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(ISSN 0097-4463)

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CARNEGIE MUSEUM OF NATURAL HISTORY4400 FORBES AVENUE * PITTSBURGH, PENNSYLVANIA 15213VOLUME 494 MARCH 1980ARTICLE 2

NONGEOGRAPHIC AND INTERSPECIFIC VARIATION IN FOUR SPECIES OF *HYLOMYSCUS* (RODENTIA: MURIDAE) IN SOUTHERN CAMEROON

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Abstract

Nongeographic and interspecific variation were studied in *Hylomyscus aeta*, *H. alleni*, *H. parvus*, and *H. stella*, which are sympatric in southern Cameroon. Karyotypes are illustrated for the first time for *H. aeta*, *H. alleni*, and *H. parvus*. Taxonomic problems within the genus, differences among the species, diagnostic characters, and the relationships of these species to other kinds of African *Hylomyscus* are discussed.

INTRODUCTION AND TAXONOMIC HISTORY

Climbing wood mice, genus *Hylomyscus*, inhabit tropical forests in Africa from near sea level to more than 2400 m. Of the eight species presently recognized (Misonne, 1974), three were named and described as recently as 1965.

The earliest named species referrable to *Hylomyscus* is *Mus alleni* Waterhouse (1838), a name based on a juvenile from the island of Fernando Po (3°50'N, 8°48'E), Equatorial Guinea, near the coast of Cameroon. In 1904, Thomas described a subadult as a topotype and

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Submitted for publication 15 May 1979.

referred specimens from Efulen and Ja River, southern Cameroon, to this species. In 1911, Thomas described and named *Epimys* [now a synonym of *Rattus* (see Hollister, 1916)] *stella* from eastern Congo [Zaire] and referred the specimens from southern Cameroon, which he originally had referred to *E. alleni*, to this new species. His only criterion for separating *E. stella* from *E. alleni* was size of skull. In the same paper, Thomas named and described *E. aeta*, from southern Cameroon, based on cranial differences between it and the sympatric *H. stella*.

In 1926, Thomas assigned all the known species of wood mice to the new genus *Hylomyscus* and designated *H. aeta* as the type species. Since that time, the name *Hylomyscus* has been either accorded generic status (by Allen, 1939; Hatt, 1940; Heim de Balzac and Aellen, 1965; Brosset et al., 1965; Rosevear, 1966 and 1969; Eisentraut, 1969), relegated to the status of a subgenus of the genus *Rattus* (by Ellerman, 1941; Simpson, 1945; Ellerman et al., 1953), or regarded as a subgenus of the genus *Praomys* (by Misonne, 1974). Herein, *Hylomyscus* is regarded as a distinct genus pending further investigation of the generic relationships of the included species.

Taxonomic problems within Hylomyscus have resulted from incomplete definitions and inadequate diagnoses of the included species, particularly of H. alleni and H. stella. Several authors (Hatt, 1940; Heim de Balzac and Lamotte, 1958; Heim de Balzac and Aellen, 1965; Brosset et al., 1965; Rosevear, 1966 and 1969) have attempted to rediagnose H. alleni and to determine both its distribution and its relationships with other species. Heim de Balzac and Aellen (1965) opted not to use the name H. alleni because its holotype was a juvenile; rather, they elevated H. a. simus Allen and Coolidge, with type locality in Liberia, to specific status and referred all mainland specimens previously identified as H. alleni to H. simus. In 1965, Brosset et al. reported five sympatric species of Hylomyscus from Gabon-H. aeta, H. simus, H. stella, plus two species (H. fumosus and H. parvus) which they described as new. Eisentraut (1969) reported the existence of three species of Hylomyscus (H. alleni, H. aeta, and H. stella) on Fernando Po and in adjacent Cameroon. Based on examination of topotypical H. alleni, he concluded that: 1) H. alleni is conspecific with the western and central African species that previously had been referred to as H. alleni (which has priority) or H. simus; 2) H. stella is a distinct species, which occurs sympatrically with H. alleni and H. aeta. Neither Brosset et al. (1965) nor Eisentraut (1969) could find any consistent mensural or karyotypic differences between H. stella and H. alleni; however, they did not attempt to identify and eliminate age and sexual variation. Rather, they differentiated these species by the "shorter

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rostrum" (no measurements given) and forward projecting incisors of *H. alleni*.

The objectives of this study, therefore, were to determine nongeographic variation (age, secondary sexual, and individual) in these four species of *Hylomyscus*, to use this information (together with karyotypic data) to refine the diagnoses, and to discuss the differences among these species in southern Cameroon.

Three specimens of a fifth species, originally named as *Hylomyscus* fumosus Brosset et al., 1965, were collected in southern Cameroon. This species differs from other *Hylomyscus* in so many cranial, external, and chromosomal characters that a separate genus (*Heimyscus*) was proposed (Misonne, 1969:125) for it (see also Misonne, 1974). Its taxonomic status will be reviewed in a separate paper.

MATERIALS AND METHODS

A total of 242 specimens, comprising seven species of *Hylomyscus*, was examined. These specimens are housed in the British Museum (Natural History—BMNH), Carnegie Museum of Natural History (CM), The Museum of Texas Tech University (TTU), and the National Museum of Natural History (USNM). The collection (192 specimens) of *Hylomyscus* from southern Cameroon (Fig. 1) housed in the Carnegie Museum, together with 21 specimens in the British Museum, served as the focus of this study; the former were collected by A. I. Good between 1914 and 1944 and by Carnegie Museum field parties in 1973, 1974, and 1978, and the latter were collected by G. L. Bates in the early 1900s. Parasites, standard karyotypes, and live tissues were obtained from specimens collected in 1978.

Each specimen was assigned to one of five age classes based on wear of teeth, ossification of skull, color of pelage, and reproductive condition: *juveniles* (age class 1)— M_3 not fully erupted; cranial sutures unossified; dorsal pelage dark gray; *subadults* (2)—molars fully erupted with cusps showing little or no wear; cranial sutures unossified; dorsal pelage showing at least some brown on tips of hairs; *young adults* (3)—all molars showing wear, but enamel lakes never connected; cranial sutures beginning to ossify; auditory bullae showing some translucence; dorsal pelage becoming redder with age (except in *H. parvus*); testes enlarged or other reproductive activity evident; *adults* (4)—molars with enamel lakes large, sometimes connected in M₂ and M₃; cranial sutures completely or nearly ossified; auditory bullae nearly translucent; *old adults* (5)—molar lakes completely connected and sometimes dished; cranial sutures completely ossified; auditory bullae translucent; dorsal pelage reddish brown.

Cranial measurements were recorded to the nearest 0.1 mm using dial calipers. The 14 measurements (four external and ten cranial) used were: total length (TL); length of tail (TA); length of hind foot, including claw (HF); length of ear from notch (ER); greatest length of skull (GLS); condylobasal length (CBL); greatest zygomatic breadth (GZB); least interorbital constriction (IOC); length of palatal bridge, from posterior edge of palatine to posterior edge of anterior palatine foramen (LPB); alveolar length of maxillary toothrow (MTR); greatest breadth across first upper molars, taken across labial crown surfaces of M_1 (M_1-M_1); breadth of braincase, posterior to zygomatic arches (BBC); length of anterior palatine foramen (APF); length of diastema, from posterior surface of alveolus of upper incisor to anterior surface of alveolus of M_1 (DST). Only external measurements taken from the more recently collected specimens were used.

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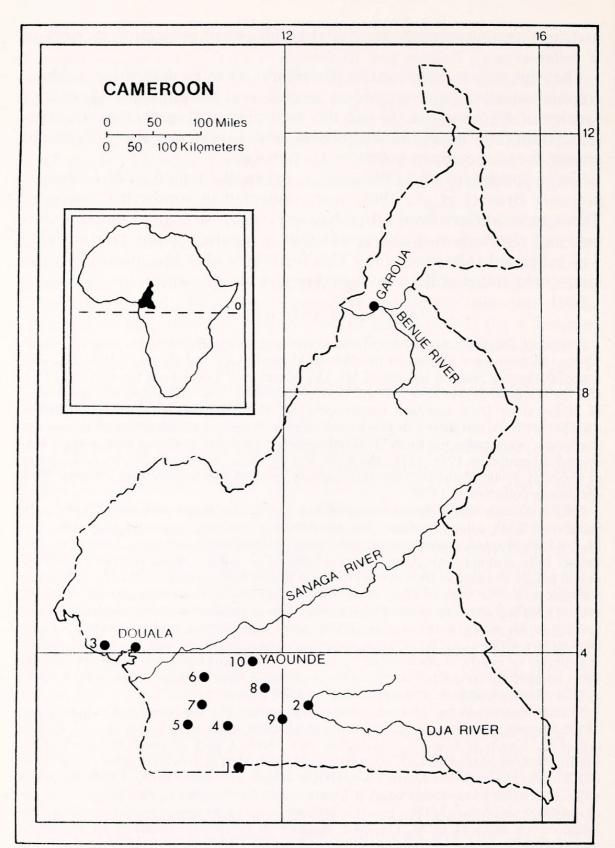


Fig. 1.—Map of Cameroon showing localities of the species of *Hylomyscus* referred to in this study: 1) 13 km S, 8 km E Ambam, $2^{\circ}16'N$, $11^{\circ}21'E$; 2) Bitye, Ja [=Dja] River, $3^{\circ}10'N$, $12^{\circ}22'E$; 3) Buea (Cameroon Mountain), $4^{\circ}11'N$, $9^{\circ}12'E$; 4) Ebolowa, $2^{\circ}54'N$, $11^{\circ}09'E$; 5) Efulen [=Efoulan], $2^{\circ}47'N$, $10^{\circ}32'E$; 6) Eseka, $3^{\circ}38'N$, $10^{\circ}47'E$; 7) Lolodorf, $3^{\circ}14'N$, $10^{\circ}44'E$; 8) Metet, $3^{\circ}23'N$, $11^{\circ}43'E$; 9) Sangmelima, $2^{\circ}52'N$, $12^{\circ}00'E$; 10) Yaoundé, $3^{\circ}52'N$, $11^{\circ}31'E$.

Univariate analyses of individual, secondary sexual, and age variation in mensural characters were conducted using the computer program UNIVAR (Power, 1970). This program generates standard statistics (arithmetic mean, standard deviation, standard error, coefficient of variation, and range) and employs a one-way analysis of variance (ANOVA, F-test) to test for significant differences (P < 0.05) among means. If the means differ significantly, the Sums of Squares Simultaneous Testing Procedure (SS-STP) is employed to identify maximal nonsignificant subsets (Gabriel, 1964). Additional statistical analyses were conducted with the Statistical Analysis System (Barr et al., 1976) and were considered significant at P < 0.05. Two-way factorial ANOVAs (with sex and age) were conducted for each species for each measurement.

No analysis of secondary sexual variation was conducted for *H. parvus* and *H. stella* because of inadequate sample sizes; thus, in these species, specimens in the same age group were pooled. When any age or sex class was not represented by a sample size greater than three, the individual measurements were recorded but those values were not used in statistical comparisons.

A minimum of ten chromosomal spreads was examined and counted from each specimen. Karyotypes are described according to Robbins and Baker (1978).

RESULTS

Nongeographic Variation

Analysis of variance-was used to assess the extent of variability associated with sex, age, and individual variation. Secondary sexual variation was determined in *Hylomyscus alleni* and *H. aeta*. Variation in selected measurements for those species is illustrated in Tables 1 and 2.

Secondary sexual variation.—A single classification ANOVA was used to test for significant differences in mensural characters between males and females of age classes 2, 3, and 4 for Hylomyscus alleni and of age classes 3 and 4 for H. aeta. In H. alleni, no significant differences between the sexes within any age class were found (Table 1). However, males of age class 4 averaged larger than females for all measurements except greatest zygomatic breadth, least interorbital constriction, length of palatal bridge, greatest breadth across first upper molars, and breadth of braincase (for these measurements, the sexes did not differ). Conversely, males of age class 3 averaged larger only in length of hind foot and females averaged larger for all other measurements except least interorbital constriction, breadth of braincase, length of palatal bridge, and length of diastema (in which the sexes did not differ). Males of age class 2 averaged larger than females in all measurements except least interorbital constriction, length of palatal bridge, and greatest breadth across first upper molars. In H. aeta (Table 2), males of age class 4 averaged larger than females for all measurements, and were significantly larger for greatest length of skull, condylobasal length, length of palatal bridge, and length of diastema; total length and length of tail averaged 10 mm larger in males than in females. Males of age class 4 even averaged larger than females of age class 5 for most measurements, although sample sizes were too

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Table 1.—Age and secondary sexual variation in selected external and cranial measurements of Hylomyscus alleni from Eseka, Cameroon. Vertical lines in the columns marked SS-STP indicate nonsignificant subsets. If sample size is less than four, values are given without statistical analyses. M and F refer to male and female, and numbers in the first column refer to age classes.

Sex and age class	N	Mean ± 2 SE	Range	CV	SS-STP
		Total l	ength	(and its in the second second	the full starts
M5	2	250, 230			
F5	1	243			
M4	16	229.2 ± 4.6	208-244	4.0	Ι
F4	7	223.3 ± 6.6	207-232	3.9	II
F3	10	215.0 ± 4.2	208-228	3.1	II
M3	28	213.6 ± 4.3	194-239	5.4	Ι
M2	13	188.8 ± 5.2	171-200	4.9	Ι
F2	10	179.6 ± 7.1	164-202	6.5	Ι
F1	1	146	_		
		Length	of tail		
M5	2	145, 135	_		
F5	1	142	_		
M4	16	133.4 ± 3.7	118-144	5.5	Ι
F4	7	128.4 ± 4.6	119-135	4.7	II
F3	10	125.6 ± 3.1	120-132	3.9	II
M3	28	125.0 ± 3.2	107-145	6.7	Ι
M2	13	109.4 ± 4.3	94-119	7.1	Ι
F2	10	104.6 ± 5.3	93-120	8.4	Ι
F1	1	81	6 - 1. 18 - 1 - 19 - 19 - 19	1	
		Length of	hind foot		
M5	2	20, 20		1	
F5	1	20			
M4	16	19.7 ± 0.3	19-21	3.1	Ι
F4	8	19.4 ± 0.4	19-20	2.7	Ī
M3	28	19.4 ± 0.2	18-20	2.9	Ī
F3	10	19.2 ± 0.3	19–20	2.2	II
M2	13	19.0 ± 0.4	18-20	3.7	II
F2	10	18.5 ± 0.3	18–19	2.8	I
F1	1	18	_	_	
		Length	of ear		
M5	2	16, 15			
F5	1	16			
M4	16	15.1 ± 0.4	14-17	5.7	I
F4	8	15.0 ± 0.5	14-16	5.0	Ī
F3	10	14.9 ± 0.4	14–16	3.8	Î
M3	28	14.6 ± 0.2	14-16	4.4	II
M2	13	13.8 ± 0.3	13-15	4.4	II
F2	10	13.5 ± 0.6	11-15	7.7	I
F1	1	12	_		

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Sex and age class	N	Mean ± 2 SE	Range	CV	SS-STP
		Greatest len	gth of skull		
M5	2	24.9, 24.5			
F5	1	24.9			
M4	15	24.8 ± 0.4	23.6-25.8	2.8	Ι
F4	8	24.5 ± 0.7	22.7-26.3	4.3	II
F3	10	23.6 ± 0.4	22.8-24.6	2.8	II
M3	27	23.5 ± 0.2	22.0-24.7	2.6	I
M2	12	21.5 ± 0.4	20.8-22.3	3.0	Ι
F2	10	21.0 ± 0.5	20.5-22.8	3.2	Ι
F1	1	19.5			
		Condyloba	sal length		
M5	2	24.4, 23.5			
F5	1	23.8	<u> </u>		
M4	15	23.6 ± 0.4	22.3-24.6	3.0	Ι
F4	8	23.5 ± 0.7	21.6-24.9	4.4	II
F3	10	22.3 ± 0.4	21.5-23.1	3.0	II
M3	28	22.2 ± 0.3	20.5-23.5	3.1	Ι
M2	12	20.1 ± 0.4	19.2-21.0	3.1	Ι
F2	10	19.6 ± 0.5	18.9-21.1	3.3	Ι
F1	1	18.0			
		Greatest zygon	natic breadth		
F5	1	12.2			
M5	2	11.8, 11.6			
F4	8	12.1 ± 3.6	11.6-13.1	4.2	Ι
M4	16	12.1 ± 1.4	11.6-12.5	2.4	I-
F3	10	11.6 ± 3.2	10.4-12.1	4.3	II
M3	28	11.4 ± 1.8	10.2-12.2	4.1	I
M2	12	10.7 ± 2.6	10.1-11.1	4.4	Ι
F2	10	10.6 ± 2.4	10.1-11.1	3.9	Ι
F1	1	10.1			
		Interorbital of	constriction		
F5	1	4.5	· · · · ·		
M5	2	4.3, 4.2			
M4	16	4.4 ± 0.05	4.2-4.5	2.2	Ι
F4	8	4.4 ± 0.09	4.2-4.5	2.9	Ι
F3	10	$4.3~\pm~0.06$	4.2-4.5	2.2	Ι
M3	28	4.3 ± 0.05	4.0-4.6	3.2	Ι
M2	12	4.1 ± 0.09	3.9-4.3	3.9	Ι
F2	10	4.1 ± 0.09	4.0-4.3	3.6	Ι
F1	1	3.9	and the second sec		
		Greatest brea	$dth M_1 - M_1$		
M5	2	4.9, 4.5	_		
F5	1	4.9	< <u> </u>		
F4	8	4.9 ± 0.14	4.7-5.2	3.9	Ι
M4	15	4.9 ± 0.09	4.6-5.2	3.4	II

Table 1.—Continued.

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Sex and					
age class	N	Mean ± 2 SE	Range	CV	SS-STP
F3	10	4.8 ± 0.07	4.7-5.0	2.2	III
M3	27	4.7 ± 0.05	4.5-5.0	3.0	II
M2	12	4.6 ± 0.10	4.3-4.9	3.8	II
F2	10	4.6 ± 0.14	4.4-4.8	4.1	Ι
F1	1	4.4	_	—	
		Breadth of	braincase		
F5	1	10.8	_		
M5	2	10.6, 10.5			
M4	16	10.8 ± 0.14	10.3-11.3	2.6	Ι
F4	8	10.8 ± 0.26	10.3-11.4	3.7	Ι
M3	28	10.5 ± 0.12	10.0-11.3	3.0	II
F3	10	10.5 ± 0.25	9.7-11.0	3.7	III
M2	12	10.3 ± 0.19	9.9-10.7	3.3	II
F2	10	10.2 ± 0.23	9.8-10.6	3.8	Ι
F1	1	9.8			
		Length of anterior	palatine foramer	1	
M5	2	4.5, 4.4			
F5	1	4.4			
M4	16	4.7 ± 0.12	4.3-5.2	5.3	Ι
F4	8	4.6 ± 0.27	3.9-5.2	8.2	II
F3	10	4.4 ± 0.13	4.2-4.7	4.5	III
M3	28	4.4 ± 0.05	4.1-4.6	2.8	II
M2	12	4.2 ± 0.14	3.7-4.6	6.2	II
F2	10	4.0 ± 0.16	3.7-4.4	6.1	Ι
F1	1	3.4	—	_	
		Length of	diastema		
M5	2	7.4, 7.3			
F5	1	7.3			
M4	15	7.3 ± 0.14	6.7-7.7	3.7	Ι
F4	8	7.2 ± 0.27	6.5-7.7	5.3	Ι
M3	28	6.7 ± 0.09	6.3-7.2	3.5	Ι
F3	10	6.7 ± 0.25	6.2-7.3	6.0	Ι
M2	12	6.1 ± 0.10	5.7-6.3	3.0	I
F2	10	5.9 ± 0.13	5.5-6.3	3.5	Ι

Table 1.-Continued.

small to test for significant differences. Males of age class 3 averaged larger than females for all measurements except length of ear from notch, length of hind foot, greatest breadth across first upper molars, and length of anterior palatine foramen (for these measurements, females averaged larger). The two-way factorial ANOVA in *H. alleni* indicated that secondary sexual variation was insignificant, in all measurements, when variation caused by age was eliminated as a factor. Analysis of *H. aeta* showed that variation caused by sex was a significant factor only in one measurement, length of palatal bridge.

Table 2.—Age and secondary sexual variation in selected cranial measurements of Hylomyscus aeta from southern Cameroon. Vertical lines in columns marked SS-STP indicate nonsignificant subsets. If sample size is less than four, values are given without statistical analyses. ns means no significant differences, M and F refer to male and female, and numbers in the first column refer to age classes.

Sex and age class	N	Mean ± 2 SE	Range	CV	SS-STP
	tale electron	Greatest leng	gth of skull	1 Transmission	
M4	3	28.1, 27.7,	_	_	
		27.4			
F5	3	27.4, 26.9,			
		26.5			
M3	10	26.0 ± 0.6	24.5-27.5	3.9	ns
F4	7	25.8 ± 0.4	25.1-26.8	2.2	
F3	10	25.7 ± 0.5	24.1-26.8	3.2	
F2	1	23.7		—	
M2	1	23.3			
		Condylobas	al length		
M4	3	26.3, 26.2,	_		
		26.0			
F5	2	25.4, 25.3	series and the		
F4	7	24.3 ± 0.4	23.7-25.1	2.2	
M3	8	24.2 ± 0.8	22.7-26.2	4.7	ns
F3	8	24.1 ± 0.7	22.4-25.5	4.2	
F2	1	22.0	<u> </u>		
M2	1	21.3		10 - 10 - 10 - 10 - 10 - 10 - 10 - 10 -	
		Interorbital c	onstriction		
F5	3	4.8, 4.7,	onstruction.		
15	5	4.6			
M4	4	4.8 ± 0.26	4.5-5.1	5.4	Ι
M3	10	4.6 ± 0.10	4.3-4.8	3.5	ÎI
F3	12	4.6 ± 0.09	4.2-4.8	3.3	II
F4	8	4.5 ± 0.11	4.2-4.6	3.5	I
F2	1	4.5		5.5	
M2	1	4.4			
	diam's a	Length of a	diastoma		
		· ·	alastema		
F5	3	8.0, 7.8, 7.5			
M4	4	7.9 ± 0.37	7.4-8.3	4.7	Ι
F4	8	7.3 ± 0.12	7.0-7.6	2.4	Ī
M3	10	7.3 ± 0.22	6.7-7.7	4.7	I
F3	12	7.1 ± 0.15	6.5-7.5	3.7	Ι
F2	1	6.7			
M2	1	6.3	the left we do not		

Variation with age.—Males and females of Hylomyscus alleni of age classes 2, 3, and 4 were grouped according to age. The ANOVA and SS-STP (results not illustrated) indicated that the three age classes differed significantly (P < 0.05) for total length, length of tail, length

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of ear from notch, greatest length of skull, condylobasal length, greatest zygomatic breadth, greatest breadth across first upper molars, length of anterior palatine foramen, and length of diastema, and that age class 2 was significantly smaller than age classes 3 and 4 for least interorbital constriction and length of palatal bridge. There were no significant differences for length of hind foot, alveolar length of maxillary toothrow, and breadth of braincase. Age and sex classes are compared separately for H. alleni in Table 1. Although sample size is low for age class 5, the measurements are within the range for all measurements in age class 4. The one specimen from age class 1 is smaller for all measurements than are those from age class 2. Age was found to be the major source of variation in all measurements of H. alleni, and in greatest length of skull, condylobasal length, greatest breadth across first upper molars, and length of diastema of H. aeta. In all other measurements, except length of palatal bridge, the major source of variation could not be determined.

Table 2 shows variation in selected measurements for *H. aeta*; significant variation was found between age classes 3 and 4 for all cranial measurements except least interorbital constriction and alveolar length of maxillary toothrow. *Hylomyscus parvus* averaged larger with increased age for all measurements, although sample sizes for age classes 3 and 5 were insufficient for statistical analyses and no specimens were available for age classes 1 and 2. In *H. stella*, specimens of age class 4 were significantly larger than those of age class 3 for all cranial measurements except least interorbital constriction and breadth of braincase. Only three specimens from age class 3 for all cranial measurements.

Individual variation.—Coefficients of variation were used as a measure of individual variation. CVs for all cranial measurements were within the ranges reported for other small rodents (Long, 1968). Highest CVs were found in external measurements, in length of anterior palatine foramina, in younger animals, and in small samples.

Variation Among Species

Mean, range, and sample size for each character for the four species of *Hylomyscus* are given for age class 4 in Table 3. Sample sizes for other age classes were too small for meaningful comparison, but those data are on file in the Museum of the High Plains and will be provided upon request. *Hylomyscus parvus* is significantly smaller (P < 0.05) than the other three species in total length, length of tail, greatest length of skull, condylobasal length, greatest zygomatic breadth, least interorbital constriction, alveolar length of maxillary toothrow, greatest breadth across first upper molars, breadth of braincase, length of

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Measure-	Hylomyscus	Hylomyscus	Hylomyscus	Hylomyscus
ment	parvus	aeta	alleni	stella
TL	190.1 (8) 180–203	223.5 (7) 210–241	228.5 (23) 207–244	237 (1)
ТА	114.5 (8) 105–124	127.5 (7) 115–142	131.3 (23) 118–144	140 (1)
HF	18.8 (8)	20.3 (7)	19.6 (24)	
	18–19	19–22	19–21	19 (1)
ER	14.5 (8) 14–15	14.9 (7) 14–16	15.0 (24) 14–17	15 (1)
GLS	20.7 (7)	26.4 (10)	24.7 (23)	25.6 (8)
	20.0–21.2	25.1–28.1	22.7–26.3	24.5–27.0
CBL	19.7 (8)	24.9 (10)	23.5 (23)	24.0 (8)
	18.7–20.4	23.7–26.3	21.6–24.9	22.4–26.0
GZB	10.7 (8)	13.3 (12)	12.1 (24)	12.0 (6)
	10.3–11.1	12.5–15.0	11.6–13.1	11.7–12.2
IOC	3.9 (8)	4.6 (12)	4.4 (24)	4.4 (8)
	3.8–4.1	4.2–5.1	4.2–4.5	4.2–4.7
LPB	4.1 (8)	4.7 (12)	4.5 (23)	4.4 (6)
	3.9–4.4	4.4–5.2	4.2–4.9	4.1–4.8
MTR	2.9 (8)	4.3 (12)	3.6 (23)	3.6 (6)
	2.8–3.0	4.1–4.5	3.4–3.8	3.4–3.7
M ₁ -M ₁	4.1 (8)	5.3 (10)	4.9 (23)	4.9 (5)
	4.0-4.3	5.1–5.7	4.6–5.2	4.8–5.0
BBC	9.4 (8)	11.8 (12)	10.8 (24)	11.1 (8)
	9.1–9.7	10.9–12.5	10.3–11.4	10.7–11.5
APF	3.9 (8)	5.2 (12)	4.7 (24)	4.9 (8)
	3.5-4.2	4.7–5.9	3.9–5.2	4.3–5.2
DST	5.9 (8)	7.5 (12)	7.2 (23)	7.3 (8)
	5.6–6.1	7.0–8.3	6.5–7.7	6.9–7.6

 Table 3.—Means and ranges for 14 measurements of four species of Hylomyscus in age class 4. Sample sizes are in parentheses. Abbreviations for measurements are given in Materials and Methods.

anterior palatine foramen, and length of diastema. *Hylomyscus aeta* is significantly larger than the other species in greatest zygomatic breadth, alveolar length of maxillary toothrow, and greatest breadth across first upper molars, and averages slightly (but not significantly) larger in greatest length of skull, condylobasal length, breadth of braincase, and length of anterior palatine foramen. No significant mensural differences were found between *H. alleni* and *H. stella*.

Karyotypes were prepared for all four species (Figs. 2 and 3). The karyotype of a female of H. stella (Fig. 2A) from Ambam is charac-

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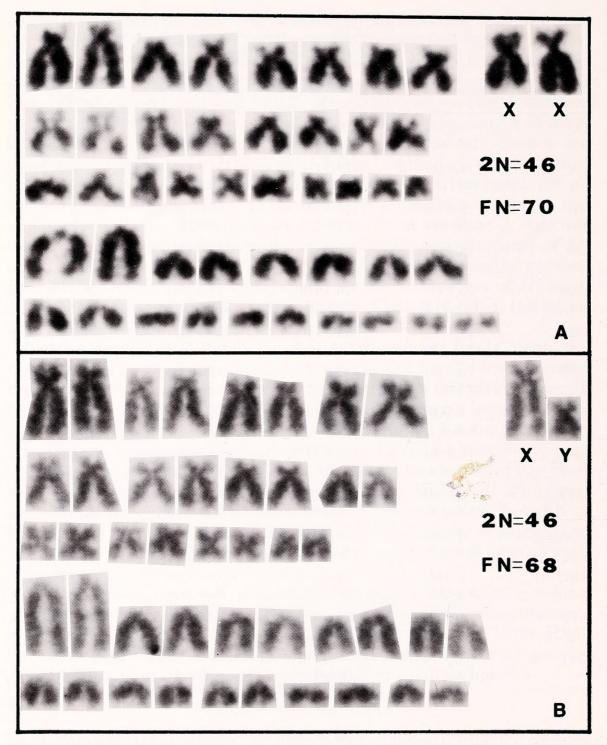


Fig. 2.—Karyotypes of *Hylomyscus*. A—*H. stella*, female, from 13 km S, 8 km E Ambam (CM); B—*H. alleni*, male, from 13 km S, 8 km E Ambam (CM).

terized by a diploid number (2N) of 46 and shows 13 pairs of biarmed autosomes (ranging from large to small), nine pairs of acrocentric autosomes (one large and the others medium to small), and a large submetacentric X. The Y chromosome in *H. stella* was described by Matthey (1963) as either a small subtelocentric or a small acrocentric.

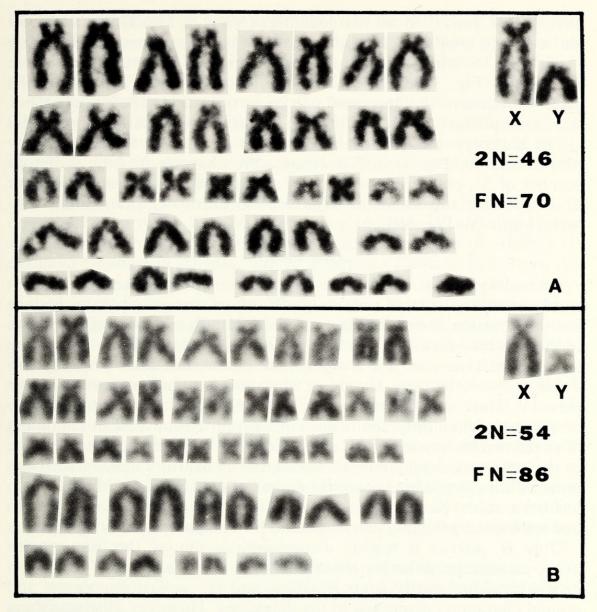


Fig. 3.—Karyotypes of *Hylomyscus*. A—*H. parvus*, male, from 13 km S, 8 km E Ambam (CM); B—*H. aeta*, male, from Buea (CM).

He reported different karyotypes from two specimens from the same locality in the Republic of the Congo. The karyotype in Fig. 2A corresponds to his "large form," which had a small subtelocentric Y.

Karyotypes of 24 (18 male and six female) specimens of *H. alleni* from three localities (1, 6, and 10, Fig. 1) were characterized by a diploid number of 46, consisting of 12 or 13 pairs of biarmed autosomes (ranging from large to small) plus nine or 10 pairs of acrocentric autosomes (Fig. 2B). The largest pair of acrocentrics has a short arm in some preparations. The X is a large subtelocentric and the Y is a small submetacentric.

Karyotypic preparations from five (four male and one female) spec-

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imens of *H. parvus* from two localities (1 and 6, Fig. 1) in Cameroon had a diploid number of 46 with 13 pairs of biarmed autosomes (ranging from large to small) plus nine pairs of medium to small acrocentric autosomes (Fig. 3A). The X is a large subtelocentric and the Y is a small subtelocentric. One small pair of acrocentrics appears fused, but this is an artifact of preparation and is not typical of other spreads.

The karyotypes of two male specimens of H. *aeta* from two localities (3 and 10, Fig. 1) in Cameroon were characterized by a diploid number of 54, consisting of 17 pairs of biarmed autosomes, nine pairs of acrocentric autosomes, a large subtelocentric X, and a small submetacentric Y (Fig. 3B).

DISCUSSION

Secondary sexual variation is not often a significant source of mensural variability in small rodents. In *H. alleni*, for example, secondary sexual variation is not significant in different age classes. The results of the two-way factorial ANOVA for *H. aeta* indicated that secondary sexual variation was not a significant factor, but data presented in Table 2 show that this source of variation becomes apparent in age class IV. Thus, secondary sexual variation may be an important source of variation when only adults are considered. Because of this, pooling of sexes results in a lower level of resolution when comparing *H. aeta* to the other species (Table 3). Likewise, mensural variation with age must be considered in taxonomic studies of *Hylomyscus*. Maximal size has been achieved by most animals referrable to age class 4, and age classes 4 and 5 probably can be pooled for comparisons among species.

Only *H. parvus* is readily distinguishable among the four species using mensural characters alone. If skulls are available, *H. aeta* can be distinguished easily from *H. alleni* and *H. stella* using dental and cranial characters discussed in the diagnoses. However, distinguishing between *H. alleni* and *H. stella* remains difficult. External and cranial measurements can be used only as an indication, and shape of skull and angle of incisors are diagnostic only within the geographic region considered by this study; these cranial and dental differences are less pronounced if specimens of *H. stella* are examined from Zaire where *H. alleni* does not occur, or if *H. alleni* is examined from western Africa where *H. stella* does not occur. Accordingly, the cranial and dental differences in sympatric populations of *H. alleni* and *H. stella* may be the result of character displacement.

Karyotypic differences may prove to be the key to accurate separation of these species. *Hylomyscus aeta* can be distinguished readily from the other three species because of differences in both diploid number and fundamental number (number of autosomal arms). *Hylomyscus parvus* exhibits both mensural and karyotypic features which facilitate identification; karyotypically it is the only one of the four species having no large acrocentric autosomes. The karyotypes of H. *alleni* and H. *stella* differ principally in fundamental number—FN = 68 in *alleni*, FN = 70 in *stella*.

The microhabitats preferred by the four sympatric species of Hylomyscus are unknown. All four were caught in the same trapline, both on the ground and in trees and bushes, at Ambam. Moreover, H. aeta, H. alleni, and H. parvus were caught in the same traps on different days in trees near Eseka.

Based on morphology, the Hylomyscus of Africa can be divided into three species groups. The H. aeta group includes H. aeta in central Africa, H. baeri Heim de Balzac and Aellen in western Africa, H. carillus (Thomas) in Angola, and H. denniae (Thomas) in eastern Africa. This group is characterized by the presence of a broad, wedgeshaped interorbital area, supraorbital ridges, relatively large molars, and less fragile skulls. The H. alleni group includes H. alleni in central and western Africa and H. stella in central and east-central Africa. This group is characterized by the presence of a biconcave interorbital area and narrow incisors and molars. The H. parvus group includes only H. parvus, in central Africa, characterized by its small size, inflated braincase, and pro-odont incisors. Standard karyotypes prepared for this study show that H. aeta differs appreciably more from representatives of the alleni and parvus groups than do representatives of those groups from each other. Additional karyotypic studies (employing banding techniques) and electrophoretic analyses may lead to a better understanding of the relationships among these species and species groups.

Following are diagnoses and descriptions of adult specimens of the four species of *Hylomyscus* where they occur sympatrically in southern Cameroon.

Hylomyscus aeta (Thomas)

Type locality.—Bitye, Ja [=Dja] River, Cameroon.

Distribution.—Forests of Cameroon, Fernando Po, Gabon, Republic of the Congo, Zaire, and western Uganda (Misonne, 1974).

Description.—Color of dorsum in adults buffy brown to reddish brown; buffy line separating white-tipped ventral pelage from dorsal pelage; juvenile pelage black to grayish-brown; basal color of dorsal and ventral pelage gray; interorbital region broad with well defined supraorbital ridges extending across parietals; frontal region wedgeshaped.

Diagnosis.—Length of maxillary toothrow greater than 4.0 mm; upper incisors opistodont (projecting posteriorly); skull illustrated by

Heim de Balzac and Aellen (1965:717–719); mammae 1p, 2i = 6; karyotype 2N = 54, FN = 86.

Hylomyscus parvus Brosset, Dubost, and Heim de Balzac

Type locality.—Belinga, Gabon.

Distribution.—Forests of Gabon, Republic of the Congo, and Cameroon.

Description.—Color of dorsum in adults chocolate brown, not noticeably reddish; tips of ventral pelage pale brown; juvenile pelage black to grayish-brown; basal color of dorsal and ventral pelage gray; skull lightly built; braincase large and rounded.

Diagnosis.—Smallest species of *Hylomyscus*; total length less than 205 mm; greatest length of skull less than 22.0 mm; greatest zygomatic breadth less than 11.5 mm; alveolar length of maxillary toothrow less than 3.2 mm; breadth of braincase less than 17.0 mm; upper incisors markedly pro-odont (projecting forward); skull illustrated by Brosset et al. (1965:149–150); mammae 1p, 2i = 6; karyotype 2N = 46, FN = 70.

Hylomyscus stella (Thomas)

Type locality.—Ituri Forest between Mawambi and Avakubi, northeastern Congo [Zaire].

Distribution.—Isolated forests of Kenya and Uganda westward to Nigeria.

Description.—Color of dorsum in adults dark reddish-brown, changing to paler reddish-brown in old adults; tips of ventral pelage white; juvenile pelage black to grayish-brown; basal color of dorsal and ventral pelage gray; interorbital constriction biconcave.

Diagnosis.—Length of maxillary toothrow between 3.4 and 3.8 mm; upper incisors slightly opistodont; nasals projecting anterior to premaxilla and incisors; skull illustrated by Brosset et al. (1965:157–158); mammae 2p, 2i = 8; karyotype 2N = 46, FN = 70.

Hylomyscus alleni (Waterhouse)

Type locality.—Fernando Po, Equatorial Guinea.

Distribution.—Forests and galleries from Central African Republic and Gabon westward to Guinea.

Description.-Color of pelage and shape of skull as in H. stella.

Diagnosis.—All mensural characters as in *H. stella*; upper incisors slightly pro-odont; premaxilla and/or incisors projecting anterior to tip of nasals; skull illustrated by Brosset et al. (1965:149–150); mammae 2p, 2i = 8; karyotype 2N = 46, FN = 68.

SPECIMENS EXAMINED

Hylomyscus aeta.—CAMEROON: 13 km S, 8 km E Ambam, 1 (CM); Bitye, Ja [=Dja] River, 9, including the holotype (BMNH); Buea, Cameroon Mtn., 2 (CM); Efulen [=Efoulan], 10 (CM); Eseka, 12 (CM); Lolodorf, 4 (CM); Metet, 1 (CM); Sangmelima, 1 (CM); Yaoundé, 2 (CM).

Hylomyscus alleni.—CAMEROON: 13 km S, 8 km E Ambam, 14 (CM); 30 km W Bertoua, 2 (TTU); Eseka, 95 (CM); Lolodorf, 3 (CM); 30 km N, 40 km E Obala, 10 (CM); 2 km W Saa, 1 (TTU); Yaoundé, 4 (CM). CENTRAL AFRICAN REPUBLIC: 10 km N M'Baiki, 2 (CM). DAHOMEY: Ayitedjou, 1 (USNM). EQUATORIAL GUINEA: Fernando Po, 2, including the holotype (BMNH). GHANA: Ahiriso, 4 (USNM); 1 mi N Berekuso, 1 (USNM); Butre, 1 (USNM). Togo: Agou, 6 (USNM).

Hylomyscus stella.—CAMEROON: 13 km S, 8 km E Ambam, 1 (CM); Bitye, 8 (BMNH); Ebolowa, 1 (CM); Efulen [=Efoulan], 9 (8 CM, 1 BMNH); Lolodorf, 4 (CM); 30 km E Nanga-Eboko, 2 (TTU); Metet, 1 (CM); Sangmelima, 1 (CM). RWANDA: 110 km W Butare, 1 (CM). ZAIRE: Ituri Forest, the holotype (BMNH); 120 km W Mambassa, 4 (CM).

Hylomyscus parvus.—CAMEROON: 13 km S, 8 km E Ambam, 4 (CM); Ebolowa, 1 (CM); Eseka, 10 (CM).

Hylomyscus baeri.—GHANA: Kade, 1 (USNM). IVORY COAST: Blekoum, 2 (USNM). Hylomyscus carillus.—ANGOLA: the holotype (BMNH).

Hylomyscus denniae.—KENYA: Mount Kenya, 7 (USNM).

"Heimyscus" fumosus.—CAMEROON: 13 km S, 8 km E Ambam, 2 (CM); Eseka, 1 (CM).

ACKNOWLEDGMENTS

Thanks are due I. Bishop of the British Museum (Natural History), R. J. Baker of The Museum of Texas Tech University, D. A. Schlitter of the Carnegie Museum of Natural History, and H. W. Setzer of the National Museum of Natural History for allowing us to examine specimens in their care. Assistance in the field was provided by D. A. Schlitter and S. L. Williams. R. K. Barnett assisted in preparation of karyotypes. Our special thanks go to the Ministry of Agriculture of the United Republic of Cameroon and to V. Belinga, Director of Forestry Services in Cameroon, and C. Njiti for assistance in obtaining necessary permits. For assistance in Cameroon, we would like to thank J. Naponic and D. Heymann. An earlier draft of this manuscript was reviewed by E. D. Fleharty (Fort Hays State University), D. A. Schlitter (Carnegie Museum of Natural History), and R. J. Baker (Texas Tech University), and was submitted by L. W. Robbins to the Department of Biological Sciences, Fort Hays State University, in partial fulfillment of the degree of Master of Science. Partial support for this study was provided by a computational grant from Kansas State University, and by grants to D. A. Schlitter from the M. Graham Netting Research Fund through a grant from the Cordelia Scaife May Charitable Trust, the Loyalhanna Foundation, and the National Geographic Society.

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