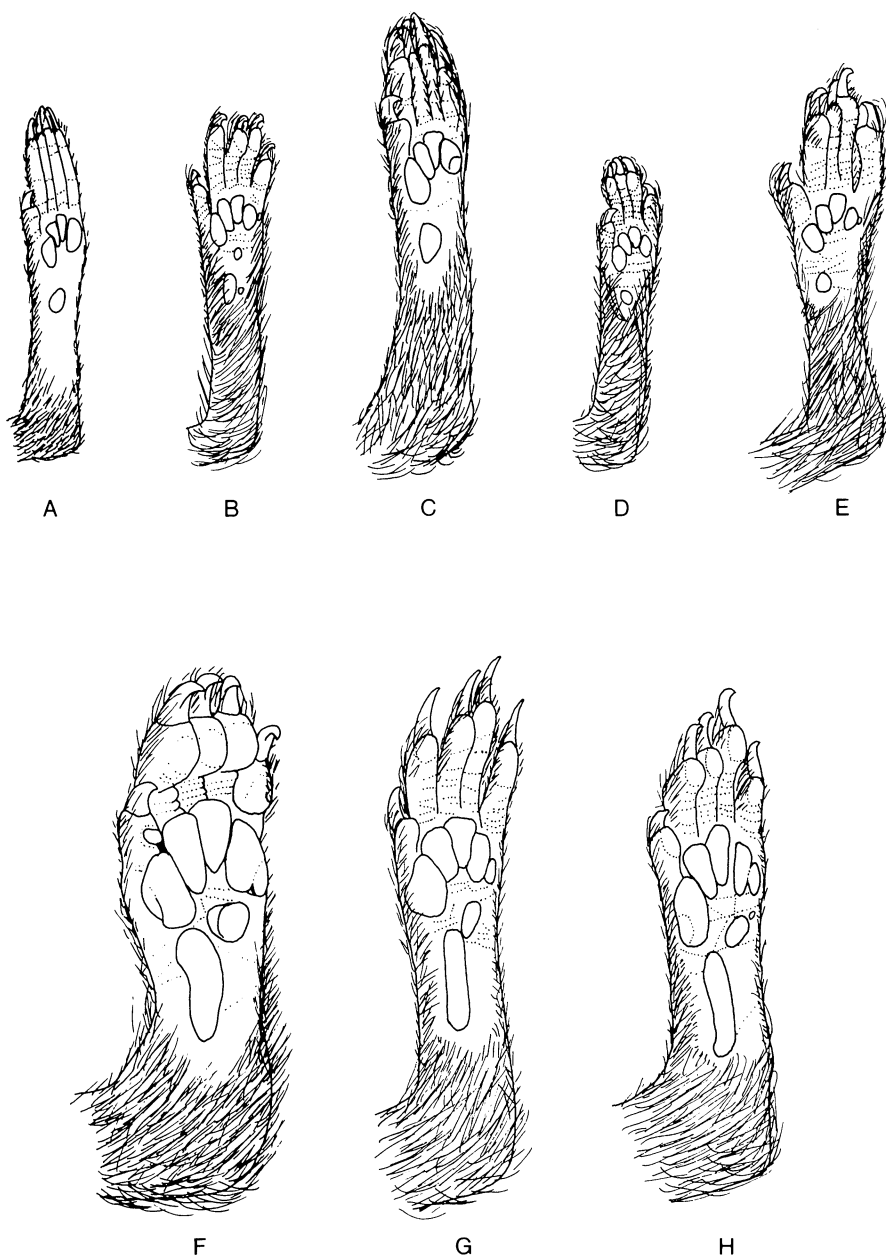


FIG. 8. Ventral surface of left hind feet, showing the position and size of pads. A) *Myosciurus pumilio*; B) *Nannosciurus melanotis*; C) *Exilisciurus concinnus*; D) *E. exilis*; E) *E. whiteheadi*; F) *Prosciurillus leucomus*; G) *Sundasciurus jentinki*; H) *S. tenuis*.

Myosciurus pumilio has pads much like those of *Exilisciurus*. The hypothenar is absent, the thenar is small, and only four interdigitals are present. However, the interdigitals of *Myosciurus* are more elongate, the toes are proportionately longer, the foot is narrower, and much less of the ventral surface is covered with hair.

It appears that there is a correlated trend in size and number of hind foot pads in the Asian genera. *Sundasciurus* and *Prosciurillus* have a full complement of foot pads, whereas *Exilisciurus* shows reductions in both size and number of pads. *Nannosciurus* is intermediate in that it has retained all pads, but the metatarsal pads are greatly reduced in size. The evidence available (see Pocock, 1923a) indicates that *S. tenuis* has the primitive state, and that the others are increasingly derived conditions. Three characters may be defined on the basis of the above discussion; these are numbered consecutively following the cranial characters.

Character 14. Metatarsal pads.

(0) Metatarsal pads normal.

(1) Metatarsal pads reduced in size.

Metatarsal pads are either normal or relatively reduced in size, as discussed above.

Character 15. Hypothenar pad.

(0) Hypothenar present.

(1) Hypothenar absent.

As discussed above, two states are present.

Character 16. Extra metatarsal pad.

(0) Extra metatarsal pad absent.

(1) Extra metatarsal pad present.

Nannosciurus melanotis typically have an extra metatarsal pad that lies lateral to the thenar; this appears to be a unique character among sciurids.

Thomas (1915) and Pocock (1923b) have shown that the morphology of the penis-bone provides a complex set of characters that is useful in studies of relationships of squirrels. Most sciurids have a single ossified portion that occurs in a variety of shapes; the callosciurines are unique in possessing an ossified blade that is hinged to the shaft, and is slightly moveable laterally. The blade projects backwards, terminating posteriorly in a tip that is often sharply pointed. In most callosciurines the blade is attached near the anterior tip of the baculum. The baculum is either nearly straight or slightly curved dorsally in most species (Pocock, 1923b).

The baculum of *Sundasciurus tenuis tahan* (Fig. 9) is typical of this assemblage, except in having the shaft shorter relative to the length of the blade than is usual. *Prosciurillus leucomus*, *Sundasciurus jentinki*, *Nannosciurus*, and *Exilisciurus* are unusual (but not unique) in having the shaft curved sharply upwards at about its midpoint, and in having the blade of the baculum nearly as long as the shaft. *Prosciurillus leucomus* and *S. jentinki* also have an unusually thick base to the baculum. *Nannosciurus melanotis* has a simple blade with a rounded, rather than acute, tip. The three species of *Exilisciurus* are unique in having a series of small, sharp denticles (serrations) on the dorsal edge of the blade; in *E. exilis* and *E. whiteheadi* the

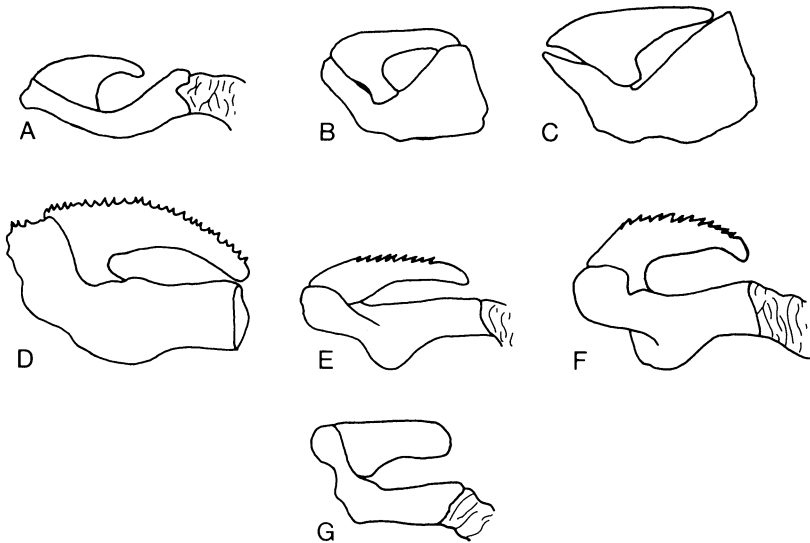


FIG. 9. Lateral view of bacula; distal is to left. A) *Sundasciurus tenuis tahan*; B) *S. jentinki* (USNM 292574); C) *Prosciurillus leucomus* (AMNH 224582); D) *Exilisciurus concinnus* (UMMZ 53158); E) *E. whiteheadi*; F) *E. exilis*; G) *Nannosciurus melanotis*. A, E, F, and G are redrawn from Pocock, 1923b.

serrations are absent from the anterior and posterior ends of the blade, whereas in *E. concinnus* the entire edge of the blade is serrated (Fig. 9).

Because bacula of only *E. concinnus*, *P. leucomus*, and *S. jentinki* are available to me, I have relied on the illustrations in Pocock (1923b) for the other species. The limitations of data restrict me to defining only three characters; examination of more material, and especially of soft anatomy of the male reproductive tract, would undoubtedly yield more characters.

Character 17. Angle of the bacular shaft.

(0) Bacular shaft with slight dorsal curve.

(1) Bacular shaft with sharp dorsal inflection near the midpoint.

In most callosciurines the shaft is straight or slightly curved, as it is in most other sciurids (Pocock, 1923b). I consider this to be the primitive condition.

Character 18. Thickness of shaft base.

(0) Width of base of bacular shaft less than one-third of length of shaft.

(1) Width of bacular shaft greater than one-half of length of shaft.

Most callosciurines have a bacular shaft that is at least three times longer than wide, and a base that is only slightly enlarged. Only *Prosciurillus leucomus*, *Sundasciurus jentinki* (this study), *S. hippurus*, and *S. lowi* (Davis, 1962) are known to have greatly thickened bases, although some thickening is present in other callosciurines (Pocock, 1923b). I consider the greatly thickened base to be derived.

Character 19. Bacular blade serrations.

- (0) Bacular blade without serrations.
- (1) Bacular blade with serrations along most of dorsal edge.
- (2) Bacular blade with serrations along entire dorsal edge.

Serrations are absent from the bacular blade in all squirrels except *Exilisciurus*. Only *E. concinnus* has serrations along the entire edge.

Although the pygmy squirrels differ in many details of their pelage, only two discrete characters can be defined.

Character 20. Ear tufts.

- (0) Absent.
- (1) Present.

Exilisciurus whiteheadi has elongate black and white hairs on its pinnae that form long gray tufts. These are unique among callosciurines.

Character 21. Facial stripes.

- (0) Absent.
- (1) Present.

Nannosciurus melanotis has unique dark and light stripes that extend from the rhinarium to behind the ear; no other callosciurine has facial stripes beyond simple dark regions adjacent to the eyes.

ANALYSIS OF NON-CRANIAL CHARACTERS.—Character states for the seven characters discussed above are summarized in Table 6, and were used to construct a phylogenetic tree (Fig. 10). The genus *Exilisciurus* is defined by two synapomorphies: absence of the hypothenar pad and presence of serrations on the bacular blade. There are no synapomorphies in this character set within *Exilisciurus*. *Nannosciurus* and *Exilisciurus* share the reduction in relative size of the metatarsal pads, and *Nannosciurus* is unique in the possession of an extra metatarsal pad and facial stripes.

All but two of the characters considered are shared in their primitive state by *Prosciurillus* and both *Sundasciurus* species. The angle of the bacular shaft is much sharper in *P. leucomus* and *S. jentinki* than in *S. tenuis*, and in this way *P. leucomus* and *S. jentinki* resemble the pygmy squirrels. The base of the bacula of *P. leucomus* and *S. jentinki* is much broader than in most other callosciurines (Pocock, 1923b); this appears to be independent of the shaft flexion. This condition appears to be a derived state not shared with *S. tenuis* or any of the pygmy squirrels.

The African pygmy squirrel *Myosciurus* was compared with the Oriental pygmy squirrels in the same manner as described above for cranial characters. External evidence of a pollex is lacking in *Myosciurus* and the Oriental pygmy squirrels, but is present in most callosciurines (Emmons, 1979; Long and Captain, 1974) and other sciurids. I have not included this trait in any analyses because it appears to be a size-related character. However, detailed examination of the Oriental pygmy squirrels might allow discrimination of usable characters, since reduction of the pollex apparently leaves the bones of the pollex intact in *Myosciurus* (Emmons, 1979).

Myosciurus is like *Exilisciurus* and *Nannosciurus* in that its metatarsal pads are reduced in size, and the hypothenar is absent; thus, allometry could cause the Oriental pygmy squirrels to share these characters because of

TABLE 6
 CHARACTER STATES FOR NON-CRANIAL CHARACTERS OF PYGMY SQUIRRELS AND REFERENCE SPECIES

Character	<i>N. melanotis</i>	<i>E. concinnus</i>	<i>E. exilis</i>	<i>E. whiteheadi</i>	<i>S. jentinki</i>	<i>S. tenuis</i>	<i>P. leucomus</i>	<i>M. pumilio</i>
14. Metatarsal pad	1	1	1	1	0	0	0	1
15. Hypothenar pad	0	1	1	1	0	0	0	1
16. Extra metatarsal pad	1	0	0	0	0	0	0	0
17. Angle of bacular shaft	1	1	1	1	1	0	1	0
18. Thickness of bacular base	0	0	0	0	1	0	1	0
19. Bacular serrations	0	2	1	1	0	0	0	0
20. Ear tufts	0	0	0	1	0	0	0	0
21. Facial stripes	1	0	0	0	0	0	0	0

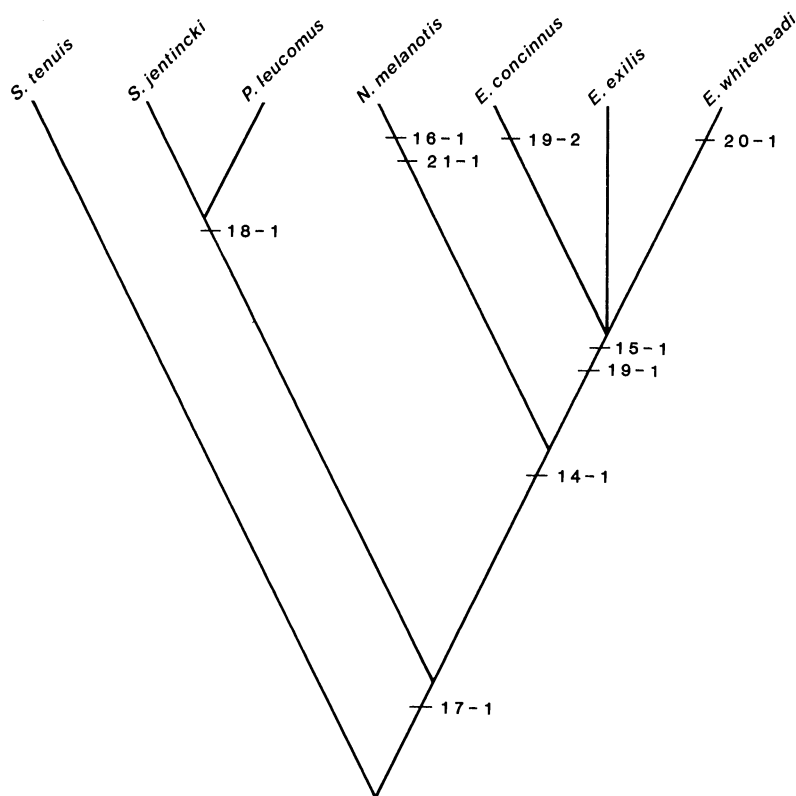


FIG. 10. Cladogram of non-cranial characters for *Exilisciurus*, *Nannosciurus*, *Prosciurillus*, and *Sundasciurus*. Bars indicate synapomorphies; numbers adjacent to the bars correspond to characters and states given in Table 6.

convergence, and caution should be used in interpreting these data. However, foot pad morphology is not strictly related to size, since the hypothenar is absent in the two *Exilisciurus* that are larger than *Nannosciurus*, which has the hypothenar. Moreover, the shape of both the feet and the individual pads of *Myosciurus* are sufficiently different from the Oriental pygmy squirrels that characters could be described that distinguish them, if that were desired. Therefore, I retain use of the foot pad characters, recognizing the need for caution in interpreting the results.

MULTIVARIATE ANALYSES OF QUALITATIVE CHARACTERS

Two multivariate methods were used to investigate the variation and covariation in qualitative characters, and the phylogenetic relationships implied by the pattern of character distribution within the study species. The first was a principal components analysis, in which the data (recoded into a matrix of presence/absence data) were entered with equal weighting. This analysis does not require assumptions of polarity; rather, species

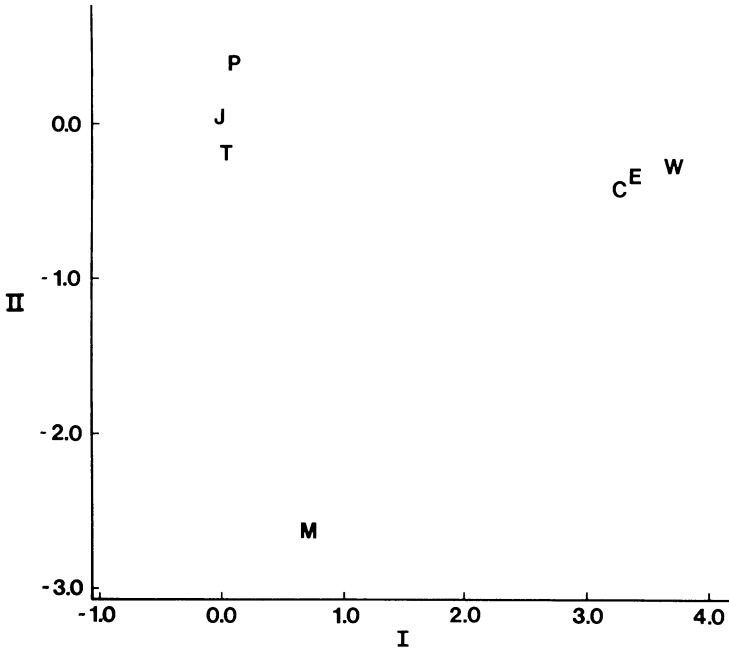


FIG. 11. Results of principal components analysis of qualitative characters of pygmy squirrels and outgroups for axes I and II, based on data in Table 7; character loadings on the axes are given in Table 8. C = *E. concinnus*; other symbols as in Figs. 5 and 6.

are grouped by generalized similarity of character states. Secondly, a Wagner Tree analysis was conducted using the polarities determined in the above discussions. This analysis allows statements to be made about relationships and ancestry, and depends on accurate assessment of polarity.

PRINCIPAL COMPONENTS ANALYSIS.—This analysis was conducted to answer two questions: 1) Can the variation present in the data set (Table 7) be reduced to a smaller number of independent (non-correlated) variables that tell us about covariation in the data; and 2) is a substantial portion of the variation correlated with body size variation, i.e., can the qualitative characters be interpreted as resulting primarily or exclusively from allometric phenomena rather than phylogenetic relationships?

Results of the analysis (Fig. 11, Table 8) show that most of the variation (61%) occurs along a single axis. Most variables show moderate to low loadings on the axis; several show very low loadings (relative size of M^3 , placement of the maxillo-premaxillary suture, palatal length, presence of an extra metatarsal pad, angle of the bacular shaft, presence of continuous serrations on the bacular blade, and presence of facial stripes). This axis primarily distinguishes the genus *Exilisciurus* from other study species (Fig. 11). The second axis (Fig. 11) reflects the rather large number of autapomorphies of *N. melanotis*, separating that species from all the others, and accounting for an additional 19% of the variation. The third in-

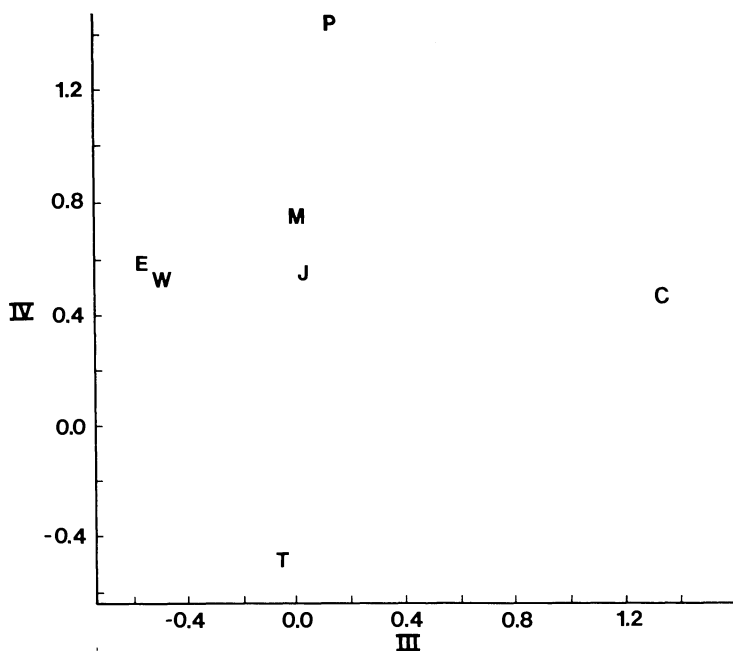


FIG. 12. Results of principal components analysis of qualitative characters of pygmy squirrels and outgroups for axes III and IV, based on data in Table 7; character loadings on the axes are given in Table 8. C = *E. concinnus*; other symbols as in Figs. 5 and 6.

dependent axis (Fig. 12) separates *E. concinnus* from the other species, especially its congeners; this axis represents about 8% of the total variation. The fourth axis (Fig. 12), which represents only about 6% of the variation, contrasts *P. leucomus* and *S. tenuis*, with other species intermediate. The remaining two axes primarily reflect differences between *E. exilis* and *E. whiteheadi* (axis 5, 3%), and the unique features of *S. jentinki* (axis 6, 2.5%).

It is apparent that most of the characters co-occur in a consistent fashion in the study species. However, not all of this variation is correlated: there are four independent axes that each contain over 5% of the total variation. Thus, to focus on my second question about variation, the effects of allometry are certainly not the only influences on the data.

Examination of Figs. 11 and 12 shows that axes II-IV are poorly correlated with body size of the species; however, axis I reflects at least a weak correlation with size. To estimate the strength of this correlation, a correlation analysis was conducted of the loadings on axis I with the logarithm of mean condylobasal length for each species. The resultant coefficient of determination (R^2) shows that 55% of the variation in loadings on axis I can be explained by the log of condylobasal length alone ($y = 17.8 - 11.3(x)$; $p < 0.05$). Because the correlation is significant, it appears that allometry may play a significant role in structuring the data set. However, because the correlation is not overly strong, and because

TABLE 7
DATA MATRIX OF CRANIAL AND EXTERNAL CHARACTERS CODED FOR WAGNER TREE ANALYSIS
(TAXA, CHARACTER NUMBERS, AND CHARACTER STATES ARE FROM TABLES 5 AND 6)

Char. No.	<i>N. melanotis</i>	<i>E. concinnus</i>	<i>E. exilis</i>	<i>E. whiteheadi</i>	<i>S. jentinki</i>	<i>S. tenuis</i>	<i>P. leucomus</i>
1.	0	1	1	1	0	0	1
2.	0	1	1	1	0	0	0
3.	0	0	1	1	0	0	0
4.	0	1	1	1	0	0	0
5.	0	1	1	1	0	0	0
6.	1	0	0	0	0	0	0
7.	1	0	0	0	0	0	0
8.	0	1	0	1	0	0	0
10.	0	0	1	1	0	0	0
11.	0	1	1	1	0	0	0
12.	1	1	1	1	1	1	0
	1	1	1	1	0	0	0
13.	1	1	1	1	0	0	0
14.	1	1	1	1	0	0	0
15.	0	1	1	1	0	0	0
16.	1	0	0	0	0	0	0
17.	1	1	1	1	1	0	1
18.	0	0	0	0	1	0	1
19.	0	1	1	1	0	0	0
	0	1	0	0	0	0	0
20.	0	0	0	1	0	0	0
21.	1	0	0	0	0	0	0

additional axes are independent of size factors, I conclude that the impact of allometry on the data set is not overwhelming. Restated, this means that an analysis of the data to determine the phylogeny of this group of squirrels may reflect some evolutionary changes that are caused by reduction in size, but that other variables that are independent of size, and thus less likely to represent parallelisms, are likely to predominate.

WAGNER TREE ANALYSIS.—An analysis of the data in Table 7 yielded a tree with a minimum length of 24 steps (consistency index = 0.92). There are two possible topologies to the tree (Fig. 13 A and B), based on differing interpretations of two characters. In Fig. 13 A, character 12 (1), palatal length, is assumed to be a synapomorphy for *Sundasciurus* and the pygmy squirrels. In Fig. 13 B, character 17 (1), angle of inflection of the bacular shaft, is assumed to be a synapomorphy for *Sundasciurus jentinki*, *Prosciurillus leucomus*, and the pygmy squirrels. In each case, the other disputed character is assumed to be convergent.

Both trees are identical in demonstrating that the pygmy squirrels are a monophyletic group. This is true whether both the *Sundasciurus* and *P. leucomus* are included as outgroups, or if each genus is used singly. It is also true that the absence of a transbullar septum in the species of *Exilisciurus* and in *Prosciurillus* is shown to be convergent in these groups, regardless of the outgroup used.

TABLE 8
 RESULTS OF A PRINCIPAL COMPONENTS ANALYSIS OF 22 QUALITATIVE CHARACTERS
 FROM SEVEN SPECIES OF TREE AND PYGMY SQUIRRELS¹
 (CHARACTER NUMBERS FROM TABLE 7)

	Axis					
	1	2	3	4	5	6
1. Transbullar septa	.22	.22	.08	.44	.08	-.47
2. Anterior infraorbital foramen	.30	.07	.05	-.03	.08	.05
3. Posterior infraorbital foramen	.21	.06	-.51	.02	.02	.02
4. Orbital notch	.30	.07	.05	-.03	.08	.05
5. Maxillary tooththrow angle	.30	.07	.05	-.03	.08	.05
6. Size of P ⁴ to M ³	-.05	-.37	-.02	.11	-.04	-.05
7. Maxillo-premaxillary suture	-.05	-.37	-.02	.11	-.04	-.05
8. Suprabullar vacuity	.21	.05	.32	-.06	-.66	-.03
10. Rostral depth	.21	.06	-.51	.02	.02	.02
11. Postorbital process	.30	.07	.05	-.03	.08	.05
12. Palatal length (state 1 to 2)	-.08	-.16	-.03	-.47	-.01	.52
Palatal length (state 2 to 3)	.25	-.30	.03	.08	.04	.01
13. Coronoid process	.25	-.30	.03	.08	.04	.01
14. Metatarsal pad	.25	-.30	.03	.08	.04	.01
15. Hypothenar pad	.30	.07	.05	-.03	.08	.05
16. Extra metatarsal pad	-.05	-.37	-.02	.11	-.04	-.05
17. Angle of bacular shaft	.08	-.06	.04	.54	-.04	.48
18. Thickness of bacular base	-.17	.24	.01	.46	-.08	.48
19. Bacular serrations (state 1 to 2)	.30	.07	.05	-.03	.08	.05
Bacular serrations (state 2 to 3)	.09	.01	.55	-.05	.06	.03
20. Ear tufts	.11	.04	-.23	-.01	-.71	-.06
21. Facial stripes	-.05	-.37	-.02	.11	-.04	-.05
Cumulative % variance	61.3	80.6	88.3	94.6	97.8	100

¹Loadings of the variables on all six definable axes are given.

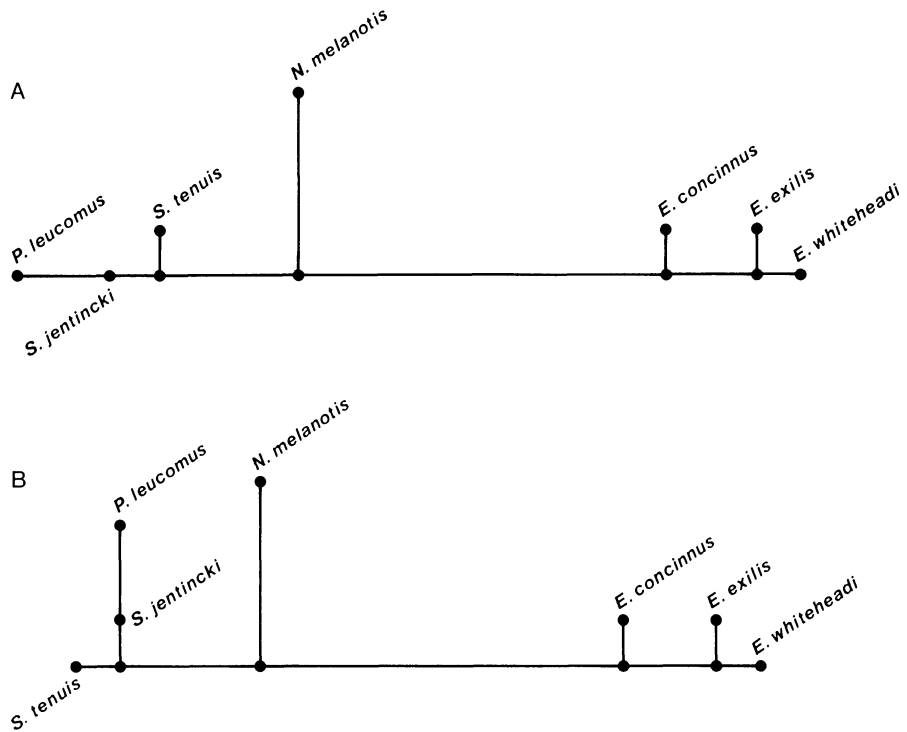


FIG. 13. Results of Wagner Tree analysis based on data in Tables 5 and 6. Coefficient of concordance = 0.92.

DISCUSSION

RELATIONSHIPS OF THE PYGMY SQUIRRELS AND CALLOSCIURINE TREE SQUIRRELS

The evidence presented above is unequivocal in demonstrating the monophyly of the three species of *Exilisciurus*, and the sister-taxon relationship of *Nannosciurus* and *Exilisciurus*. This is in contrast to the classification proposed by Moore (1959), who placed them in different subtribes. The sole character that Moore used to distinguish the two subtribes, the presence or absence of transbullar septa, is here shown to result from convergence.

The relationships of the species used as outgroups in this study are less clear. Both cranial and non-cranial characters consistently provide evidence that *Sundasciurus jentinki* is more similar to the pygmy squirrels than is *S. tenuis*. Perhaps more importantly, one derived character (bacular base width) unites *S. jentinki* with *Prosciurillus leucomus*, and one (bacular inflection) is shared by *S. jentinki*, *P. leucomus*, and the pygmy squirrels. Only one character included in this study, relative length of the palate, appears to be a synapomorphy of the two species of *Sundasciurus*.

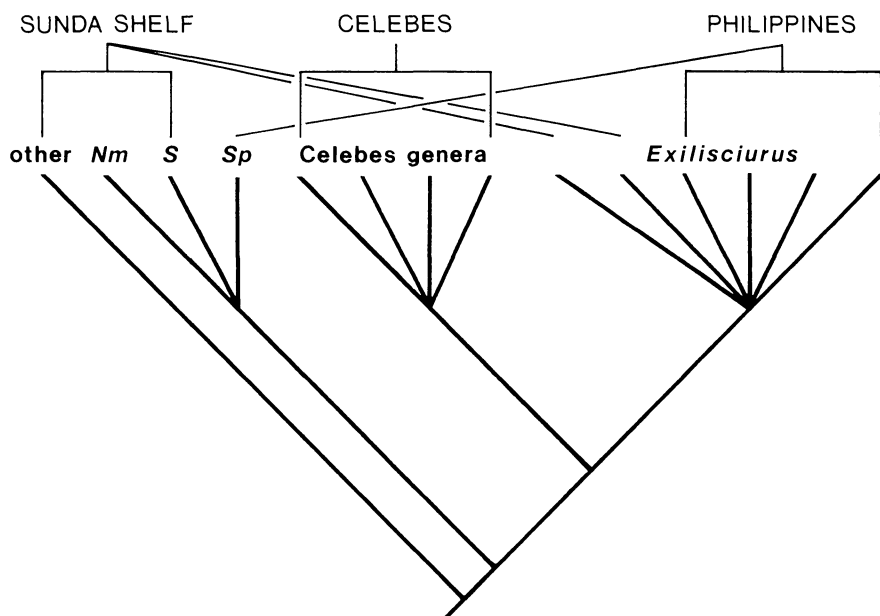


FIG. 14. Phylogenetic relationships of pygmy squirrels and their relatives hypothesized by Moore (1959), also showing the geographic distribution of each.

Because the purpose of this study was to examine relationships of the pygmy squirrels, I did not gather data that would pertain specifically to the larger tree squirrels. Thus, I do not regard this study as providing conclusive evidence of the paraphyly of *Sundasciurus*. Nevertheless, the implication of paraphyly is clear, and the relationships of species in *Sundasciurus* and *Prosciurillus* are obviously in need of review. In spite of my uncertainty regarding the status of *Sundasciurus*, I do feel that discarding the absence of transbullar septa as a useful character within the Callosciurini makes the retention of the subtribe Hyosciurina untenable, since that character was the only one regarded by Moore (1959) as a unique synapomorphy for that group. Therefore, the subtribes Callosciurina and Hyosciurina should be disregarded in future classifications, with all included genera to remain within the tribe Callosciurini Simpson 1945.

ORIGIN AND ZOOGEOGRAPHIC HISTORY OF THE PHILIPPINE PYGMY SQUIRRELS

One of the principal reasons that this study was initiated was the zoogeographic implication of Moore's (1959) classification of callosciurine squirrels, which placed the three endemic genera of squirrels on Celebes (*Hyosciurus*, *Prosciurillus*, and *Rubrisciurus*) and *Exilisciurus* in a distinct subtribe, the Hyosciurina. If we assume that the Hyosciurina are derived

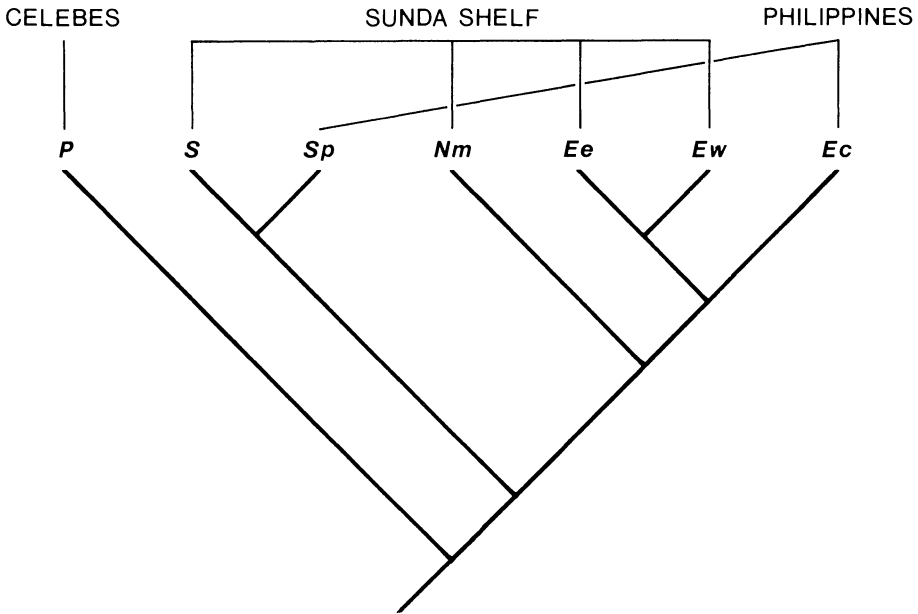


FIG. 15. Phylogenetic relationships of *Exilisciurus*, *Nannosciurus*, *Prosciurillus*, and *Sundasciurus* hypothesized in this study and the geographic distribution of each taxon. One species group of *Sundasciurus* occurs in the southern Philippines (see text).

from *Callosciurini* on the Sunda Shelf, as is strongly implied by Moore, then it follows that 1) all speciation in the *Hyosciurina* has taken place on Celebes, 2) except that *Exilisciurus* dispersed back to the Sunda Shelf (perhaps via the Philippines) and speciated further there. Such a conclusion (Fig. 14) would be of importance in understanding the apparently complex zoogeographic history of mammals in the area of Wallace's Line.

However, reanalysis of the relationships of these squirrels contradicts Moore's interpretation. The analyses presented here, summarized in Fig. 15, strongly indicate the monophyly of the two pygmy squirrel genera. The phylogenetic relationships of *Prosciurillus* and *Sundasciurus* in this diagram should be regarded as provisional because of the problem of paraphyly within *Sundasciurus*. As noted earlier, one species-group of *Sundasciurus*, the *S. philippinensis* group, occurs in the southern Philippines (Heaney, 1979); their relationships are not clear at this time, but they do appear to be rather distantly related to *Sundasciurus jentinki* and *S. tenuis*, which are most similar to the pygmy squirrels. The one unique character of the *Hyosciurina*, absence of transbullar septa, is here shown to be convergent in *Prosciurillus* and *Exilisciurus*. Given the highly divergent morphology of the three Celebesian genera in the *Hyosciurina* (Moore, 1959), their monophyly becomes questionable.

The phylogenetic tree of the species presented here implies a zoogeographic pattern far less complicated than the one implied by Moore (Fig. 15). I hypothesize that much of the evolution of the pygmy squirrels

and their relatives took place on the Sunda Shelf. Dispersal of callosciurines to the oceanic island of Celebes has occurred at least once, and perhaps three times (once for each extant genus). Dispersal into the oceanic portion of the Philippines by callosciurines has occurred at least twice, one time involving the *Sundasciurus* of the Mindanao faunal region, and once involving the *Exilisciurus* of the same area. The origin of the ancestors of *E. concinnus* apparently took place prior to speciation of *E. exilis* and *E. whiteheadi*, but the timing of dispersal into the Philippines is not necessarily the same as the timing of the speciation itself.

A glance at the map of the known occurrence of *E. concinnus* (Fig. 3) does not indicate an obvious pattern of distribution on the islands in the southern portion of the archipelago. However, comparison with Fig. 16 provides a dramatic explanation of the distribution. It is known that sea level dropped to ca. 120 m below present level during the late Pleistocene, with maximum depth occurring about 18,000 years ago (Bloom, 1983; Hopkins, 1982). One can estimate the extent of late Pleistocene land masses in the Philippines by drawing a line at the current -120 m bathymetric line (Fig. 16). *Exilisciurus concinnus* is known to occur on all of the large and most medium-sized islands that probably were part of the late Pleistocene Mindanao mega-island. There is no evidence that they occur on the adjacent oceanic islands, even though these islands are often less than 10 km from Mindanao or Leyte (e.g., Camiguin; see Heaney, 1984b). Although habitat destruction may have reduced recent lowland populations, it appears that these squirrels now occur primarily as isolated populations at moderate to high elevations. The low level of geographic variation within *E. concinnus* indicates that it comprised a single widespread, interbreeding population during the late Pleistocene. This is consistent with evidence that temperatures in Southeast Asia were 4° to 5°C cooler during the late Pleistocene, causing current montane vegetation to be widespread at lower elevations (Medway, 1972; Heaney, 1984a). It is apparent that pygmy squirrels did not cross salt-water barriers within the Philippines.

DWARFING, ALLOMETRY, AND PHYLOGENETIC ANALYSIS OF SQUIRRELS

The analyses presented above indicate that allometry has played a significant role in influencing both quantitative and qualitative characteristics of Southeast Asian pygmy squirrels. I will review briefly the features found to be associated with differences in body size, and will then discuss a general approach for identifying and removing such influences from a phylogenetic analysis.

PCA of metric cranial characters indicated that among the pygmy squirrels about 67% of the total variation was due to size differences; all characters loaded moderately on this axis. In an analysis that included three larger species as outgroups, it was found that 95% of the total variation was on the first axis, and related to size.

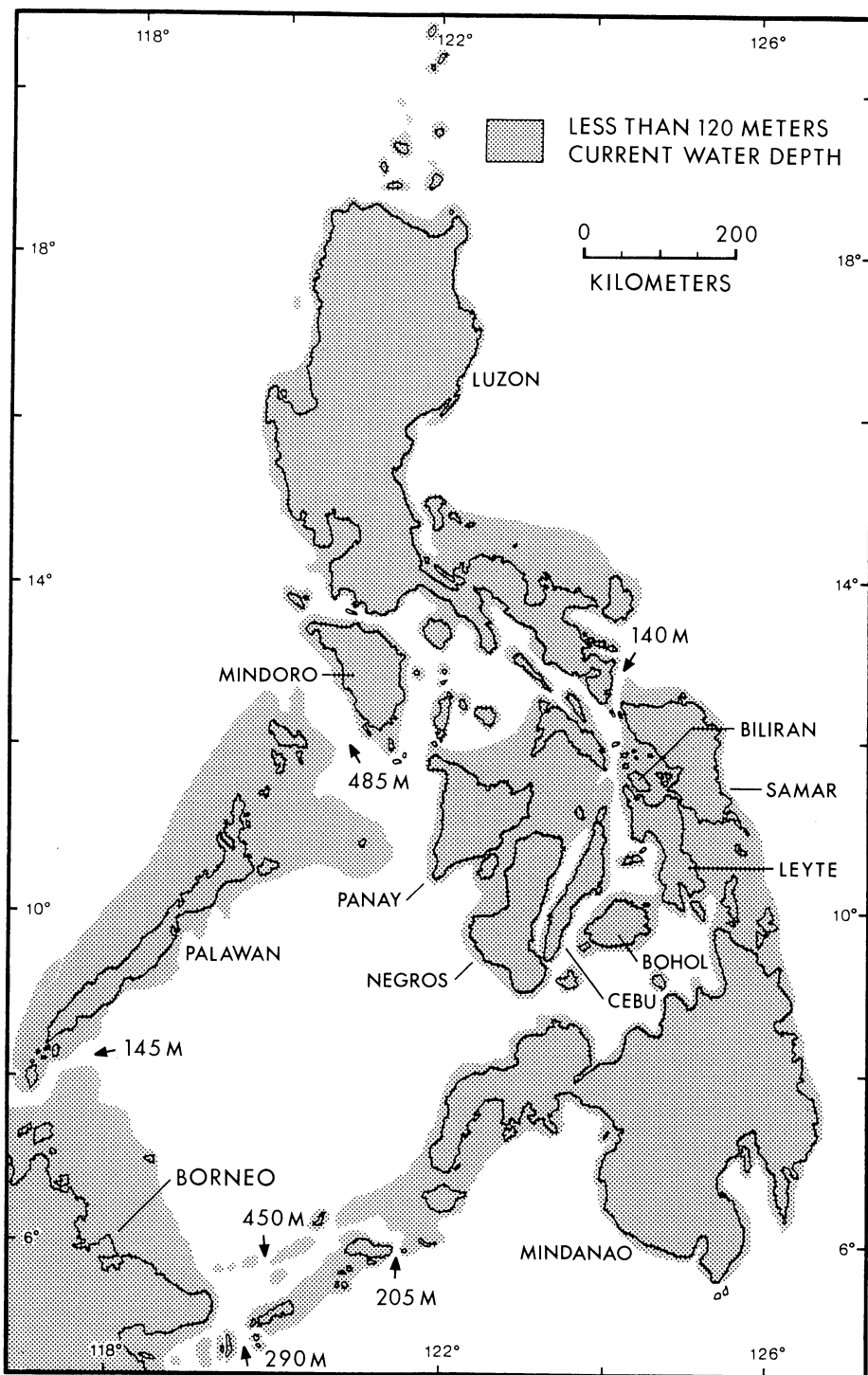


FIG. 16. Map of the Philippine islands, showing the probable extent of late Pleistocene islands, based on the current position of the -120 m bathymetric line.

A comparison with an unrelated pygmy squirrel, the African *Myosciurus pumilio*, indicated that an elongate rostrum was typical of all of these pygmy squirrels, and so was not a reliable synapomorphy for the Southeast Asian pygmy squirrels. Six other characters (palatal length, coronoid process shape, shape of the infraorbital foramen, maxillary tooththrow angle, length of the postorbital process, and reduction of the metatarsal pads) also seem to be associated with dwarfing due to allometric effects, but show evidence of enough variation that close similarities probably reflect synapomorphies. However, because these traits are associated with dwarfing, general similarity of these characters should not be relied on heavily in comparisons between taxa that are thought to be only distantly related on the basis of other presumably more reliable characters.

A PCA of qualitative characters shows that most variation (61%) lies along a single axis, and that axis is correlated with cranial size ($R^2 = 55\%$). Thus, size may contribute about 30% (0.61×0.55) of the variation in that data set. However, this includes those characters that are true synapomorphies that happen to be correlated with size, and so the actual contribution of allometric convergence may be less.

The results of this study suggest that future analysis of phylogenetic relationships among squirrels should discriminate between characters that are useful indicators of higher level relationships, those that are useful only at lower levels (within genera or species-groups), and those that are due to allometry alone. In the first group, I would place details of the male reproductive tract and the position of cranial sutures relative to unambiguously defined landmarks. In the second group, I would place characters of the interdigital and metatarsal pads, angle of the tooththrows, relatively small differences in size of teeth, minor differences in bullar morphology, differences in rostral depth and length, and other small differences in the size and position of processes, vacuities, and foramina, and possibly losses or reduction of digits, including the pollex. In the group of features strongly associated with allometry are such characters as relative orbit length, relative expansion of the braincase, degree of basicranial inflection, and angle of the zygomatic plate. Because my sample of species is small, I am sure that additional characters can be added to this list, and some characters may be moved from one "level of usefulness" to another.

The general approach to identifying characters shared by squirrels due to allometry rather than phylogeny used here has been 1) selection of an ecologically similar, same-sized reference species for comparison with the group under study, 2) identification of characters shared only by the reference species and the dwarfed study species, and removal of those characters as being unreliable indicators of phylogeny, 3) estimation of the percentage of the variation in the remaining characters that may be related to allometric trends, and 4) reexamination and possible removal of additional ambiguous characters. This approach could be adapted for use in comparable situations where, for example, convergence is suspected due to development of fossorial habits or gliding adaptations.

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APPENDIX I

The following fluid-preserved specimens were examined in compiling lists of external characters summarized in Table 6.

Exilisciurus concinnus. PHILIPPINES: LEYTE OF SAMAR. UMMZ 53158, 53159.

Exilisciurus exilis. INDONESIA: KALIMANTAN: Labuan Bini. USNM 199008; Segah River. USNM 199009.

Exilisciurus whiteheadi. MALAYSIA: SABAH: Mt. Kinabalu. USNM 292634, 292637, 292644, 292648, 301010, 301011.

Nannosciurus melonotis borneanus. INDONESIA: KALIMANTAN: Sanggau District, Kapuas River. USNM 142270; Sungai Matan. USNM 145606, 145607; Upper Pasir River. USNM 154407; Labuan Bini. USNM 199007.

Prosciurillus leucomus. INDONESIA: CENTRAL SULAWESI: Sungei Sadaunta, 3000 ft (910 m) AMNH 224587, 224588.

Sundasciurus jentinki. MALAYSIA: SABAH: Mt. Kinabalu; Kamaranga. USNM 292582.

Sundasciurus tenuis. MALAYSIA: JOHORE: Endau River, Johore bank. USNM 112523-524; INDONESIA: SUMATRA: Tapanuli Bay. USNM 114552.

APPENDIX II

The following specimens of *Prosciurillus leucomus*, *Sundasciurus jentinki*, and *S. tenuis* were used as reference samples in multivariate analyses of cranial morphology; data are summarized in Table 1.

Prosciurillus leucomus. INDONESIA: CELEBES (= Sulawesi) Id. Paleheh River (2 USNM); Teteamoet (12 USNM); Toli Toli (1 USNM).

Sundasciurus jentinki. MALAYSIA: SABAH. Mt. Kinabalu, Kiau, 3100 ft (940 m) (7 MCZ); Mt. Kinabalu, Kemberanga (1 MCZ); Mt. Kinabalu, Lumu Lumu (13 MCZ); Mt. Kinabalu, 3000 ft (910 m) elev. (1 AMNH).

Sundasciurus tenuis. MALAYSIA: SELANGOR. 16 km N Kuala Lumpur on Pahang Road (7 USNM).

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