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ON THE COVER: REPRODUCTION OF ADOLF BERNHARD MEYER'S PLATE OF "*CRAUROTHRIX LEUCURA*" (= *ECHIOTHRIX LEUCURA*) FROM HIS 1899 ARTICLE, "SÄUGETIERE VOM CELÉBES- UND PHILIPPINEN-ARCHIPEL." MODERATELY LARGE WITH A LEAN BODY, LONG HEAD, BRISTLY DARK GRAY UPPERPARTS, WHITE UNDERPARTS, MOSTLY WHITE TAIL THAT IS LONGER THAN HEAD AND BODY, DELICATE FRONT LEGS AND SMALL FEET BUT ROBUST HIND LEGS WITH LARGE AND ELONGATE HIND FEET, AND VERY LARGE EARS, SPECIES OF *ECHIOTHRIX* ARE TERRESTRIAL, NOCTURNAL, ADAPTED TO PRIMARILY AN EARTHWORM DIET, AND OCCUR ONLY ON THE INDONESIAN ISLAND OF SULAWESI.

MUSSER & DURDEN: *ECHIOTHRIX LEUCURA* AND *E. CENTROSA*

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MORPHOLOGICAL AND GEOGRAPHIC  
DEFINITIONS OF THE SULAWESIAN SHREW  
RATS *ECHIOTHRIX LEUCURA* AND *E. CENTROSA*  
(MURIDAE, MURINAE), AND DESCRIPTION  
OF A NEW SPECIES OF SUCKING LOUSE  
(PHTHIRAPTERA: ANOPLURA)

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GUY G. MUSSER AND LANCE A. DURDEN



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(PHTHIRAPTERA: ANOPLURA)

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## ABSTRACT

Among the 15 known genera of murine rodents endemic to the island of Sulawesi, is the shrew rat genus *Echiothrix*. Physically large (length of head and body = 182–235 mm; weight = 215–310 g) with a bicolored tail typically longer than head and body (100%–135% of head and body length), elongate hind feet (48–55 mm), large ears (31–35 mm), long and thin muzzle, spinous fur, and tiny molars relative to size of skull (length of molar row = 12%–13% of occipitonasal length), *Echiothrix* was named and described in 1867 and through the years has been treated as monotypic or containing up to three species. Results from analyses of morphometric traits derived primarily from cranial and dental measurements document the presence of two species. *Echiothrix leucura* (Gray, 1867) is restricted to the northern peninsular mainland east of the Gorontalo region (00°31' N, 123° 03' E). This distribution is concordant with that of four other murids endemic to the northeastern tip of the northern peninsula: *Bunomys fratrorum*, *Taeromys taerae*, *Rattus xanthurus*, and *R. marmosurus*. *Echiothrix centrosa* Miller and Hollister, 1921 (*Echiothrix brevicula* Miller and Hollister, 1921, is a synonym), is documented by specimens from the northern peninsula west of the Gorontalo region and in the central portion of the island; 19 other murine species are also known only from the core of Sulawesi. Whether the range of *E. centrosa* extends to the eastern, southeastern, and southwestern peninsulas is at present unknown. *Echiothrix leucura* has a more elongate skull compared with *E. centrosa* (greater lengths of skull, rostrum, diastema, and bony palate), a wider interorbital region, larger braincase, narrower bony palate and mesopterygoid fossa, shorter incisive foramina, and appreciably larger molars; the two species also differ in frequencies of particular molar cusps and cusplets. Both species of *Echiothrix* are nocturnal, terrestrial, and occupy habitats in tropical lowland evergreen rain forest. Natural history observations made in the field for *Echiothrix centrosa* show it to be primarily vermivorous; other natural history observations derived from field work in central Sulawesi are provided. One aspect of that natural history is the ectoparasitic load borne by *E. centrosa*. This shrew rat is host to at least four species of ticks (*Haemaphysalis kadarsani*, *Haemaphysalis hystriensis*, *Haemaphysalis* sp. and *Amblyomma* sp.), a tiny fur mite (*Listrophoroides echiothrix*), mesostigmatid mites belonging to the genus *Laelaps*, currently undetermined chiggers, a flea (*Farhangia quattuordecimdentata*), and a new species of sucking louse described herein as *Polyplax beaucournui*. This louse has tibiotarsal claws adapted for grasping slender soft hairs in the pelage and not the wide host spines; female lice also attach their eggs only to these slender hairs. The closest relative of *Echiothrix* is probably *Paucidentomys vermidax*, another Sulawesian endemic shrew rat that is also vermivorous but lacks molars and has been collected only in montane forests. The present report documents morphological and distributional limits of species in *Echiothrix*, places one of those species in an ecological and parasitological landscape, and generally contributes to knowledge covering endemic murid species diversity and identifying unique zoogeographical areas on Sulawesi.

## INTRODUCTION

*Echiothrix* and the two species of this genus defined here, along with four other genera and five species of described shrew rats—*Melasmsothrix naso*, *Tateomys rhinogradoides* and *T. macrocerus* (Musser, 1982), *Sommeromys macrorhinos* (Musser and Darden, 2002), and *Paucidentomys vermidax* (Esselstyn et al., 2012)—and two additional undescribed genera are among the 15 known genera and more than 50 species of murids endemic to the island of Sulawesi (Musser, in press). Of these shrew rats, the diversity of species in *Echiothrix*, their range over the island, and their associated ecologies are

feebly documented and require serious inquiry. To alter that lack of information for such an interesting and unique product of murine evolution on Sulawesi is our purpose here.

Our investigation into the nature of *Echiothrix* concentrates on describing results from two primary research endeavors. One looks to define limits of the species in *Echiothrix* employing examples of the genus housed in collections of museums in North America, Europe, and Asia. It is from these voucher specimens that we have gathered data concerning color and texture of the fur; qualitative aspects of physical build and cranial conformation; external, cranial, and dental measurements; morphology of the

incisors and molars; and geographic and elevational distributions on Sulawesi. Supplemental information comes from field journals and publications. We also include ecological observations for one of the species (*E. centrosa*) made by Musser during the time he worked in central Sulawesi. Results reflect an alpha-level systematic contribution that frames species limits based upon our interpretation of present morphological and geographic data, a hypothesis readily testable by using a combination of qualitative anatomical, morphometric, and molecular approaches drawn from additional material collected in unsurveyed regions of Sulawesi.

The other goal provides results from surveying skins for ectoparasites of *Echiothrix* with a focus on sucking lice (Insecta, Anoplura). Many groups of sucking lice are host specific and phyletically track their hosts (Kim, 1985, 1988; Light and Hafner, 2007; Smith et al., 2008): “Among insects, no group is more specialized for parasitism than are lice (Phthiraptera) because they are probably the only insect parasites to spend their entire life cycle, from egg to adult, on one host” (Grimaldi and Engel, 2005: 278). While we found lice on skins of only one of the two species of *Echiothrix* (*E. centrosa*), the discovery allowed us to name and describe the new species, *Polyplax beaucournui*. New research will have to determine whether the new louse infests only *E. centrosa* or it also parasitizes *E. leucura* or any other species of *Echiothrix* that might be identified in future surveys of small mammals on Sulawesi. Because of the intimate bond between parasite and the parasitized, morphological and eventually molecular comparisons among the *Polyplax* residing on different species of *Echiothrix* might add another set of data potentially useful for discerning species limits of the hosts. In the meantime, the new record broadens the inventory of sucking louse species (in *Polyplax* and *Hoplopleura*) found on endemic Sulawesi rodents in general (Musser et al., 2010) and murines in particular (Durden, 1986a, 1986b, 1987, 1990; Durden and Musser, 1991, 1992; Musser and Durden, 2002).

Our exposition of *Echiothrix* is presented in the following parts: (1) materials and methods covering the sections relevant to

both the shrew rat and its ectoparasites; (2) gazetteer of collection localities and record of specimens examined from each locality; (3) introduction to the genus, which includes the nomenclatural history of the two other generic names that in the past have been attached to *Echiothrix*, indication of the type species, an emended generic diagnosis, and a notice of the species contained in the genus; (4) an account of *E. leucura*, the type species of the genus; (5) the account of *E. centrosa*; (6) natural history observations pertaining to *E. centrosa*; (7) brief discussion of particular anatomical systems showing adaptation to a vermivorous diet; (8) description of the new species of louse and records of other ectoparasites infesting *Echiothrix* (based on *E. centrosa*); (9) a closing section (Coda) in which we briefly comment on the phylogenetic affinity of *Echiothrix*, and include an overview of anopluran sucking lice recorded from endemic Sulawesi murines.

Responsibilities for the contents are divided: Musser contributed the basic anatomical, morphometric, and distributional data and analyses used in the taxonomic revision of *Echiothrix*, along with the ecological observations and significance of particular anatomical systems as pertains to vermivory. Description of the new sucking louse, the records of other groups of ectoparasites, and overview of Sulawesi sucking lice springs from Durden’s research. We integrated our individual efforts, carefully reviewed each other’s contribution, and share responsibility for the finished product.

## MATERIALS AND METHODS

### THE SHREW RATS

**INSTITUTIONS AND SPECIMENS:** The definitions of species documented here are determined from examination of specimens stored in the following institutions: the American Museum of Natural History, New York (AMNH); Natural History Museum (formerly British Museum of Natural History), London (BMNH); Field Museum of Natural History, Chicago (FMNH); Museum Zoologicum Bogoriense, Cibinong, Java (MZB; now the Indonesian National Museum of Natural History, also known as

the Research Center in Biology–Lembaga Ilmu Pengetahuan Indonesia); Naturhistorisches Museum Basel, Switzerland (NMB); Nationaal Museum of Natural History Naturalis (formerly the Rijksmuseum van Natuurlijke Historie), Leiden (RMNH); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Specimens referenced by catalog number in gazetteers, tables, text, and figure legends are preceded by one of these acronyms. Some specimens are also cited by Archbold Sulawesi Expedition field numbers (ASE).

Many of the generic and specific traits described here are those associated with a dry skin (usually stuffed as a museum study specimen) and an associated skull—one type of standard museum preparations. Color descriptions of fur, ears, feet, and tail of *E. leucura* are derived from those museum specimens—Musser's field work did not take him to the geographic regions where that species resides. Color descriptions of *E. centrosa* come primarily from his field journals (stored in Mammalogy Archives, AMNH) where he recorded coloration and other details of freshly caught rats. His collection also includes fluid-preserved whole specimens or skinned carcasses that were initially fixed in 10% formalin, soaked for several days in water, and finally stored in 70% ethanol. From this material comes descriptions of stomach morphology and topography of palmar and plantar regions.

**MEASUREMENTS:** Values for external dimensions are from two groups of specimens. One consists of samples Musser collected in central Sulawesi. For each of these specimens he measured total length; length of tail (LT); length of the dorsal distal white tail segment (taken from the distal border of the basal brown portion to tip of the tail along the dorsal surface); length of hind foot, including claw (LHF); and length of ear, from notch to crown (LE). He took these measurements soon after the rat was caught, and also obtained a value for body weight (WT, in grams).

The second group contains specimens in museums caught and prepared by other collectors. They recorded total length, lengths of tail and hind foot, sometimes length of ear, but not weight. Musser used their value for

length of tail, and measured length of the distal white tail segment on the dry study skin; value for ear length, when available, was sometimes ignored because it was unclear how preparators measured that dimension. Values for length of hind foot were usually ignored and instead Musser measured those distances on the dry skins. He also did not use total length from either group in any analyses, but subtracted length of tail from it to obtain a value for length of head and body, which is a more useful metric.

In the laboratory, several measurements were made on specimens from both groups. The number of scale rings per centimeter on the tail was counted about one-third the distance from its base. To measure lengths of overfur and guard hairs on the dorsum, Musser placed a ruler at a right angle to the skin surface on the back near the rump and recorded the approximate mark where ends of the bunched hairs rested; the technique is unsophisticated and the results imprecise, but provides a descriptive estimate of lengths for those pelage constituents.

Using handheld dial calipers, Musser measured the following cranial and dental dimensions to the nearest 0.1 mm; shorter dimensions (BBP, LIF, BIF, BMF, LB, and dimensions of toothrows and individual molars) were measured under a dissecting microscope. Dimensional limits are illustrated in figure 1; abbreviations are used in the tables.

ONL	occipitonasal length (= greatest length of skull; distance from tip of the nasals to posterior margin of the occiput)
ZB	zygomatic breadth (greatest breadth across the zygomatic arches)
IB	interorbital breadth (least distance, as viewed dorsally, across the frontal bones between the orbital fossae)
LR	length of rostrum (from tip of the nasal bones to the posterior margin of the zygomatic notch)
BR	breadth of rostrum (greatest breadth across the rostrum, including the bony nasolacrimal capsules)

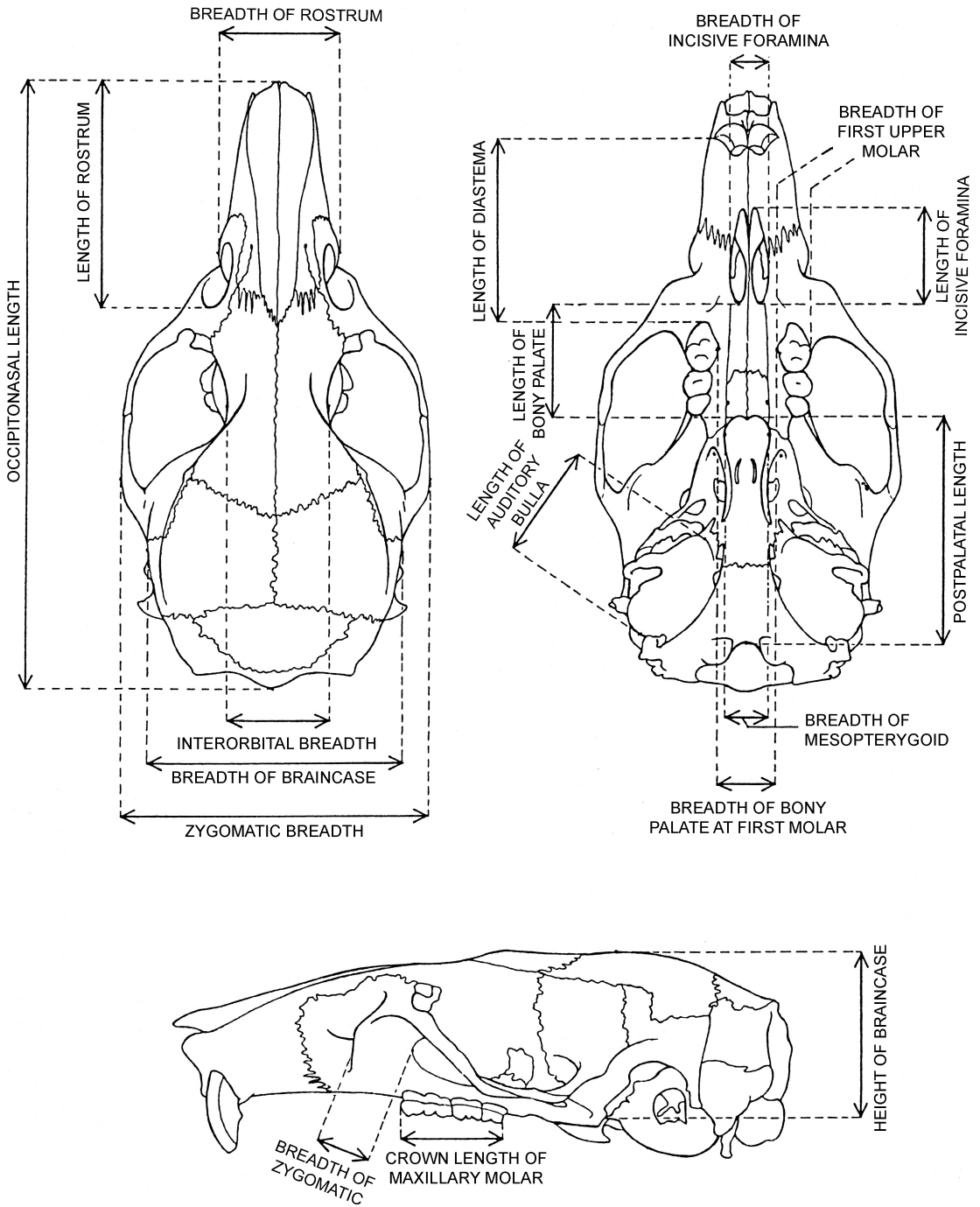


Fig. 1. An adult *Bunomys chrysocomus* illustrating limits of cranial and dental dimensions measured. Additional definitions are provided in the text.

BBC	breadth of braincase (measured from just above the squamosal root of each zygomatic arch)		of first lower molar, excluding the root, to posterior enamel face of third lower molar)
HBC	height of braincase (from top of the braincase to the ventral surface of the basisphenoid)	clm1–3	crowns length of mandibular molar row (from anterior enamel face of first lower molar to posterior enamel face of third lower molar)
BZP	breadth of zygomatic plate (distance between the anterior and posterior edges of the zygomatic plate)	BM1	breadth of first upper molar (taken across widest part of molar)
LD	length of diastema (distance from posterior alveolar margins of upper incisors to anterior alveolar margins of first upper molars)	bm1	breadth of first lower molar (taken across widest part of molar)
PPL	postpalatal length (distance from the posterior margin of the palatal bridge to posterior edge of the basioccipital—ventral lip of the foramen magnum)		
LBP	length of bony palate (distance from posterior edge of incisive foramina to posterior margin of the bony palate)		
BBPM1	breadth of bony palate at first molar (least distance between lingual alveolar margins of first molars)		
LIF	length of incisive foramina (distance from anterior to posterior margin of one of the foramina)		
BIF	breadth across incisive foramina (greatest distance across both foramina)		
BMF	breadth of mesopterygoid fossa (distance from one edge of mesopterygoid fossa to the other)		
LB	length of ectotympanic (auditory) bulla (greatest length of the bullar capsule, excluding the bony eustachian tube)		
ALM1–3	alveolar length of maxillary molar row (from anterior alveolar rim of first upper molar to posterior alveolar rim of third upper molar)		
alm1–3	alveolar length of mandibular molar row (from anterior alveolar rim of first lower molar to posterior alveolar rim of third lower molar)		
CLM1–3	crowns length of maxillary molar row (from anterior enamel face		

In the multivariate analyses used to generate principal-components and discriminant-function graphs, values for alveolar length of the maxillary molar row (ALM1–3) instead of crown length of the molar row (CLM1–3) were used. The molars are very small, particularly the third molar, and some were lost when skulls were cleaned. By using alveolar length, a complete set of variables for the analyses could be employed, even when teeth were missing, and the largest possible sample sizes assembled.

**AGE AND SEX:** Specimens could consistently be placed into one of the following age groups: **old adult** (body size usually among the largest in a sample; clothed in adult pelage; occlusal surfaces of molars worn nearly to tops of roots so cusp patterns are obliterated, the crowns worn into shallow basins with either intact or eroded margins); **adult** (body size among the largest in a sample; covered in adult pelage; molars worn; occlusal surfaces retain outlines of major cusps, but their enamel margins are worn low so that dentine is broadly exposed forming shallow basins; labial cusplets obliterated); **young adult** (body size usually smaller than older adults; covered in fresh adult fur; molars slightly worn; enamel borders of cusps much higher than the enclosed dentine, which has a restricted exposure; laminae, cusps, and labial cusplets are discrete); **juvenile** (body size among smallest in a sample; covered in juvenile pelage, which is easily recognizable compared to the adult coat; upper and lower third molars unerupted or if erupted usually unworn).

These roughly defined age groups are unequally represented among samples: old



TABLE 1  
Differences in Means of Cranial and Dental Variables between Sexes in Samples of *Echiothrix centrosa* and *E. leucura*

Mean  $\pm$  1 SD are listed; probability values (P) are derived from t-tests. Samples (consisting of young-to-old adults) from different localities had to be combined to obtain a sufficiently large number of specimens for testing the significance of sexual differences.

Variable	<i>E. centrosa</i> Pinedapa and Kuala Navusu <sup>a</sup>			<i>E. leucura</i> Rurukan, Tondano, Gunung Masarang, Temboan <sup>b</sup>		
	♀N = 8	♂N = 11	P	♀N = 10	♂N = 6	P
ONL	51.8 $\pm$ 1.32	51.8 $\pm$ 1.27	0.984	55.1 $\pm$ 1.18	54.7 $\pm$ 2.17	0.682
ZB	23.5 $\pm$ 0.86	23.0 $\pm$ 0.67	0.168	23.6 $\pm$ 1.06	23.5 $\pm$ 1.38	0.949
IB	6.5 $\pm$ 0.18	6.7 $\pm$ 0.23	0.108	7.3 $\pm$ 0.30	7.4 $\pm$ 0.17	0.309
LR	20.4 $\pm$ 0.82	20.3 $\pm$ 0.75	0.805	22.4 $\pm$ 1.00	22.3 $\pm$ 1.35	0.907
BR	7.5 $\pm$ 0.29	7.5 $\pm$ 0.34	0.646	7.4 $\pm$ 0.53	7.3 $\pm$ 0.35	0.846
BBC	18.7 $\pm$ 0.25	18.7 $\pm$ 0.36	0.949	19.3 $\pm$ 0.45	19.6 $\pm$ 0.21	0.078
HBC	14.0 $\pm$ 0.25	14.2 $\pm$ 0.31	0.119	14.6 $\pm$ 0.53	15.1 $\pm$ 0.41	0.076
BZP	3.4 $\pm$ 0.21	3.4 $\pm$ 0.24	0.720	3.5 $\pm$ 0.16	3.5 $\pm$ 0.35	0.899
LD	18.3 $\pm$ 0.68	18.3 $\pm$ 0.81	0.922	19.1 $\pm$ 1.00	18.7 $\pm$ 1.08	0.522
PPL	18.3 $\pm$ 0.31	18.1 $\pm$ 0.50	0.330	18.4 $\pm$ 0.90	18.3 $\pm$ 1.13	0.867
LBP	9.8 $\pm$ 0.25	9.9 $\pm$ 0.51	0.468	12.2 $\pm$ 0.62	11.9 $\pm$ 0.81	0.424
BBPM1	4.9 $\pm$ 0.24	5.0 $\pm$ 0.25	0.616	4.7 $\pm$ 0.62	4.6 $\pm$ 0.39	0.866
BMF	2.6 $\pm$ 0.11	2.6 $\pm$ 0.10	0.856	2.3 $\pm$ 0.19	2.3 $\pm$ 0.19	0.893
LIF	9.7 $\pm$ 0.62	9.5 $\pm$ 0.38	0.463	9.4 $\pm$ 0.63	9.2 $\pm$ 0.71	0.563
BIF	3.2 $\pm$ 0.16	3.2 $\pm$ 0.24	0.430	3.3 $\pm$ 0.28	3.2 $\pm$ 0.42	0.714
LB	6.1 $\pm$ 0.15	6.1 $\pm$ 0.15	0.562	6.1 $\pm$ 0.17	6.1 $\pm$ 0.21	0.542
ALM1-3	6.5 $\pm$ 0.12	6.3 $\pm$ 0.26	0.097	7.3 $\pm$ 0.42	7.3 $\pm$ 0.38	0.873
BM1	2.0 $\pm$ 0.05	2.0 $\pm$ 0.07	0.967	2.3 $\pm$ 0.11	2.4 $\pm$ 0.10	0.510

<sup>a</sup> Localities 3 and 4 for *E. centrosa* in gazetteer and on the map in figure 2; both places are from lowlands in the same general region.

<sup>b</sup> Localities 2-4 and 6 for *E. leucura* gazetteer and on the map in figure 2.

adults and juveniles are scarce, adults and young adults are most common. Old adults, adults, and young adults were combined into samples from which cranial and dental measurement values were obtained for multivariate analyses and univariate descriptive statistics. Recognition of relative age classes was important for identifying relative age of holotypes and gauging the position of particular specimens showing incongruous distributions in principal-components and canonical-variate ordinations.

Males and females were not separated in any of the statistical analyses. Examined side by side, size differences in adult skulls of males and females within a single species collected from the same area appeared negligible. This observation was reinforced by results from determining significance of differences between means for cranial and dental variables of each sex (t-test) in samples of *Echiothrix centrosa* and *E. leucura* (ta-

ble 1). Within each of the species, differences between means were not significant across all variables—sex is a trivial contribution to intrasample nongeographic variation of cranial and dental variables.

Results of principal-components analysis of each species (not illustrated here) did not reveal a different pattern in variation among the cranial and dental variables due to sex. The distribution of specimen scores projected onto first and second components for each species produced a single cloud of thoroughly intermixed points for males and females—polygons enclosing maximum dispersion of scores representing each sex, and ellipses outlining 95% confidence limits for cluster centroids broadly overlapped.

Weak sexual dimorphism in cranial and dental variables generally characterizes nongeographic sexual variation among muroid rodents. For examples of sigmodontines, see Carleton and Musser (1989, 1995 [*Microryz-*

TABLE 2  
**Population Samples Employed in Univariate and Multivariate Analyses of Cranial and Dental Variables for Species of *Echiothrix***

Localities, along with elevations and geographic coordinates, are referenced in the gazetteers and marked on the distribution map. Brackets enclose total number of specimens for each species. Specimens measured are identified in footnote.

Species and population sample <sup>a</sup>	<i>N</i>
<i>Echiothrix leucura</i>	[16]
NORTHEAST	
Northeast (Rurukan, Tondano, Gunung Masarang, Temboan)	
<i>Echiothrix centrosa</i>	[30]
NORTHCENTRAL	
Molinggapoto	3
Bumbulan	1
CORE	
Kuala Navusu–Pinedapa	19
Sadaunta–Besoa (Sungai Sadaunta, Kulawi, Winatu, Gimpu, Besoa)	7

<sup>a</sup> *E. leucura*—Rurukan: AMNH 101243, 101245–101248; BMNH 97.1.2.46. Tondano: RMNH 21066–21069. Gunung Masarang: BMNH 97.1.2.45. Temboan: RMNH 21065; USNM 217802, 217804, 217806–217808, 217906.

*E. centrosa*—Molinggapoto: USNM 200266, 200268, 200269. Bumbulan: AMNH 153013. Kuala Navusu: AMNH 225678–225681, 225683–225685. Pinedapa: FMNH 43409; RMNH 21064; USNM 219715, 219740, 219741, 219743, 219744 (holotype of *Echiothrix brevicula*), 219746–219749, 219751. Sungai Sadaunta: AMNH 225043, 225044, 226815. Kulawi: BMNH 40.385. Winatu: USNM 218706 (holotype of *Echiothrix centrosa*). Gimpu: USNM 219742. Besoa: USNM 219750.

*omys* and *Oligoryzomys*], Carleton et al. (1999 [*Sigmodon*]; 2009 [*Oecomys*]), Voss (1991 [*Zygodontomys*]), and Emmons and Patton (2012 [*Juscelinomys*]); for murine examples, see Carleton and Robbins (1985 [*Hybomys*]), Carleton and Martinez (1991 [*Dasyomys*]), Carleton and Van der Straeten (1997 [*Lemniscomys*]), Maryanto (2003 [*Rattus argentiventer*]), Carleton and Byrne (2006 [*Otomys*]), Carleton and Stanley, 2005, 2012 [*Hylomyscus* and *Praomys*]), Helgen and Helgen (2009 [*Pseudohydromys*]), Musser (unpublished data [*Bunomys*, *Margaretamys*, *Rattus facetus*, and *Coccyomys*]), Heaney et al. (2006 [*Apomys*, *Batomys*, and *Limnomys*]), and Balete et al. (2012 [*Soricomys* and

*Archboldomys*]). A striking exception is the sigmodontine *Oryzomys couesi* (Carleton and Arroyo-Cabrales, 2009).

STATISTICAL ANALYSES: Standard univariate descriptive statistics (mean, standard deviation, and observed range) were calculated for population samples (identified in table 2) as well as for each species and are listed in tables throughout the text. Principal-component and discriminant-function analyses were computed using original cranial and dental measurements transformed to natural logarithms. Principal components were extracted from a variance-covariance matrix, and canonical variates were extracted from the discriminant-function analyses; loadings (correlations) of the variables are given as Pearson product-moment correlation coefficients between the extracted principal components or canonical variates and the log-transformed input variables. Probability levels denoting the significance of the correlations in both kinds of analyses are unadjusted. Analyses are based on 16 cranial and two dental measurements from intact skulls of adults (young to old). The statistical packages in SYSTAT 11 for Windows, Version 11 (2005), were used for all analytical procedures.

ANATOMY: Terminology follows Brown (1971) and Brown and Yalden (1973) for particular external features of the head and limbs; Bugge (1970) for cephalic arteries; Wahlert (1985) for cranial foramina; Carleton (1980), Musser and Newcomb (1983), Carleton and Musser (1984), Musser and Heaney (1992), and Voss (1988) for cranial morphology; and Rinker (1954), Turnbull (1970), and Satoh and Iwaku (2006, 2008) for cranial musculature. Names of cusps and cusplets of maxillary (upper) and mandibular (lower) molars are indicated in figure 9 where sources of the terminology are explained in the legend.

STOMACH CONTENTS: Musser recorded in his field journal the contents found in stomachs of some freshly caught rats. Some samples were preserved in ethanol, which he examined later in the laboratory under a dissecting microscope. He supplemented this material by extracting stomachs from fluid-preserved animals. Stomachs were removed by severing the posterior end of the esophagus and the anterior section of the duodenum.

The isolated stomach was bisected along the midfrontal plane; contents were transferred to a white ceramic dish and examined with a dissecting microscope. In addition to remains of ingested foods, stomachs contained soft and spinous hairs, most likely ingested during grooming. Stomachs emptied in the field are still attached to the gastrointestinal tract of carcasses preserved in fluid at AMNH. Those stomachs extracted in the laboratory are stored, with their contents, in leakproof vials in the fluid collection at AMNH. The stomachs illustrated in figure 11 were fully distended and dissected from adults.

One captive *Echiothrix centrosa* was supplied with a range of forest foods to determine what would be accepted or rejected.

**GEOGRAPHY:** The island of Sulawesi consists of a central region from which four arms, or **peninsulas** radiate (see distribution map in fig. 2): the **northern peninsula**, which ends in a northeastern jog; the **eastern peninsula**; the **southeastern peninsula**; the **southwestern peninsula**. We use these informal labels when describing distributions of the two species of *Echiothrix* over the island, and refer to the central portion as **Sulawesi's core**, or simply "**core**."

In the text we refer to the **west-central highlands** or **west-central mountain block**, which forms the western portion of Sulawesi's core. It is the region of foothills, peaks, and interior valleys situated above 100 m and lying roughly west of Danau Poso and extending from the Palu area in the north to Pegunungan Latimojong in the south. For our purposes here it excludes the coastal strip along the shores of the Makassar Strait simply because no nonvolant mammals have been collected there. A suite of mammals, from shrews to rats, have been collected only in the west-central region: a few species are found in tropical lowland evergreen rain forest covering lower altitudes on foothills and in valleys, but most occur at higher altitudes in montane forests (Musser et al., 2010).

Another area of endemism of relevance to distributions of *Echiothrix* is the **northeastern tip of the northern peninsula east of Gorontalo** (see the distribution map in fig. 2).

We use the Indonesian terms **sungai** (stream or small river), **kuala** (stream discharging

directly into the sea), **danau** (lake), **gunung** (mountain), **pegunungan** (mountain range), **pulau** (island), **kepulauan** (archipelago), **selat** (strait), **tanjung** (cape) and **teluk** (bay).

Localities from which samples were collected, along with the institutional acronyms and catalog number of each specimen examined, are listed in a gazetteer of collection localities for each species. No specimen of *Echiothrix* is listed that Musser did not personally examine. Descriptions of locality and elevations (given here in meters but may have been originally recorded in either meters or feet) were taken from labels attached to skins. These basic data were enhanced where necessary by relevant information from field journals, other archival material, and published expeditionary accounts and gazetteers; sources are cited in the locality entry.

Spelling of locality names are those approved by the United States Board on Geographic Names in the Gazetteer of Indonesia, Third Edition, volumes 1 and 2, published by the Defense Mapping Agency, Washington, D.C., in 1982 (referenced as USBGN Indonesia, 1982). Some localities could not be located in that gazetteer but were found on the topographic map sheets described below; other spellings come from Musser's field notes.

Coordinates for some collection localities were found in USBGN Indonesia (1982) or the Gazetteer of Celebes published in 1944 through the Hydrographic Office of the United States Navy Department (HOUSND Celebes, 1944). Coordinates for most of Harry C. Raven's collection localities were estimated from his personal copy of a Dutch map of Celebes on which he had marked his camp sites and travel routes (Overzichtskaart van het eiland Celebes, Schaal 1:1,250,000, "met aanduiding van de politieke indeeling, de organisatie van het bestuur, de bestaande en nog aan te leggen verkeerswegen en van de groote cultuur- en industriele centra" ("indicating the political divisions, the organization of the administration, the existing and the still to be built road system, and the large cultural and industrial centers"). Samengesteld op last van de N.I. Regeering ("Created at the request of the N.I. [= Nederlands Indië = Dutch East Indies] Government"). Published in 1909), and referred to in the text as "Raven's map."

Coordinates for Musser's collection localities, as well as height above sea level for places for which altitudes were not recorded by collectors, were estimated from "JOINT OPERATIONS GRAPHIC-GROUND" topographic maps, scale 1:250,000, compiled by Mapping and Charting Establishment RE, 1969, and published by the Director of Military Survey, Ministry of Defence, United Kingdom, 1970, or by the Army Map Service, Washington, D.C. (sheets NA 51-9 [1967], NA 51-12 [1967], NA 51-14 [1967], SA 50-8 [1971], SA 51-1 [1970], SA 51-5 [1967], and SA 51-14 [1967], SB 50-8 [1966], SB 51-1 [1970]).

**FORESTS:** The tropical rain forests embracing the habitats of Sulawesi's species of *Echiothrix* will be described broadly in the accounts of species by applying three of the forest formations categorized by Whitmore (1984): tropical lowland evergreen rain forest, tropical lower montane rain forest, and tropical upper montane rain forest. Whitmore's descriptions of these different forest landscapes are illuminating and, as he notes, an extension and elaboration of P.W. Richards (1952) classic work *The Tropical Rain Forest*, which readers will also find informative (a second edition was published in 1996).

#### THE SUCKING LOUSE (*POLYPLAX*)

**INSTITUTIONS:** Paratypes of the new species of *Polyplax* are deposited in the collections of the American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); private collection of L.A. Durden (LAD), the Museum Zoologicum Bogoriense, Cibinong, Java (MZB); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The holotype and allotype are deposited in the USNM.

**PROCEDURES AND ABBREVIATIONS:** Host shrew rats were collected by G.G. Musser. Lice were removed from pelts by L.A. Durden. Description of the new species of louse presented in this paper follows the format and terminology of morphological structures and setae used by Musser et al. (2010). Drawings of entire lice conventionally illustrate dorsal structures to the left of the midline and ventral features to the right.

Measurements were made using a calibrated micrometer inserted into the eyepiece of a high-power phase-contrast Olympus BH2 microscope. Drawings and measurements of lice were made by L.A. Durden.

Abbreviations for anatomical structures used in the description of the new species of louse are as follows:

ApHS	apical head setae
DAcHS	dorsal accessory head setae
DAnHS	dorsal anterior head setae
DCAS	dorsal central abdominal setae
DLAS	dorsal lateral abdominal setae
DMHS	dorsal marginal head setae
DMsS	dorsal mesothoracic setae
DPaHS	dorsal preantennal head setae
DPHS	dorsal principal head setae
DPoCHS	dorsal posterior central head setae
DPTS	dorsal principal thoracic setae
SpAtHS	supraantennal head setae
StAS	sternal abdominal setae
SuHS	sutural head setae
TeAS	tergal abdominal setae
VCAS	ventral central abdominal setae
VLAS	ventral lateral abdominal setae
VPaHS	ventral preantennal head setae
VPHS	ventral principal head setae

#### GAZETTEER AND SPECIMENS

Listed below are the localities at which the 25 specimens of *Echiothrix leucura* and 39 examples of *E. centrosa* we examined were collected. The number preceding each place keys to the same numbered locality on the map in figure 2 (right panel).

##### *Echiothrix leucura*

1. **Manado** (also spelled "Menado"), 01° 30' N, 124° 50' E, coastal plain near sea level: the holotype ("No. 1499" in BMNH). Tate (1936: 586) restricted the type locality to Manado. Specimen "a" (a mount with the skull still inside, in the collection at RMNH), as listed by Jentink in his *Catalogue systématique des Mammifères* (1888: 73).
2. **Rurukan**, 01° 21' N, 124° 52' E: 800 m, AMNH 101243, 101245–248; 1098 m, BMNH 97.1.2.46.
3. **Tonsealama** (also known as "Tonsea"; "Toelap West, Tonsea lama" is notation on skin label),

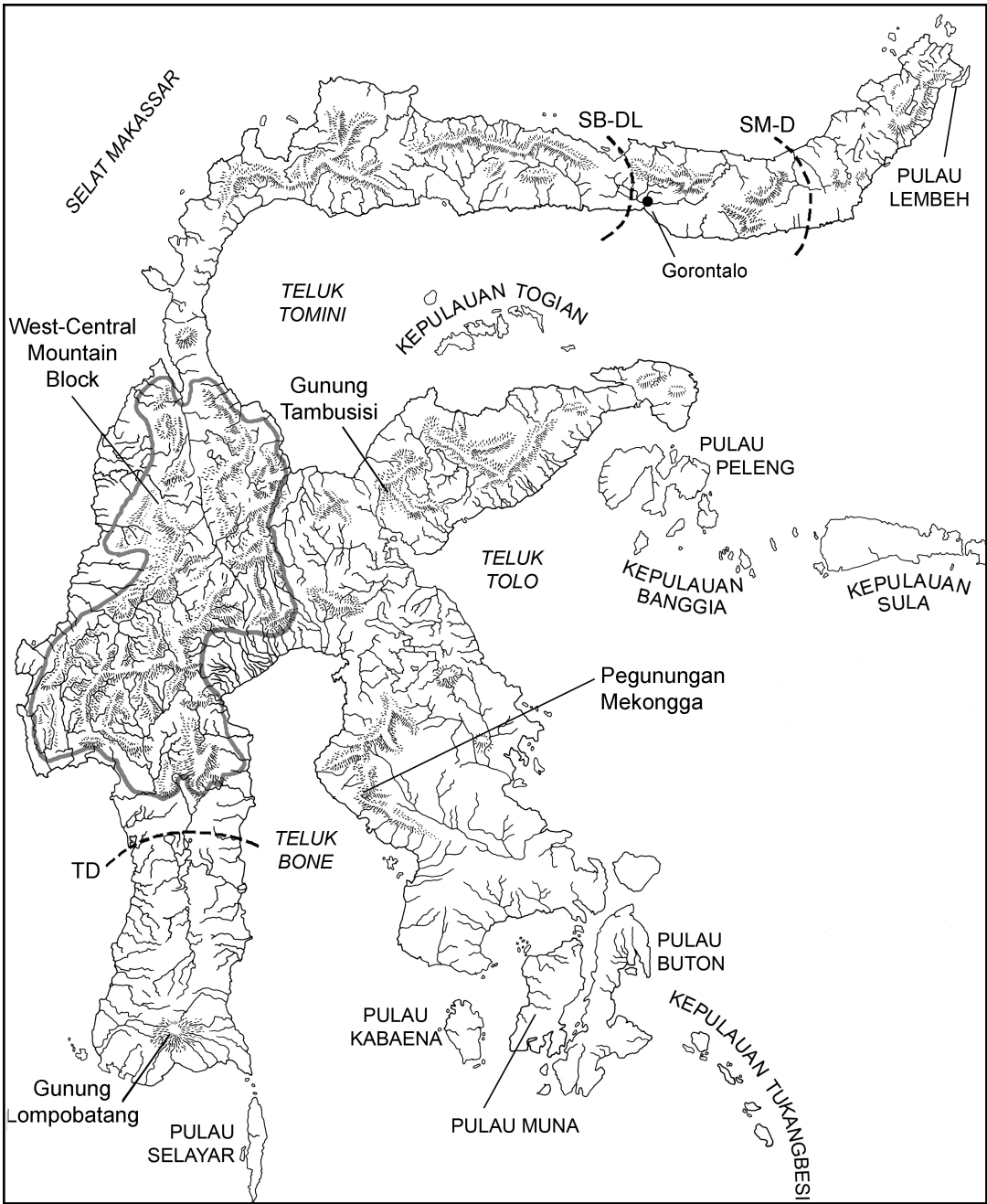


Fig. 2. (above) The island of Sulawesi and environs, showing Sulawesi's four peninsulas and its "core" or central portion. Boundaries separating regions of endemism discussed here are indicated by dashed lines: **SM-D** = lowland reaches of the Sungai Onggak Mongondaw and Sungai Onggak Dumoga; **SB-DL** = lowlands of the Sungai Bone and Danau Limboto; **TD** = Tempe Depression. (opposite page) Collection localities for samples of *Echiothrix leucura* and *E. centrosa*. Numbers key to localities described in the gazetteer. Note the range of *E. leucura*, which is east of SM-D.

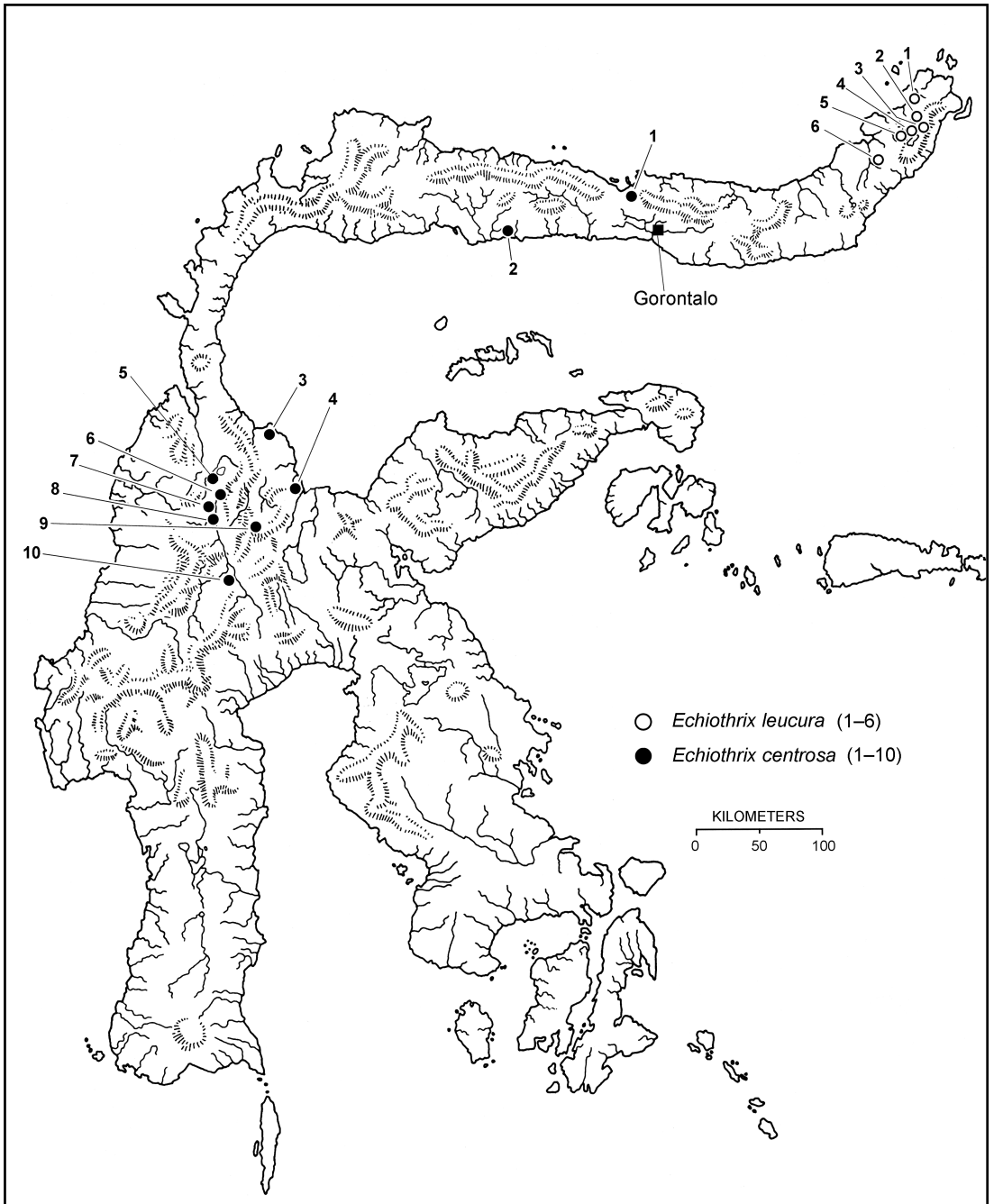


Fig. 2. Continued.

- 01° 19' N, 124° 55' E, 600–700 m (estimated from Sheet NA 51-12): MZB 5627–5630. **Tondano**, 01° 19' N, 124° 54' E, 600–700 m (estimated from Sheet NA 51-12): RMNH 21066–69.
4. **Gunung Masarang**, 01° 19' N, 124° 51' E, 1098 m: BMNH 97.1.2.45.
  5. **Tomohon**, 01° 19' N, 124° 49' E, 700–800 m (estimated from Sheet NA 51-12): NMB 1111/4760, 1184, 1209.
  6. **Temboan**, 01° 05' N, 124° 40' E (estimated from Raven's map), 500 m (estimated from Sheet NA 51-12): RMNH 21065 (formerly USNM 217805); USNM 217802–804, 217806–808, 217906. Temboan, on Kuala Kalait, "is a new clearing of eight houses and lies from Mt. Sapoetan south, 55° west and about six miles from Loboec," as noted by Raven in his field journal that is stored in the Mammal Division Library, USNM).

*Echiothrix centrosa*

1. **Molinggapoto** (spelled "Molengkapoti" and "Molengkapota" on specimen labels), 00°47' N, 122° 52' E, less than 100 m: USNM 200266–269.
2. **Bumbulan**, 00° 29' N, 122° 04' E, coastal plain near sea level: AMNH 153013.
3. **Malakosa, Kuala Navusu**, 00° 58' S, 120° 27' E (estimated from Sheet SA 51-1): 31 m, AMNH 225683; 38 m, AMNH 225678, 225679, 225684; 46 m, AMNH 225680; 155 m, AMNH 225685; 107 m, AMNH 225681; 122 m, AMNH 225682. The locality is shown on the detailed map in Musser et al. (2010: 81).
4. **Pinedapa**, 01° 25' S, 120° 35' E (estimated from Raven's map), 31 m: USNM 219715, 219737, 219738, 219740, 219741, 219743, 219744 (holotype of *Echiothrix brevicula*), 219745–749, 219751; FMNH 43409 (formerly USNM 219736, part of the type series); RMNH 21064 (formerly USNM 219739). H.C. Raven penned in his field journal (p. 125; January, 1918) that "Pinedapa is a new kampong [village] at the base of the main mountains of Central Celebes. The kampong is on the level but some of the clearings are on the slopes to the north-west of the kampong. The immediate kampong is surrounded by heavy forest. The distance to the sea is about five miles." Pinedapa is shown on the detailed map in Musser et al. (2010: 16).
5. **Valley of Sungai Miu, Sungai Sadaunta** (also spelled "Sidaonta" or Sidaunta); tributary on right side of Sungai Miu, 01° 23' S, 119° 58' E (estimated from Sheet SA 50-8): 803 m, AMNH 225045; 884 m, AMNH 225043 and 225046; 930 m, AMNH 226815; 939 m, AMNH 225047; 985 m, AMNH 225044. See the detailed map in Musser et al. (2010: 17).

6. **Kulawi**, 01° 27' S, 119° 59' E, 758 m: BMNH 40.385. Shown on the detailed map in Musser et al. (2010: 16).
7. **Winatu**, 01° 34' S, 119° 58' E, 762 m: USNM 218706 (holotype of *Echiothrix centrosa*).
8. **Gimpu**, 01° 36' S, 120° 02' E, 400 m: USNM 219737, 219742. Locality is also indicated on the detailed map in Musser et al. (2010: 16).
9. **Besoa**, approximately 01° 30' S, 120° 25' E; USNM 219750. Besoa is a region southwest of Rano Rano visited by H.C. Raven who described it as "a large level plain, undoubtedly a former lake bed, surrounded by mountains, which are covered by heavy forests; the tops of most of the mountains are above 2,000 meters, the level plain is said to be about 1,300 meters, or perhaps more. The plain is perhaps 2 or 3 miles wide by about 3 miles long..." (Riley, 1924: 3).
10. **Tuare** (recorded as "Toarebada" on skin label, and either "Toware" or "Toare" on some maps), 01° 54' S, 120° 10' E, 800 m (estimated from Sheet SA 50-8): USNM 219714.

*ECHIOTHRIX* GRAY, 1867

*Echinotrix* Alston, 1876: 83.

*Craurothrix* Thomas, 1896a: 246.

Gray (1867: 599) based his diagnostic description of *Echiothrix* (which he did not formally label as a diagnosis) on an intact skin and partial skull of an adult in which the molars are worn to the degree that their occlusal surfaces are basined instead of cuspidate (fig. 3):

Head elongate. Nose elongate, compressed, concave on the sides; apex produced, acute; underside with short close bristles and a small central groove; nostrils apical, lateral. Fur soft, crisp, with abundance of bristles, flat and channeled at the base cylindrical and tapering at the tip; those of the under part of the body being white and more slender. Ears nakedish. Feet covered with short adpressed hairs. Tail elongate, cylindrical, nearly bald, with rings of square scales. Skull elongate; face very much produced, elongate, compressed; palate rounded in front, flat behind, with an elongated aperture in the middle of its length, more than twice as long as broad; the hinder part of palate with three equally long longitudinal grooves; nose flat above; nasal bones very long, slender. Cutting-teeth white; upper short, with two well-marked subcentral longitudinal grooves; lower elongated, arched, rather compressed, rounded and smooth in front. Grinders [molars]...

moderate-sized; the front much the largest; the hinder smallest and subcircular; the front upper rounded on the inner, and with two folds on the outer side; the second upper with one fold on the outer side, the lower front with a slight subcentral fold on the inner side. Crowns of the teeth flat; the front upper with two and the others with a single cross ridge, less distinctly marked in the hinder teeth. *Hab.* Australia. The skull is very much longer and more slender than in any species of *Mus* or of *Muridae* in the Museum Collection. The face is very slender, compressed, flat on the sides and above. The fissure on the side of the nose from the base of the infraorbital foramen is short and small, compared with those in the typical *Muridae*. The grinders [molars] are nearly erect; the crowns of the grinders are worn and concave between the ridges of the enamel.

Two other names have been proposed to replace Gray's appellation. "The following attempt at a natural arrangement of the gnawing mammals is the result of a revision of the genera of that order," wrote Alston in his "On the Classification of the Order Glires" published in 1876. There Alston provided a short diagnosis and emended *Echiothrix* to "*Echinothrix*" without explanation for doing so. *Echiothrix* is derived from the Greek *echinos*, referring to "hedgehog," and *trichos*, meaning "hair," and by combining the Greek words, Gray likely meant to highlight the shrew rat's crisp, prickly coat—hair like that of a hedgehog.

Twenty years later, in a report "On Mammals from Celebes, Borneo, and Philippines recently received at the British Museum," Thomas (1896a: 246) proposed *Craurothrix* (the Greek *krauros* means "brittle") to replace Alston's *Echinothrix*, and Gray's *Echiothrix*, because "*Echinothrix*" had already been proposed in 1853 for a group of sea urchins (the Greek *echinos* also means "sea urchin"). Thomas (1896b: 1018) listed *Craurothrix* as the valid name in his "On the Genera of Rodents: an Attempt to bring up to Date the current Arrangement of the Order." But in the next two years, Thomas (1898: 397) reverted to *Echiothrix*, explaining

As I have now joined those who think that names should be retained as originally spelt, whether classically right or wrong (except in the

case of obvious misprints), I am now prepared to consider that Peters's *Echinothrix* of 1853 does not preoccupy Gray's *Echiothrix* of 1867, and therefore again recognize the latter term. Those who are not of this opinion must call it *Craurothrix*. That the missing out of the letter *n* is not a misprint is shown by Gray having written on the type skin what appears to be '*Echithrix*,' might be '*Echiothrix*,' but is certainly not '*Echinothrix*.'

Thomas's acceptance of *Echiothrix* anticipated the rules that would come to govern original spellings of scientific names as promulgated in Article 32.2 and 32.3 of the International Code of Zoological Nomenclature (4th ed., 1999: 39): "The original spelling of a name is the 'correct original spelling,'" and "The correct original spelling of a name is to be preserved unaltered ...." Gray's (1867) *Echiothrix* is the valid generic name for the large-bodied Sulawesi shrew rat.

Gray's (1867: 599) original characterization of *Echiothrix*; Alston's (1876: 83) brief diagnosis, which is simply a synopsis of Gray's portrayal; and Ellerman's (1941: 269) short account of characters in his "The Families and Genera of Living Rodents," provided some diagnostic traits but lacked others so a generic emendation of those three author's contributions is provided below.

**TYPE SPECIES:** *Echiothrix leucura* Gray, 1867: 600 (fixation by monotypy; see ICZN, 1999: 71, article 68.3).

**EMENDED DIAGNOSIS:** A genus in Murinae within Muridae (as delimited by Musser and Carleton, 2005) that is distinguished from all other described murine genera by the following combination of traits: (1) species terrestrial in habitus; (2) dorsal pelage covering head and body dark gray or bluish gray, coarse and bristly, overhair coat composed mostly of wide flexible, and channeled spines intermixed with slender soft hairs; (3) ventral coat white (some individuals with russet stain), coarse but softer than dorsal pelage, demarcation between upperparts and underparts sharp and conspicuous; (4) muzzle elongate, mask encircling each eye, ears gray and large relative to body size; (5) tail typically longer than combined length of head and body (ranges of mean values for LT/LHB are 103.8%–116.0% for *E. leucura*,



and 112.8%–126.0% for *E. centrosa*), tail scales moderately large (7–8 rows per cm), the rings of scales slightly overlapping, with one, two, or three hairs associated with each scale (tail appears scantily haired), basal one-fourth to one-half dark gray to brownish gray on dorsal surface and sides, rest of tail white (ranges for dorsal white length–tail length is 47%–67% for *E. leucura* and 44%–73% for *E. centrosa*); (6) forearms short and slender, front feet moderately large but delicately built, claws sturdy but not elongate, digits white, dorsal surfaces of carpal regions white or speckled with patches of gray, three central digits of front foot longer than lateral digit, palmar surface adorned with three interdigital pads, a thenar, and a hypothenar; (7) hind foot elongate, digits white, dorsal surfaces of metacarpal regions white or speckled with patches of gray, three middle digits very long compared with much shorter lateral digits, plantar surface with full complement of plantar pads (four interdigitals, a thenar, and a hypothenar), but thenar and hypothenar very small relative to plantar surface; (8) two pairs of teats, both inguinal in position; (9) testes large relative to body size (16%–23%); (10) symphysis of mandible flexible, so tips of lower incisors can be spread apart up to 7 mm; (11) rostrum long and slender, interorbital and postorbital margins bounded by moderately high ridges, zygomatic arches moderately sturdy and flare from sides of skull, posterior zygomatic root situated low on braincase, braincase boxlike (wide and deep), occiput deep, no cranial flexion; (12) zygomatic plate moderately wide, its anterior margin projecting beyond dorsal maxillary root of zygomatic arch, its posterior edge even with the anterior margin of the first upper molar; (13) squamosal intact, not perforated by a subsquamosal foramen; (14) alisphenoid struts typically absent; (15) incisive foramina long and wide, set in middle of diastemal region; (16) molar rows parallel or bowed toward midline, bony palate long with its posterior margin projecting well beyond the molar rows to form a bony shelf, palatal surface with moderately deep palatine grooves, posterior palatine foramina at level of either second or third upper molars; (17) moderately long and wide sphenopalatine vacuities; (18) pterygoid

plates appear absent but are reduced to slim and inconspicuous ridgelike vestiges, narrow platforms undefined by discrete margins, and apparently transformed into a vertical component in the outer wall of the mesopterygoid fossa in some specimens; (19) auditory bulla moderately large relative to skull size, the ectotympanic (bullar) capsule covering all but a narrow wedge of periotic, posterodorsal wall of carotid canal formed by bullar capsule; (20) large stapedial foramen, no sphenofrontal foramen or squamosal-alisphenoid groove, indicating a carotid arterial pattern widespread within Murinae (character state 2 of Carleton, 1980; pattern 2 described by Voss, 1988); (21) dentary elongate, long and narrow ramus (diastema) between incisor and molar row, very small coronoid process, large condyloid (articular) process, end of alveolar capsule forming large labial bulge just posterior to coronoid process; (22) upper incisors typically white (dentine and enamel unpigmented), small and short relative to skull size, emerging from rostrum at a right angle (orthodont), each anterior face with two shallow grooves; (23) each lower incisor long and awl shaped with elongate wear facets, anterior faces smooth, dentine white and enamel either white or tinted pale yellow; (24) maxillary molars with three roots, mandibular molars with two; (25) molars brachydont, cusp rows forming cuspidate occlusal patterns that transform into basins with only moderate wear, third molar very small relative to others in tooththrow; (26) no cusp t7 on upper molars, and no other occlusal embellishments (such as an enamel ridge projecting from anterolingual surface of cusp t8 anteriorly to posterior margin of lingual cusp t4, a labial enamel ridge connecting anterolabial margin of cusp t9 with posterolabial margin of cusp t6, or a comparable but shorter ridge projecting from the anterior surface of cusp t5 to meet the posterior margin of cusp t3 near the cingulum, all typical of some other murines with more complicated enamel occlusal patterns—the New Guinea *Coccyzomys* is an example [Musser and Lunde, 2009]), posterior cingulum present in one species but absent in the other; (27) anteroconid formed of large anterolingual and anterolabial cusps, anteroconid cusp absent, anterolabial cusp

present at low frequency or missing from second and third lower molars depending upon the species, anterior labial cusplets not present on any lower molars, but posterior labial cusplet present at a low frequency on most teeth, posterior cingulum present on first and second lower molars in one species, missing from those molars in another; (28) stomach unilocular-pouched, glandular epithelium confined to a pouch situated on the greater curvature within the lumen of the stomach; (29) sperm head long and sickle shaped, with single apical hook that lacks ventral processes, spermatozoal tail long; (30) karyotype,  $2N = 40$ ,  $FN_a = 72$  (total of autosomal arms) and  $FN_t = 75$  (total number of arms, including XY), for *E. centrosa*.

CONTENTS: Two species are currently recognized, *Echiothrix leucura* and *E. centrosa*, both endemic to Sulawesi.

Between 1867 and 1920, *Echiothrix* was regarded as monotypic with *E. leucura*, the type species, occurring east of Gorontalo in the northeastern end of the northern peninsula (Alston, 1876; Jentink, 1883; Thomas, 1896b; Trouessart, 1897; Meyer, 1899). In 1921, Miller and Hollister (1921: 67) described two additional species, both from the central part of Sulawesi. *Echiothrix centrosa* was based on samples from "the interior of Middle Celebes," the Besoa region, Gimpu, Tuare, and Winatu. *Echiothrix brevicula* was applied to a sample from Pinedapa, "about 5 miles inland from the Gulf of Tomini, near Mapane, Middle Celebes." Tate (1936), in his treatise covering some Indo-Australian Murinae, discussed *E. leucura* and referred to the two taxa described by Miller and Hollister as species. Subsequent rodent compendia and regional lists of species, however, demoted *centrosa* and *brevicula* to either subspecies of *E. leucura* (Ellerman, 1941; Laurie and Hill, 1954) or synonyms (Corbet and Hill, 1992; Musser and Carleton, 1993). By 2005, Musser and Carleton had recognized two species, *E. leucura* and *E. centrosa*, which are the two we define here. Geography, morphometric differences in cranial and dental variables, and different cusp patterns of maxillary and mandibular molars comprise the anatomical distinctions between the two species. The outlines of geographic range and phenetic interpretation of species diversity

in *Echiothrix* sketched here is a hypothesis that should be tested by analyses of DNA sequences.

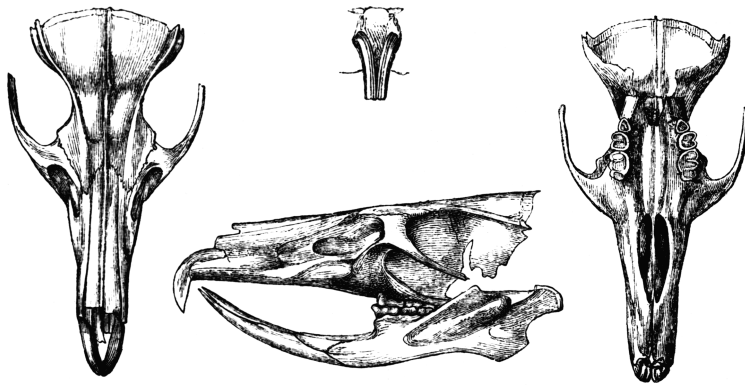
The first of the two accounts of species that follow consists of a description of *Echiothrix leucura*, the type species of the genus. Musser has not worked in the region where this species occurs and knows it only from his study of material held in museum collections. The geographic and morphological traits characteristics of *E. leucura* form the standard to which comparable characteristics of *E. centrosa* will be compared.

Musser did encounter *E. centrosa* in his fieldwork and the report on that species derives from material he collected (skins, skulls, rats preserved in fluid, and chromosomal preparations), descriptions of freshly trapped animals recorded in his field journals, and specimens obtained by other collectors now stored in collections of museums (skins and skulls). Information on spermatozoal and stomach morphologies, karyotype, and external characteristics of juveniles will be included—this kind of information is not available for *E. leucura*.

The accounts cover the following information: (1) description of the holotype and type locality; (2) emended diagnosis; (3) reference to the gazetteer where specimens are identified; (4) etymology of the scientific name (5) summary of geographic and elevational distributions; (6) description; (7) comparisons with other species; (8) geographic variation in phenetic characters; (9) allocation of a synonym (relevant to *E. centrosa*).

#### *Echiothrix leucura* Gray, 1867

HOLOTYPE: "No. 1499," which is Gray's catalog number. To learn more about this specimen, Musser queried Paula Jenkins at the Natural History Museum in London, who wrote (in litt., 1999) that the "specimen has apparently never been registered using the four-digit system, however, these Gray catalogue numbers are also traditionally accepted as register numbers." "It is," she continued, "listed in one of Gray's catalogues ... as: '1499 Skull a. the specimen fig. [the skull was illustrated in Gray, 1867: 599] Skin in a bottle in the Colln.' There is no locality given here." Paula also checked Thomas'



*Echiothrix leucura.*

Fig. 3. The holotype of *Echiothrix leucura*, a reproduction of the partial skull illustrated in Gray's (1867: 599) original description.

catalog and noted that "no number is given; the entry reads: 'a. Sk. ad. male Australia. Type of genus and species.'" The identity of the collector was not recorded. Musser examined the holotype but at the time he took no measurements. The holotype is an adult male and consists of a dry skin and skull. Except for the damaged head, the skin is whole. The skull is incomplete (fig. 3): anterior portion of the nasals, nearly all of the skull behind the orbit, and posterior half of each zygomatic arch are missing. The mandible is intact; upper and lower incisors and molars are present. The few measurements that could be made on the holotype are listed in table 3.

**TYPE LOCALITY:** Manado (01° 30' N, 124° 50' E; locality 1 in gazetteer and fig. 2), coastal plain near sea level, the northeastern tip of the northern peninsula of Sulawesi, Propinsi Sulawesi Utara, Indonesia.

Gray (1867) indicated the specimen he described to have come from "Australia." No other reference to the actual provenance of the specimen exists. Paula Jenkins could not locate any additional information in the archives of the Natural History Museum (London). Subsequent researchers recognized that the holotype was not collected in Australia. Sixteen years after Gray's description was published, Jentink (1883: 177) reported two additional specimens:

The type-specimen of this interesting species is in the British Museum and has been described

by the late Gray as inhabiting Australia. A second specimen is in the Dresden Museum; it was brought from Menado, North-Celebes, some years ago. The specimen now before me is, as far as I know, the third representant of this species. I think it not improbable that Gray's locality (Australia) is incorrect and that later investigations will prove that it exclusively is an inhabitant of Celebes.

Tate (1936: 585–586) discussed specimens in the American Museum of Natural History that had been collected by G. Heinrich at Rurukan and noted that this locality is "at the extreme northeast of the Celebes and within a few miles of Menado, whence came the specimen in the Dresden Museum alluded to by Jentink," and wrote that "In absence of evidence to the contrary the type locality of *E. leucura* may be restricted to Menado, north Celebes, making our series practically topotypical."

**EMENDED DIAGNOSIS:** Traits associated with external and cranial morphology as enumerated in the generic diagnosis also characterize *Echiothrix leucura*. The species differs from *E. centrosa* in possessing (1) a longer body and hind foot, but a shorter tail in relation to length of head and body; (2) a larger skull (as indexed by the greater mean values for occipitonasal and rostral lengths; interorbital breadth; height and breadth of braincase; and lengths of diastema, bony palate, and postpalatal region), but shorter incisive foramina and narrower rostrum,

TABLE 3  
Age, Sex, and Measurements (mm) for Holotypes  
Associated with Species of *Echiothrix*<sup>a</sup>

	<i>E. leucura</i>		<i>E. centrosa</i>	
	<i>leucura</i> BMNH 1499		<i>centrosa</i> USNM 218706	<i>brevicula</i> USNM 219744
Age	Adult		Young adult	Adult
Sex	♂		♂	♂
LHB	—		215	198
LT	—		265	240
LT/LHB	—		123	121
(%)				
LHF	—		53	55
LE	—		—	—
ONL	—		54.8	51.6
ZB	—		23.7	23.7
IB	7.3		7.7	7.0
LR	—		22.3	20.2
BR	6.6		7.7	7.5
BBC	—		19.6	19.0
HBC	—		14.9	14.7
BZP	3.6		3.8	3.7
LD	—		19.7	18.2
PPL	—		19.2	17.7
LBP	—		10.3	9.7
BBPM1	4.0		4.6	5.3
BMF	—		2.2	2.6
LIF	—		10.2	9.3
BIF	3.4		3.3	3.4
LB	—		5.9	5.9
ALM1–3	6.7		6.5	6.7
CLM1–3	6.8		6.3	6.5
BM1	2.2		2.1	2.0
alm1–3	6.3		6.5	6.2
clm1–3	6.8		6.5	6.5

<sup>a</sup> Values for external measurements were transcribed from skin labels, except for the hind feet of *centrosa* and *brevicula*, which were measured by M.D. Carleton on the dry skins. Cranial and dental dimensions of *leucura* were measured by P. Jenkins; comparable dimensions of *centrosa* and *brevicula* were measured by M.D. Carleton.

bony palate, and mesopterygoid fossa; (3) larger molars and slightly more complex cusp patterns; (4) cusp t3 occurring at a higher frequency on second upper molar, a posterior cingulum typically present on first and second upper molars, (5) an anterolabial cusp present at a low frequency on second and third lower molars, posterior labial cusplets on all lower molars in some specimens, and a posterior cingulum present on first and second lower molars in most individuals surveyed.

SPECIMENS EXAMINED: Total 25 (see Gazetteer and Specimens).

ETYMOLOGY: The species name *leucura* is derived from the Greek *leukos* meaning “white.” Whether Gray meant to highlight the white ventral coat of *Echiothrix* or its white incisors (“cutting-teeth white,” as Gray, 1867: 300, described them) is unknown, although we suspect the latter. Many species of murines have white underparts but not many possess incisors with white enamel layers.

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS: Voucher specimens indicate *Echiothrix leucura* is endemic to the northeastern end of the northern peninsula east of the Gorontalo region (00° 31' N, 123° 03' E; see the map in fig. 2). All specimens come from the mainland between coastal lowlands and approximately 1000 m (see gazetteer), an elevational interval that would be covered by tropical lowland evergreen rain forest.

The geographic range of *E. leucura* is concordant with the distributions of several other mammalian species: the macaque *Macaca nigra* (Fooden, 1969; Groves, 1980, 2005); and the murids, *Bunomys fratrorum*, *Taeromys taerae*, *Rattus xanthurus*, and *R. marmosurus* (Musser and Carleton, 2005, unpublished MS.).

DESCRIPTION: Gray (1867: 600) provided a short description of *E. leucura*:

Fur dark grey brown, varied with black-tipped hairs on the back and sides; sides of nose, cheeks, throat, chest, and underside of limbs white; feet moderate, covered above with dark-brown hair; tail yellow, black at the base; cutting-teeth white; whiskers long, black, rather rigid. Length of body and head 9½ inches; tail imperfect; hind feet about 2 inches. *Hab.* Australia; British Museum, male? Tail imperfect.

His account does not do justice to the species. *Echiothrix leucura* is moderately large (table 4) with a lean body, long head, bristly dark gray or bluish gray upperparts, white underparts, mostly white tail that is longer than head and body, delicate front legs and small feet but robust hind legs with large and elongate hind feet, and very large ears (fig. 4; Musser, 1990: fig. 3). The skull shows specializations such as a long and slender

TABLE 4  
**Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weight (g) Derived From Samples of Adult *Echiothrix leucura* and *E. centrosa*<sup>a</sup>**  
 Mean  $\pm 1$  SD, observed range (in parentheses), and size of sample are provided. Mean values were used to compute LT/LHB. Specimens measured are listed in footnotes.

Species and sample <sup>b</sup>	LHB	LT	LHF	LE	WT	LT/LHB (%)
<i>E. leucura</i>						
NORTHEAST						
Rurukan	217.8 $\pm$ 12.26 (198–230) 5	226.0 $\pm$ 10.93 (212–240) 5	52.6 $\pm$ 1.52 (51–54) 5	32.4 $\pm$ 0.89 (31–33) 5	—	103.8 $\pm$ 3.77 (100–108) 5
Tondano	208	242	50	—	—	116
Temboan	213.0 $\pm$ 12.00 (196–230) 8	246.3 $\pm$ 15.98 (220–270) 8	54.1 $\pm$ 1.81 (50–55) 8	—	—	115.5 $\pm$ 3.96 (111–124) 8
<i>E. centrosa</i>						
NORTHCENTRAL						
Molinggapoto	190	240	51.8 $\pm$ 1.72 (50–54) 4	—	—	126
Bumbulan	216	245	51	35	—	113
CORE						
Kuala Navusu	213.0 $\pm$ 8.81 (197–225) 8	245.9 $\pm$ 7.71 (235–258) 7	52.4 $\pm$ 0.74 (51–53) 8	33.3 $\pm$ 0.71 (32–34) 8	267.3 $\pm$ 33.45 (220–310) 7	114.6 $\pm$ 4.24 (109–119) 7
Pinedapa	197.0 $\pm$ 7.76 (182–205) 12	239.6 $\pm$ 6.20 (230–250) 12	50.3 $\pm$ 1.91 (48–55) 12	—	—	122.0 $\pm$ 4.61 (118–135) 12
Sungai Sadaunta	213.8 $\pm$ 3.54 (210–219) 6	241.2 $\pm$ 6.11 (230–247) 6	53.2 $\pm$ 1.72 (50–55) 6	34.8 $\pm$ 1.17 (33–35) 6	237.5 $\pm$ 20.92 (215–270) 6	112.8 $\pm$ 2.40 (110–116) 6
Besoa	190	240	53	—	—	126
Winatu	215	265	53	—	—	123

<sup>a</sup> Musser collected and measured the samples from Kuala Navusu and Sungai Sadaunta, and also measured the dry hind foot in the other samples. Those specimens not collected by him were measured by the collectors G. Heinrich, H.J.V. Sody, J.J. Menden, and H.C. Raven; none took weights and Raven did not measure ear length. We cannot verify the accuracy of the values, especially those obtained by G. Heinrich who collected the specimens from Rurukan in the northern peninsula. In Musser’s experience, Heinrich sometimes included part of the tail when he measured head and body, and sometimes the rump in his measure of tail length; we suspect the former for the Rurukan sample.

<sup>b</sup> *E. leucura*—Rurukan: AMNH 101243, 101245–101248. Tondano: RMNH 21068. Temboan: RMNH 21065; USNM 217802–217804, 217806–217808, 217906.

*E. centrosa*—Molinggapoto: USNM 200266–200269. Bumbulan: AMNH 153013. Kuala Navusu: AMNH 225648–225685. Pinedapa: FMNH 43409; RMNH 21064; USNM 219738, 219741, 219743, 219744 (holotype of *Echiothrix brevicula*), 219745–219749, 219751. Sungai Sadaunta: AMNH 225043–225047, 226815. Besoa: USNM 219750. Winatu: USNM 218706 (holotype of *Echiothrix centrosa*).

rostrum and a lack of pterygoid plates; the incisors are white or cream, and the molars are very small relative to skull size. The following description is drawn from adults; we have not seen examples of juvenile *E. leucura*, but their external characteristics are likely similar to juvenile *E. centrosa*, which are described in the account of that species.

**Fur:** The glossy dorsal coat of adults is harsh and bristly to the touch (not rigidly spiny as in hedgehog fur) and 15–20 mm long. It is composed of underhairs (or

“wool” hairs; Voss, 1988) that form a thin underfur layer, and longer overhairs (also called “awns”; Voss, 1988) comprising the overfur. The underhairs are soft, fine, wavy, and unpigmented along their entire lengths. The overfur layer consists mostly of wide and flat flexible spines, each with a channel extending along the dorsal surface, and a sharp tip. The base of each spine is unpigmented but the remainder is gray, which ranges in tone from pale gray near the unpigmented base to dark gray distally to

*Abh. Ber. K. Zool. Anthr. Ethn. Mus. Dresden 1898/9 Nr. 7*

*Meyer: Säugethiere Cölöbes II. Taf. IX*



*Craurothrix leucura* (Gr.)

*nat. Grösse*

Fig. 4. Reproduction of Meyer's (1899) color plate of "*Craurothrix leucura*" (= *Echiothrix leucura*) rendered from animals collected at Tomohon (locality 5 in gazetteer and on map in fig. 2).

the tip. In adults showing molt from old to new fur, the old spines have faded to straw brown, but those in the new layer proliferating through the skin are dark bluish gray. Scattered among the spines are softer thin hairs, each unpigmented except for a gray subterminal band. Guard hairs are inconspicuous because they are scattered throughout the coat and barely extend beyond the overfur layer; each is thin and round with an unpigmented base, long blackish subterminal band, and silvery tip. Overall, the fresh dorsal fur is dark gray or dark bluish gray frosted with white along the back but lightens to gray on sides of the head and body; old, worn pelage fades to pale straw brown.

The ventral coat of adults is 8–10 mm long on animals from low elevations but 10–13 mm thick over rats from higher places and consists of underhairs and overhairs but no guard hairs. Hairs forming the underfur are soft, fine, and wavy; those constituting the overfur are narrow, flat, and soft spines, each with a dorsal channel from base to near the tip. Texture of the coat is soft to slightly harsh to the touch but not spinous. Underhairs and overhairs are unpigmented in most specimens, so the ventral pelage, from tip of the muzzle to base of the tail, is overall white and sharply demarked from the gray dorsal coat. A few animals from Temboan show buffy or buffy orange patches on the chest and abdomen.

The white ventral coat is best appreciated in living rats or freshly prepared specimens. Some museum preparations, especially study skins stored since the early 1900s, appear pale yellow because the yellow dry skin shows through the fur or the hairs are stained with fatty oils (some of the skins from Temboan, for example, are obviously stained with yellowish deposits, so the entire animal appears to have a yellowish tint) and the underparts are yellow-orange (oily debris adheres to the hairs, and some skins are greasy yellow because subcutaneous fat was either not or incompletely removed before the skin was stuffed).

Fur covering the head of adults is pigmented like that clothing the body; throat and cheeks are white, chromatically indistinguishable from chest and abdomen. Rhinarium and lips are pink. Behind each ear is a

crescent-shaped pale gray patch of soft, fine and short hairs that provides a whitish-gray crescent-shaped tuft around the base of each ear. The only obvious facial pattern is formed by blackish-brown eyelids and a circle of darker hairs around each eye, which on some individuals are more expansive and form a mask. All species have an array of mystacial, submental, superciliary, subocular, genal, and interramal vibrissae adorning the head; the longest mystacial extend beyond the ears when laid back over the head (see Brown, 1971, for descriptions of these sensory hairs and terminology). Some of the hairs lack pigment (appearing silvery), the rest are black or dark brown, and all have glossy surfaces.

**Ears:** Pinnae are very large relative to size of head and body (table 4). We have not seen living *E. leucura*, but the pinnae appear and feel rubbery in freshly caught *E. centrosa*, and while they seem naked, they are covered on inner and outer surfaces by short, fine, dark hairs that form a short and inconspicuous fringe along the dorsal internal rim of each pinna. Color of the ears is glossy dark gray with a pinkish tinge in living *E. centrosa*. We suspect texture and coloration to be similar in live *E. leucura*. Dried ears of stuffed museum skins lack the rubbery texture of the live animal and have dried to dark brown.

**Tail:** In samples of adults, average length of tail exceeds combined head and body length (LT/LHB = 103.8%–116.0%; table 4). The tail is squarish in cross section and bicolored: in living animals, dorsal and lateral surfaces of the basal one-third to one-half range from dark gray to blackish gray, the rest of the tail, including the entire ventral surface, is glistening white (dorsal white length/tail length = 47%–67%; table 5). In some material collected in the late 1800s and early 1900s, the pigmented basal portion of the tail has darkened to black and the white region altered to pale yellow, reflecting stain from the subcutaneous fat in the tail. Gray (1867: 600), for example, wrote of the holotype, “tail yellow, black at base.” White tail segments are yellowish in all of H.C. Raven’s material (stored at USNM), which was collected in the early 1900s. Slightly overlapping rings of moderately large scales (7–8 scale rings per cm, counted on the basal third of the tail) cover the tail. One, two, or three fine hairs (as

TABLE 5  
**Absolute Lengths (mm) of Dorsal White Tail Segment and Length of Tail, and Length of Dorsal White Segment Relative to Length of Tail (%) In Samples of *Echiothrix***  
 Mean  $\pm$  1 SD and observed range in parentheses are listed.

Species and sample	<i>N</i>	Length of dorsal white segment	Length of tail	Dorsal white length/tail length
<i>E. leucura</i>				
Rurukan, Temboan	12	139.2 $\pm$ 14.59 (110–155)	236.7 $\pm$ 16.58 (212–270)	58.5 $\pm$ 7.04 (47–67)
<i>E. centrosa</i>				
Sungai Sadaunta, Kuala Navusu, Pinedapa	20	142.0 $\pm$ 19.42 (110–180)	239.6 $\pm$ 6.20 (230–250)	59.1 $\pm$ 7.38 (44–73)

long as one or two scales) emerge from beneath each scale. The tail appears to be scantily haired because the hairs are fine, inconspicuous, and vary in number per scale (instead of three at each scale, the usual pattern in murines), and the scutellation is exposed. Scale hairs are brown in the pigmented basal portion of the tail but unpigmented (silvery) in the white region.

**Legs and feet:** The front legs are short and slender, particularly the forearms. Each front foot has four slender digits ending in unpigmented stout claws and a tiny stubby thumb (pollex) bearing a nail (fig. 4). The middle digits are the longest, the medial second digit shorter, and the lateral fifth digit extending about to the base of the adjacent digit. Dorsal surface of the metacarpal region and digits are white, covered with silvery hairs. Ungual tufts are sparse, consisting of one or two short hairs confined to the end of each digit, leaving the claws uncovered. Three interdigital pads along with a moderately large thenar and small hypothenar mounds form most of the naked palmar surface (fig. 4), which ranges from unpigmented to dark gray (palmar surfaces of live *E. centrosa* have a rosy tinge reflecting the subcutaneous arterial circulation).

While the front claws are stout, moderately long, gently arched, and sharp, they are not excessively large relative to length of digits and size of the front foot (fig. 4). By contrast, the montane Sulawesi shrew rats *Melasmothrix naso*, *Tateomys rhinogradoides*, and *Paucidentomys vermidax*, all consumers of earthworms, bear elongate curved claws

that are very long relative to size of the foot (Musser, 1982; Esselstyn et al., 2012).

The hind legs are large and robust. Hind feet are long and very narrow; the first (hallux) and fifth digits are much shorter than the three much longer middle digits, which are all about the same length (fig. 4). The claw of the hallux barely reaches the base of the second digit, and the claw of the fifth digit extends to about middle of the second digit. Dorsal surfaces of the metatarsal region are either white (covered with unpigmented hairs), or white with small patches of gray speckling; digits are typically white. Conspicuous silvery unguis cover bases of the ivory-colored stout claws. Each naked, dark gray plantar surface is adorned by six moderately fleshy pads: four interdigital mounds (forming a cluster at the bases of the digits), a tiny pimplelike hypothenar, and a short and narrow ridgelike thenar (both are very small and inconspicuous relative to plantar surface). The hind claws are curved and sharp tipped and moderately long relative to the length of the digits and hind foot, proportionally similar to the configuration seen in Sundaic *Berylmys bowersii* and *Sundamys muelleri* (Musser and Newcomb, 1983: 15; fig. 15).

**Teats:** Two pairs of inguinal teats are characteristic of all female shrew rats surveyed (12 *E. leucura*, 15 *E. centrosa*). Tate (1936) and Ellerman (1941) reported three pairs, which is incorrect.

**General cranial features:** The cranial configuration of *E. leucura* is illustrated in the portrait of a skull from Rurukan (fig. 5; the





Fig. 5. Cranium and left dentary of *Echiothrix leucura* (AMNH 101246; ONL = 56.6 mm, CLM1-3 = 6.6 mm), an adult female from Rurukan. X2.

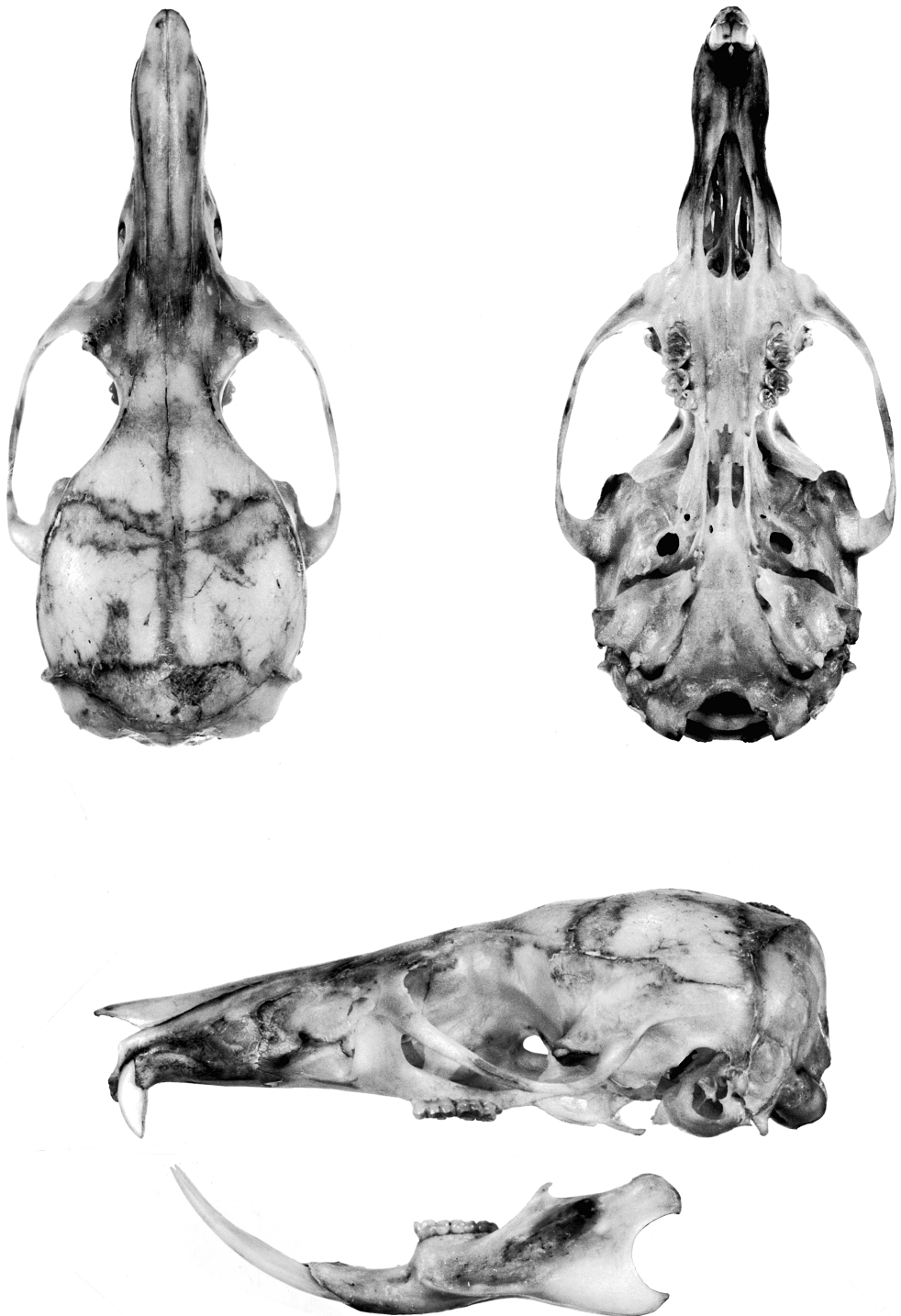


Fig. 6. Cranium and left dentary of *Echiothrix centrosa* (AMNH 225043; ONL = 52.5 mm, CLM1–3 = 6.0 mm), an adult female from Sungai Sadaunta. X2.

skull of *E. centrosa* from Sungai Sadaunta is portrayed in fig. 6). A long (about 40% of occipitonasal length) and narrow (about 38% of braincase breadth; table 6) rostrum is typical; from a lateral view, the rostrum tapers from its highest point level with the zygomatic plates distally to the incisors. The smooth sides are broken near the base of the rostrum by low nasolacrimal capsules that barely bulge beyond the rostral walls (and are hardly evident in dorsal or ventral views). Pointed tips of the nasals overhang the external nares and are either even with or project slightly beyond anterior edges of the premaxillaries; posterior borders of the nasals extend well beyond the premaxillary-frontal suture (by 14% of nasal length). The zygomatic plate is moderately wide, its maxillary root originating posterior to the nasolacrimal bulge and above and in front of the first molar; its anterior margin is typically convex, is usually also inclined, and joins the dorsal maxillary root to form a conspicuous notch between the anterior edge of the plate and lateral side of the skull (as seen from dorsal perspective). The posterior edge of the zygomatic plate sits above the anterior one-third of the first molar. A tall and narrow infraorbital foramen is the usual configuration. The tendon of the superficial masseter muscle attaches to a small bony swelling or roughened raised area on the anteroventral corner of the zygomatic plate. Robust zygomatic arches bow appreciably outward; the maxillary and squamosal roots of each arch are united by a short jugal. The squamosal root of each zygomatic arch originates low on the outer braincase wall and its posterior margin extends as an indistinct ridge along the braincase to disappear well before the occiput.

A moderately wide interorbital region is usual. Its dorsolateral borders are defined by conspicuous ridges that extend along dorsolateral margins of the postorbital region (but never wide enough to form narrow shelves) and to the braincase where they form low but prominent temporal ridges that disappear anterior to the occiput (just before the lamboidal ridges). The otherwise smooth braincase is squarish (as seen from dorsal perspective) and deep (as viewed from the side) with a domed roof. A rectangular

portion of the parietal drops below the dorsolateral margin of the braincase almost to the top of the zygomatic root; this projection and the squamosal form the wall of the braincase. The inner sidewalls of the braincase are smooth, without squamosalisphenoid grooves. Sides of the braincase are vertical from the temporal beading to squamosal roots of the zygomatic arches. The occipital region is moderately deep and roofed by the interparietal in the middle and dorsal segment of the exoccipital on either side. The boundary between squamosal and exoccipital is marked by prominent lamboidal ridges. The posterior wall of the occiput is vertical (in lateral view) and even with the posterior boundaries of the occipital condyles. The squamosal above each auditory (ectotympanic or bullar) capsule and just anterior to the lamboidal ridge is complete (not penetrated by a subsquamosal foramen).

As seen from the ventral perspective, the moderately long incisive foramina (about 50% of diastemal length; table 6) are located in the center of the diastema and form an elongate teardrop in outline. Just behind the upper incisors is a slitlike interpremaxillary foramen. Except for a pair of grooves that increase in depth from front to back, the bony palate is smooth, its posterior margin projects well past the third molars to form a bony shelf. A pair of large posterior palatine foramina penetrate the palate at the maxillopalatine suture opposite either first or second upper molars. Maxillary molar rows are either parallel or bow medially toward the back of the bony palate. The mesopterygoid fossa is narrow and its dorsolateral walls are perforated by two wide and moderately long sphenopalatine vacuities that expose the medial borders of the presphenoid and basisphenoid.

Each ectotympanic bulla (= bullar capsule) is moderate in size (about 11% of the occipitonasal length) and bears a wide and long bony eustachian tube. The medial sagittal plane of each bullar capsule is oriented ventromedially, so the capsules appear to rest on the basicranium and project toward the midline rather than more nearly vertical (an orientation similar to that seen in the Philippine *Tarsomys apoensis* [Musser and Heaney, 1992: 23, fig. 9]). The bullar capsule does not

cover the entire surface of the enclosed periotic bone, leaving exposed a thick posteromedial wedge and a narrow flange extending forward between the ectotympanic and basioccipital. The carotid canal is bounded by part of the periotic, adjacent ectotympanic, and lateral border of the basioccipital (pattern is closely similar to that illustrated for Philippine *Chrotomys* [Musser and Heaney, 1992: 78, fig. 43]). All specimens possess a large stapedial foramen penetrating the crevice (the petromastoid fissure) between the bullar capsule and the periotic. A middle lacerate foramen, either spacious or narrow, separates the bullar capsule from the posterior margin of the alisphenoid.

In lateral view, a narrow flange of periotic is exposed along the anterodorsal margin of the bullar capsule. The capsule and periotic are separated from most of the squamosal by a broad postglenoid foramen that is confluent with a ventral middle lacerate foramen. The mastoid portion of the periotic is slightly inflated, its outer surface without perforations.

Within the orbit, the ethmoid foramen is small and the optic foramen large, a typical murine pattern. Orbitosphenoid, alisphenoid, and frontal bones join to form a solid section of the braincase wall, unbroken by a sphenofrontal foramen. Sphenopalatine and dorsal palatine foramina are separate, a pattern similar to that found in species of *Rattus* (Musser, 1982: 22).

**Pterygoid region:** Osseous structure of the pterygoid region of *Echiothrix* is extremely simplified: the pterygoid plates have regressed and are represented only by diminutive remnants. Among murines, this osteological design of the pterygoid-alisphenoid region is repeated only in the Philippine shrew rat *Rhynchomys* (see the cranial illustrations in Musser and Heaney [1992: 78] and Balete et al. [2007: 293]) and the Sulawesi shrew rat *Paucidentomys* (Esselstyn, et al., 2012). The best way to appreciate this severe modification is to first describe the pterygoid region in the Sulawesi *Maxomys dollmani*, which expresses a pattern common to nearly all other murines, especially those from the Indomalayan region, Sulawesi, Philippines, New Guinea, and Australia (see the cranial illustrations in Musser, 1982,

1991; Musser and Newcomb, 1983; Musser and Holden, 1991; Musser and Heaney, 1992; Flannery, 1995; Musser et al., 2008; Musser and Lunde, 2009; Heaney et al., 2012; Balete et al., 2012), as well as species in Europe and Africa (see the cranial drawings in Happold, 2013).

In *Maxomys dollmani*, each pterygoid plate forms a long and wide shelf bounded on the medial side by a hamular process and defined laterally by a smooth margin; the palatine bone forms the plate's anterior half and the pterygoid bone its posterior section (fig. 7D). Nearly all of the ventral surface of the pterygoid plate anterior to the foramen ovale is shallowly excavated and forms the pterygoid fossa. The posterolateral and posterior edges of the plate converge behind the foramen ovale to form a wide and smoothly rounded ridge, which defines the anterolateral border of the spacious medial lacerate foramen separating the pterygoid plate and posterior margin of the alisphenoid from the ectotympanic bullar capsule. Just medial to this pterygoid ridge is a deep groove for the infraorbital branch of the stapedial artery. The spot where the artery leaves the groove and passes to the dorsal surface of the pterygoid plate defines the posterior opening of the alisphenoid canal. Medial to the foramen ovale is the sizeable opening of the transverse canal.

As seen from lateral perspective (fig. 8D), a bony alisphenoid strut is not present in *Maxomys dollmani*, a loss resulting in the coalescence of the foramen ovale accessorius and masticatory-buccinator foramina (see fig. 48 in Musser and Newcomb, 1983: 457, showing the configuration when an alisphenoid strut is present). Exposed to view is the anterior opening of the alisphenoid canal, the open canal itself, the foramen ovale and the defining lateral margin of the pterygoid plate. Emerging from the foramen ovale is a shallow trough for the masticatory and buccinator divisions of the maxillary nerve.

In *Echiothrix*, the pterygoid plates have disappeared as major horizontal structural entities and only remnants remain, as seen from ventral perspective of skulls (fig. 7A–C). In all three views of *E. centrosa*, most of the alisphenoid bone extends to the base of the hamular process without meeting a

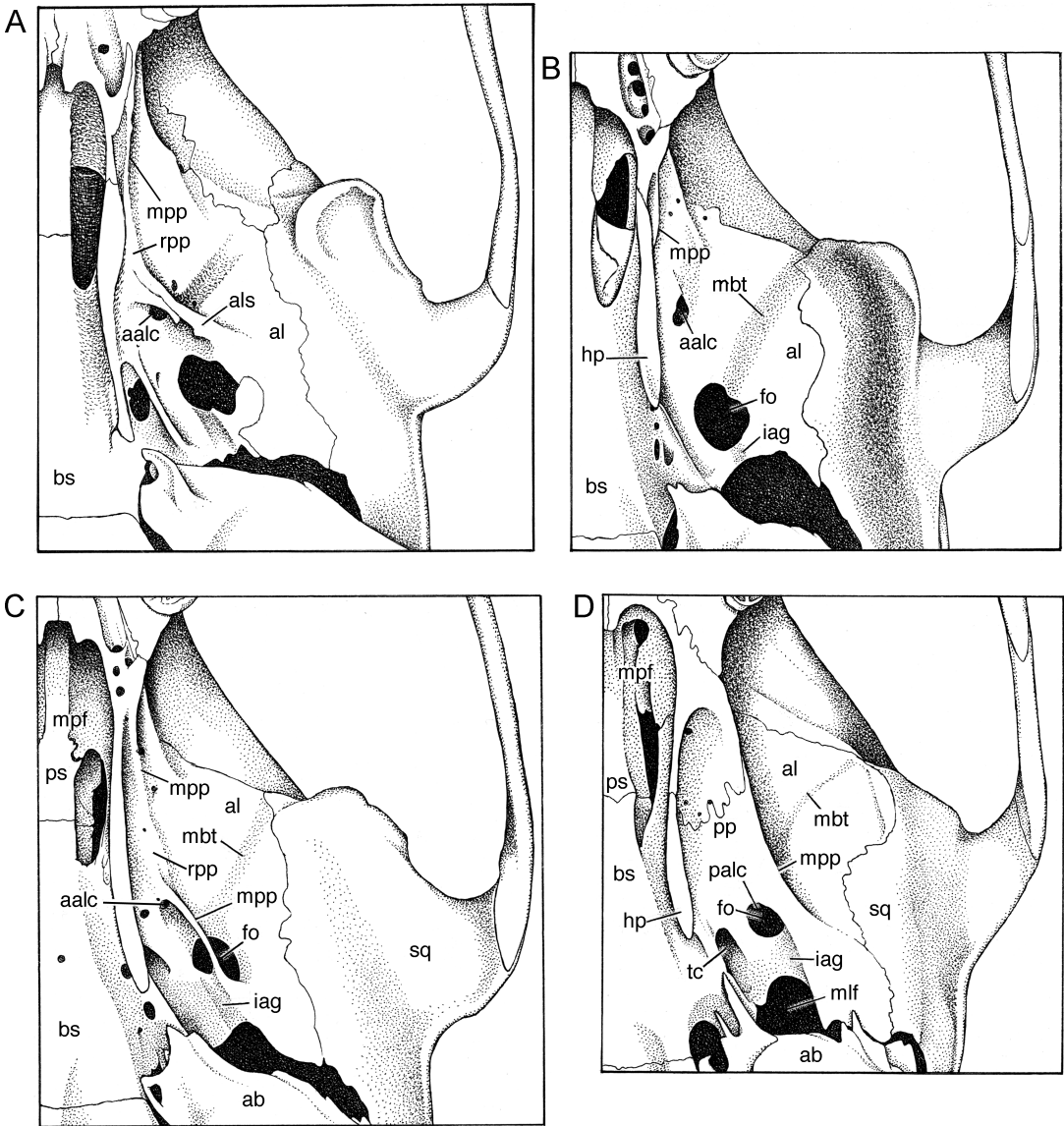


Fig. 7. Ventral views of crania showing variation in the specialized configuration of the alisphenoid region in *Echiothrix* as represented by *E. centrosa* (A, AMNH 225043; B, AMNH 225683; C, AMNH 225679), contrasted with the usual conformation found in nearly all other murines as represented by *Maxomys dollmani* (D, AMNH 224862). Abbreviations: **aalc**, anterior opening of alisphenoid canal (see fig. 8); **ab**, auditory bulla; **al**, alisphenoid; **als**, alisphenoid strut; **bs**, basisphenoid; **fo**, foramen ovale; **hp**, hamular process; **iag**, groove in which the infraorbital artery courses; **mbt**, trough for masticatory and buccinator divisions of maxillary nerve; **mlf**, middle lacerate foramen; **mpf**, mesopterygoid fossa; **mpp**, margin of pterygoid plate; **palc**, posterior opening of alisphenoid canal; **pp**, pterygoid plate; **ps**, presphenoid; **rpp**, platformlike remnant of pterygoid plate; **sq**, squamosal; **tc**, transverse canal.

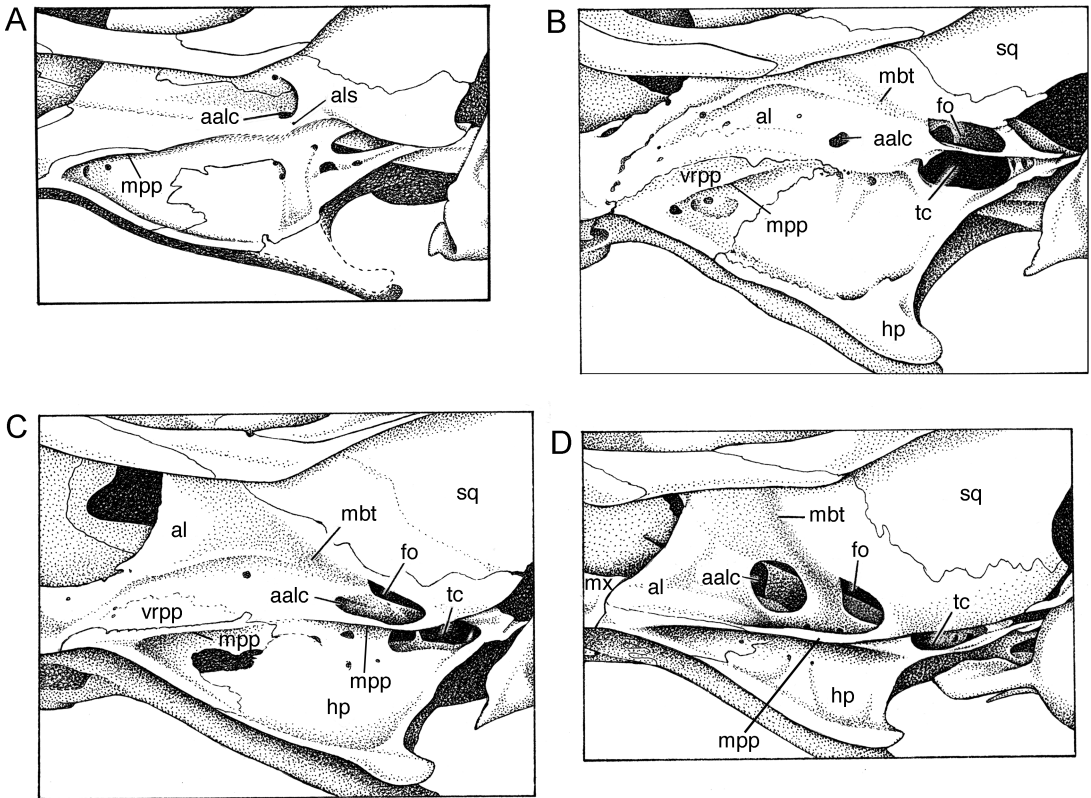


Fig. 8. Lateral views of the same specimens diagrammed in figure 7 showing variation in the specialized configuration of the alisphenoid region in *Echiothrix* as represented by *E. centrosa* (A, AMNH 225043; B, AMNH 225683; C, AMNH 225679) contrasted with the usual conformation found in nearly all other murines as represented by *Maxomys dollmani* (D, AMNH 224862). Abbreviations are the same as in figure 7, except for the following: **mx**, maxillary; **vrpp**, vertical remnant of the pterygoid plate.

generous horizontal pterygoid plate (panel A) and the entire outer surface of the alisphenoid is exposed. Aside from tiny scattered nutrient foramina, only two major openings are present in the alisphenoid: the anterior opening of the alisphenoid canal forms a small round or irregular aperture anterior to the much larger and spacious foramen ovale. Emerging from the latter is a shallow trough for the masticatory and buccinator divisions of the maxillary nerve. Between the foramen ovale and the large middle lacerate foramen is a shallow groove in which the infraorbital artery courses. In some specimens, a continuation of the groove can be detected between the anterior rim of the foramen ovale and the anterior opening of the alisphenoid canal (fig. 7C) but in others the groove exists only

between the middle lacerate foramen and the foramen ovale (fig. 7A–B). Apparently the infraorbital artery courses along the surface of the alisphenoid in *Echiothrix* but in *Maxomys* is concealed by the pterygoid plate and is exposed only between the middle lacerate foramen and foramen ovale, the latter marking the posterior opening of the alisphenoid canal.

Variation in vestiges of the pterygoid plate is also shown in figure 7. The skull in panel A retains an alisphenoid strut to which a sliver of pterygoid plate margin is attached; forward of the strut is a slight ridgelike remnant of the anterior margin of the plate. Panel B reflects the configuration of the alisphenoid region in many examples of *Echiothrix* where a short sliver of the anterior plate margin is

the only sign of the pterygoid plate from ventral perspective. The skull depicted in panel C preserves a narrow ridgelike relic of the anterior plate margin and a slim crescent of bone representing the posterolateral margin of the pterygoid plate; stippling that connects the anterior part of the bony crescent with the relict anterior plate margin outlines a narrow ledge (remnant of the pterygoid plate) undefined by a discrete lateral margin; a comparable narrow ledge or platform is found in many examples of *Echiothrix*.

The alisphenoid region, as seen from lateral perspective, of the same three specimens of *E. centrosa* that are illustrated in figure 7 is shown on panels A–C in figure 8. In panel A, a bit of the pterygoid plate margin is evident as is an alisphenoid strut, which is typically absent in most examples of *Echiothrix*. The anterior opening of the alisphenoid canal is small (also seen in panels B and C), in contrast to the comparable spacious opening in *Maxomys* (panel D). Vestiges of the pterygoid plate margin are also evident in panels B and C. So is the encroachment of what appears to be a low vertical remnant of the pterygoid plate into the alisphenoid. This vertical remnant apparently represents the transformation of a horizontal pterygoid ridge—the usual murine conformation—into a vertical surface that, along with the lower portion of the alisphenoid, forms the outer wall of the mesopterygoid fossa (mpf in fig. 7); this vertical remnant varies in extent among specimens of *Echiothrix*, ranging from the expanse illustrated in panels B and C to a thin sliver just above the ridgelike pterygoid margin. In most species of murines, such as *Maxomys dollmani* (panel D), the alisphenoid extends from its suture with the squamosal ventrally to the base of the pterygoid plate and anteriorly to the maxillary (mx) just behind the molar row. The outer wall of the mesopterygoid fossa is formed only by the alisphenoid.

**Cephalic arterial pattern:** All specimens of *Echiothrix leucura* (and *E. centrosa*) surveyed possess a carotid arterial plan that is primitive for members of the subfamily Murinae (character state 2 of Carleton, 1980; pattern 2 described by Voss, 1988; conformation dia-

grammed for *Oligoryzomys* by Carleton and Musser, 1989), but derived for muroid rodents in general. The pattern is reflected in certain cranial foramina and osseous landmarks seen in cleaned skulls. No sphenofrontal foramen penetrates the bony junction of orbitosphenoid, alisphenoid, and frontal bones; no squamosal-alisphenoid groove scores the inner surface of each wall of the braincase; and the stapedia foramina is neither minute nor absent. Instead, there is a large stapedia foramen in the petromastoid fissure, and a shallow groove (iag in fig. 7B–C) extending from the middle lacerate foramen (mlf in fig. 7D) to the foramen ovale (fo in fig. 7B–D). This disposition of foramina and grooves indicates that the stapedia artery branches from the common carotid and enters the periotic region through a large stapedia foramen. The infraorbital branch of the stapedia artery exits the periotic through the middle lacerate foramen, courses in a short groove (between middle lacerate foramen and foramen ovale), and continues on the outside of the skull at the base of the hamular process to disappear into the braincase through the anterior opening of the alisphenoid canal from which it emerges to course through the anterior alar fissure into the orbit. The supraorbital branch of the stapedia is absent; the arterial supply to the orbit is furnished by the distal part of the infraorbital branch. This circulatory plan is common among murines (Musser and Newcomb, 1983; Musser and Heaney, 1992) and is also found in some North and South American cricetids (Carleton, 1980; Voss, 1988). The derived murine version of the carotid arterial supply is contrasted with the primitive configuration and another more derived pattern, both of which are found within other muroid rodents as documented by Bugge (1970), Carleton (1980), Carleton and Musser (1989), and Voss (1988).

**Mandible:** Each gracile dentary is elongate, particularly the diastemal portion between the incisor and anterior margin of the first molar (fig. 5). On the dorsal rim of the ramus behind the molar row, the coronoid process is a minute triangular projection, and the long rim between it and the large and long condyloid (articular) process is either straight or slightly concave (very shallow sigmoid

notch). The posterior margin of the dentary between the large condyloid and angular processes is deeply concave (outlining a half circle). A large bulge on the side of the dentary behind the coronoid process and even with the dorsal rim marks the posterior termination of the incisor sheath (alveolus). Masseteric ridges on the lateral surface of each dentary are pronounced.

**Dentition:** Upper incisors are small, short, and narrow, and emerge from the rostrum at a right angle (orthodont in form; see Thomas [1919] and Hershkovitz [1962: 103] for definitions of incisor configurations). The anterior face of each incisor is scored by two shallow grooves (fig. 3). Dentine is white (unpigmented) as is the enamel in most specimens, but a few show a pale yellow tinge in the enamel layers. In live *E. centrosa*, the teeth appear ivory and emit a translucent quality; we suspect the teeth appear similar in live *E. leucura*. Enamel layers form the face and anterolateral third of each incisor, and dentine the remainder, a configuration similar to that found in most murines (as illustrated for *Rattus* in Musser and Heaney, 1992: 79).

Beyond their emergence from the anterior body of the dentary, the lower incisors are awl shaped—each is long, slim, gently curved, and with a sharp tip and elongate wear (occlusal) facet; enamel layers are smooth, without grooves. While the dentine is white, the enamel layers range from white to a pale yellow tinge—usually the distal portion of each incisor is unpigmented but the basal portion pale yellow. The extent of the enamel layer is similar to the pattern seen in most murines, *Rattus*, for example (Musser and Heaney, 1992: 79, fig. 46). The full length of each long incisor is slender and although gracile in form the tooth is not weak. Two-thirds of the incisor is contained in a sheath within the body of the dentary where it ends between coronoid and condyloid processes in an elongate bulge on the lateral surface of the dentary. This bony enclosure provides the incisor with foundational strength for stabbing prey (see Natural History Particulars of *E. centrosa*).

Every maxillary molar is secured by three roots. The alveolar patterns illustrated for *Maxomys wattsi* (Musser, 1991: 32, fig. 18)

are also usual for *Echiothrix*. Each first and second molar is anchored by large anterior and lingual roots along with a smaller posterior holdfast; each third molar is held in place by three roots of about the same size. There are two large roots beneath each of the mandibular molars.

The brachydont molars are small and molar rows are short relative to size of skull (13% of occipitonasal length; table 8); the rows are either parallel or curve gently posteriorly toward the midline of the bony palate. Molars grade in size within each row: the first is the largest, the third the smallest, which is the usual configuration observed in most species of murine rodents (Carleton and Musser, 1984). Like many murines, the cusp rows incline caudad, so that within each maxillary row the first molar overlaps the second and that tooth leans slightly against the third; the third molar in each mandibular row inclines against the second, which slightly overlaps the first molar. The rows of cusps on each tooth are moderately close to one another, a condition usually associated with inclined rows of cusps; in murines with widely separated rows, the cusps are typically erect.

Occlusal surfaces of maxillary molars are formed by simple rows of low cusps and lack the complexities found in more complicated patterns that characterize some other murines (fig. 10, upper row). For example, there is no cusp t7, which is a prominent feature on the occlusal surface in certain murine genera (*Lenothrix*, for example; fig. 9); cusp rows stand free, unconnected by labial or lingual enamel bridges (stephanodont crests as described by Misonne, 1969: 55); although close to one another, cusps t4 and t8 do not coalesce along their lingual margins until they are worn to the cingulum; the anterior cingular face on each first molar is smooth, without a shelflike ridge or small cusp (a cingular ridge, often bearing a small cusp, is a usual element on the first molar in *Rattus hoffmanni*, for example; Musser and Holden, 1991: 348). An occasional specimen of *E. leucura* shows an auxiliary cusp behind cusp t1 on the first molar (fig. 10A).

On the first upper molar, the labial and central cusps in each row are transversely aligned; the lingual cusps t1 and t4 are



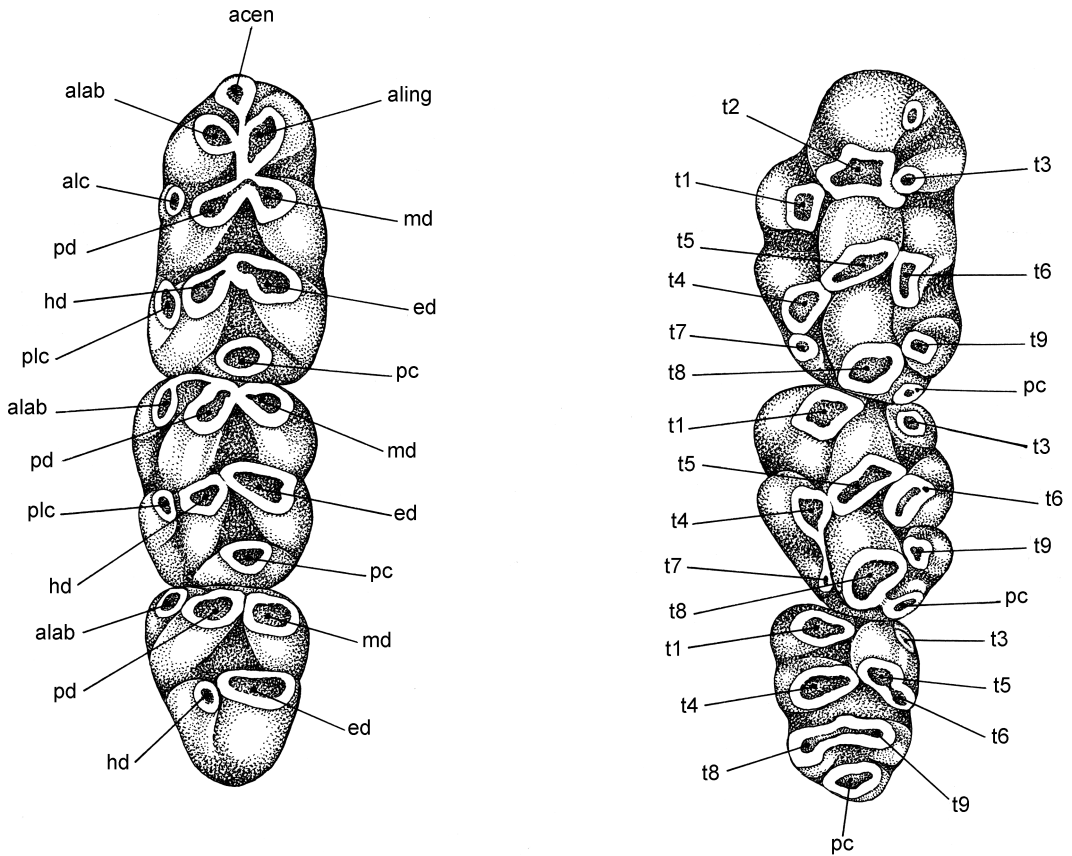


Fig. 9. Nomenclature of dental structures using right maxillary (upper) and mandibular (lower) molars of *Lenothrix canus*. Maxillary molars (right toothrow): cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix "t"; pc = posterior cingulum. Mandibular molars (left toothrow): the anteroconid (**acen**), anterolabial cusp (**alab**), and anterolingual cusp (**aling**) form the anteroconid; an anterior labial cusplet (**alc**) is present on the first lower molar, and posterior labial cusplets (**plc**) occur on the first and second lower molars; primary cusp rows are formed by the protoconid (**pd**) and metaconid (**md**), and the hypoconid (**hd**) and entoconid (**ed**); a posterior cingulum (**pc**) sits at the back of each molar (adapted from van de Weerd, 1976: 44).

situated well back of the first and second rows, respectively. A posterior cingulum occurs on nine of the 10 specimens surveyed (sample size is small because teeth are missing from some specimens or in others the occlusal surfaces are too worn to identify a posterior cingulum). The posterior cingulum extends from the back of cusp t8 in the form of a ridge, a triangular projection, or a large cusp projecting labially to form a portion of the occlusal surface (as exemplified by *Lenothrix*; fig. 9).

On the second molar, the first row of cusps is represented by cusp t1, which is

always present, and cusp t3, which is present in only about half the sample surveyed. A posterior cingulum was located on nine of 10 specimens.

Cusp t1 is present on the small third molar, but cusp t3 is not. Cusps 4, 5, and 6 form a structure that is usually chevron shaped. Cusps 8 and 9 form a posterior lamina in some specimens, but in others only a single structure is present, representing either cusp t8 only or completely merged cusps t8 and t9; the third molar lacks a posterior cingulum.

Occlusal topography of each mandibular molar consists primarily of chunky transverse

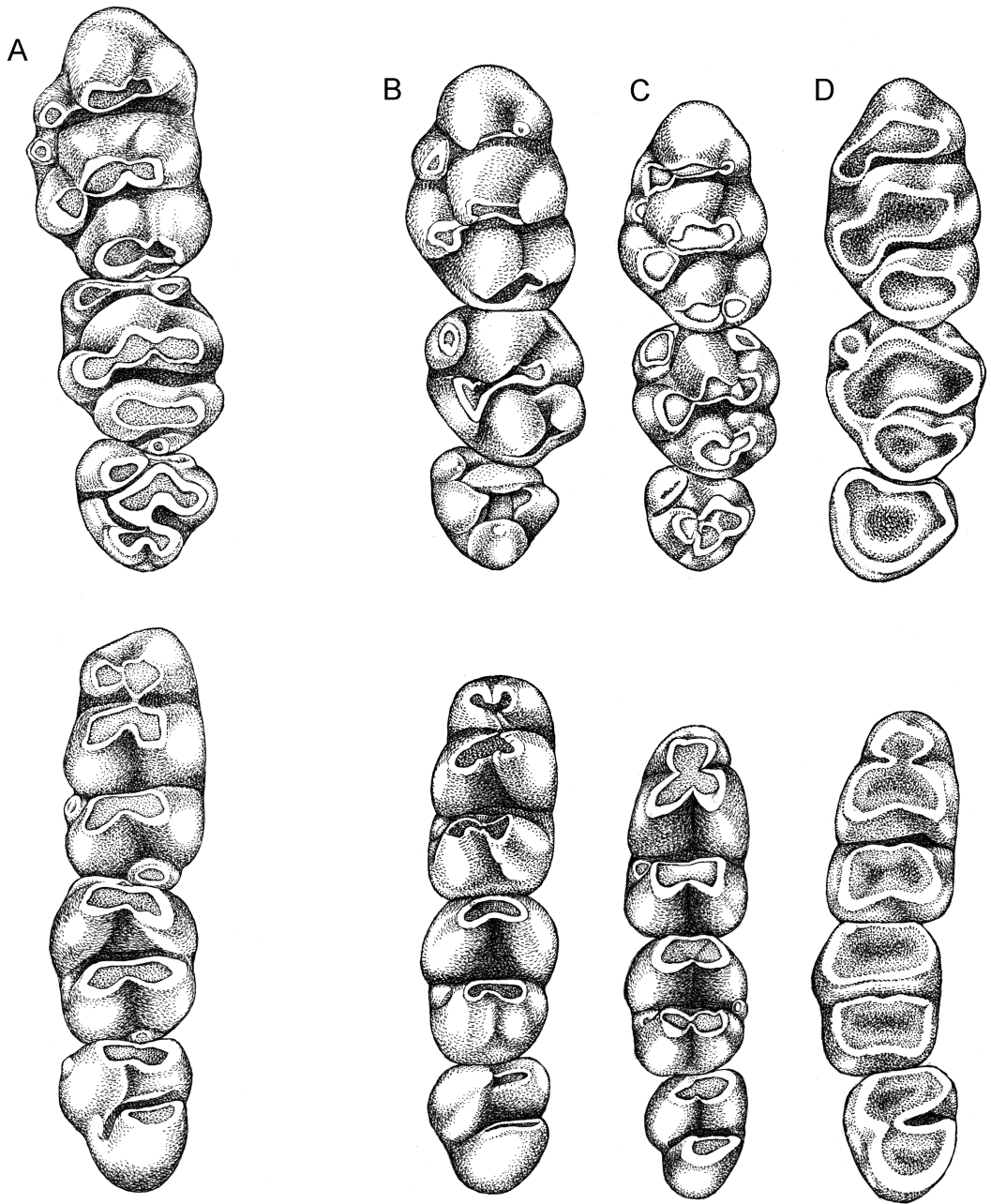


Fig. 10. Occlusal views of left maxillary (top row) and mandibular (bottom row) molar rows in four specimens of *Echiothrix* (lingual margin of each row is on the left, labial on the right). **A**, young adult *E. leucura* (USNM 217807, Temboan; CLM1-3 and clm1-3 = 7.5 mm). The next three drawings portray wear stages in *E. centrosa*: **B**, juvenile (USNM 219719, Tuare; CLM1-3 = 6.4 mm, clm1-3 = 6.6 mm); **C**, young adult (AMNH 225680, Kuala Navusu; CLM1-3 and clm1-3 = 6.5 mm); **D**, adult (AMNH 225683, Kuala Navusu; CLM1-3 = 6.5 mm, clm1-3 = 6.4 mm).

rows, each representing the fusion of two cusps (fig. 10, lower row). A large posterior cingulum, generally elliptical in cross section, occurs on the first lower molar in 11 of the 12 specimens surveyed, and a much smaller posterior cingulum could be identified on the second molar in seven of 10 specimens. Located at the front of the first molar is a chunky anteroconid composed of large anterolabial and anterolingual cusps (no antero-central cusp was found on any of the specimens) that have merged to form a large oblong lamina (without discernable cusp boundaries in some specimens, but clearly formed from two cusps in others) either slightly or much narrower than the lamina behind it. None of the molars bear anterior labial cusplets; various frequencies of occurrence of posterior labial cusplets on all molars along with anterolabial cusps on the first and second molars comprise minor components of the occlusal surface.

**COMPARISONS:** Cranial and dental morphometrics as well as qualitative cusp differences and geographic distributions between *E. leucura* and *E. centrosa* will be offered in the account of the latter species.

**GEOGRAPHIC VARIATION:** The samples of *E. leucura* used in analyses of morphometric traits come from four places and each analytical sample is small. There is insufficient material and geographic coverage for any serious analysis of geographic variation in external, cranial, and dental traits. We can report that features of fur coloration along with lengths of head and body, tail, hind foot, and ear among adults show hardly any differences from place to place other than that ascribed to individual, age, and sexual variation. Nor do definable groups emerge when cranial and dental measurements are subjected to principal-components analysis. The distribution of specimen scores for the samples from Rurukan, Gunung Masarang, Tondano, and Temboan projected on the first and second principal components (not illustrated here) intermix to form a single large cluster. If significant geographic variation exists within the range of *E. leucura*, it will have to be demonstrated in the future by obtaining larger samples from more places and adding analyses of DNA sequences to results derived from morphometric inquiry.

*Echiothrix centrosa* Miller and Hollister, 1921

*Echiothrix brevicula* Miller and Hollister, 1921:67.

**HOLOTYPE:** USNM 218706, the skin and skull of an adult male (original number 3077) collected January 9, 1917, by H.C. Raven. The skin was prepared as a conventional stuffed museum preparation; the skull and mandible are complete; all teeth are present. External, cranial, and dental measurements along with other data are listed in table 2.

**TYPE LOCALITY:** Winatu (01° 34' S, 119° 59' E; locality 7 in gazetteer and on the map in fig. 2), 762 m, in the core of the island, Propinsi Sulawesi Tengah, Indonesia.

**EMENDED DIAGNOSIS:** *Echiothrix centrosa* is similar to *E. leucura* in aspects of physical size as well as coloration and texture of fur but differs in other traits: (1) a shorter body and hind foot, but a longer tail in relation to length of head and body; (2) a smaller skull (as indexed by the lesser mean values for occipitonasal and rostral lengths; interorbital breadth; height and breadth of braincase; and lengths of diastema, bony palate, and postpalatal region), but longer incisive foramina, narrower rostrum, and wider bony palate and mesopterygoid fossa; (3) smaller molars with less complex cusp patterns: (4) cusp t3 occurs at a lower frequency on the first upper molar, a posterior cingulum is rarely present on the first and second upper molars; (5) an anterolabial cusp is absent from the second and third lower molars, posterior labial cusplets occur at low frequencies on the first and second lower molars but are absent from the third lower molar, and neither the first or second lower molar bears a posterior cingulum.

**SPECIMENS EXAMINED:** Total 39 (see Gazetteer and Specimens).

**ETYMOLOGY:** Miller and Hollister used *centrosa* to reference the provenances of their samples (Gimpu, Winatu, Besoa, and Tuare) from the central region of Sulawesi.

**GEOGRAPHIC AND ELEVATIONAL DISTRIBUTIONS:** Voucher specimens are from two localities on the northern peninsula and several places in the core of the island (see gazetteer and the map in fig. 2). Although collection sites are spotty, and expansive landscapes of Sulawesi are without records, the specimens at hand indicate that *E.*

*centrosa* ranges throughout the northern peninsula west of the Gorontalo region (00° 31' N, 123° 03' E) and into the core of the island. All specimens come from the mainland between coastal lowlands and approximately 1000 m (see gazetteer), an interval that would be covered by tropical lowland evergreen rain forest.

The actual distribution of *E. centrosa* south of the northern peninsula is unknown. There are no records from the eastern, southeastern, or southwestern peninsulas. However, there are no reasons to think the species does not occur in tropical lowland evergreen rain forest on at least the eastern and southeastern peninsulas. Whether it also occurred on the southwestern peninsula before most of the lowland forest was removed and the landscape converted to agriculture (see Fraser and Henson, 1996; Whitten et al., 1987) or is present in remnant tracts of lowland forest (as described by Froehlich and Supriatna, 1996) is not known. Samples of subfossil murines excavated from caves in the southern part of the southwestern peninsula include species of *Bunomys*, *Maxomys*, *Paruromys*, *Taeromys*, *Lenomys*, and *Rattus*, but no *Echiothrix* (Musser, 1984, also unpublished MSS.).

**DESCRIPTION:** Physical size and external features (color and texture of fur; lengths of head and body, hind foot, and ear; length of tail and its pigmentation pattern; and number of teats) of *E. centrosa* closely resemble those attributes shown by *E. leucura* (see description of that species). Descriptions of the skull, mandible, incisors, and molars for *E. leucura* also describe the basic shapes in these structures for *E. centrosa* except for the differences in cranial measurements and proportions along with size differences in molars and contrasts in their occlusal topographies, which are described below in the section covering comparisons.

Here we provide descriptions of a few characteristics of *E. centrosa*, primarily derived from material Musser collected, which are not currently available for *E. leucura*.

**Testes and spermatozoal morphology:** The testes are large relative to body size (16%–23% of head and body length; table 14), the scrotal sac is densely haired, and the hairs behind the penis are stained by a brownish-

yellow exudate. There is no gross external sign of a midventral gland.

Gross morphology of the spermatozoa of *Echiothrix centrosa* has been described by Breed and Musser (1991; reported as *E. leucura*). Basically, the asymmetrical sperm head is long and sickle shaped, the apical hook is short, ventral hooks are not present, and the tail is long (see the table of measurements and micrograph of the spermatozoa in Breed and Musser, 1991: 4 and 8, respectively).

**Stomach morphology:** *Echiothrix centrosa* has a unilocular-pouched stomach, that is, it combines aspects of what Carleton (1973) regards as the two basic morphological designs within muroid rodents—unilocular-hemiglandular or bilocular-discoglandular. Carleton (1973: 10) described a unilocular-hemiglandular stomach as:

single-chambered with a shallow incisura angularis that scarcely extends beyond the esophageal opening ... the corpus is spacious, with a broad fornix ventricularis. Distribution of cornified and glandular linings coincides closely with the basic stomach divisions: cornified epithelium is found in the corpus while glandular epithelium is limited mainly to the antrum. The bordering fold crosses the lesser curvature at the apex of the incisura angularis and the greater curvature at a locus opposite the incisura angularis.

This single-chambered hemiglandular morphology, in which the glandular zones are separated by a smooth bordering fold and the incisura angularis is shallow, forms the gastric conformation that Carleton (1973, 1980) suggested represents the primitive evolutionary state among muroid rodents. The general unilocular-hemiglandular design is common to Sulawesi species in which the diets are composed of insects and fruit (*Margaretamys*); fruit, small seeds (*Haeromys*); fruit, vegetative and flowering plant parts, insects (*Lenomys* and *Eropeplus*); small vertebrates, arthropods, snails, earthworms (oligochaetes), fruit, fungi (*Bunomys*); primarily fruit, some insects (*Taeromys*); and mostly fruit (*Rattus*). In these species, the extent of glandular epithelium lining the antrum relative to the area of cornified epithelium of the corpus resembles the pattern exemplified by *Rattus hoffmanni*

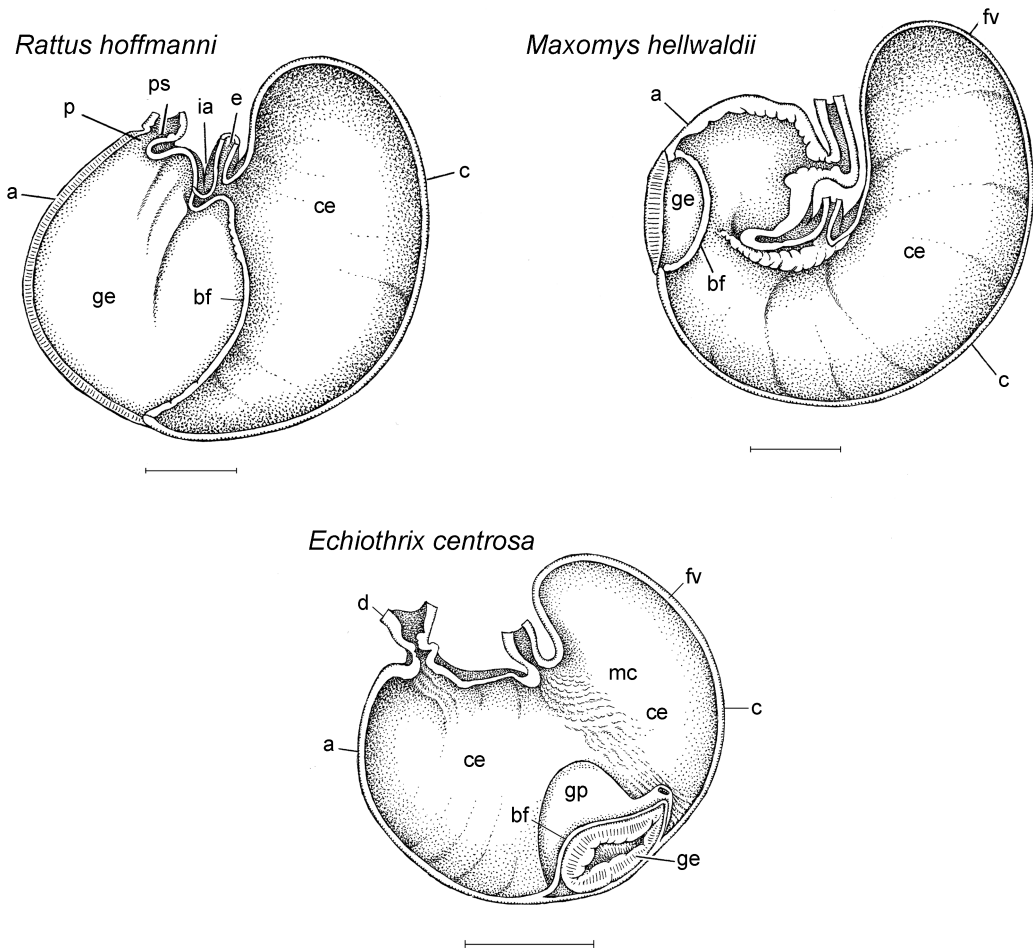


Fig. 11. Ventral views of the unilocular-hemiglandular stomach (in midfrontal section) of *Rattus hoffmanni* (AMNH 226041) and the bilocular-discoglandular stomach of *Maxomys hellwaldii* (AMNH 224939) contrasted with the unilocular-pouched stomach of *Echiothrix centrosa* (AMNH 225043). Abbreviations: **a**, antrum; **bf**, bordering fold; **c**, corpus; **ce**, cornified squamous epithelium; **d**, anterior end of duodenum; **e**, posterior end of esophagus; **fv**, fornix ventricularis; **ge**, glandular epithelium; **gp**, glandular pouch; **ia**, incisura angularis; **mc**, muscular walls of the corpus; **p**, pylorus; **ps**, pyloric sphincter. Scale lines = 10 mm.

as illustrated in figure 11, with a range of variation in which the glandular portion does not extend beyond the level of the esophageal orifice to a configuration where the glandular lining penetrates the corpus well past the esophageal opening.

In Carleton's view (1973: 10), a bilocular-discoglandular stomach has:

a deep incisura angularis that projects well past the esophageal opening, thereby imparting a more strongly defined bipartite condition .... The fornix ventricularis arches further beyond

the esophageal orifice than in a unilocular stomach, and recurves slightly toward the esophagus. The size of the corpus, especially the fornix ventricularis section, varies greatly between individuals, the degree of distension corresponding to the amount of food contained. The walls of the antrum are conspicuously muscular, particularly near the pyloric orifice. The zone of glandular epithelium, surrounded by a distinct bordering fold, is restricted to a small disc-shaped area on the greater curvature. Cornified epithelium covers the remainder of the antrum and corpus.

A bilocular-discoglandular pattern is the stomach morphology common to *Maxomys hellwaldii* (fig. 11) and other Sulawesi species in that genus. A spacious fornix ventricularis inclines toward the esophagus and projects cranial beyond the esophageal opening, the incisura angularis is deep, and the walls of the antrum are muscular. The corpus and most of the antrum is lined with muscular cornified squamous epithelium. Glandular epithelium is restricted to a small patch in the antrum on the ascending portion of the greater curvature; the glandular zone is bounded by a bordering fold. Fruit, arthropods, snails, earthworms, and small vertebrates are consumed by *M. hellwaldii*.

The stomach of *Echiothrix centrosa* (fig. 11) is unilocular and pouched. "Unilocular" because the corpus and antrum are not separated by a bordering fold, which transforms the bulk of the stomach into a single chamber, and the incisura angularis is shallow (either even with the esophageal orifice or barely extending beyond it). "Pouched" because the entire corpus and antrum is lined with cornified squamous epithelium, and glandular epithelium occurs only in a pouch situated on the greater curvature within the lumen of the stomach opposite the esophageal orifice. This pouch is lined with thick glandular epithelium and connects with the main chamber of the stomach through a small aperture at the end of a funnel-shaped or tubular neck. (We are indebted to Michael Carleton [in litt., 2013] for identifying *Echiothrix*'s stomach conformation as unilocular-pouched.)

The possible correlation of stomach design and diet will be explored below in the section covering natural history aspects of *E. centrosa*.

**Karyotype:** The chromosomal composition has been recorded for a male *E. centrosa* (AMNH 225682) collected at Kuala Navusu:  $2N = 40$ ,  $FN_a = 72$  (total of autosomal arms) and  $FN_t = 75$  (total number of arms, including XY). Autosomes comprise 14 pairs of submetacentrics with the first pair the largest and the others ranging in size from moderately large to small, two pairs of small acrocentrics, and three pairs of small metacentrics; the presumed X chromosome is a small submetacentric, the Y a small acrocentric

(Musser, 1990: fig. 10; documented as *E. leucura*).

**Juveniles:** All the information provided in the preceding descriptions of *E. centrosa* and *E. leucura* is derived from adults. We have seen only two juveniles, both *E. centrosa*: a skin and skull from Pinedapa (USNM 219737) and skull only from Tuare (USNM 219714). All molars are erupted and exhibit a degree of wear similar to the juvenile molars of USNM 219714 illustrated in figure 10. The dorsal pelage is brown and the ventral coat off-white in the juvenile from Pinedapa; although we have not seen live or freshly caught juveniles, we suspect the skin is discolored and colors in the live rat were likely grayish brown and pure white. The feet and most of the tail are white (with slight greasy discoloration). Fur covering upperparts from shoulders to rump is spinous but softer, without the rigid texture of the adult coat. The spines are long, and about half the width of adult spines (but still flat, flexible, and grooved), so the curly and soft underfur layer forms more of the coat than it does in adults, which is why the fur feels less bristly to the touch. Legs and sides of the body are covered with softer fur, composed mainly of soft and curly underhairs through which are scattered flattened, long spines. Mask on the face (around each eye) and pigmentation pattern of the tail is like that of adults. Ears are dry and brown, but were probably rubbery and dark gray in life. The ventral fur is soft to the touch and composed of both thin hairs and thicker flat hairs; the latter are much narrower than those in the adult coat.

COMPARISONS: Miller and Hollister (1921: 67) diagnosed *Echiothrix centrosa* as:

Like *Echiothrix leucura* Gray, of North Celebes; but more grayish, less buffy, in color; with more cream-buff, less yellowish, underparts and inner surfaces of limbs. Ears smaller; teeth smaller, the length of entire upper tooth row about equal to that of first and second molars of *leucura*.

Farther along in the description, Miller and Hollister remarked that the new species

is like *Echiothrix leucura* of North Celebes in size and proportions of the skin and skull; except that it has smaller ears and smaller teeth. In color it is conspicuously different from a

TABLE 6  
**Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples for *Echiothrix leucura* and *E. centroso***  
 Mean  $\pm$  1 SD and observed range in parentheses are listed.

Variable	<i>E. leucura</i>					<i>E. centroso</i>				P value (KN-P versus S-B)
	All samples N = 30	Northcentral			Core					
		Molinggapoto N = 3	Bumbulan N = 1	Kuala Navasu-Pinedapa N = 19 "brevicauda"	Sadaunta-Besoa N = 7 "centroso"					
ONL	55.0 $\pm$ 1.56 (51.7-57.8)	52.3 $\pm$ 1.27 (51.4-53.7)	53.0	51.8 $\pm$ 1.26 (50.1-54.2)	53.4 $\pm$ 1.16 (51.5-54.8)	**				
ZB	23.5 $\pm$ 1.14 (21.5-25.2)	22.6 $\pm$ 0.31 (22.3-22.9)	23.8	23.2 $\pm$ 0.78 (21.8-25.1)	23.5 $\pm$ 0.95 (21.4-24.3)	—				
IB	7.3 $\pm$ 0.26 (6.9-7.9)	7.4 $\pm$ 0.17 (7.3-7.6)	7.3	6.6 $\pm$ 0.22 (6.2-7.0)	7.1 $\pm$ 0.33 (6.7-7.7)	**				
LR	22.4 $\pm$ 1.10 (20.0-24.0)	20.9 $\pm$ 0.81 (20.3-21.8)	20.7	20.4 $\pm$ 0.76 (19.2-22.3)	21.2 $\pm$ 1.04 (19.9-22.3)	—				
BR	7.3 $\pm$ 0.46 (6.7-8.3)	7.0 $\pm$ 0.00 (6.8-8.1)	7.1	7.5 $\pm$ 0.31 (6.8-8.1)	7.6 $\pm$ 0.28 (7.2-8.0)	—				
BBC	19.4 $\pm$ 0.40 (18.5-20.0)	18.4 $\pm$ 0.50 (17.9-18.9)	18.8	18.7 $\pm$ 0.31 (18.0-19.2)	19.1 $\pm$ 0.28 (18.8-19.6)	**				
HBC	14.8 $\pm$ 0.53 (13.5-15.5)	13.9 $\pm$ 0.31 (13.2-14.2)	14.6	14.1 $\pm$ 0.30 (13.6-14.7)	14.5 $\pm$ 0.34 (14.1-15.0)	*				
BZP	3.5 $\pm$ 0.24 (3.1-4.0)	3.6 $\pm$ 0.10 (3.5-3.7)	3.8	3.4 $\pm$ 0.22 (3.1-3.8)	3.6 $\pm$ 0.35 (3.1-4.0)	—				
LD	19.0 $\pm$ 0.99 (16.7-20.5)	18.2 $\pm$ 0.85 (17.3-19.0)	18.5	18.2 $\pm$ 0.74 (17.3-19.9)	19.2 $\pm$ 0.73 (18.0-20.1)	*				
PPL	18.4 $\pm$ 0.95 (16.9-20.3)	17.7 $\pm$ 0.25 (17.5-18.0)	18.3	18.1 $\pm$ 0.43 (17.0-19.0)	18.3 $\pm$ 0.59 (17.5-19.2)	—				
LBP	12.1 $\pm$ 0.69 (10.9-13.1)	11.1 $\pm$ 0.15 (10.9-11.2)	10.4	9.9 $\pm$ 0.41 (9.0-10.8)	10.5 $\pm$ 0.36 (10.0-11.1)	**				
BBPM1	4.6 $\pm$ 0.53 (3.0-5.2)	4.6 $\pm$ 0.58 (4.3-5.3)	5.0	4.9 $\pm$ 0.24 (4.4-5.3)	4.9 $\pm$ 0.43 (4.3-5.3)	—				
BMF	2.3 $\pm$ 0.18 (2.0-2.6)	2.1 $\pm$ 0.12 (2.0-2.2)	2.5	2.6 $\pm$ 0.10 (2.4-2.8)	2.4 $\pm$ 0.12 (2.2-2.6)	**				
LIF	9.3 $\pm$ 0.65 (8.2-10.3)	9.1 $\pm$ 0.71 (8.5-9.9)	9.4	9.7 $\pm$ 0.49 (8.8-10.7)	10.0 $\pm$ 0.51 (9.1-10.7)	—				
BIF	3.3 $\pm$ 0.33 (2.7-3.9)	3.3 $\pm$ 0.15 (3.1-3.4)	3.4	3.2 $\pm$ 0.21 (2.8-3.5)	3.6 $\pm$ 0.17 (3.3-3.7)	**				

TABLE 6  
(Continued)

		<i>E. centrosa</i>						
		All samples			Northcentral		Core	
Variable	<i>E. leucura</i> <i>N</i> = 16	<i>N</i> = 30	Molinggapoto <i>N</i> = 3	Bumbulan <i>N</i> = 1	Kuala Navusu-Pinedapa <i>N</i> = 19* <i>brevicula</i> *	Sadaunta-Besoa <i>N</i> = 7** <i>centrosa</i> *	P value (KN-P versus S-B)	
LB	6.1 ± 0.18 (5.8-6.5)	6.0 ± 0.15 (5.7-6.3)	5.8 ± 0.15 (5.7-6.0)	5.9	6.1 ± 0.15 (5.8-6.3)	6.1 ± 0.11 (5.9-6.2)	—	
ALM1-3	7.3 ± 0.39 (6.6-8.0)	6.4 ± 0.20 (5.9-6.7)	6.4 ± 0.25 (6.3-6.6)	6.2	6.4 ± 0.22 (5.9-6.7)	6.4 ± 0.17 (6.1-6.6)	—	
BM1	2.3 ± 0.10 (2.2-2.5)	2.1 ± 0.08 (1.9-2.3)	2.1 ± 0.00	2.1	2.1 ± 0.06 (1.9-2.1)	2.1 ± 0.12 (1.9-2.3)	—	

\*\* =  $P \leq 0.01$ ; \* =  $P \leq 0.05$ ; — = not significant.

series of *leucura* from Temboan, North Celebes; the yellowish-buff tints of *leucura* are replaced by vinaceous-gray, especially noticeable on the flanks; and the belly is a whitish cream-buff rather than deep yellowish-buff.

In the following contrast between *E. leucura* and *E. centrosa*, the taxon *brevicula*, also described by Miller and Hollister and also from the central part of Sulawesi, is included as a synonym of *E. centrosa*. Reasons for doing so are set forth below in the section explaining allocation of the synonym.

In the samples at hand of *E. centrosa* and *E. leucura*, which includes the material examined by Miller and Hollister, and contrary to their observations, we see differences in size and proportions of external measurements. Mean values for length of head and body (206.0 mm for *E. centrosa*, 215.8 mm for *E. leucura*;  $P = 0.013$ ) and length of hind foot (51.5 mm and 53.5;  $P = 0.003$ ) are significantly different—*E. centrosa* averages smaller. Means for length of tail (240.9 mm for *E. centrosa*, 240.2 mm for *E. leucura*;  $P = 0.877$ ), however, are statistically identical—therefore, *E. centrosa* has on average a shorter body and hind foot but a longer tail relative to length of head and body (sample sizes are  $N = 30$  for *E. centrosa* and  $N = 13$  for *E. leucura* for all three variables).

Other external differences between *E. centrosa* and *E. leucura* that were described by Miller and Hollister are not apparent to us. Both species have dark gray to bluish-gray dorsal coats; both have underparts that are either all white (in live animals) or white with patches or streaks of buff, orange, or pale rust (the rust may be a stain because the hairs in these colored places have pigmented debris adhering to them while hairs in the white region are clean); both show a similar color pattern on the tail, including length of the dorsal white portion (means of dorsal white length/tail length are 59.1% for *E. centrosa* and 58.5% for *E. leucura*; table 5); and both possess two pairs of inguinal teats.

To Miller and Hollister, the smaller ears of *centrosa*—as well as *brevicula*, the other taxon they described from central Sulawesi—were diagnostic in relation to *E. leucura*. But their descriptions of the new



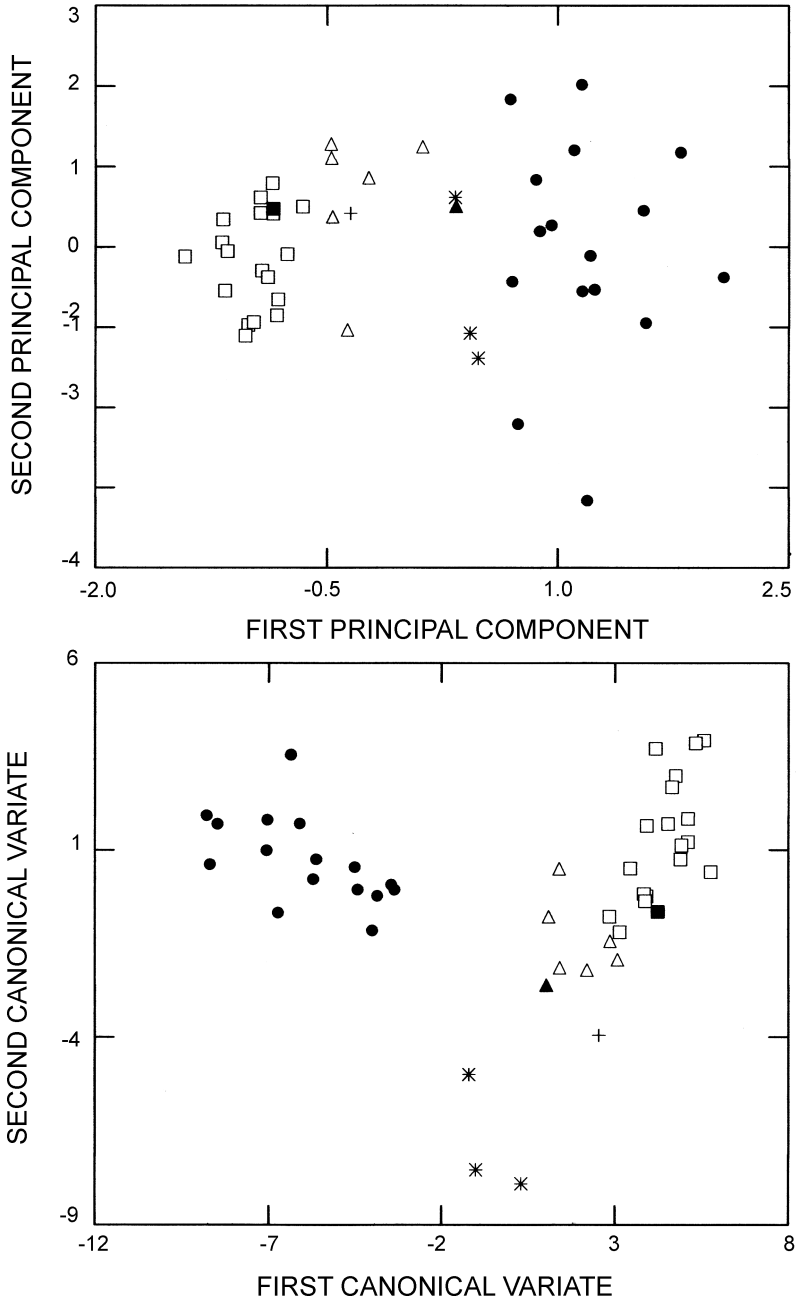


Fig. 12. Scatterplots of specimen scores representing the sample of *Echiothrix leucura* (filled circle;  $N = 16$ ) and the four population samples of *E. centrosoa* ( $N = 30$ ; Molinggapoto = asterisk, Bumbulan = cross, Kuala Navusu-Pinedapa = square, Sadaunta-Besoa = triangle) projected on first and second principal components extracted from principal-components analysis (upper), and on first and second canonical variates extracted from discriminant-function analysis (lower) of 16 cranial and two dental log-transformed variables. Scores for holotypes: *Echiothrix centrosoa* (filled triangle, Winatu in Sadaunta-Besoa sample) and *Echiothrix brevicula* (filled square, Pinedapa in Kuala Navusu-Pinedapa sample). See table 7 for correlations (loadings) of variables with extracted components or canonical variates and for percent variance explained in both ordinations.

TABLE 7  
**Results of Principal-Components and Discriminant-Function Analyses Comparing Samples of *Echiothrix leucura* and *E. centrosa***

Correlations (loadings) of 16 cranial and 2 dental log-transformed variables are based on 16 *E. leucura* and 30 *E. centrosa*. See figure 12.

Variable	Correlations (loadings)			
	Principal components		Discriminant function	
	PC1	PC2	CV1	CV2
ONL	0.73***	0.56***	-0.66***	0.12
ZB	0.15	0.65***	-0.07	-0.08
IB	0.75***	0.10	-0.71**	-0.36**
LR	0.72***	0.54***	-0.64***	0.09
BR	-0.19	0.58***	0.28	0.28
BBC	0.58***	0.39**	-0.55***	-0.21
HBC	0.57***	0.50***	-0.51***	0.03
BZP	0.29*	0.49***	-0.18	-0.35*
LD	0.33*	0.77***	-0.18	0.04
PPL	0.13	0.66***	-0.06	0.03
LBP	0.94***	0.13	-0.91***	-0.06
BBPM1	-0.32*	0.80***	0.35*	-0.06
BMF	-0.72***	0.25	0.62***	0.48***
LIF	-0.29*	0.72***	0.37**	0.08
BIF	-0.01	0.81***	0.06	-0.22
LB	0.03	0.02	-0.13	0.40**
ALM1-3	0.82***	-0.10	-0.88***	0.29
BM1	0.84***	0.03	-0.86***	0.16
Canonical correlation			0.981	0.931
Eigenvalue	0.028	0.020	25.832	6.457
% Variance	38.1	26.8	67.2	16.8

\*\*\* =  $P \leq 0.001$ ; \*\* =  $P \leq 0.01$ ; \* =  $P \leq 0.05$ .

taxa and comparisons were based on material obtained by H.C. Raven, who did not measure length of ear on freshly caught rats. Miller and Hollister simply measured ears (from the notch) on the dry museum skins; because such ears are shriveled and their lengths contracted, they recorded smaller values than would be obtained from freshly caught animals. They reported, for example, 29.4 mm for the holotype of *centrosa* and 28.1 mm for the holotype of *brevicula*. Musser also measured the ear (from notch to crown of pinna) on specimens he collected within the geographic ranges of *centrosa* and *brevicula* and did not encounter any ear length less than 32 mm, a value within the range of measurements obtained by G. Heinrich for a sample of *E. leucura* from Rurukan (table 4).

Except for its smaller ears and teeth, *E. centrosa* was considered by Miller and

Hollister to be similar to *E. leucura* in cranial size and proportions. In addition to the contrast in molar size, (see below), there are—contrary to the perceptions of Miller and Hollister—impressive distinctions between the two species in certain cranial dimensions and proportions. Univariate mean differences in cranial variables show that, compared with *E. leucura*, the central Sulawesi *E. centrosa* has a shorter skull and narrower interorbit, a shorter but wider rostrum, smaller braincase, shorter diastema and postpalatal region, shorter but wider bony palate, wider mesopterygoid fossa, and longer incisive foramina (table 6).

The univariate mensural cranial and dental differences are also summarized by results from multivariate analyses (fig. 12). There the top scatterplot contains the distribution of specimen scores for all population samples of *E. centrosa* and *E.*

TABLE 8  
**Descriptive Statistics for Measurements (mm) of Maxillary and Mandibular Molar and Alveolar Rows Derived from Samples of *Echiothrix leucura* and *E. centrosa***

Mean  $\pm$  1 SD, observed range in parentheses, and size of sample are listed.

Species	Maxillary			Mandibular		
	ALM1-3	CLM1-3	BM1	alm1-3	clm1-3	bm1
<i>E. leucura</i>	7.2 $\pm$ 0.38 (6.6-8.0) 19	7.0 $\pm$ 0.29 (6.6-7.5) 19	2.3 $\pm$ 0.10 (2.2-2.5) 20	6.9 $\pm$ 0.32 (6.3-7.5) 19	7.1 $\pm$ 0.29 (6.5-7.5) 17	1.8 $\pm$ 0.11 (1.7-2.0) 16
<i>E. centrosa</i>	6.4 $\pm$ 0.20 (5.9-6.7) 33	6.3 $\pm$ 0.17 (6.0-6.5) 26	2.1 $\pm$ 0.08 (1.9-2.3) 33	6.3 $\pm$ 0.22 (5.9-6.7) 33	6.4 $\pm$ 0.15 (6.1-6.7) 33	1.6 $\pm$ 0.10 (1.5-1.7) 33

*leucura* projected on the first and second principal components. Scores for specimens in population samples from regions west of Gorontalo in the northern peninsula (Molinggapoto, Bumbulan) and from the core of the island (Sadaunta-Besoa, and Kuala Navusu-Pinedapa) with small skulls and molars are scattered in the left half of the plot; these are samples of *E. centrosa*. Specimen scores for samples from the north-eastern portion of the northern peninsula east of the Gorontalo region, animals with larger skulls and molars, fall in the right half of the ordination: these scores identify *E. leucura*. Covariation among most variables indicates size to be the primary influence for dispersion of the scores along the first component, as indicated by the many positive and high correlations on that axis ( $r = 0.57-0.94$ ). Four variables yielded moderate to high negative correlations ( $r = -0.19$  to  $-0.72$ ; table 7), which point to the broader rostrum, bony palatal bridge, and mesopterygoid fossa along with a longer incisive foramina relative to skull size (indexed by occipitonasal length) in *E. centrosa* compared with *E. leucura*. The patterns of significant loadings of cranial and dental measurements are generally mirrored by the univariate mean contrasts (table 6).

Results of discriminant-function analysis (which identifies the variables most strongly separating the centroids of predefined population samples) provide a sharper resolution of morphometric affinity among samples, but the pattern is generally similar to that illuminated by results of the principal-components analysis. Individual specimen scores projected on first and second canonical variates form two nonoverlapping constella-

tions (fig. 12, bottom): scores for *E. leucura*, with the larger skulls and molars, fall in the left half; points representing *E. centrosa*, with smaller skulls and molars, are contained in the right half. Size is the force separating scores along the first variate as indicated by covariation among most of the same variables that proved significant in the principal-components analysis (table 7). Here, the analysis again shows that *E. centrosa* has a shorter skull and rostrum, narrower inter-orbit, smaller braincase, shorter bony palate, and smaller molars (as measured by alveolar length of maxillary molar row and breadth of first upper molar) ( $r = -0.51$  to  $-0.91$ ), but a wider rostrum, bony palate, and mesopterygoid fossa, coupled with a longer incisive foramina ( $r = 0.28-0.62$ ) compared with *E. leucura*.

Miller and Hollister noted the contrast in molar size between *E. centrosa* and *E. leucura*, and the difference is striking as shown by the univariate means for lengths of maxillary molar rows: 6.4 mm for *E. centrosa* and 7.0 mm for *E. leucura* (table 8). Furthermore, there is no overlap in the observed range of values. Mean differences in lengths of the mandibular molar rows is comparable (6.4 mm for *E. centrosa* and 7.1 mm for *E. leucura*), although there is slight overlap in the observed range of measurements. The shorter maxillary and mandibular molar rows in *E. centrosa* are related to its smaller molars compared with those of *E. leucura*, as estimated by means for breadth of first upper molars (table 8).

Contrast in molar size is not the only dental distinction between the two species. The molars of *E. centrosa* also have less complex occlusal surfaces, as indicated by the

TABLE 9  
Presence or Absence of Particular Cusps and  
Cusplets on Maxillary and Mandibular Molars in  
Samples from *Echiothrix leucura* and *E. centrosa*<sup>a</sup>

	<i>E. leucura</i>	<i>E. centrosa</i>
<b>MAXILLARY MOLARS</b>		
<b>Cusp t3</b>		
M2		
+	42 (5)	25 (5)
–	58 (7)	75 (15)
M3		
+	14 (1)	15 (3)
–	86 (6)	85 (17)
<b>Posterior cingulum</b>		
M1	90 (9)	4 (1)
+	10 (1)	96 (22)
–		
M2		
+	90 (9)	5 (1)
–	10 (1)	95 (20)
<b>MANDIBULAR MOLARS</b>		
<b>m1</b>		
Posterior labial cusplet		
+	83 (10)	46 (12)
–	17 (2)	54 (14)
Posterior cingulum		
+	92 (11)	0
–	8 (1)	100 (26)
<b>m2</b>		
Anterolabial cusp	30 (3)	0
+	70 (7)	100 (26)
–		
Posterior labial cusplet		
+	40 (4)	19 (5)
–	60 (6)	81 (21)
Posterior cingulum		
+	70 (7)	0
–	30 (3)	100 (26)
<b>m3</b>		
Anterolabial cusp		
+	30 (3)	0
–	70 (7)	100 (26)
Posterior labial cusplet		
+	20 (2)	0
–	80 (8)	100 (26)

<sup>a</sup> Number of individuals with or without the cusp or cusplet is expressed as a percentage of the entire sample of each species; actual number of specimens with or without the trait is in parentheses. Data are derived from juveniles and young adults, age classes showing little or moderate wear; in older specimens, the occlusal surfaces consist of a series of enamel-ringed dentine basins in which the discrete cuspidation has been obliterated. Provenances of samples are identified below.

TABLE 9  
(Continued)

*E. leucura*: northeastern arm of the northern peninsula (Rurukan, Tondano, and Temboan).

*E. centrosa*: northern peninsula (Molinggapoto and Bumbulan) and Core (Kuala Navusu, Pinedapa, Sungai Sadaunta, Winatu, Gimpu, Besoa, and Tuare).

None of the specimens examined showed an antero-central cusp as part of the anteroconid, or anterior labial cusplets on any of the three mandibular molars.

difference between the two species in frequency of occurrence of particular cusps and cusplets (table 9, fig. 10). In the maxillary molars, cusp t3 occurs at a lower frequency on the second molar in *E. centrosa* (25%) compared with *E. leucura* (45%), and a posterior cingulum is present on the first and second molars in only 1% of the sample of *E. centrosa* but present in 90% of the sample of *E. leucura*. In the mandibular molars, an anterolabial cusp is not present on either the second or third molars in *E. centrosa* (occurs in 30% of the sample of *E. leucura*); none of the specimens of *E. centrosa* surveyed showed a posterior cingulum on the first and second molars (frequency is 92% on the first molar and 70% on the second molar in *E. leucura*); and a posterior labial cusplet is present on the first molar in 46% of the sample, on the second molar in 19%, and not present on the third molar in the sample of *E. centrosa* (92% on the first molar, 40% on the second, and 20% on the third molar are the frequencies for *E. leucura*).

**GEOGRAPHIC VARIATION:** Except for the 19 specimens in the Kuala Navusu–Pinedapa sample, the other population samples are small. Three from Molinggapoto and one from Bumbulan are the only specimens we have examined from the northern peninsula west of the Gorontalo area, and the seven in Sadaunta-Besoa are the only specimens from middle elevations in central Sulawesi west of the lowlands in which Kuala Navusu and Pinedapa are located. Without larger samples from more places, especially from transects that would connect the current collection localities, we cannot provide a definitive pattern of geographic variation using external traits and measurements from cranial and dental variables. For now only a few

comments covering the different population samples is possible.

The specimens from Molinggapoto and Bumbulan have white underparts without patches of pigmentation. Both all-white underparts and white ventral coats with patches or streaks of buff or rust occur in the samples from the core of Sulawesi. More specimens from the northern peninsula both east and west of Gorontalo are needed to determine the frequency of occurrence of all-white versus partially pigmented underparts in the population there.

The pattern of covariation among cranial and dental variables as revealed by principal-components and discriminant-function analyses places the specimen from Bumbulan within or close to the cluster of specimen scores representing the Sadaunta-Besoa sample (fig. 12). Its physical size and fur color are indistinguishable from specimens of comparable age in the Sadaunta-Besoa sample, at least those individuals with all-white underparts.

In the ordinations generated by multivariate analyses, scores for the Sadaunta-Besoa sample cluster close to those representing the Kuala Navusu–Pinedapa sample, both in principal components and canonical variate scatter plots (fig. 12). There are some perceptible differences between the two samples. Animals from the lowlands at Kuala Navusu and Pinedapa have slightly shorter ventral coats and slightly smaller skulls than do those in the Sadaunta-Besoa sample, differences that will be elaborated upon in the section below where the reasons are given for treating *brevicula* as a synonym of *E. centrosa*. Again, the significance of these observations within the context of revealing geographic variation in external and cranial traits is elusive without samples from intervening regions between the two population samples and without samples from elsewhere in the core of the island and the various peninsulas.

The specimens from Molinggapoto are geographically closest to the range of *E. leucura*, but their cranial and dental morphometric attributes, along with molar occlusal cusp patterns, link them with the specimen from Bumbulan and those collected in the core of Sulawesi. However, there are a few

morphometric differences, which are graphically summarized in the canonical variate scatterplot in figure 12. There, along the first axis, the specimen scores for Molinggapoto are aligned in the right half of the ordination along with scores for the samples from Bumbulan and central Sulawesi, all of which we identify as *E. centrosa*; scores for *E. leucura*, with larger skulls and molars, fall into the left half of the graph. But along the second axis, the points for Molinggapoto are separated from those representing the other examples of *E. centrosa*. Compared with that material, the Molinggapoto sample has a relatively wider interorbital region and zygomatic plate, narrower mesopterygoid fossa, and smaller bullae, as indicated by the high positive and negative correlations for these variables (table 7).

Future attempts to recover any patterns of geographic variation within what is identified as *E. centrosa* here will depend on study of additional material collected from a greater expanse of Sulawesi and analyses of molecular as well as morphometric data.

ALLOCATION OF SYNONYM: *Echiothrix brevicula* Miller and Hollister, 1921: 67. The holotype is USNM 219744, the skin and skull (measurements are listed in table 3) of an adult male collected January 29, 1918, by H.C. Raven. The type locality is Central Sulawesi, Pinedapa (01° 25' S, 120° 35' E; locality 4 in gazetteer and on the map in fig. 2), Propinsi Sulawesi Tengah, Indonesia.

The Latin *brevis* means "short" (also connotes "small" and "narrow"), and Miller and Hollister used *brevicula* to reflect what they perceived to be the smaller size of the specimens in the sample from Pinedapa as compared with their sample of *E. leucura* from Temboan in the northeastern end of the northern peninsula and *E. centrosa* from the west-central highlands. Miller and Hollister (1921: 68) diagnosed *Echiothrix brevicula* as follows:

Differs from *Echiothrix leucura* and *E. centrosa* in smaller size; smaller hind feet; much more vinaceous, less buffy or yellowish, coloration; darker underparts, buff or reddish-buff rather than yellowish or whitish; and smaller, less narrowed skull. Ears and teeth small, as in *centrosa*.

The authors remarked that the new species “is easily separated from *E. leucura* and *E. centrosa* by its small size, peculiar coloration, and the less narrowed skull. It has small ears and small teeth as in *E. centrosa*.”

Our sample of *brevicula* includes the type series Raven obtained at Pinedapa and the sample Musser collected from Kuala Navusu; both localities are in the coastal lowland region east of the west-central highlands (see gazetteer and the map in fig. 2). Specimens from each place are inseparable in physical size, color of fur, morphometric traits associated with the skull and molars, and molar occlusal patterns formed by cusps and cusplets. We subjected cranial and dental measurements from all the samples identified here as *E. centrosa* to principal-components analysis and on the resulting scatterplot (not illustrated here) the scores representing specimens from Pinedapa and Kuala Navusu intermingle to form a tight cluster. The two geographic samples were combined to form a single population sample (Kuala Navusu–Pinedapa) used to generate the multivariate analytical results illustrated in figure 12.

Specimens that can be assigned to what Miller and Hollister would have identified as *centrosa* consist of the holotype from Winatu and collections from Tuare, Besoa, Gimpu, Kulawi, and Sungai Sadaunta, all localities in the west-central highlands west of the eastern coastal lowlands containing Kuala Navusu and Pinedapa (see the maps in Musser et al., 2010: 16, 81).

The type series of *brevicula* from Pinedapa does differ in magnitude of two external measurements from the series collected by Raven at Temboan, which is the sample Miller and Hollister used as their representative of *leucura*. Means for length of head and body (197.0 mm for *brevicula*, 215.4 mm for *leucura*;  $P = 0.003$ ) and length of hind foot (50.3 mm and 54.7 mm;  $P = 0.0001$ ) are significantly different, but means for length of tail are not (239.6 mm and 250.0 mm;  $P = 0.082$ ). (Sample sizes are  $N = 12$  for *brevicula* from Pinedapa and  $N = 7$  for *N. leucura* from Temboan.) The Temboan sample has a larger body and longer hind foot than the series from Pinedapa, and the tail is shorter relative to length of head and body; this is the

same pattern of differences seen between all samples of *E. leucura* and all samples of *E. centrosa* (including *brevicula*) that we presented previously (see comparisons in the account of *E. centrosa*).

In contrast, the distinction between *brevicula* and *centrosa* as noted by Miller and Hollister cannot be corroborated by us. We compared external measurements from the type series of *brevicula* (Pinedapa;  $N = 12$ ) with the specimens Miller and Hollister assigned to *centrosa* (Gimpu, Winatu, and Besoa;  $N = 3$ ). Means for length of head and body (197.0 mm for *brevicula*, 206.7 mm for *centrosa*;  $P = 0.37$ ), length of tail (239.6 mm and 233.3 mm;  $P = 0.80$ ) and length of hind foot (50.3 mm and 51.7 mm;  $P = 0.25$ ) are not significantly different.

Specimens (all adults) that Musser collected from Sadaunta (representing *centrosa*;  $N = 6$ ) and those he obtained from Kuala Navusu (representing *brevicula*;  $N = 7$ ) are closely similar in physical size as indexed by means for length of head and body (215.3 mm for *brevicula*, 213.8 mm for *centrosa*;  $P = 0.70$ ), length of tail (249.9 mm and 241.2 mm;  $P = 0.25$ ), and length of hind foot (52.3 mm and 53.2 mm;  $P = 0.29$ ), but the Sadaunta sample has slightly larger ears (33.3 mm and 34.8 mm), although the difference is not statistically significant ( $P = 0.23$ ); see also table 4. The sample from Kuala Navusu has a larger mean weight (267.3 g) than that from Sadaunta (237.6 g), just the opposite of expectation if *brevicula* were physically smaller as Miller and Hollister claimed.

Coloration and texture of the fur is similar in the samples of *centrosa* and *brevicula*. Both contain specimens with dark gray or dark bluish-gray dorsal coats and white ventral coats, with some individuals showing buffy or rusty streaks on the chest and abdomen. One difference is the shorter ventral fur on the specimens from Kuala Navusu and Pinedapa; all were taken between 31 and 122 m, specimens representing *centrosa*, with slightly softer and longer fur, are from 400–985 m. Another difference is that the dorsal coat is somewhat softer in the specimens comprising the Sadaunta-Besoa sample compared with the slightly harsher and stiffer fur typical of animals in the Kuala Navusu–Pinedapa series.

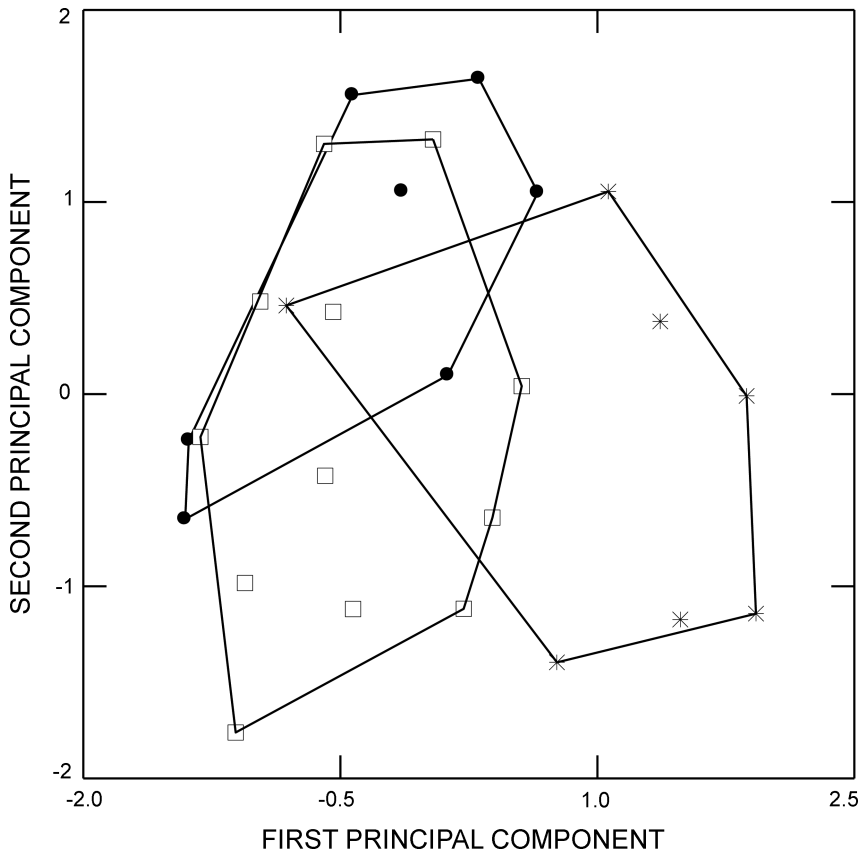


Fig. 13. Scatterplot of specimen scores representing the sample of *Echiothrix* “*centrosa*” (Sadaunta-Besoa; asterisk;  $N = 7$ ) and the two population samples of *E. “brevicula”* (Kuala Navusu–Pinedapa; filled circle = Kuala Navusu, empty square = Pinedapa;  $N = 19$ ) projected on first and second principal components extracted from principal-components analysis of 16 cranial and two dental log-transformed variables. See table 10 for correlations (loadings) of variables with extracted components and for percent variance explained.

It is unclear what Miller and Hollister saw when they described *brevicula* as having a “less narrowed skull” than either *leucura* or *centrosa*—perhaps they meant a skull *less narrow*, with the implication that it was wider than those in the samples of *leucura* and *centrosa*. Specimens in the samples from Pinedapa and Kuala Navusu, as well as those from landscapes to the west at higher elevations (the Sadaunta-Besoa population sample), do have appreciably smaller skulls compared with the northeastern peninsular *E. leucura*, as does all the material at hand from places west of the Gorontalo region (figs. 5, 6; table 6).

Restricting the focus to the core of Sulawesi, there are significant differences in

univariate means between the Kuala Navusu–Pinedapa (*brevicula*) and Sadaunta-Besoa (*centrosa*) samples for eight cranial dimensions. Most means for the Kuala Navusu–Pinedapa sample average smaller, including interorbital breadth as well as breadth and height of braincase, three variables that could be used conceivably to index degree of cranial narrowness—in this case *brevicula* actually has a *more narrowed skull*, not a “less narrowed skull,” as contrasted with *centrosa*. Significant differences between means for other variables highlight the average longer skull in *centrosa*, its longer diastema and bony palate, wider incisive foramina, but narrower mesoptery-

TABLE 10  
Results of Principal-Components Analyses  
Comparing Samples of *Echiothrix* "*centrosa*"  
(Sadaunta-Besoa) and *E. "brevicula"* (Kuala  
Navusu-Pinedapa)

Correlations (loadings) of 16 cranial and 2 dental log-transformed variables are based on 16 *E. leucura* and 30 *E. centrosa*. See figure 13.

Variable	Correlations	
	PC1	PC2
ONL	0.80***	0.26
ZB	0.44*	-0.18
IB	0.60***	0.00
LR	0.70***	0.33
BR	0.39*	0.21
BBC	0.68***	0.11
HBC	0.72***	-0.16
BZP	0.56**	-0.79***
LD	0.83***	0.26
PPL	0.23	0.03
LBP	0.74***	-0.11
BBPM1	0.46*	0.18
BMF	-0.30	0.34
LIF	0.59**	0.21
BIF	0.80***	0.36
LB	-0.28	-0.07
CLM1-3	-0.11	-0.41*
BMI	0.02	-0.18
Eigenvalue	0.013	0.006
% Variance	35.1	16.0

\*\*\*  $P \leq 0.001$ ; \*\*  $P \leq 0.01$ ; \*  $P \leq 0.05$ .

goid fossa (table 6). For the other cranial measurements, as well as the dental variables, there are no significant differences in mean values between the Kuala Navusu-Pinedapa and Sadaunta-Besoa samples. Keep in mind the dissimilar sample sizes involved ( $N = 19$  for Kuala Navusu-Pinedapa,  $N = 7$  for Sadaunta-Besoa), each containing a range in age from young-to-old adults.

The mensural differences noted here are reflected in a principal-components ordination where most of the scores for Sadaunta-Besoa congregate to the right along the first axis of the scatter plot but overlap those signifying the Kuala Navusu-Pinedapa sample to the left (fig. 13), a pattern influenced by the moderate to large positive correlations for 13 of the 18 variables ( $r = 0.39-0.83$ ; table 10) a measure of the average larger means for some measurements in the Sadaunta-Besoa series. Whether these univari-

ate mean distinctions seen in samples at hand measure real geographic variation in the two populations will have to be determined by study of larger samples equal in number of specimens and equal in age classes. Nevertheless, present evidence from phenetic traits associated with skins, skulls, and teeth persuades us that the sample from Kuala Navusu and Pinedapa, corresponding to what Miller and Hollister described as *E. brevicula* (originally based on the sample from Pinedapa), represents a coastal lowland population of *E. centrosa* with slightly shorter ventral fur, harsher dorsal coat, and some cranial dimensions that average smaller. This specific homogeneity is reinforced by sucking lice (Anoplura): hosts in the Kuala Navusu-Pinedapa sample as well as those in the west-central highlands (Sadaunta-Besoa sample) are parasitized by the same species of louse, *Polyplax beaucournui*, n. sp. (see the section describing ectoparasites of *Echiothrix*).

#### NATURAL HISTORY PARTICULARS OF *ECHIOTHRIX CENTROSA*

Information presented here comes from Musser's experience with *E. centrosa* when he worked in tropical lowland evergreen rainforests along Sungai Sadaunta in Sulawesi's west-central highlands (camp sites are indicated on the map in Musser et al., 2010: 17) and east of there at Kuala Navusu (shown on the map in Musser et al., 2010: 81) on the coastal plain bordering Teluk Tomini. Musser's observations, summarized from his field journals (stored in Mammalogy archives, AMNH) cover habitat, diet, miscellaneous behavior, function of spinous fur, reproductive aspects, nests, and the species of murines found in association with *E. centrosa* at Sungai Sadaunta and Kuala Navusu.

**HABITAT:** All specimens of *E. centrosa* obtained by Musser were trapped in primary tropical lowland evergreen rain forests in the watershed of Sungai Sadaunta and lowlands containing Kuala Navusu. Summaries of ambient air temperatures, relative humidity, and days of rainfall compared with days of trapping for Sungai Sadaunta and Kuala Navusu are listed in table 11. Ten to 12 consecutive wet months and up to two



TABLE 11  
 Ambient Air Temperatures, Relative Humidity, and Rainfall Patterns at Sungai Sadaunta and Kuala Navusu<sup>a</sup>

Variable	Sungai Sadaunta	Kuala Navusu
Elevation (m)	758	30
Recording period	Sept. 16–Dec. 16, 1974	Aug. 28–Nov. 30, 1975
Air temperature (°C; means and ranges)		
minimum	19.4 (17–21)	23.1 (22–24)
maximum	24.0 (21–20)	27.2 (23–31)
Relative humidity (%; ranges)		
morning	92–100	94–100
midday	60–98	78–100
evening	88–100	94–100
Days of recording	92	95
Days of rainfall	56	64
Rainfall days/recording days (%)	61	67

<sup>a</sup> Minimum and maximum recordings were collected during a 24-hour period. At the indicated elevations, thermometers were placed just above the ground beneath the canopy in primary forest. Intensity of rainfall ranged from sprinkles to rain falling day and night. Data are from Musser's field journals (stored in Mammalogy Archives, AMNH). Mean annual rainfall in both areas is about 3000 mm (Whitten et al., 1987: 25).

consecutive dry months dry months are the rainfall patterns for the drainage basin of Sungai Sadaunta, which places it in a "permanently humid" zone. Five to six consecutive wet months and three or fewer consecutive dry months are usual for Kuala Navusu on the eastern coastal plain, a "slightly seasonal" region (see Whitten et al., 1987: 22). Mean annual rainfall in both areas is about 3000 mm (Whitten et al., 1987: 25).

Examples of the forest habitats occupied by the shrew rats around Kuala Navusu are depicted in figures 14 and 15; images of streamside habitats along Sungai Sadaunta can be found in Musser (1982: 26–29).

Along Sungai Sadaunta and at Kuala Navusu, traps were placed on the ground, on top of decaying tree trunks lying on the forest floor, and above ground at different levels in the understory. Cage-type live traps, Sherman live traps (10 inch), Victor snap traps, Museum Special snap traps, and Conibear (single spring #110) body gripping traps were employed. In both areas, all *E. centrosa* were taken only with the Conibear traps set at ground level, two in runways along decaying tree trunks resting in hillside forest near a stream or wet ravine, 12 on decaying tree or palm trunks spanning

streams in dense streamside forest. Summaries of habitats at trapping sites are provided in table 12.

**DIET:** *Echiothrix centrosa* is an aggressive earthworm (oligochaete) predator. Earthworms form the primary component of its diet, but a variety of insects along with geophilomorph centipedes are also eaten (table 12). Musser determined the foods eaten by examining contents of stomachs (table 12) and offering different foods to a captive young adult male (AMNH 225682/ASE 3448) caught by the tail in a Conibear trap at Kuala Navusu on October 15, 1975 (table 13). The following descriptions of feeding behavior of the male are summarized from Musser's observations recorded at camp.

**Earthworms:** *Echiothrix* sports a unique set of adaptations for handling earthworms. The upper incisors are short, their anterior surfaces scored by shallow grooves, the cutting edges chisel shaped; the lower incisors are long and slender, with smooth faces and sharp tips. The connection between mandible and cranium is loose, and the dentary symphysis is flexible, which allows tips of the lower incisors to be spread apart up to 5–7 mm. When the mouth is open, the lower incisors curve upward from the lips, and

resemble two long, slender, and sharp-tipped miniature white tusks. Held close together (adducted), they form a stabbing lance; with the tips separated (abducted), they are transformed into either a two-pronged spear or a forcepslike gripping instrument. When the mouth is closed and the molars are occluded, tips of the lower incisors rest against the palate just behind the upper incisors. The loose articulation between mandible and cranium allows the rat to open its flexible mouth (gape is about 25 mm) and pull the mandible back and down, so lower incisor tips are 4 mm behind the uppers—it is the mandible that is retracted, not the lower lip, which remains in place. The rat can also launch the lower incisors forward beyond the lips; during all the times Musser watched the rat feeding, the lower lips appeared stationary and the lower incisors were propelled beyond the lips and then retracted into a sheathlike lip receptacle. This behavior and the feeding action described below were observed by Musser who offered the rat individual earthworms or arthropods by hand.

When the rat reaches for an earthworm, it thrusts the lower incisors beyond the lips and separates the tips (this is a purposeful action, as the incisors do not automatically separate as the mouth opens); the two incisor tips form a V. A thick earthworm is immobilized by the rat driving each sharp incisor tip into each side of the worm; a thin worm is held between the incisors in a forcepslike clamp. Whether impaled by the incisor spear or gripped by the incisor forceps, the earthworm is held against the upper incisors, with the uppers pressing down into the earthworm and against the lowers as the rat draws the earthworm up through its paws.

When offered an earthworm the rat quickly seizes it with its incisors and then clasps it between the front feet, pressing it against claws and digital pads of each foot. While clasping the worm between the digits and simultaneously holding it by the lower incisors, the rat jerks its own head upward in a series of rapid thrusts. The worm is hauled up through the digits, which are usually held stationary, and clasped so tightly that with each upward heave of the rat's head the earthworm is stretched and its gastrointestinal contents squeezed out and ejected onto

the ground. Sometimes the front feet are wrenched downward to squeeze the earthworm. In this manner the apparently distasteful gastrointestinal contents are removed and the earthworm, now a hollow tube of muscle and other tissue, is pulled up through the front feet and into the mouth. When a small worm was drawn toward the mouth, the lower incisors were opened and then closed lower on the worm's body; a larger worm required the rat to retract its incisors and then thrust them into the worm lower down on its body. Sometimes when very hungry, the rat seems to jab, pull, and suck the earthworm up quickly, then jab and tug again. Usually the bulk of the worm is pulled and swallowed this way and only when the worm tore apart did the rat stop to chew the last part that went into his mouth. Similarly, if the entire earthworm is sucked in without breaking, the rat chews only the last bit; when chewing, it retracts the lower incisors, so they either do not or barely project beyond the lips and upper incisors.

The rat seems to mostly swallow earthworms without chewing, especially the smaller ones; some medium-sized earthworms (8–10 cm long) were pulled apart and others were bitten into segments and then swallowed. There was minimal chewing. Smaller earthworms (4–6 cm) were grasped by the forcepslike clamp of the lower incisors and virtually inhaled without holding them between the front feet. The rat is so quick in acquiring an earthworm, and so swift in consuming it, that several feeding sessions in afternoon light were required before Musser was able to appreciate the process. Medium-sized and smaller earthworms were usually consumed in 1–9 seconds, 15 or 17 seconds at the most (see table 13).

The observed feeding action explains why earthworm segments found in stomachs are empty tubes, and why the front feet become covered with slime while the mouth remains relatively clean. In addition to remains of earthworms, contents of stomachs revealed a muddy fluid smelling of earthworms, partly resulting from the gastrointestinal residue of small earthworms that were swallowed intact and partly from the mucous and muddy liquid cleaned from the front feet after consuming a larger earthworm. *Echiothrix* does not wipe its front feet on the ground or



Fig. 14. Tropical lowland evergreen rain forest on terrace behind camp at Kuala Navusu, 38 m, the habitat of *Echiothrix centrosa*. A tall canopy *pohon benoa* (*Octomeles sumatrana*) on the right and subcanopy *Neolamarckia macrophylla* on the left bracket a dense understory of shrubs, tree saplings, ferns, young palms—mostly *Licuala celebica*, *Livistona rotundifolia*, and rattan rosettes of *Calamus* and *Daemonorops*—and a small clearing formed when a subcanopy ebony (*Diospyros macrophylla*) was uprooted during a storm. Photographed in 1975.

on leaves (the cleaning behavior typical of the Sulawesi shrew rat *Melasmothrix naso*) but cleans them with its tongue, swallowing the slime and muddy fluid. During one particular session, the rat was fed about 25 grams of medium-sized and small earthworms, and only after all were offered and eaten did he clean himself, shaking each front foot in the air several times, then licking one paw by holding the forearm with its opposite paw, and repeating the process on the other foot.

The behavior described above was observed when the rat was provided with medium-sized (8–10 cm long) and small (4–6 cm long) earthworms. Below are two examples of the rat's behavior when given larger worms. When Musser fed the rat an earthworm 15 cm long and 6 mm thick, the rat grabbed the worm, extended the lower

incisors 4–5 mm beyond the lips and separated the tips for about the same distance. He speared the worm from below while at the same time sinking his upper incisors in from above. He then manipulated the worm until one end was up and in the mouth. He proceeded as he usually did with smaller worms, but thrust the lower incisors deeper into the earthworm and held the tips farther apart so each tip penetrated a side of the worm; Musser could see the lower incisors penetrate the worm and the gut contents spurt out with each thrust. At times, the earthworm broke into segments as it was pulled up through the paws. The rat finished with a piece in his mouth and then quickly stabbed segments that had fallen to the cage floor, transferring each to his mouth. The lower incisors were actually thrust forward



Fig. 15. Tropical lowland evergreen rain forest on hillsides above rocky stream bed, Kuala Navusu, 38 m. During the night, *Echiothrix centrosa* (AMNH 225678; see table 12) and *Rattus hoffmanni* were caught upstream where a decaying tree trunk spanned the rocky creek bed; the squirrels *Prosciurillus alstoni* and *Rubricsiurus rubriventer* were taken during the day on the same spot. The rats *Maxomys hellwaldii* and *Paruromys dominator* were frequently trapped on this hillside forest as well as six other species of murines (see table 12). Photographed in 1975.

TABLE 12  
 Summary of Microhabitats in Primary Tropical Lowland Evergreen Rain Forest and Stomach Contents for Specimens of *Echiothrix centrosa* Collected in Central Sulawesi, 1974–1975

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and stomach contents
<b>Sungai Sadaunta</b> 225046 (2123) 225043 (2124)	994	Oct 1974	On decaying, wet, and moss-covered trunk (25 cm in diameter) of <i>wanga</i> palm ( <i>Pigafetta filaris</i> ) bridging stream; wet, mossy hillside forest cover steep slopes down to stream banks. <b>Stomach:</b> 225046 partially full, scarce remnants of earthworm tissue, two small geophilomorph centipedes, skin and tissues of small beetle larvae (one is a cursorial larva), fragments of small adult beetle, soft hairs from fur, many small pebbles, small woody fragments; 225043 mostly full of earthworm segments, also pieces of head capsule and sclerites from one beetle larva.
255047 (2319)	939	Nov. 1974	On huge (1 m diameter) rotten, wet tree trunk lying across upper headwater tributary of Sungai Sadaunta; trap 1.5 m above stream level. Trunk covered with moss; also supports small shrubs, rosettes of seedling palms, small green plants, orchids, and ferns—these plants cover trunk but not densely. Away from either side of the stream, steep banks choked with ferns, shrubs, rotting moss-covered trunks and limbs from old tree-falls, rise to forested terraces on either side. <i>Wanga</i> palms ( <i>Pigafetta filaris</i> ) and understory figs ( <i>Ficus</i> sp.) common along stream borders. <b>Stomach:</b> distended with thick wormy fluid and semidigested remains of many small earthworms; spinous hairs, overhairs, guard hairs (taken in during grooming); small pebbles.
225044 (2327)	985	Nov. 1974	On decaying, wet and smooth tree trunk lying across both banks of main headwater tributary of Sungai Sadaunta and 30 cm above water surface. <b>Stomach:</b> partially full, pieces of several small earthworms, a few rhinotermitid termite remains, and fragments of small adult beetle (pair of wings, legs).
225045 (2392)	805	Nov. 1974	On decaying tree limb spanning a channel of Sungai Sadaunta, 1.5 m off ground. Limb part of old tree-fall resting on terrace, and extends from top of boulders on terrace (1.5 m above stream) to opposite bank of stream where other remains of tree-fall form mound of decaying wood on stream bank. Area wet; shrubs, ferns form underbrush; <i>wanga</i> ( <i>Pigafetta filaris</i> ) dominant palm, understory figs ( <i>Ficus</i> spp.) common; ground muddy, partially concealed by leaf litter, dry beneath some rocks and wood piles. <b>Stomach:</b> partially full, wormy fluid, small chunks of one small semidigested earthworm, many fragments of rhinotermitid termites, many wings and sclerite fragments probably from small beetles; very small pebbles and woody debris.
226815 (4319)	939	Mar. 1976	On large (1 m diameter) decaying tree trunk 6 m long that lays from high terrace (3 m above water) down across stream at angle to other bank. Trunk densely covered with ferns, monocot shrubs, smaller plants that form good cover for rats using trunk to cross stream. <b>Stomach:</b> pieces of at least one small earthworm, possibly another, and remains of small adult beetle.
<b>Kuala Navusu</b> 225683 (3174)	38	Sept. 1975	On decaying large tree trunk (35 cm diameter) spanning wet ravine on terraced hillside in tall intact hillside forest. Caught the rats <i>Maxomys hellwaldii</i> and <i>Rattus hoffmanni</i> and the squirrel <i>Rubrisciurus rubriventer</i> nearby on same terrace. <b>Stomach:</b> nearly empty, a few spiny hairs (ingested during grooming), and muddy fluid containing tiny segments of semidigested earthworms.

TABLE 12  
(Continued)

Locality, AMNH and (ASE-field) numbers	Elevation (m)	Date	Trap site and stomach contents
225685 (3181)	55	Sept. 1975	On decaying tree limb (25 cm diameter) spanning steep tributary of main stream; the large limb is part of huge canopy tree that fell down hill in intact hillside forest, trunk still rests on hill providing path on which rats can run downslope. Caught rat <i>Paruromys dominator</i> on same spot. <b>Stomach:</b> full with wormy fluid and remains of one large and one small earthworm; also fragments of small adult beetle (legs, wings, elytra).
225684 (3333) 225679 (3505)	38	Oct. 1975	On decaying tree trunk (25 cm diameter) bridging stream and 1.5 m above water level. Slopes just above stream covered by short, dense partially scrubby forest, dense undergrowth; tall trees grow farther back from stream margins. <b>Stomach:</b> 225684 full of wormy fluid containing one large earthworm (15 cm long, 6 mm diameter), segments of another, and a small intact earthworm; stomach of 225679 distended with small earthworms, also fragments of small insects (wings and mouth parts), and a few spinous hairs (ingested during grooming).
225682 (3448)	122	Dec. 1975	In runway beneath rotting tree trunk lying on hillside above rocky ravine; runway 15 cm wide extending length of limb (4.5 m); parts of trunk covered with shrubs, leaf litter, and debris, so runway partially concealed. Understory dense, young fan palms ( <i>Livistona rotundifolia</i> ), the endemic palm <i>Licuala celebica</i> , species of rattan, and variety of shrubs; closed understory canopy with scattered tall trees nearby; ravine shaded, cool, moist, staying that way much longer than exposed higher slopes away from ravine. Caught <i>Maxomys hellwaldii</i> and <i>Bunomys andrewsi</i> in same spot. See table 11 for foods eaten during captivity.
225678 (3527)	38	Oct. 1975	On section of decaying tree trunk (20 cm diameter) spanning steep tributary of main stream. Caught the squirrels <i>Prosciurillus alstoni</i> and <i>Rubrisciurus rubriventer</i> on same spot on different dates during day and the rat <i>Rattus hoffmanni</i> at night. <b>Stomach:</b> full of earthworm remains along with fragments of cockroach nymph.
225681 (3600)	107	Nov. 1975	In runway (20 cm wide) along side of very rotten tree trunk (10 m long, 30 cm wide) lying downslope on steep hillside above stream. Good hillside forest, relatively dense understory, slopes densely covered with leaf litter and debris; undergrowth of shrubs, palm rosettes, tree seedlings, and saplings provide good ground cover. Trunk covered by shrubs, huge clumps of rattan. <b>Stomach:</b> full, mostly pieces of purple larvae from large beetles mixed with small beetle larvae, pieces of cockroach nymph, two segments of small earthworm, fragments of small geophilomorph centipedes, few fragments of rhinotermitid termites—predominately insects.
225680 (3653)	46	Nov. 1975	On slender section of tree trunk (8 m long, 15 cm diameter) spanning bend in main stream 1.5 m above rocky stream bottom. Good streamside forest; stream banks support dense cover of shrubs, ferns and small plants; tall trees and palms back on stream terraces provide dense canopy over the water. Caught the rat <i>Paruromys dominator</i> in same spot during a different night. <b>Stomach:</b> filled with segments of one large earthworm, skin fragments from an old earthworm meal; remains of rhinotermitid termites, and small unidentified insect larva.

from the lip sheath, the tips separated and driven into the body of the worm, like a two-pronged spear.

The second example shows the rat's reaction to an earthworm 23 cm long and 1 cm thick, which was consumed in 3.5 minutes; during the first 2 minutes he stopped eating at intervals and cleaned his front feet of sticky slime that was hindering manipulation and ingestion of the worm. The rat started at the head end by thrusting the separated lower incisors forward and spearing the worm, which was so thick that he had to spear it about three times, nearly severing the earthworm, and he separated the segment from the remaining body and ate it. Because the worm was long and thick bodied, the rat had to eat slowly and take in short segments, about 5 mm long. He seemed to have difficulty swallowing some of these segments, spitting them out onto the ground and breaking them apart with the incisors before picking up and ingesting the resultant fragments. Eventually he worked down the worm, gradually taking larger segments after he got past the thick middle; nearly all thrusts of the separated incisors (spread about 4 mm) through this thick part of the worm penetrated the body about 2 mm and either held the worm against the upper incisors while the rat pulled its head back and up, or were instantly retracted and thrust forward again until the worm was almost severed again and the segment pulled off the main body. Several times the rat moved the incisors up, retracted, thrust again, moved the worm up a bit, then thrust again and held the worm tight while the rat pulled its head back and up in rapid sequence. After the anterior third of the earthworm was consumed, the rest was eaten more quickly with the rat pulling and then cutting 5-cm segments; finally he slurped in the last 7 cm, leaving his front feet covered with muddy fluid and slime. A cord of gastrointestinal contents mimicking the shape of the worm was left lying on the leaf litter. By licking and shaking his front feet, he cleaned them of worm fluid and slime; this was followed by cleaning his lips, rhinarium, and finally face. The earthworm slime was viscous and thick, and the rat had to forcefully pull apart his feet several times because they kept sticking together.

We lack data about size of earthworms selected by the shrew rat during a night's foraging, but suspect that very large earthworms would be avoided, unless perhaps very hungry. Only remains of medium-sized (8–10 cm long) and small earthworms (4–6 cm long) were found in the stomachs surveyed, and those smaller worms are consumed more quickly (usually between 1 and 9 seconds) than very large worms that take minutes to eat, which would leave the rat exposed for a longer time to potential nocturnal predators.

*Bunomys chrysocomus*, *B. andrewsi*, and *Maxomys hellwaldii*, which occur in the same habitat as *Echiothrix centrosa* in the west-central highlands as well as the eastern coastal plain (see tables 15 and 16) include earthworms in their diets, but they are less efficient consumers. All three grab an earthworm with the incisors and quickly transfer it to the front feet where it is held in the same way as *Echiothrix* does. *Bunomys* and *Maxomys* do not pull the earthworm up through the front paws but bite and pull apart a segment (usually 1 cm long), chew it, then bite and pull off another segment until the earthworm is consumed. None of these rats squeeze the gastrointestinal contents out, but eat everything—the worm is writhing right up to the last few millimeters and the rat's front feet and muzzle are covered with the worm's stomach and intestinal contents (basically a thick muddy liquid) along with sticky mucous. Because *Echiothrix* squeezes the gastrointestinal contents out of the medium-sized earthworm, nothing is left but the hollow body—the last third or fourth of the earthworm appears lifeless, and only the rat's paws are covered with muddy fluid and slime.

Compared with *Echiothrix*, the two species of *Bunomys* and *Maxomys hellwaldii* take longer to consume earthworms. Earthworms averaging 5 cm long were consumed in 3 to 14 sec by captive *Bunomys chrysocomus*; earthworms 10 cm long were completely ingested after 57 to 145 sec. One *B. chrysocomus* took 5 min to eat a 15 cm long annelid that it first had to bite into several pieces. Medium-sized and small earthworms are consumed in 16–54 sec by *Bunomys andrewsi*, and in 17–42 sec by *Maxomys hellwaldii*. Earthworms of comparable size are usually

eaten in 9 sec or less by *Echiothrix centrosa* (table 13; data summarized from Musser's field journals). None of the *Bunomys* or *Maxomys* individuals observed swallowed the earthworm whole as *Echiothrix centrosa* did with small and some medium-sized earthworms, but bit off segments that were generally chewed and then ingested.

**Beetle (Coleoptera) larvae:** The shrew rat was offered a large beetle larva (12 cm  $\times$  1 cm), which he attacked quickly, thrusting the spread lower incisors into the thorax behind the head capsule and penetrating the tough skin. The rat then withdrew the incisors and ignored the grub. Musser retrieved it and found three places where the exoskeleton had been split by the splayed incisor tips. When the rat attacked a medium-sized earthworm he spread the lower incisor tips 2–4 mm apart but for something like the large grub, or very large earthworm, he opened the incisors wider and lunged with incisors thrust out and spread, moving very quickly.

A huge beetle larva (10 cm  $\times$  2 cm) was offered, which the rat tried to eat; he opened his mouth wide and got purchase on the larva but could not penetrate the tough skin, and after several attempts abandoned the grub. Musser retrieved the larva, cut it open and offered it to the rat. This time the rat used his lower incisors to scoop out the soft insides of the abdomen and left the head capsule, thorax, and tough abdominal skin on the cage floor.

All smaller beetle larvae (5 cm  $\times$  5 mm) offered were readily accepted and entirely consumed. Larvae of this size are not sucked up like the earthworms; rather the rat holds the larva between its front digits, bites into one end and pulls up, then chews, bites again, pulls its head up again and chews. He took longer to consume a beetle larva than to consume several medium-sized or large earthworms.

A large adult beetle was offered and the shrew rat attacked it as he had other adult insects, biting at the head and thorax; however, after several attempts he shied away from the beetle. His incisors made shallow dents in the sclerites of the thorax but nowhere else. Musser retrieved the insect and sliced open its thorax and abdomen and

again offered it to the shrew rat; this time he eagerly consumed the soft insides. Apparently the thickly sclerotized exoskeleton of large adult beetles is too hard to penetrate, and no such remains were found in stomachs of other *Echiothrix* examined.

**Other insects:** The rat was offered a small green cicada (Hemiptera: Cicadidae), which he first seized with the incisors and then transferred to his front feet, manipulating it until the head was up. He then bit the insect's head and proceeded to consume head, thorax, and abdomen—wings and legs were discarded (a behavior common to Sulawesi murines that prey on winged stages of insects). Two katydids (Orthoptera: Tettigoniidae) and two adult cockroaches (Blattodea) were attacked, handled and eaten in the same manner (table 13).

A mole cricket (Orthoptera: Gryllotalpidae) was offered to the rat, which he chased around the cage and eventually pinned to the cage floor with his front feet. He began eating the posterior end but the cricket easily crawled away. The shrew rat did not seem to know how to dispatch this particular cricket. However, later another mole cricket was offered, this one 6 cm long, which was attacked and finally eaten in 6.5 minutes.

**Snails:** Snails are consumed but probably infrequently and likely only small ones. Musser offered the shrew rat a snail 2.5 cm in diameter. He tried to break the shell by biting it but could only flake off a few pieces of the outer layer; then he attempted to bite off pieces near the opening but was unsuccessful and dropped the snail. After extracting the soft snail body, Musser offered it to the shrew rat but this was also ignored. The shrew rat did accept a small snail 10 mm in diameter and consumed the soft body extracted by Musser in 106 seconds. Of the other shrew rats Musser collected, none had remains of snails in their stomachs.

**Rejected foods:** Fruits from a variety of trees, shrubs, woody and herbaceous vines, palms, other plant parts, ferns, and several kinds of fungi were offered to the captive shrew rat but were always ignored; no evidence of these kinds of foods was found in the contents of stomachs.

**Yearly dietary regimen:** An aspect of understanding the complete range of foods



TABLE 13  
 Earthworms and Insects eaten by a Captive *Echiothrix centrosa*<sup>a</sup>

Date (1975)	Food and other information
Oct. 17	Ate 6 medium-sized earthworms early in evening, then a few more during the night.
18	Ate 2 large earthworms (12 cm long, 5 mm wide) and 8 medium-sized (8–10 cm long, 2–3 mm wide) at one feeding bout, 3 small earthworms (5–7 cm long) an hour later, and 4 small earthworms after another hour; sniffed around the empty cage floor for more.
19	Consumed 8 medium-sized earthworms at one feeding session.
20	Ate 12 medium-sized earthworms at one feeding; about an hour later unhesitatingly began eating a large beetle larva (6 cm long, 1.5 cm wide) consuming only the anterior half, but finished the other half later during the night.
21	Consumed 11 medium-sized earthworms at one feeding session; 1 small green cicada about an hour later; an hour after the cicada was consumed offered 2 beetle larvae (6 cm long by 8 mm wide), which were prodded for a while but eventually consumed (ate the softer insides of the larvae first and then bit off pieces of the exoskeleton and underlying tissue).
22	Ate 1 large earthworm and 18 medium-sized ones at first feeding, then 12 medium-sized earthworms about an hour later; offered tiny earthworms (4 cm long and 1 mm wide), ate one of the larger earthworms, picked up some of the others, manipulated them, but instead of ingesting any simply dropped them to the cage floor where they remained ignored. About half an hour later offered a katydid, but this was ignored.
23	Woke in the afternoon at 2 pm sniffing around, was then offered 2 beetle larvae (6 cm long and 8 mm wide; these have a purple body fluid and when squeezed the larvae turn deep purple), which the shrew rat consumed, eating everything; looked about the cage, then went back to sleep. About 6:30 P.M. offered a mole cricket, which the rat grabbed but was unsuccessful in eating (see text). Gave it a huge beetle larva (10 cm long and 2 cm wide), and the rat scooped out the soft insides of the abdomen (see text). A bit later he was offered a smaller beetle larva (5 cm long, 5 mm wide), which he ate readily and without problems. Afterward, the rat consumed 2 large earthworms and 20 small ones; then he cleaned himself and settled to a corner of the cage.
24	At 7:00 pm, fed the rat all the earthworms collected from a very wet decaying section of trunk that was half clay; 21 worms, 18 g worth; 6 were 18 cm long but narrow (1–3 mm), the rest were of medium size. Ate all 21, afterward ate 7 more medium-sized earthworms, which seemed to fill him because he had trouble swallowing the last worm as if esophagus and stomach were full. Rat took 19 sec to consume one large worm; times for 11 medium-sized worms were 5, 3, 15, 3, 3, 8, 5, 2, 3, 17, and 3 sec.
25	At 2:00 pm, fed the shrew rat 2 adult cockroaches (each 2.5 cm long), one was fully consumed (except for wings and legs) in 30 sec, the other in 59 sec; 1 beetle larva 3.5 cm long was eaten in 42 sec; 1 large beetle larva 5 cm long was consumed in 5 min; a small snail (10 mm in diameter) eaten in 106 sec; and 1 mole cricket 6.5 cm long was eaten in 6.5 min. Later during the night fed him 13 g of earthworms with the following individual feeding times: 9, 4, 25 (trouble swallowing because worm became stuck between lower incisors), 3, 4, 2, 5, 2, 5, 3, 2, 2, and 3 sec.
26	During the night offered several earthworms and after they were consumed offered a large adult beetle, which he was unsuccessful at capturing (see text). Later fed the rat two katydids, which he unhesitatingly attacked and consumed.
27	Ate 1 beetle larva 40 mm long and one 20 mm long; offered an adult cockroach 4 cm long that was ignored. Then he ate 18 g of medium-sized earthworms. Later offered a snail 2 cm in diameter, which was ignored (see text).
28	Ate 11 medium-sized earthworms (3, 1, 9, 9, 5, 3, 8, 6, 3, 5, 6 sec) and one very large earthworm (145 sec).
29	Ate 2 beetle larvae (each 4 cm long and 7 mm wide)—time 78 and 120 sec. Then consumed 7 earthworms (12, 18, 5, 7, 7, 3, and 9 sec).
30	Ate a few earthworms and small beetle larvae (a meager offering because Musser was running out of food to offer the rat).
31	In the afternoon gave the rat 25 g of large to medium-sized earthworms; ate all but one medium-sized worm and left it on the cage floor—he was clearly satisfied.
Nov. 1	Offered 2 beetle larvae 2 cm long and three larvae 4 cm long, all were quickly consumed; afterwards the rat ate several medium-sized earthworms and a very large earthworm that took him 3.5 min to consume (see text)

<sup>a</sup> Data from a young adult male (AMNH 225682/ASE 3448) caught at Kuala Navusu during October, 1975. Information summarized from Musser's field journals (stored in Mammalogy Archives, AMNH).

consumed by a species is any seasonal variation in dietary composition during a yearly cycle. Stomach contents from Musser's collection of *E. centrosa*, consisting of adult males and females, obtained during a period of seven months (September to March) suggests that throughout most of a year, and probably the full 12-month cycle, earthworms form the predominant prey as compared with insects and other invertebrates. This is a reasonable hypothesis springing from available data, but requires testing by study of food preferences during an entire year derived from larger samples of shrew rats living throughout a more expansive geographic region of Sulawesi. Such an inquiry should also determine the dietary composition of postweaning juvenile shrew rats to determine the relative percentages of earthworms versus insects or other invertebrates in their diets, along with size of the prey.

Earthworms should be accessible to shrew rats year-round in the Sungai Sadaunta watershed and along the coastal plain that encompasses Kuala Navusu. Neither region is typified by strongly seasonal rainfall patterns (Whitten et al., 1987: 21 note that the "climate of Sulawesi is best described with reference to rainfall since temperature is relatively constant [table 11], and other climatic variables such as wind velocity, evaporation and humidity change within even small areas"). Ten to 12 consecutive wet months and up to two dry months are the rainfall patterns for the drainage basin of Sungai Sadaunta, which places it in a "permanently humid" zone (Whitten et al., 1987: 22). Kuala Navusu is located in a "slightly seasonal" region where generally five or six consecutive months are wet and three consecutive months or less are dry (Whitten et al., 1987: 22). During the 57-day period in which the rats were captured along Sungai Sadaunta, there were 23 days without rain or with only sprinkles; rainfall during 34 of the days averaged 35.2 mm with a range of 1–175 mm. At Kuala Navusu where examples of *E. centrosa* were caught during a 45-day period, there were 19 days with no rain or sprinkles only; rainfall during 26 of the days averaged 38.2 mm with a range of 1–230 mm. October is usually the driest month

in both areas (Musser's experience, and assertions by the local people). Even during the relatively driest interval, earthworms were available as prey for *E. centrosa* for they were found in stomachs of rats trapped during that period, and Musser collected samples of earthworms from different parts of the forest (see below).

**Prey distribution in the forest:** Although *Echiothrix centrosa* (and presumably *E. leucura*) preys primarily on earthworms, soft-bodied coleopteran larvae are also taken, as well as other kinds of insects (mole crickets, katydids, cockroaches, and rhinotermitid termites were either found in contents of stomachs or accepted and consumed by the captive shrew rat), and geophilomorph centipedes. Near camp on the Kuala Navusu (August 28–November 30, 1975), Musser searched for places on the forest floor where *Echiothrix centrosa* might find invertebrates, particularly earthworms, and during the night after a rain located earthworms scattered on the clear ground surface, beneath leaf litter, or in pools of water near the stream. During the day he found them in rotting sections of tree trunks and limbs or in the underlying soil. He also found burrows, each marked by a pile of processed soil, some as tall as 5 cm. Several small worms occupied a single burrow and were found 5–15 cm below the ground surface. Burrows were always on well-drained slopes or stream terraces. Because the earthworms are spotty in their distribution, it is difficult to provide any meaningful estimate of worms available to *E. centrosa* per unit area. Musser did find one place on a steep hillside above a wet ravine where a piece of wood had decayed into slivers. The soil was stable. He collected 21 earthworms (8 grams total) within a square meter; all occurred throughout the soil from near the surface to a depth of 15 cm.

The most common site for both large and small earthworms was within and beneath rotting trunks and limbs from old tree falls. At a certain stage of decomposition the wood becomes soft and is mixed at soil level with a dense gray or bluish-gray claylike layer; the worms are in this layer, and in passages within the damp and rotting pulpy wood.

In addition to earthworms, decaying sections of old tree falls lying on the forest floor

also provide habitat for a variety of other invertebrates, some of which are eaten by *E. centrosa*. Musser tore apart a long section of rotting trunk (5 m long, 30 cm in diameter) lying on a terrace about 3 m above a stream. The pulpy wood was saturated with water and the underlying claylike layer nearly liquefied. Pigs had ripped open the trunk in places. Musser extracted 30 grams of invertebrates (excluding termites—the terrestrial rhinotermitid termites, which infested the entire trunk and were too numerous to collect and weigh): 21 earthworms (some large, up to 13 cm long, most were smaller, 5–8 cm), three mole crickets, and six adult and nymphal cockroaches.

**Prey procurement:** Musser observed only captive *Echiothrix* held in a cage. While he did not see shrew rats at night searching for food in the forest, some inferences regarding behavior in procuring prey can be made based on the physique of the shrew rat. *Echiothrix* has a long muzzle, very large ears, a tail that is longer than combined head and body, delicate front legs with small feet and moderately large and stout claws, and strong hind legs with elongate and robust hind feet (fig. 4). The long muzzle reflects the underlying long and narrow bony rostrum containing extended turbinals, likely well suited for probing in loose leaf litter and sniffing out earthworms. Large ears may also help detect scraping movement of prey as they move through and beneath decaying leaves on the forest floor. The front claws are not as large relative to body size and don't seem to be as adapted for digging as those seen in species of either *Melasmothrix* and *Tateomys* (Musser, 1982) or *Paucidentomys* (Esselstyn et al., 2012), the other Sulawesi shrew rats; the claws of *Echiothrix* are stout and appear sufficiently robust to excavate earthworms from moist subsurface soil layers and to dig into old tree falls lying on the forest floor where the wet wood has decayed to a soft and spongy texture. One female *E. centrosa*, caught in a Conibear trap set on a decaying limb bridging the Sungai Sadaunta, had soil and debris matted on the fur beneath the chin and on parts of the front legs. In addition to excavating earthworms, we can imagine the rat separating loose leaf litter and other debris on the forest floor with its muzzle

and front feet, and pouncing on the uncovered earthworms and small arthropods, sometimes inadvertently ingesting small pebbles and woody fragments (found in some stomachs). Should a predator approach, its presence might be picked up by the large ears and escape accomplished by the rat instantly leaping away in unpredicted directions.

**MISCELLANEOUS BEHAVIOR:** When the shrew rat sits, resting or during feeding, its body rests on the entire lengths of the hind feet, the rump about 5 mm off the ground and the tail lying stretched out behind, so the weight is on the hind feet and an appreciable length of the tail. It stands and moves about only on its digits and interdigital pads.

The captive rat was quiet most of the time. When he vocalized he never squealed or screamed but emitted a rusty eh-eh-eh-eh with a slight warbling quality.

**SPINOUS FUR:** Function of the spinous dorsal pelage of *E. centrosa* (and *E. leucura*) is unknown. It is unlikely that predators are deterred by the spines because the long and broad spines are flexible, and the dorsal coat is unlike the bristly and rigid spiny fur of porcupines and hedgehogs. Furthermore, Musser never saw the captive shrew rat erect the hairs of the dorsal coat, even when disturbed. Avian predators, presumably owls because the shrew rats are nocturnal, would simply use their talons to seize the shrew rats, then fly to their roosts and pick the rats apart with their sharp beak, avoiding the spinous hairs. The endemic Sulawesi palm civet, *Macrogalidia musschenbroekii*, which Musser encountered on his transects, is an agile and aggressive predator and could stalk and capture a shrew rat, crunching it between the jaws without hindrance from the spinous fur (the other viverrid occurring on Sulawesi, the nonnative *Viverricula indica*, is a bumbling and inept rodent predator judged from Musser's observations). Nocturnal snakes are the other kind of predators, and by manipulating the shrew rat so the head is swallowed first and the fur laid back against the skin they can swallow a rat without any resistance from the flexible spines in the coat.

One possible function of spinous fur was suggested to Musser by Joe T. Marshall, who trapped rodents throughout Thailand. He

thought the spinous hairs would trap drops of water coming off wet vegetation, misty air, or rain and suspend them long enough for the rat to shake the drops from the fur before they wet the skin. In tropical lowland habitats where ambient temperatures and relative humidity are high (table 11), drying fur would be problematic for nonamphibious species if the fur became soaked to the skin. At the prompting of David Johnson, formerly a curator in the Mammal Division at USNM, Marshall sprinkled two Thai spinous-furred *Maxomys surifer* and two soft-furred *Rattus rattus*. The broad and flat flexible spines in the dorsal coat of *M. surifer* are channeled with the concave surface facing dorsally on the back. Marshall's (1988: 402) observations are worth repeating:

The two *M. surifer* shook themselves periodically and remained reasonably dry, whereas the two *R. rattus* stayed still and soon became waterlogged. In shaking, a spiny rat ... starts at the nose, and a spasm of spiral shaking at right angles to the backbone proceeds rapidly rearward to the rump. The possession of concave spines plus the habit of shaking them seems to be a device for keeping the animal dry during a rain storm. The broad spines catch the drops so that they can be shaken off all at once.

To test Marshall's observations, Musser sprinkled a caged *Echiothrix centrosa* and a *Margaretamys beccarii*; the latter is a small-bodied arboreal rat with spinous dorsal pelage very similar in texture to the fur of *Echiothrix* (Musser, 1981). The shrew rat did not shake its fur but simply ran from the water source and covered in a corner of the cage. The *Margaretamys* shook its body in a fashion similar to the motion described by Marshall for *Maxomys surifer*. As the water hit the fur of both the *Echiothrix* and *Margaretamys*, it collected into drops held by surface tension to tips and channeled surfaces of the broad spines and tips of the soft overhairs and guard hairs. The drops remained attached for a minute or so before breaking up and running down the hairs to wet the underfur and skin. The drops were flung off the fur when the *Margaretamys* shook its body, and had the shrew rat not been so timid it would have shaken off the drops in a similar manner.

When Musser sprinkled soft fur, such as that covering species of *Bunomys* held in cages, the water also collected as drops at the tips of the hairs. Droplets quickly coalesced into large drops, which sank deeper into the fur, still adhering to the hairs without falling to the skin, but soon flowed downward to wet the skin; none of the *Bunomys* shook themselves and their fur would have become soaked had Musser continued sprinkling them. So, with both small and large drops, the rat can remain relatively dry by shaking the drops off shortly after they hit the fur; if the rat waits too long the water sinks to the skin.

It is important that rats keep their fur dry. Droplets from mist and dripping vegetation that fall on the fur can be shaken off with the fur retaining its insulation qualities. The fur would become soaked should rats fall into a stream or have to run through shallow pools. In the ambient environments along the Sungai Sadaunta and at Kuala Navusu where temperatures and relative humidity are high (table 11), it would be difficult for the animals to dry their pelage, thus impairing the insulative quality of the coat and possibly producing deleterious changes in body temperature; also time required to dry and groom the fur would impose on time necessary for foraging. Some soft-furred rats that Musser trapped in cage live traps, such as *Bunomys chrysocomus* were soaked because the trap had been placed too close to the spray from waterfalls, or the rat had knocked the trap into a stream, or the trap was unprotected from a night's rain. Back at camp, the animals made no attempt to dry their fur; by day's end, the coat was partially dry from evaporation and despite the rat's attempts to fluff out the fur, it remained matted and difficult to groom; some animals did not recover their health. This was the typical reaction observed for most of the soaked soft-furred species trapped alive.

Whether one function of a dorsal spinous coat is to deter accumulation of water is an aspect that requires more rigorous inquiry. However, the reaction of the rats to being sprinkled or soaked bears on results from setting traps on decaying tree trunks and limbs spanning streams and ravines, highlighting the importance of these pathways

TABLE 14  
**Dates of Collection, Sex and Age, Physical Size, Reproductive Aspects and Pelage Condition of Adult *Echiothrix centrosa* Collected at Sungai Sadaunta and Kuala Navusu**

Measurements are in millimeters, weight in grams. Measurements of testes (T) include the epididymis and are from the fluid-preserved carcasses and intact specimens. All females have two pairs of inguinal teats. Information is extracted from specimens and Musser's field journals (stored in Mammalogy Archives, AMNH).

Locality, Specimen (AMNH)	Date	Sex and age	Physical size					Reproductive aspects and pelage	T/LHB (%)
			LHB	LT	LHF	LE	WT		
<b>Sungai Sadaunta (1974)</b>									
225046	Oct. 4	♂ Adult	213	247	53	33	235	Testes large and scrotal, 45 mm long; full adult pelage.	21
225043	Oct. 5	♂ Adult	216	246	55	36	270	Testes large and scrotal, 48 mm long; full adult pelage.	22
225047	Nov. 6	♀ Young adult	219	241	54	35	225	Teats small, not lactating; full adult pelage.	—
225044	Nov. 7	♂ Adult	215	240	53	34	225	Testes large and scrotal, 41 mm long; full adult pelage.	19
225045	Nov. 30	♀ Adult	210	230	50	35	215	Teats large, lactating; in full adult pelage.	—
226815	Mar. 17 (1976)	♂ Old adult	215	243	54	36	255	Testes large and scrotal, 45 mm long, sperm in epididymis; in full adult pelage.	21
<b>Kuala Navusu (1975)</b>									
225683	Sept. 12	♀ Adult	221	245	52	34	275	Left uterine horn with 3 embryos (each 10 mm long), right horn with 6 scars, teats large, lactating; full adult pelage.	—
225685	Sept. 13	♀ Adult	221	241	53	34	293	Teats large but not lactating; vagina closed; molting on head, neck and along sides of body and parts of back.	—
225679	Oct. 24	♀ Young adult	208	247	52	33	248	Teats tiny, white bumps barely visible on skin; vagina sealed; full adult pelage.	—
225684	Oct. 2	♂ Old adult	225	258	53	33	310	Testes large and scrotal, 46 mm long, copious sperm in epididymis; molting in broad mottled pattern from eyes over top of head and body to rump.	20
225682	Oct. 15	♂ Young adult	197	—	53	33	—	Testes tiny and abdominal; full adult pelage.	—
225678	Oct. 28	♂ Adult	213	253	53	32	235	Testes large and scrotal, 35 mm long, few sperm in epididymis; full adult pelage except for small patches in front of eyes and on thighs.	16

TABLE 14  
(Continued)

Locality, Specimen (AMNH)	Date	Sex and age	Physical size					Reproductive aspects and pelage	T/LHB (%)
			LHB	LT	LHF	LE	WT		
225681	Nov 7	♂	219	242	51	34	290	Testes large and scrotal, 50 mm long, sperm in epididymis; full adult pelage.	23
225680	Nov 12	♂ Young adult	200	235	52	33	220	Testes small and abdominal; full adult pelage except for patch on top of muzzle.	—

over natural bridges for rats. In the regions where Musser worked, heavy rains cause streams and rivers to rise, often to the level of flooding their banks, and filling hillside ravines that are normally dry. Tree and palm trunks or tree limbs extending from one stream terrace to the other that are resting on terraces high enough to escape inundation from runoff provide reliable crossing points for rats, woody connections allowing them quick access to the forest on the other side without becoming soaked. At times of low water, rats may use crossing places where they can scramble across on exposed stones or decaying pieces of a tree fall scattered on the stream bed, but during flood the higher links formed by downed trunks and limbs are safer. All six of the shrew rats caught along the Sungai Sadaunta were taken on tree or palm trunks or limbs connecting opposite stream terraces; six of the eight *E. centrosa* caught at Kuala Navusu were also trapped on similar kinds of bridges over streams and wet ravines (table 12). Examples of the majority of the species of murines caught along Sungai Sadaunta and at Kuala Navusu (tables 15, 16) were also trapped on decaying sections of tree falls spanning streams and ravines (Musser's field journals).

**REPRODUCTIVE INSIGHTS:** The six examples of *E. centrosa* from Sungai Sadaunta and the eight from Kuala Navusu that Musser collected consist of old adults, adults, and young adults; most were obtained during September, October, and November. The old adults and adults were sexually mature (females with large teats, either lactating or not, and containing embryos; males with large scrotal testes and sperm in the epididymis), and the young adults sexually immature (females with tiny teats, vagina sealed; males with small abdominal testes). All the specimens from Sungai Sadaunta and Kuala Navusu are listed in table 14 and provide examples of general reproductive status in relation to body size, pelage condition, and date of collection.

Presumed litter size is documented by only one female (AMNH 225683) caught September 12, 1975, at Kuala Navusu, which had three embryos (each 10 mm long) in the left horn of the uterus (table 13); gestation period is unknown.

Although the period of time during which the rats were collected is short (September to November, one record in March) and the sample size of animals small (14), the data indicate that adults are reproductively active from September to November and likely through to March.

Whether mating activity and birth is year-round or seasonal cannot be determined with the present information, but possibly shrew rats become sexually mature and bear young throughout the year. Neither the west-central highlands containing the watershed of Sungai Sadaunta nor the coastal plain to the east at Kuala Navusu are typified by strongly seasonal rainfall patterns (see preceding section); it is unlikely that nesting sites and prey resources are available during the entire year.

**NESTS:** Unfortunately, Musser was unable to locate nesting sites in the forest. Observations on nest construction are based on a captive young adult male collected at Kuala Navusu. The rat was provided with a fresh pile of dry leaves into which he burrowed and slept. Eventually as the leaves compressed, the rat arranged them about him in a loosely constructed partial sphere; after the leaves were compressed even more, he slept on top of the mound in a shallow round depression and did not attempt to build a high enclosure even though there were plenty of leaves scattered on the cage floor. Only when Musser gathered all the leaves and piled them in a corner did the rat burrow into them rather than sleeping on top.

**SYMPATRY:** *Echiothrix centrosa* shares its forest habitat with other species of murines that are also endemic to Sulawesi. Along with *E. centrosa*, samples of 15 other species were collected in streamside and hillside forests along Sungai Sadaunta (table 15); samples of nine species were collected in addition to *E. centrosa* in the Kuala Navusu area (table 16). Many were taken in the same traplines that yielded *E. centrosa*.

Our understanding of the ecological interactions between *E. centrosa* and the other species is limited to the observational data listed in the categories (elevation, terrestrial or arboreal, number of teats, litter size, and diet) presented in tables 15 and 16. One interactive aspect that is of special interest

is the possible resource competition between *E. centrosa* and the other murines that also include earthworms in their diet. In the forests along the Sungai Sadaunta, the terrestrial and nocturnal *Bunomys chrysocomus*, *Bunomys andrewsi*, *Maxomys hellwaldii*, and *Maxomys dollmani* devour earthworms, although they comprise only one element in each of their diets (table 15). Of these species, *B. chrysocomus* was the most frequently collected (43% of the total specimens representing all species), samples of the four species combined make up 52% of the murines trapped (table 15). At Kuala Navusu, *Maxomys hellwaldii* and *Bunomys andrewsi* are the only potential vermivorous competitors with *E. centrosa*; the former was common and easily caught (69% of the total sample of all species), the latter less so (5%). At both Sungai Sadaunta and Kuala Navusu, *E. centrosa* constituted less than 2% of all specimens collected.

Judged by relative numbers of each species trapped, the anecdotal evidence suggests that along the Sungai Sadaunta, *Bunomys chrysocomus* would be the most important earthworm competitor with *Echiothrix centrosa*. This potential competition is strengthened because both species were trapped in environments that remain wet and humid—streamside habitats and at the bottom of hillsides adjacent to streams—and not on steep slopes and ridgetops that tend to dry out sooner than streamside environs.

*Maxomys hellwaldii* is the obvious competitor with *Echiothrix centrosa* for earthworms at Kuala Navusu. Here the competition may not be as potentially intense. *Maxomys hellwaldii* was trapped in a range of habitats, from streamside to ridgetops; *E. leucura* was taken only in streamside environments.

At both places, these observations need to be bolstered by more rigorous study of relative dietary composition over the course of a 12-month cycle or longer that incorporates both dry and wet periods before any significant conclusions regarding competition among these earthworm-eating rodents can be drawn. Some questions that require answers come to mind. What percent of the diet of *B. chrysocomus* and *M. hellwaldii* consists of earthworms compared with the

dietary components of *E. centrosa*? Are earthworms taken during both wet and dry periods throughout a year by *M. hellwaldii* and *B. chrysocomus* or do other foods comprise the bulk of their diets during certain months? Are there certain times of the year when *E. centrosa* consumes fewer earthworms and more insects and other invertebrates? What is the availability of earthworms and other invertebrates, and their respective mass for consumption, in streamside habitats during a 12-month cycle or longer? Do postweaning juveniles have the same dietary range as adults during a given surveyed period of months (the data we discuss are obtained from adults)?

Another aspect requiring investigation is the abundance of *Echiothrix centrosa* relative to the other earthworm consumers along Sungai Sadaunta and at Kuala Navusu, especially the more abundant *Bunomys chrysocomus* and *Maxomys hellwaldii*. Examples of those two species were readily caught by live traps and kill traps (a cage-type live trap, 10 inch Sherman live traps, Victor and Museum Special snap traps, and Conibear traps), but only the Conibears took *E. centrosa*. Musser baited all the traps with a mixture of oatmeal, raisins, bacon, and peanut butter. Earthworms were used as bait for a few nights, but they attracted more *B. chrysocomus* and *M. hellwaldii* and, during the early morning, birds. Whether the relatively low densities we record for *E. centrosa* at both localities is real or an artifact of trapping technique is unknown. Any future study of competition between *E. centrosa* and other syntopic murine earthworm consumers will have to include firm data on relative densities of these vermivore predators.

#### SOME MORPHOLOGICAL ADAPTATIONS FOR VERMIVORY

In the previous sections, we have described various anatomical characteristics of the two species of *Echiothrix*. Some of these are related to acquiring and processing a specialized diet consisting mostly of earthworms, and behavioral aspects of seizing and ingesting that particular kind of prey were discussed in Natural History Particulars of *Echiothrix centrosa*. Here we extract some

of those anatomical systems and briefly explain why they appear to be significant adaptations for a vermivorous diet, at least in *Echiothrix*.

**SKULL:** General conformation of the cranium behind the rostrum is not unlike other murines: the interorbital region is moderately wide, the zygomatic arches are robust and flare out from the sides of the cranium, the zygomatic plate is moderately wide with a narrow anterior spine (shallow zygomatic notch), and the boxy braincase is wide and deep (see figs. 5 and 6 and cranial portrayals of various species in Musser and Newcomb, 1983) showing expansive surfaces for origin of the temporal musculature.

The notable specializations in the skull involve the rostrum and pterygoid region. The very long, slim, and tapered rostrum is distinctive and encloses long sets of turbinals covered in nasal mucosa. This extended surface of epithelium likely enhances olfactory sensitivity that may be required to distinguish the scent of earthworms from ambient background odors redolent in the strong vegetative and earthy fragrances emanating from wet and decaying leaves, rotting tree falls, wet moss, and soil. Also, Samuels (2009: 880) has suggested that rostral elongation "increases the velocity of closing the mouth, which facilitates the capture of prey."

Morphology of the pterygoid region of *Echiothrix* is extremely simplified. As we have described previously (see description of *E. leucura*), the pterygoid plates no longer exist as significant structures and are represented by only inconspicuous vestiges (see figs. 7 and 8). This transformation from the common design likely includes modification of the pterygoid musculature.

We have not dissected musculature in the pterygoid region and do not know whether those muscle groups would show changes from the usual murine condition that might be correlated with loss of the typical horizontal and wide pterygoid plates. Still, it is productive to conjecture on possible modifications of the relevant muscle groups, speculations that can be tested by actual dissection. Two primary muscles, the external and internal pterygoids, originate from the pterygoid-alisphenoid region of muroid rodents



TABLE 15  
***Echiothrix centrosa* and 15 Sympatric Species of Murines Collected in Primary Lowland Tropical Evergreen Rain Forest at Sungai Sadaunta in the West-Central Highlands (1973–1976)**  
 Information was gathered during 1973–1976 and is summarized from Musser's field journals (stored in Mammalogy Archives, AMNH).

Species	N (total = 463)	N/463 (%)	Elevational range of collection sites (m)		Arboreal- Terrestrial		Test formula	Litter size	Diet
			Terrestrial	Arboreal- Terrestrial					
<b><i>Echiothrix centrosa</i></b>	<b>6</b>	<b>1.3</b>	<b>803–985</b>	+	—	<b>0 + 2 = 4</b>	<b>3</b>	<b>Primarily earthworms, some arthropods</b>	
<i>Margaretomys beccarii</i>	12	2.6	600–675	—	+	1 + 2 = 6	2	Fruit, arthropods, snails, small vertebrates	
<i>Taeromys callitrichus</i>	2	0.4	884–915	+	—	1 + 2 = 6	1	Fruit, ferns	
<i>Taeromys celebensis</i>	8	1.7	675–1006	—	+	1 + 2 = 6	2–3	Fruit	
<i>Maxomys dollmani</i>	8	1.7	854–1006	+	—	2 + 2 = 8	?	Fruit, arthropods, snails, earthworms, small vertebrates	
<i>Maxomys helwaldtii</i> <sup>1</sup>	47	10.2	675–1006	+	—	1 + 2 = 6	2–4	Fruit, arthropods, snails, earthworms, small vertebrates	
<i>Maxomys muschenbroekii</i> <sup>1</sup>	13	2.8	675–960	+	—	2 + 2 = 8	?	Fruit, insects	
<i>Rattus hoffmanni</i>	43	9.3	675–1068	+	—	1 + 3 = 8	4–5	Fruit	
<i>Rattus facetus</i>	50	10.8	457–1006	—	+	1 + 2 = 6	1–3	Fruit	
<i>Paruromys dominator</i>	51	11.0	675–1067	—	+	1 + 2 = 6	2–5	Fruit	
<i>Crunomys celebensis</i>	1	0.2	824	+	—	2 + 2 = 8	?	Insects	
<i>Haeromys minahassae</i>	2	0.4	924–1000	—	+	1 + 2 = 6	2	Fruit	
<i>Lenomys meyeri</i>	2	0.4	915	+	—	0 + 2 = 4	1	Fruit, forbs, leaves, ferns, insects	
<i>Bunomys chirysocomus</i>	199	43.0	675–1037	+	—	0 + 2 = 4	1–2	Fruit, arthropods, snails, earthworms, small vertebrates	
<i>Bunomys</i> , n. sp.	17	3.7	823–1006	+	—	0 + 2 = 4	1–2	Mostly fungi	
<i>Bunomys andrewsi</i>	2	0.4	675	+	—	0 + 2 = 4	1–2	Fruit, arthropods, snails, earthworms, small vertebrates	

<sup>1</sup> These are provisional determinations as listed here and in table 16. Whether the samples represent true *Maxomys helwaldtii* and *M. muschenbroekii*, with type localities in the northeastern end of the northern peninsula (east of the Gorontalo region), or are from different reproductively isolated lineages, has yet to be assessed (see Achmadi et al., 2013).

TABLE 16  
*Echiothrix centrosa* and the Nine Sympatric Species of Murines Collected in Primary Lowland Tropical Evergreen Rain Forest at Kuala Navasu in the Coastal Lowlands East of The West-Central Highlands  
 Information was gathered during 1975 and is summarized from Musser's field journals (stored in Mammalogy Archives, AMNH).

Species	N (total = 435)	N/435 (%)	Elevational range of collection sites (m)		Terrestrial	Arboreal- Terrestrial		Teat formula	litter size	Diet
			30-122	43-122		+	+			
<i>Echiothrix centrosa</i>	8	1.8	30-122	43-122	+	—	0 + 2 = 4	3	Primarily earthworms, some arthropods	
<i>Margaretomys beccarii</i>	4	0.9	43-122	61-152	—	+	1 + 2 = 6	2	Fruit, arthropods, snails, vertebrates	
<i>Taeromys celebensis</i>	3	0.7	61-152	30-300	—	+	1 + 2 = 6	2-3	Fruit	
<i>Maxomys helwaldi</i>	300	69.0	30-300	122	+	—	1 + 2 = 6	2-4	Fruit, arthropods, snails, earthworms, small vertebrates	
<i>Maxomys muschenbroekii</i>	1	0.2	122	30-214	+	—	2 + 2 = 8	?	Fruit, insects	
<i>Rattus hoffmanni</i>	18	4.1	30-214	122-152	+	—	1 + 3 = 8	4-5	Fruit	
<i>Rattus facetus</i>	3	0.7	122-152	30-300	—	+	1 + 2 = 6	1-3	Fruit	
<i>Paruromys dominator</i>	68	15.6	30-300	76-152	—	+	1 + 2 = 6	2-5	Fruit	
<i>Haeromys minahassae</i>	9	2.1	76-152	30-122	—	+	1 + 2 = 6	2	Fruit	
<i>Bunomys andrewsi</i>	21	4.8	30-122		+	—	0 + 2 = 4	1-2	Fruit, arthropods, snails, earthworms, small vertebrates	

(Greene, 1935; Rinker and Hooper, 1950; Rinker, 1954; Turnbull, 1970; Voss, 1988; Satoh, 1997; Satoh and Iwaku, 2004, 2006, 2008).

The external pterygoid muscle (*M. pterygoideus externus*) originates from the lateral surface of the anterior third of the pterygoid plate, from the adjacent surface of the alisphenoid bone anterior to the groove for the masticatory-buccinator nerves, and from the segment of the maxillary just behind the molar row; it inserts on the medial surface of the articular (condyloid) process of the dentary (origin and insertion is nicely visualized in fig. 6 in Thorington and Darrow [1996, as the "lateral pterygoid"] and in figs. 10 and 11 in Satoh and Iwaku [2004]; also see Turnbull, 1970: 231). Acting together, the external pterygoids protract the mandible—depressing the lower jaw in the case of *Echiothrix*, and launching the incisors forward to either spear an earthworm or grip it in the forcepslike V of the incisor tips. In the shrew rat, the bulk of this muscle may originate mostly on the broad alisphenoid and bit of maxillary just behind the third molar because the anterior lateral margins of a pterygoid plate are represented only by vestigial ridgelike bony slivers; between origin on the alisphenoid and portion of the maxillary, possibly with some fibers on the vestigial pterygoid margins, and insertion on the robust condyloid process, the muscle's action may be only moderately suppressed over what it would be in a murine showing the usual pterygoid configuration, such as seen in *Maxomys* (figs 7D, 8D), *Onychomys*, (Satoh and Iwaku, 2006), or *Rattus* (Turnbull, 1970), for example. Retaining substantial external pterygoid muscles would be critical for *Echiothrix's* ability to depress the mandible and extend it forward so the long, slender, and sharp-tipped incisors can be thrust beyond the tips of the upper incisors. The mylohyoid group of muscles, especially the digastric complex, would join the external pterygoids in depressing the mandible (open the jaw) and would also act to retract it.

The internal pterygoid muscle (*M. pterygoideus internus*) originates from the pterygoid fossa (which is the ventral surface of the pterygoid plate, usually excavated to some degree) and inserts on the medial surface of

the angular process and dorsal surface of its inflected ventral border (see fig. 6 in Thorington and Darrow [1996, identified as “medial pterygoid”], figs. 10 and 11 in Satoh and Iwaku [2004], fig. 12 in Satoh and Iwaku [2006], and p. 231 in Turnbull [1970] where origin and insertion is diagrammed). Acting together and in concert with the temporal and masseter muscles, the internal pterygoids elevate the mandible (close the jaw); acting alternately they pull the mandible from side to side; and overall assist in mastication.

Landry (1970: 363) has coined the name “mandibular sling”

for the combined masseter and internal pterygoid muscles, acting together upon the angle of the jaw to pull it anterodorsally. The masseter pulls across the outer face of the mandible, the internal pterygoid across the inner, so that each muscle acting alone expends some fraction of its force in twisting the mandible along its antero-posterior axis, but the average direction of pull in the sagittal plane of the mandible is about the same, and they should be considered together as that mass of muscle the force of which acts at the back end of the ventral side of the jaw both to occlude the cheek teeth and to drag the jaw forward.

While the large angular process on the dentary of *Echiothrix* provides expansive surface for insertion of the internal pterygoid on its medial surface (as well as the superficial masseter), the site of origin is problematic because there is no pterygoid fossa. Possibly origin is on the cramped posterior portion of the alisphenoid or on the ventral surface of the narrow shelf that represents a remnant of a pterygoid plate in some specimens (see fig. 7C). Likely the muscle is smaller and the force capable of being exerted weaker than its counterpart in a murine like *Maxomys* or in those muroids in which dissection has revealed large and substantial internal pterygoids, the usual configuration (examples are the murines *Rattus* and *Apodemus* [Turnbull, 1970; Satoh, 1997; Satoh and Iwaku, 2008]; the sigmodontine ichthyomyines, *Oryzomys*, and *Sigmodon* [Rinker, 1954; Voss, 1988], the neotomines *Onychomys*, *Peromyscus*, and *Reithrodontomys* [Rinker and Hooper, 1950; Rinker, 1954; Satoh and Iwaku, 2006]; cricetines [Satoh

and Iwaku, 2004]; and arvicolines [Kesner, 1980; Satoh, 1997]).

The internal pterygoid muscles, noted Rinker and Hooper (1950: 9) “should be important in crushing and grinding actions of the molar teeth and in gnawing actions of the incisors,” an observation based on dissection of two species of *Reithrodontomys*. But *Echiothrix*’s molars are very small relative to size of the skull and the cusps low in relief; there is little crushing and grinding of prey. Watching the shrew rat feed (see above), Musser noticed periodic bouts of chewing, only seconds in duration, but typically earthworms, the primary dietary constituent, were either cut into segments and swallowed without mastication or swallowed intact. And there is no functional gnawing—the earthworm is seized using the incisors, either by stabbing or gripping it with the lower incisors and held against the uppers in the process already described (see discussion of diet). Elevating the mandible to close the jaws may rest mainly with the temporal and masseter muscles rather than with the internal pterygoids. Judging from osteological landmarks, the temporal and masseter complex are well developed in *Echiothrix*. In most muroids, the temporalis (which usually consists of separate parts) originates on the side of the cranium at the back of the orbit, and the squamosal and ventral projection of the parietal; it is bounded anteriorly by the frontal forming the posterior rim of the orbit, dorsally by the temporal ridge and posteriorly by the lamboidal crest. Insertion is on the tip of the coronoid process and anteromedial surface of the dentary between the coronoid process and the end of the molar row (Rinker, 1954; Turnbull, 1970; Satoh and Iwaku, 2006, 2008). *Echiothrix*’s spacious postorbital region, high braincase, and patent temporal and lambdoidal ridges provide expansive surface area for the origin of the temporalis. Although the tip of the coronoid is small, the anteromedial margin of the dentary between the coronoid tip and the end of the molar row (the retromolar fossa) is extensive. Origins for the different parts of the masseter complex involve the side of the rostrum forming the medial boundary of the infraorbital canal, the zygomatic plate, and the zygomatic arch; insertion is on various

portions of the lateral surface of the dentary (Rinker, 1954; Turnbull, 1970; Satoh and Iwaku, 2006, 2008). These bony surfaces are also ample in area, including the robust zygomatic plate and arch. Without the necessity to gnaw, and need for only minimal mastication of food, substantial internal pterygoid musculature and an elongate surface on which it can originate are no longer indispensable, especially when the temporal and masseter muscle complexes remain sufficiently sizeable to take over action of closing the jaw.

Michael Carleton (in litt., 2014) provided us with another possible function of the internal pterygoid muscles in *Echiothrix*. He wonders

whether the rudimentary pterygoid plate necessarily implies reduction in size of the internal pterygoids and their diminished importance in feeding. Perhaps they are no longer so important in mastication [as described by Landry's mandibular sling, or the propalinal swing formulated by Kesner (1980)], but their origin may have been reoriented to enhance manipulation of the mandibles and splaying of the lower incisors. Because the incisor tips are separating to form a V, then they must be pivoting at the base of the mandibular symphysis, and some contracting force must be applied to the rear of each hemi-mandible to animate the symphyseal fulcrum. Which muscle groups would enable this exceptional mobility of the long, saber-like incisors, the remarkable abduction of their tips, and independency of the rami motion? The internal pterygoids, it seems to me, are preadapted to provide that medial vector force through medial migration of its origin onto the walls of the pterygoid wings [vrpp in fig. 8B, C]. Only slight migration of the internal pterygoid origin onto the outer wall of the mesopterygoid fossa would be required to impart a more medial vector component to its action, compared with the predominantly anterior force vector as propounded by the sling hypothesis, and perhaps coupled with the rearward prolongation of the mandible's angle and corresponding change in the insertion of the internal pterygoid. In essence, the evolutionary result is a pterygoid "plate" that has been readjusted to a more vertical aspect from its ancestral horizontal position, typical of most muroids. Ultimately, of course, actual dissection is needed to describe the size, origin-insertions, and fiber direction of the shrew-rat's jaw muscles.

**MANDIBLE:** The dentary is long and low but not structurally delicate (figs. 5, 6). Compared to most murine species, it is stretched from front to back, especially the body of the dentary posterior to the molar row and the ramus anterior to the tooth row. The long body of the dentary forms a strong bony casing in which two-thirds of the slender, gently curved, and sharp-tipped incisor is tightly held, a strong handle absorbing the force when the dentary and free end of the incisor is thrust forward to impale the target prey (see Natural History Particulars of *Echiothrix centrosa*).

**DENTITION:** Molars and incisors of *Echiothrix* contrast sharply with the dentition of most murines, designs that are thought typical for gnawing and processing food by rigorous crushing and grinding actions. *Echiothrix* has small and delicate molars relative to the size of the skull. Length of the molar row is 12–13% of the occipitonasal length; percentages are 15%–18% for murines of about the same body size in *Rattus*, *Maxomys*, and *Bunomys*, for example, and many other Indo-Australian genera (compiled from Musser's records). Although occlusal surfaces are tuberculate, the cusps are low and wear rapidly to form series of dentine basins outlined by enamel rims (fig. 10). With a diet consisting of soft-bodied arthropods, primarily earthworms in the case of *Echiothrix*, that are swallowed whole or cut into segments and swallowed without mastication or only minimal chewing, molar occlusal surfaces play a minimal triturating function as invertebrate segments pass through the buccal cavity to the esophagus.

Form of the incisors and degree of enamel pigmentation also reflect adaptations to a vermivorous diet. The upper incisors emerge from the rostrum at a 90° angle to the ventral surface of the rostrum and the occlusal surface of the molar row (orthodont in configuration), and that exposed segment is short, as well as narrow; the enamel layers either lack pigment or are tinged with pale yellow or orange, usually near their exit from the premaxillaries; the anterior margins are scored with shallow grooves. Overall configuration of the upper incisors suggests a short chisellike instrument, suited to chop earthworms or other soft-bodied invertebrates

such as coleopteran and other insect larvae into segments before they are ingested, an action aided by the grooved enamel faces, which facilitate penetration of the incisor tips into pliant earthworm and larval tissues.

The segments of the lower incisors emerging from the dentaries curve slightly upward as long and slim tusklike structures with sharp tips. Enamel layers are either unpigmented or tinged with pale yellow or orange near their exit from the bony incisor sheath. Because the mandibular symphysis is flexible, the incisor tips can be splayed into a V. We previously described how the incisors can be used to procure prey, by either stabbing it or gripping it between the incisor tips. And when the jaw is closed, the prey is held against tips of the upper incisors. The entire complex is geared toward efficiently procuring earthworms and processing them into the mouth, either as cut segments or as whole worms.

The reduction of enamel pigmentation in the incisor's enamel layers of *Echiothrix* is significant. Most rodents possess incisors in which the enamel layers are densely orange due to the deposition of iron (Møinichen et al., 1996; Wen and Paine, 2013). It is generally accepted that "the primary function of the pigmentation is to harden the enamel and maximize the differential wear between the enamel and the [softer] dentine to produce a sharp chisel-like tooth" (Strait and Smith, 2006: 703). The deposition of iron forming the red enamel on the teeth of soricine shrews is also thought to make the enamel harder and more resistant to wear (Strait and Smith, 2006). The mostly unpigmented enamel on the incisors of *Echiothrix* is obviously strong enough to process soft-bodied invertebrates, and at some point in the evolutionary history of the genus, natural selection has eliminated much of the iron as necessary to the functional integrity of the incisor actions—basically the energy demands related to iron deposition has been minimized. *Echiothrix* uses its incisors to procure soft-bodied invertebrates, not for cropping vegetation, digging, removing bark, or felling trees, all activities requiring strong biting forces that would be enhanced by iron in the enamel layers.

Upper and lower incisors in which the enamel is either unpigmented or only tinged with pale yellow are also typical of the other vermivorous Sulawesi shrew rats *Melasmothrix naso*, the two species of *Tateomys* (Musser, 1982) and *Paucidentomys vermidax* (Esselstyn et al., 2012) as well as the Philippine species of *Rhynchomys* (Musser and Heaney, 1992; Balette et al., 2007).

**STOMACH MORPHOLOGY:** As described previously, the stomach of *Echiothrix centrosa* (fig. 11) generally corresponds to the unilocular and pouched configuration discussed by Carleton (1973: 28)—we have not examined stomachs of *E. leucura* but assume the anatomy to be similar to that of *E. centrosa*. The bulk of the stomach (the combined corpus and antrum) forms a single chamber lined with cornified squamous epithelium that is thickened and muscular in places; thick glandular epithelium is restricted to a pouch *within* the lumen of the stomach that connects with the main stomach chamber through a small aperture at the tip of a funnel-shaped or tubular neck. This configuration obtained in all 13 stomachs examined.

Among muroid rodents surveyed for their stomach morphology, the gastric structure of *E. centrosa* most closely resembles the unilocular-pouched stomachs of the South American sigmodontine *Oxymycterus rufus* (Carleton, 1973, reported as *O. rutilans*; Vorontsov, 1979) and the deomyine *Lophuromys sikapusi* (Genest-Villard, 1968), but in both of those species the glandular epithelium is entirely confined to a diverticulum or pouch ("glandular diverticulum" or "isolated blind chamber" in Vorontsov's description, 1979: 184) located on the *outside* of the greater curvature; a minute opening connects this glandular pouch with the main lumen of the stomach (Carleton, 1973: 16, fig. 5; Vorontsov, 1979: 185, fig. 100). Gross conformation of the stomach in many other species of *Lophuromys* is similar to that of *L. sikapusi* (Dieterlen, 1976: fig. 29).

The gastric configuration is different in *E. centrosa* because the glandular pouch is contained *within* the lumen of the stomach—not along its outside border—and connects with the lumen by an aperture at the end of a funnel-shaped neck (fig. 11).

The relationship of this specialized gastric morphology (glandular diverticulum either outside or inside the stomach lumen) to diet is obscure. While some dietary components of *Oxymycterus* and *Lophuromys* overlap with those of *Echiothrix*, the former two enjoy a broader range of foods than the latter. *Oxymycterus rufus* (Suarez, 1994, reported as *O. rutilans*; Musser and Carleton [2005] explain why the name *rufus* should be used in place of *rutilans*) and *O. nasutus* (Barlow, 1969), for example, consume mainly insects—earthworms, snails, centipedes, plant tissues, and seeds are taken but comprise minor components of the diet. *Lophuromys sikapusi*, as reported by Dieterlen (2013b: 256) is:

Insectivorous and omnivorous. Forages by searching and digging in dead leaves or litter, where ants, termites, other small or large insects, millipedes, earthworms, mollusks and even carrion are devoured opportunistically. May also eat soft fallen fruits and small seeds of certain tree species.

Dieterlen also summarized reports of other researchers who recorded foods consumed by *L. sikapusi* in Central African Republic, Uganda, Nigeria, DR Congo, Rwanda, and Côte d'Ivoire; insects, earthworms, and plant material in different combinations were the primary dietary constituents, and there is sufficient data from some regions to show seasonal changes in the diet. But omnivory is not special to *L. sikapusi*, for most species of *Lophuromys* “are omnivorous, and include a large proportion of insects and other invertebrates in the diet” (Dieterlen, 2013a: 239). By contrast with *Oxymycterus* and *Lophuromys*, *Echiothrix centrosa* can be labeled as a vermivore that supplements its primary diet with arthropods (chiefly soft bodied, such as coleopteran larvae and rhinotermitid termites; and geophilomorph centipedes; see tables 12 and 13).

These dietary comparisons are derived from examining stomach contents and offering captive rats different food items, and while informative at one level are a long way from meeting Carleton's (1973: 37) observation that:

A thorough accounting of a species' food preferences, and more importantly the nutritional value derived from those foods, would

entail study of the complete alimentary canal and associated glands from mouth to anus (and back again in instances of coprophagy).

The significance of a glandular diverticulum or pouch located within the stomach lumen, as in *Echiothrix centrosa*, but outside the lumen along the greater curvature, as in *Oxymycterus* and *Lophuromys*, is unclear, but its role in digestion is likely similar. Insects, Carleton (1973) noted, are biochemically heterogeneous, a statement that could also be applied to earthworms and other kinds of invertebrates consumed by these rats. The digestive process in all three genera may conform to Carleton's (1973: 39) suggestion that

the concentration of gastric glands in an enclosed diverticulum achieves a stomach entirely lined with cornified squamous epithelium. ... With the large mass of fundic glands of the pouch these rodents may accomplish some digestion of both the carbohydrate (pouch closed) and protein (pouch opened?) fractions of their diet before the food bolus passes into posterior segments of the gut.

Finally, we note that not all Sulawesi murines that include worms and insects in their diet possess the same gastric morphology seen in *Echiothrix*. For example, *Bunomys chrysocomus*, *Bunomys andrewsi*, and *Maxomys hellwaldii*, all sympatric with *E. centrosa*, consume earthworms, a variety of insects and other arthropods, snails, small vertebrates, and fruit. *Bunomys* has a unilocular-hemiglandular stomach morphology very similar to that of *Rattus hoffmanni* illustrated in figure 11. Bilocular-discoglandular is the design common to samples of *Maxomys hellwaldii* (fig. 11). Is digestion of the carbohydrate and protein components of earthworms and soft-bodied insects more efficient in the stomach of *Echiothrix* as compared with the processes breaking down these fractions in stomachs of the other genera? We don't know and can only apply Carleton's (1973: 39) conclusion, derived from a survey of stomach morphology among certain groups of muroid rodents, to the variation in gastric design and diet noted above:

The function(s) of the various gastric patterns evident in muroid rodents is still much in

question. Clearly more basic information on gastric histology and histochemistry, rate of food passage, nature of gastric symbionts, and food habits is needed to more precisely interpret the adaptive significance of the divergent kinds of stomachs.

#### ECTOPARASITES OF *ECHIOTHRIX CENTROSA*

Here we record the sucking lice (Anoplura, Polyplacidae), fleas (Siphonaptera, Pygiopsyllidae), hard ticks (Acari, Ixodidae), and mites (Acari, Laelapidae, Atopomelidae, and Trombiculidae [chiggers]) obtained from the fur of adult *E. centrosa* collected along the Sungai Sadaunta and at Kuala Navusu. We focus on the louse, which is an undescribed species of *Polyplax* represented by adults of both sexes, nymphs, and eggs. It is described in the next section and followed by short accounts of the other ectoparasites recorded as parasitizing *E. centrosa*.

#### THE NEW SUCKING LOUSE *Polyplax beaucournui*, new species

**TYPES:** Holotype male, allotype female, and 18 paratypes (4 males, 12 females, 1 second instar Nymph, 1 third instar Nymph) ex *Echiothrix centrosa* (AMNH 225044, adult male; Rodentia, Muridae, Murinae) collected by G.G. Musser at Sungai Sadaunta (1°23'S, 119°58'E; see gazetteer and fig. 2), 985 m, Propinsi Sulawesi Tengah, Indonesia, on 7 November 1974.

Two paratypes (1 female, 1 first instar Nymph) ex *E. centrosa* (AMNH 225045, adult female), collected by G.G. Musser at Sungai Sadaunta, 884 m, Propinsi Sulawesi Tengah, Indonesia, on 30 November 1974. One female ex *Echiothrix centrosa* (AMNH 225681, adult male), collected by G.G. Musser at Malakosa, Kuala Navusu (0°58'S, 120°27'E), 350 m, Propinsi Sulawesi Tengah, Indonesia, on 7 November 1975.

**DISTRIBUTION:** Known only from the collections itemized above, all from *Echiothrix centrosa*. *Polyplax beaucournui* may parasitize *E. centrosa* throughout its geographic and altitudinal ranges.

**DEPOSITION OF SPECIMENS:** Holotype, allotype, and six paratypes (1 male, 2 females,

1 first instar nymph, 1 second instar nymph, 1 third instar nymph) deposited in USNM. Other paratypes deposited in AMNH, BMNH, MZB, and private collection of L.A.D.

**ETYMOLOGY:** This species is named for Jean-Claude Beaucournu (Université de Rennes, France) in recognition of his exemplary studies of ectoparasites, especially fleas, his enduring friendship, and his collaborative studies with us on ectoparasites of mammals in southeast Asia, including Sulawesi.

**DIAGNOSIS:** *Polyplax beaucournui* is a fairly typical member of its genus. It does not have extreme morphological adaptations that are present, for example, in the congeneric *P. melasmothrixi*, which parasitizes the endemic Sulawesi shrew rat, *Melasmothrix naso* (see Durden and Musser, 1992), or in *Hoplopleura musseri*, which parasitizes another endemic Sulawesi rat, *Maxomys musschenbroekii* (see Durden, 1990). Nevertheless, *P. beaucournui* is unique and adults can be distinguished from all other described species of *Polyplax* based on a combination of the following characters.

In the male, the genitalia differ from those of all other known *Polyplax*, especially the very small, subcircular parameres and the small protuberance borne on each of them. The shape of the posterior arms of the basal apodeme is also distinctive. Other diagnostic characters are: (1) the shape of the thoracic sternal plate; (2) the shape of the paratergal plates and the lengths of the paratergal setae borne on them; (3) the presence of 2 DAChS next to the DPHS with all 3 of these setae aligned in a row and borne on distinct protuberances; (4) the narrow dorsal abdominal tergites, especially the very narrow plates 5 and 6.

The female of *P. beaucournui* can be identified using a combination of the following characters: (1) the morphology of the genitalia, including the shapes and associated setae of the subtriangular subgenital plate and gonopods VIII; (2) the shape of the thoracic sternal plate; (3) the shape of the paratergal plates and the lengths of the paratergal setae; (4) the presence of two DAChS next to the DPHS with all three of these setae aligned in a row and borne on distinct protuberances.

Nymphal stages of *P. beaucournui* are presumably also unique, but immature stages of very few species of *Polyplax* have been described (Kim, 1987) and none have previously been described that were collected from mammal species native to Sulawesi. The immature stages of the spiny rat louse, *Polyplax spinulosa* (Burmeister) have been described (Kim, 1987) and this louse parasitizes commensal *Rattus* throughout most of the world including nonnative *Rattus* species on Sulawesi (Durden, 1987). The three dorsal setae inserted in a row in the posterior head region (1 DPHS and 2 DACHS) that are also present in adult males and females are unusual and are probably diagnostic for all three nymphal stages of *P. beaucournui*. As in adults of both sexes, these setae are borne on distinct small protuberances in the third instar nymph of *P. beaucournui*, which is even more unusual for the genus. These characters can be further assessed when the immature stages of other species of *Polyplax*, particularly native species from Sulawesi, are described.

**DESCRIPTION: Male** (fig. 16A–D): Length of holotype, 1.05 mm; mean for series ( $N = 5$ ), 1.00 mm; range, 0.95–1.05 mm. Head and thorax well sclerotized.

**Head:** Broad, about as broad as long, with squarish but distinctly crenulated anterior margin; lateral margins somewhat curved, broadening toward thorax. Two SHS, 2 DMHS, 1 DPoCHS, 1 DPHS, 2 DACHS, 1 SpAtHS, 1 SpAtCHS, 2 DAHS, 2 ApHS, 1 VPHS, and 1 VPaHS on each side. DPHS and both DACHS each borne on small protuberance and aligned in a row. **Antennae:** Five segmented with basal segment much larger than other segments.

**Thorax:** About as broad as long. Thoracic sternal plate (fig. 16B), shield shaped with rounded apical projection, rounded anterolateral margins and acute, elongate posterior margin. Mesothoracic spiracle moderate in size (0.023 mm in diameter) with 1 small DMsS and 1 fairly long DPTS (0.11 mm in length) medial to spiracle. **Legs:** Forelegs small with small tibiotarsal claw; midlegs and hindlegs larger with progressively larger tibiotarsal claws; all coxae subtriangular.

**Abdomen:** Wider than thorax. Eight dorsal plates; plates 4–8 narrow, especially plates 5

and 6 which are extremely reduced; 1 DCAS anteriorly, followed by 2 TeAS on plate 1, 8 TeAS on each of plates 2–4, 10–12 TeAS on each of plates 5–6, 8 TeAS on plate 7 and 4 TeAS on plate 8; TeAS on plates 2–4 alternating in length between long and short; other TeAS long; 5 long DLAS present on each side. Eight fairly broad ventral plates anterior to subgenital plate; 5 StAS on plate 1, followed by 4 StAS on each of plates 2–3, 6 StAS on plate 4, 6–7 StAS on each of plates 5–7, and 4 StAS on plate 8; all StAS long except lateral seta on each side on plate 4.

**Paratergal plates** (fig. 16C): Present on segments 2–8; plates I–VI all subtriangular with lateral posteroapical angles acuminate; plates II–VII each with spiracle; plates I–IV each with 1 apical seta slightly longer than other apical seta on same plate; plates VI–VII each with 2 long apical setae; 4 small setae also present on plate I; all plates differentially sclerotized as shown (fig. 16C).

**Genitalia** (fig. 16D): Subgenital plate broader anteriorly with two lacunae; anterior lacuna with acuminate lateral margins and two long setae inserted anteriorly; posterior lacuna smaller without associated setae and lacking acuminate lateral margins; aedeagal basal apodeme much longer than parameres with small extension at tip of each posterior arm; parameres, small, subcircular but with lateral extension and small posterior protuberance; pseudopenis long, extending well beyond parameres and extruding from tip of abdomen.

**Female** (fig. 17A–D): Length of allotype, 1.28 mm; mean for series ( $N = 14$ ), 1.25 mm; range, 1.13–1.47 mm.

**Head, thorax, and legs:** As in male unless noted otherwise. Thoracic sternal plate (fig. 17B) with anterolateral margins projecting slightly more anteriorly than in male. Mesothoracic spiracle diameter, 0.12 mm.

**Abdomen:** Dorsally, with 2 rows of 2 DCAS anteriorly followed by 11 fairly broad dorsal plates; plates 1 and 2 each with 6 TeAS, plates 3–9 each with 6–9 TeAS, plate 10 with 5 TeAS, plate 11 with 3 TeAS; lateral TeAS on plates 1 and 2 distinctly shorter than medial TeAS on same plate; 5 DLAS present on each side. 12 fairly broad pregenital plates ventrally; plates 1–3 each with 4



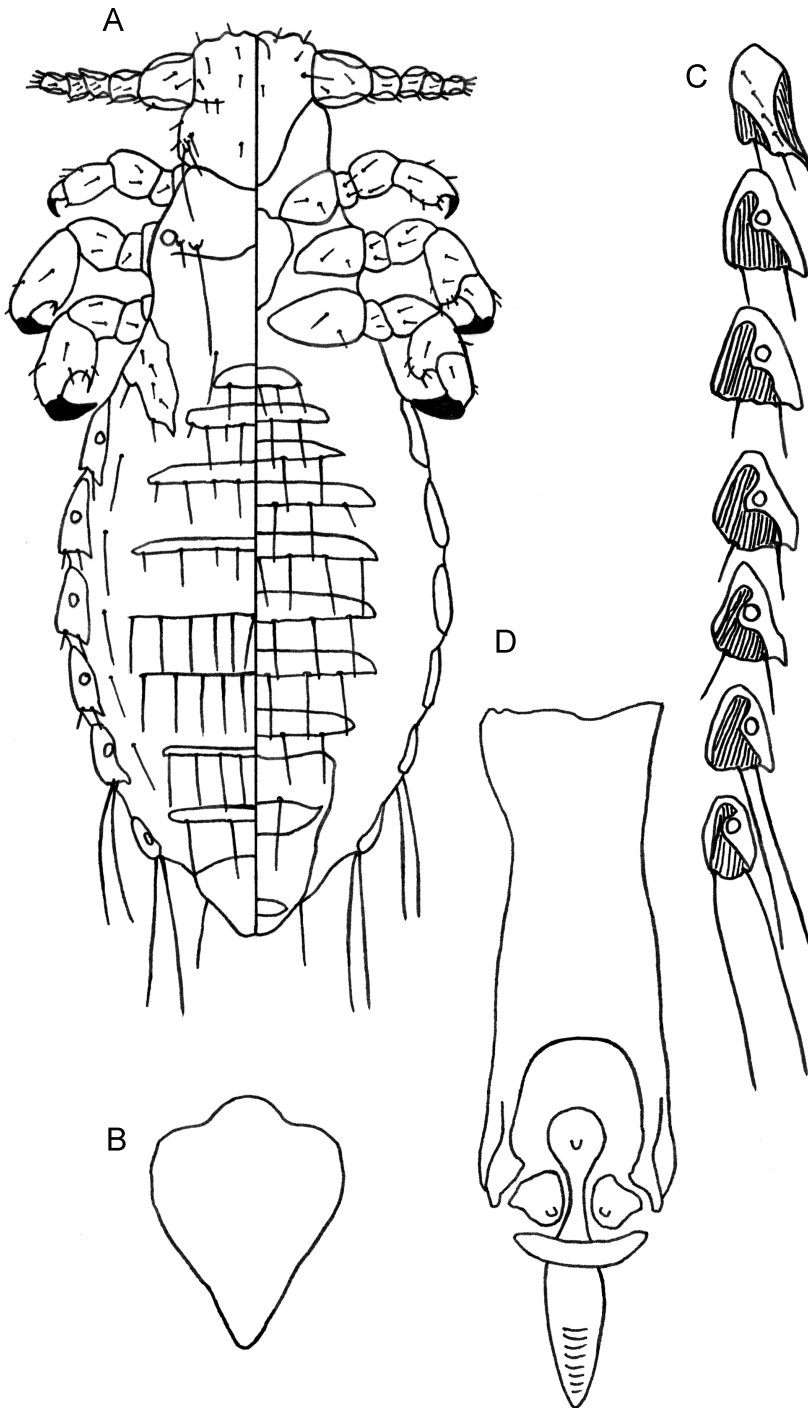


Fig. 16. *Polyplax beaucournui*, n. sp., male. **A**, dorsoventral view of entire male (dorsal morphology is shown to the left of the midline, ventral morphology to the right); **B**, thoracic sternal plate; **C**, paratergal plates; **D**, genitalia.

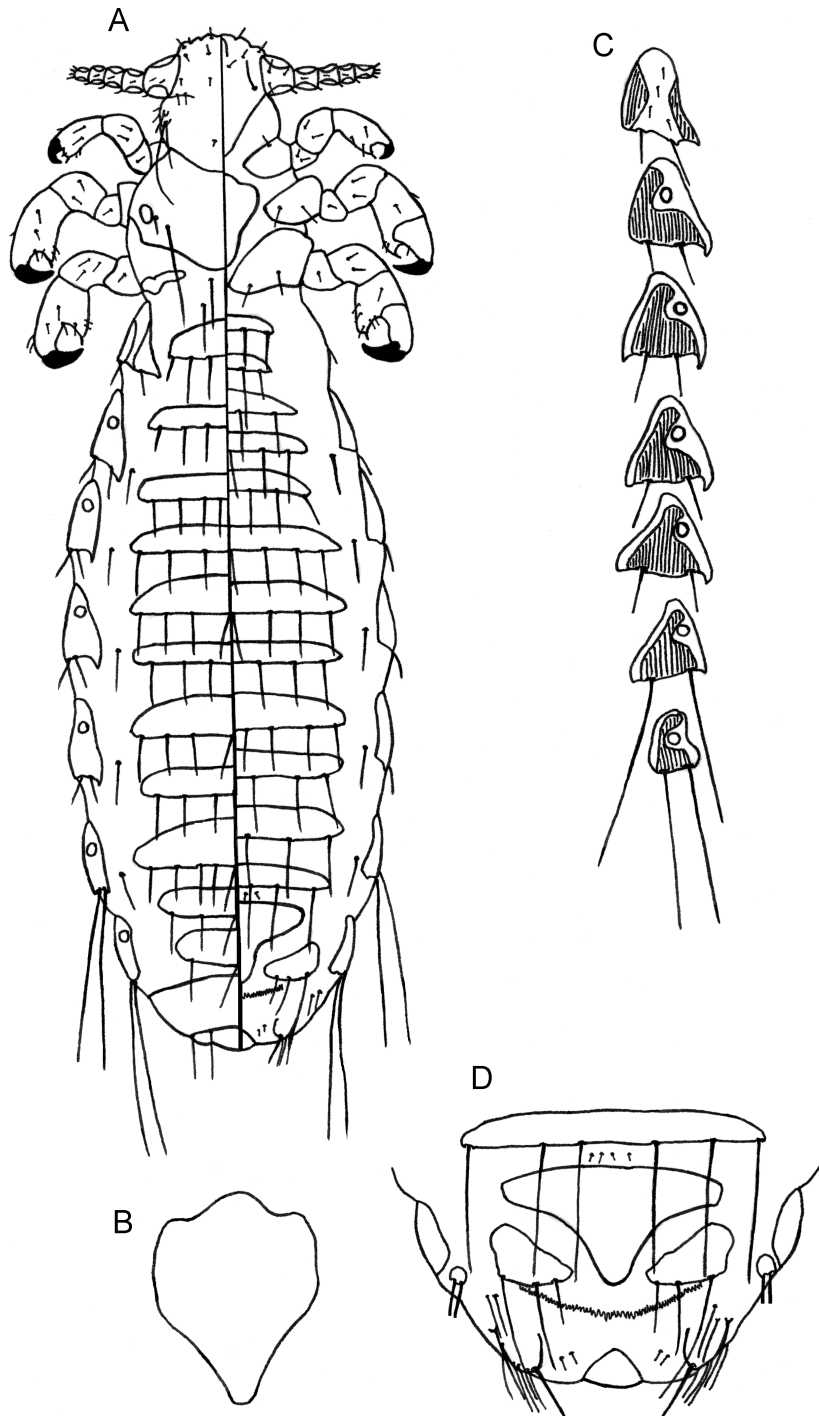


Fig. 17. *Polyplax beaucournui*, n. sp., female. **A**, dorsoventral view of entire female (dorsal morphology is shown to the left of the midline, ventral morphology to the right); **B**, thoracic sternal plate; **C**, paratergal plates; **D**, genitalia.

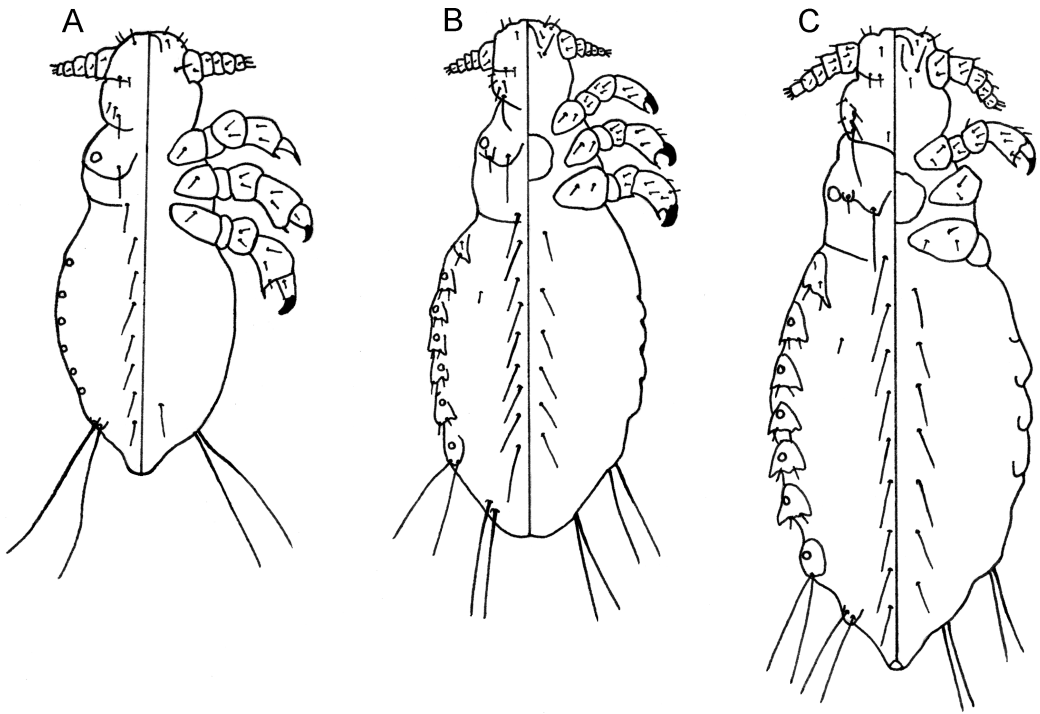


Fig. 18. *Polyplax beaucournui*, n. sp., nymphal stages—dorsoventral views of entire nymphs (dorsal morphology is shown to the left of the midline, ventral morphology to the right). A, first instar nymph; B, second instar nymph; C, third instar nymph.

StAS, plate 4 with 5 StAS, plates 5–11 each with 6–8 StAS; lateral StAS on plate 2 distinctly shorter than medial StAS on same plate. 5 VLAS present on each side.

*Paratergal plates* (fig. 17C): More or less as in male but with both apical setae on plates III–V about equal in length.

*Genitalia* (fig. 17D): Subgenital plate subtriangular with smoothly convex anterior margin, slightly concave posterolateral margins and broadly rounded posterior apex; 4 small medial setae immediately anterior to anterior margin. Gonopods XIII subtriangular each with 3 long setae, with lateral seta extending beyond apex of abdomen. Gonopods XI each with robust apical seta; 3 long setae inserted laterally and 3–4 long setae inserted anteriorly to gonopods XI; 2 tiny setae medial to gonopod XI on each side; vulvar fimbriae distinct.

**First instar nymph** (fig. 18A): Length (1 specimen): 0.48 mm.

*Head*: Broadly rounded anteriorly and laterally. Two SHS, 1 DPTS, 2 DACHS, 1 DPaHS, 2 ApHS, 1 VPHS, and 1 VPaHS on each side; insertions of DPTS and both DACHS aligned in a row. *Antennae*: Five segmented with basal segment larger than other segments.

*Thorax*: Broader than head with distinct mesothoracic spiracle and DPTS; thoracic sternal plate absent. *Legs*: All legs about equal in size, but tibiotarsal claws progressively increasing in size from forelegs to hind legs; coxae subtriangular.

*Abdomen*: Wider than thorax; paratergal plates lacking but paired, long lateral setae present on segment 8 borne on small protuberance; no other lateral abdominal setae; no abdominal tergites or sternites present; 8 long DCAS present on each side; 1 long VCAS located posteriorly on each side.

**Second instar nymph** (fig. 18B): Length (1 specimen): 0.82 mm

*Head and thorax:* As in first instar nymph unless stated otherwise. Anterior margin of head slightly crenulated; lateral margins of head less rounded than in first instar; 2 DMHS present on each side (in addition to other head setae listed for first instar); midlegs and hind legs distinctly larger than forelegs; subcircular thoracic sternal plate present; small DMsS present next to DPTS and borne on small protuberance.

*Abdomen:* Wider than thorax; 9 long DCAS, 6 long VCAS, and 1 small DLAS present on each side. Two pairs of long posterolateral setae present, the anterior pair borne on the most posterior paratergal plate.

*Paratergal plates:* Seven partially formed plates present on segments II–VIII; plates I–VI subtriangular; plates II–VII each with distinct spiracle.

**Third instar nymph** (fig. 18C): Length (1 specimen): 0.64 mm (note: the third instar nymph specimen is shorter than the second instar nymph specimen; normally, the opposite would be expected; however, the second instar specimen had an extended, blood-engorged abdomen and the third instar specimen had not fed resulting in a compressed abdomen).

*Head and thorax:* As in first instar nymph unless stated otherwise. Anterior margin of head distinctly crenulated. Two DMHS and 1 DPoCHS present on each side (in addition to other head setae listed for first instar). DPHS and both DACHS each borne on small protuberance; midlegs and hind legs (except coxae) missing on both sides; subcircular thoracic sternal plate present; small DMsS present next to DPTS and borne on small protuberance.

*Abdomen:* Wider than thorax; 9 long DCAS, 7 long VCAS, and 1 small DLAS present on each side. Two pairs of long posterolateral setae present, the anterior pair borne on the most posterior paratergal plate, the posterior pair borne on small protuberance. *Paratergal plates:* Seven well-formed plates present on segments II–VIII; plates I–VI subtriangular; plates II–VII each with distinct spiracle.

**HOST AND PARASITE RELATIONSHIPS:** Eggs (nits) of *P. beaucournui* were attached only to the guard hairs or thin overhairs of the dorsal pelage (fig. 19) and never on the

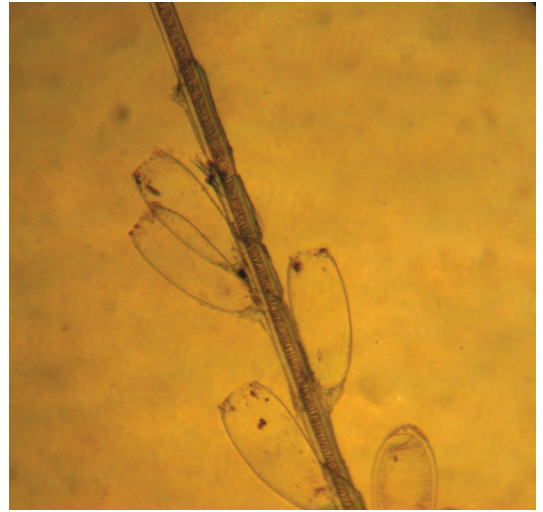


Fig. 19. *Polyplax beaucournui*, n. sp., ova (nits) attached to guard hairs in the dorsal coat of *Echiothrix centrosa*. All ova shown had hatched previously; cement and egg bases where other ova were previously attached are also visible.

spines that characterize *E. centrosa* or on the underfur hairs. The eggs shown in figure 19 had hatched previously because the operculum (“cap”) is absent on each of them. Nevertheless, as with other species of Anoplura, many hatched eggs remain cemented to the host hairs. Cement egg bases of *P. beaucournui* with partial remains of hatched eggs are also visible in figure 19.

The diameters of different hair types of *P. beaucournui* at their maximum width and at the hair base where *P. beaucournui* lice would typically be present (at the skin surface where they feed on host blood) are listed in table 17. Also listed in that table are the tibiotarsal claw gap sizes for different sexes and nymphal stages of *P. beaucournui*. Although each louse specimen has six legs in life, some legs or leg segments were broken in some of the desiccated (i.e., brittle) specimens that were removed from study skins of *E. centrosa*. Also, if tibiotarsal claws were not slide mounted in a completely flat plane, their gap widths could not be reliably measured. For these reasons, the sample sizes for tibiotarsal claws listed in table 17 are lower than would initially be expected from the total number of louse specimens available.

TABLE 17  
**Hair Diameter Measurements (mm) for *Echiothrix centrosa* and Claw-Opening Diameters for Its Louse, *Polyplax beaucournui***

Dorsal spines, guard hairs, thin hairs of the overfur and underfur hairs are components of the fur covering upperparts of head and body; ventral overhairs and underfur hairs form the coat covering the underparts.

	N	Mean	Range
<i>Echiothrix centrosa</i>			
Dorsal spines max. diameter	5	0.393	0.230–0.480
Dorsal spines diameter at base	5	0.072	0.057–0.085
Dorsal guard hairs max diameter	3	0.141	0.090–0.202
Dorsal guard hairs diameter at base	3	0.032	0.021–0.044
Dorsal thin hairs max. diameter	3	0.109	0.065–0.140
Dorsal thin hairs diameter at base	3	0.029	0.022–0.040
Dorsal underfur hairs max. diameter	8	0.022	0.018–0.026
Dorsal underfur hairs diameter at base	8	0.011	0.010–0.013
Ventral overhairs max. diameter	2	0.160	0.150–0.170
Ventral overhairs diameter at base	2	0.033	0.021–0.044
Ventral underfur hairs max. diameter	8	0.022	0.019–0.025
Ventral underfur hairs diameter at base	8	0.012	0.010–0.013
<i>Polyplax beaucournui</i>			
Male claw I opening	3	0.032	0.031–0.033
Male claw II opening	5	0.061	0.052–0.068
Male claw III opening	5	0.067	0.063–0.075
Female claw I opening	11	0.031	0.028–0.038
Female claw II opening	15	0.065	0.058–0.075
Female claw III opening	9	0.068	0.060–0.078
Nymph, 3rd instar, claw I opening	2	0.029	0.028–0.030
Nymph, 2nd instar, claw II opening	2	0.043	0.042–0.044
Nymph, 1st instar, claw II opening	2	0.033	0.032–0.034
Nymph, 1st instar, claw III opening	2	0.046	0.045–0.047

Regardless, the data in table 17 highlight some important findings with respect to the host-parasite relationships between *Echiothrix centrosa* and *Polyplax beaucournui*. Firstly, the claw gap sizes of males, females, and all nymphal stages of *P. beaucournui* are not large enough to be able to grasp the dorsal spines, guard hairs, or thin overhairs of the dorsal coat of *E. centrosa* or the overhairs of its ventral pelage at their maximum diameter. Similarly, only the largest claws of a few male and female lice could grasp the smallest host spines at their base. This, combined with the fact that louse eggs were never recorded on host spines, strongly suggests that, even though these spines are characteristic of *E. centrosa*, they are almost certainly avoided by *P. beaucournui*. The measurements listed in table 17 show that adults of *P. beaucournui* can, however, adequately grasp any of the other hair types

of *E. centrosa* at or near their bases. Conversely, although few samples were available for analysis, claws of nymphal *P. beaucournui* are clearly not large enough to grasp some of these hairs at their bases. Therefore, nymphs must mainly grasp the smaller underfur hairs that have sufficiently small diameters for all measured nymphal claws to be able to grasp. These data suggest there could be a partial microhabitat segregation between adults and nymphs of *P. beaucournui* in the pelage of *E. centrosa*, with adults frequenting the bases of the larger hairs (but avoiding the spines) and nymphs occurring near the bases of the underfur hairs.

*Polyplax beaucournui* could be host-specific to *E. centrosa* in Central Sulawesi or it could infest both this murid and the congeneric *E. leucura* in the northeastern arm of the northern peninsula. This question can be

answered when lice are collected and examined from *E. leucura*. Although study skins of two specimens of *E. leucura* (BMNH 97.1.2.45 and 97.1.2.46) were carefully examined, no lice were found on them.

#### OTHER ECTOPARASITES OF *ECHIOTHRIX*

ORDER SIPHONAPTERA (FLEAS), FAMILY PYGIOPSYLLIDAE: *Farhangia quattuordecimdentata* Mardon and Durden, 2003. Allotype ♀ and 1 paratype ♀ ex *Echiothrix centrosa* (AMNH 225043; listed in original description as *Echiothrix leucura*), collected by G.G. Musser at Sungai Sadaunta, 884 m, Propinsi Sulawesi Tengah, Indonesia, on 5 October 1974. Central Sulawesi.

The principal hosts of fleas belonging to the genus *Farhangia* are considered to be tree squirrels, and most other specimens of *F. quattuordecimdentata* have been collected from the endemic Sulawesi pygmy tree squirrel *Prosciurillus murinus* (see Musser et al., 2010). However, in addition to *E. centrosa*, this flea has been recorded from another endemic Sulawesi rodent, the murid *Margaretamys beccarii*. Mardon and Durden (2003) provide collection data including host information for all known specimens of this flea. The genus *Farhangia* is only known from Sulawesi (3 species) and Borneo (1 species) and some morphological traits suggest that members of this genus are inefficient jumpers and therefore are probably nest-associated fleas (Traub, 1980). The specimens of *F. quattuordecimdentata* from *E. centrosa* and *M. beccarii* may represent atypical host associations or they could indicate reduced host specificity or less reliance on squirrels as hosts for this flea species. To date, no flea species that are host-specific to either species of *Echiothrix* have been collected.

SUBCLASS ACARI, ORDER IXODIDA, FAMILY IXODIDAE (HARD TICKS): In this section, some tick collections have HH (Harry Hoogstraal) accession numbers whereas others have RML (U.S. National Tick Collection) accession numbers. The HH collection is now incorporated into the U.S. National Tick Collection on the campus of Georgia Southern University, Statesboro, Georgia.

*Amblyomma* sp.: Two larvae (RML 122184) ex AMNH 225044, 6 nymphs, 4 larvae (RML 122185) ex AMNH 225045, 4 larvae ex AMNH 225046, all from *E. centrosa*, Central Sulawesi, Sungai Sadaunta, Nov. 1974, G.G. Musser.

These nymphs do not match known nymphal stages of any of the other species of *Amblyomma* known to occur on Sulawesi (Durden et al., 2008).

In addition to *E. centrosa*, ticks of this genus have been collected from a suite of other mammal hosts living in Sulawesi: shrews (the commensal *Suncus murinus*), pigs (*Sus celebensis* and the domestic *Sus scrofa*), water buffalo (*Bubalus bubalis*, nonnative), humans, domestic dog (nonnative), two endemic squirrels (*Rubrisciurus rubriventer* and *Hyosciurus heinrichi*), nine other species of endemic murid rodents (*Bunomys fratrorum* and *B. andrewsi*; *Margaretamys beccarii*; *Maxomys hellwaldii* and *M. musschenbroekii*; *Paruromys dominator*; *Rattus hoffmanni*, *R. xanthurus*, and *R. facetus* [recorded as *R. marmosurus*]); and two nonnative murines (*Rattus tanezumi* [recorded as *R. rattus*] and *R. exulans*) (Durden et al., 2008).

*Haemaphysalis (Ornithophysalis) kadarsani* Hoogstraal and Wassef, 1977: One paratype nymph (MZB 1525, HH 45,046) ex *E. centrosa* (listed in original description as *E. leucura*), Central Sulawesi, Malakosa, Kuala Navusu, Coll.: G.G. Musser.

New specimen: 1 male (RML 121405) ex *E. centrosa* (AMNH 225682), Central Sulawesi, Malakosa, Kuala Navusu, elevation 122 m, 15 Oct. 1975, G.G. Musser (tick removed from host study skin by L.A.D. on 12 April 1994).

This tiny tick (the smallest known species of *Haemaphysalis*, a genus that comprises 166 known species worldwide) is known only from Central Sulawesi (Durden et al., 2008), with most adult specimens reported by Hoogstraal and Wassef (1977) collected (by Musser) from another endemic murid, *Paruromys dominator*, which is sympatric with *Echiothrix centrosa*. Morphologically, Hoogstraal and Wassef (1977) considered *H. kadarsani* to be closest to *H. (O.) sciuri*, which parasitizes tree squirrels in the Philippines (Mindanao). No molecular phylogenetic analyses have been undertaken to further

investigate the evolutionary relationships among species in the genus *Haemaphysalis*, including *H. kadarsani* and *H. sciuri*.

*Haemaphysalis (Kaiseriana) hystricis* Sulpino, 1897: Two nymphs, 3 larvae (RML 122187) ex *E. centrosa* (AMNH 225046), Central Sulawesi, Sungai Sadaunta, Nov. 1974, G.G. Musser.

In addition to Sulawesi, this tick is known from Vietnam, Laos, Taiwan, the Ryuku Islands, northeastern India, northern Myanmar, Thailand, and Sumatra (Durden et al., 2008). Adults mainly parasitize ungulates (especially suids and cervids) whereas immature stages parasitize rodents (Durden et al., 2008). Besides *E. centrosa*, Durden (1986a) recorded *H. hystricis* from samples of three murid species collected in the northeastern end of the northern peninsula of Sulawesi; *Bunomys fratrorum*, *Maxomys hellwaldii*, and *Maxomys musschenbroekii*—all are Sulawesi endemics, and *B. fratrorum* occurs only in forests of the northeastern arm.

*Haemaphysalis* sp.: Five nymphs (RML 122186) ex *E. centrosa* (AMNH 225045), Central Sulawesi, Sungai Sadaunta, Nov. 1974, G.G. Musser. These nymphs do not match *H. kadarsani* or any of the other Sulawesi species of this genus for which nymphs have been described (Durden et al., 2008).

In addition to *E. centrosa*, unidentified immature stages belonging to the genus *Haemaphysalis* have been collected from other mammal hosts living in Sulawesi: shrews (the endemic *Crocidura elongata*, and the commensal *Suncus murinus*), rusa (*Rusa timorensis*, nonnative), three endemic squirrels (*Rubrisciurus rubriventer*, *Hyosciurus heinrichi*, and *H. ileile*), 10 other species of endemic murid rodents (*Bunomys fratrorum*, *B. andrewsi*, and *B. chrysocomus*); *Maxomys hellwaldii*, *M. musschenbroekii*, and *M. watsi*; *Paruromys dominator*; *Taeromys* sp.; *Rattus hoffmanni*, *R. facetus* [recorded as *R. marmosurus*], and three nonnative murines (*Rattus tanezumi* [recorded as *R. rattus*], *R. argentiventer*, and *R. exulans*) (Durden et al., 2008).

SUBCLASS ACARI, ORDER MESOSTIGMATA, FAMILY LAELAPIDAE: The following specimens were collected from *E. centrosa* from Central Sulawesi: Five female specimens

ex AMNH 225044; 1 female ex AMNH 225045, 2 females ex AMNH 225046 (all from Sungai Sadaunta, Oct–Nov. 1974, G.G. Musser); 2 females ex USNM 219738 (Pinedapa, 21 Jan. 1918, H.C. Raven); 1 female ex BMNH 40.385 (Koelawi, 29 Dec. 1938, W.J.C. Frost).

Musser's field notes reveal that laelapid mites are common on *E. centrosa*. Virtually all endemic Sulawesi rodents examined in the field by Durden were heavily infested with laelapid mites; often there were more than 100 of these mites on a single host individual (Durden, 1986b). These mites, including the specimens from *E. centrosa*, were forwarded to D. Gettinger (University of Central Arkansas) in 2006 but have not yet been identified.

SUBCLASS ACARI, ORDER SARCOPTIFORMES, FAMILY ATOPOMELIDAE (FUR MITES): *Listrophoroides (Marquesania) echiothrix* Bochkov et al., 2004: Holotype male plus 20 male and 20 female paratypes ex *E. centrosa* (FMNH 43409), Central Sulawesi, Pinedapa, 7 Feb. 1918, H.C. Raven.

New specimens ex *E. centrosa* from Central Sulawesi as follows: Two specimens ex AMNH 225044, 1 specimen ex AMNH 225047 (both from Sungai Sadaunta, Nov. 1974, G.G. Musser); 1 specimen ex AMNH 225681, 3 specimens ex AMNH 225682 (both from Kuala Navusu, Oct. 1975, G.G. Musser). These specimens were forwarded to A.A. Bochkov (Russian Academy of Sciences, St. Petersburg) in 2009.

This tiny fur mite appears to be host-specific to *E. centrosa*; however, as with the louse *Polyplax beaucournui*, it could also parasitize *E. leucura*. The male and female of *L. echiothrix* were described and illustrated by Bochkov et al. (2004).

SUBCLASS ACARI, ORDER TROMBIDIFORMES, FAMILY TROMBICULIDAE (CHIGGERS): Eighteen specimens ex *E. centrosa* (AMNH 225047, Central Sulawesi, Sungai Sadaunta, Nov. 1974, G.G. Musser).

These specimens were removed from the host study skin by L.A.D. in April 1994 and forwarded to M.L. Goff (Chaminade University, Hawaii) later that year but have not yet been identified or described. Based on these specimens and on Musser's field notes, chiggers also appear to be common on *E. centrosa*.

## CODA

PHYLOGENETIC AFFINITY OF *ECHIOTHRIX*

Illuminating the species diversity in *Echiothrix* has been the thrust of our report, within a format where two species are diagnosed, described, and compared, and their geographic and elevational ranges outlined based on available specimens for study. Attendant biological subjects organized under the banners of natural history, morphological adaptations for vermivory, and ectoparasites are elucidated as a garnish to the accounts of species. Recovering the phylogenetic alliance of *Echiothrix* within the more than 125 extant genera of Murinae is the subject of a different inquiry. While we do not explicitly address kinship, we are compelled here to seal our exposition of *Echiothrix* with a historical review of its postulated affinities, its present position in Murinae, and brief speculation as to its actual relationship.

From the time it was originally described to the present, *Echiothrix* has been treated as a member of Murinae (in Muridae) in most regional faunal treatises, classifications, and other kinds of rodent compendia (Alston, 1876; Thomas, 1896b; Trouessart, 1897; Meyer, 1899; Tate, 1936; Sody, 1941; Ellerman, 1941; Simpson, 1945; Misonne, 1969; Laurie and Hill, 1954; Carleton and Musser, 1984; Corbet and Hill, 1992; Pavlinov et al., 1995; McKenna and Bell, 1997; Musser and Carleton, 2005; Aplin and Helgen, 2010). The prominent exception is Oldfield Thomas who in his classification of rodents (Thomas, 1896b) listed *Echiothrix* (under the name *Craurothrix*) in Murinae, but who two years later (Thomas, 1898: 397–398) suggested the genus be transferred to Rhynchomyinae, which contained the long-nosed Philippine shrew rat *Rhynchomys*. Thomas carefully compared two specimens of *Echiothrix* from the northern peninsula of Sulawesi with *Rhynchomys*, and concluded that:

in spite of the absence of any tendency towards a reduction in the dentition, there is a genuine relationship between the two forms. In the Celebean animal the general shape of the skull is very similar to that found in *Rhynchomys*: the peculiar anterior nasal bulging is present; the braincase is similarly smooth and rounded; the supraorbital and temporal ridges, although

present, are very small; the zygomatic root is slightly slanted back; and the posterior palatal region is strikingly similar to that of *Rhynchomys* both in the breadth and shape of the posterior nares, and the entire suppression of the external pterygoids. The incisors again—or at least the upper ones—in size, proportions, and position are more like those of *Rhynchomys* than of ordinary murines.

On the other hand, the molars of *Echiothrix* are absolutely murine, and show no trace of reduction or any other peculiarity. The third molar is, of course, present above and below, and is of full murine proportions. On the whole it seems probable that we have in *Echiothrix* a form which bears to *Rhynchomys* ... the first commencement of a line of modification which culminates in a genus sufficiently distinct to demand subfamily separation from the main trunk of the Murinae. If this be true, it would then probably be best to include all the members of the diverging branch within the special subfamily, even if nearer to the trunk than to the extremity, and I would therefore suggest ... that *Echiothrix* should be transferred to the Rhynchomyinae, a name which would be particularly suitable owing to the long snout being the most obvious character that the two genera have in common. It is, of course, just possible that when unworn teeth of *Rhynchomys* are examined they will show a structure quite incompatible with the view that this form is related to *Echiothrix*, but it seems to me that the many cranial characters which the two forms have in common render this possibility very unlikely.

In a review of Indo-Australian mammals in reference to Wallace's Line, Raven (1935: 188–189) indicated the Sulawesi *Echiothrix* to be related to the Philippine *Rhynchomys*, an alliance probably influenced by Thomas's suggestion.

Tate (1936: 585) entertained a different supposition of affinity: "In view of the *Rattus*-like character of its molar teeth, *Echiothrix* must be regarded, in spite of the reduced size of those teeth and its elongate rostrum, as a strongly specialized off-shoot of the *xanthurus* group of *Rattus* [also endemic to Sulawesi]. ... it is quite unrelated to *Rhynchomys* of Philippines ...."

Ellerman (1941: 269) disagreed, writing in his compendium on families and genera of rodents this rebuttal to both Thomas and Tate:



Thomas transferred this genus [*Echiothrix*] to the Rhynchomyinae; but its molars and incisors are not abnormally reduced as they are in *Rhynchomys*, while the cranial characters could have been evolved independently in the two genera owing to similar diet or habits. Tate regards it as an offshoot of the *Rattus xanthurus* group; but this seems one of the few genera in the subfamily with simple teeth that is clearly and definitely not only distinct from *Rattus* but about as far from *Rattus* as it can be. That it may have been derived from *Rattus* appears beside the point; probably every living simple-toothed member of the group was. But that it is very far removed from that genus to-day there can be little doubt.

By 1969, Misonne (1969: 159) concluded from a survey of murine dentitions that *Echiothrix* is “certainly Murinae” but at the same time “cannot be clearly allocated.” Subsequent researchers have endorsed *Echiothrix*’s ambiguous position: in their list of Rodentia of the world, Pavlinov et al. (1995: 174) listed the genus as Muridae incertae sedis, as did Aplin and Helgen (2010: 46) in their table describing tribal level classification of extant Murinae. These two reports bracket that of Musser and Carleton (2005: 903), who isolated *Echiothrix* in its own “Division” within Murinae, which was simply stating incertae sedis in a different way.

In opposition to the explicit views of Thomas and Tate, Ellerman correctly assessed the cranial and dental similarities between *Rhynchomys* and *Echiothrix* as an example of convergence, not close phylogenetic alliance. Analyses of DNA sequences unambiguously relate *Rhynchomys* to endemic Philippine murines (Jansa et al., 2006), nesting the genus in a clade containing *Chrotomys* and *Soricomys*, a cluster that in turn bears a sister relationship to *Archboldomys*—all are endemic to the Philippine Archipelago (Balet et al., 2012).

We suspect that eventually results from analyses of DNA sequences will demonstrate *Echiothrix* to be a member of a clade containing some of the other described endemic Sulawesi shrew rats, namely *Melasmothrix*, *Tateomys*, and *Paucidentomys*. Of these, *Echiothrix* will likely turn out to be most closely allied to *Paucidentomys*, as Esselstyn et al. (2012) have already suggested.

#### SUCKING LICE (ANOPLURA)

There are more than 50 species of murid rodents that are endemic to Sulawesi and nearby islands, and likely more await discovery (Musser, ms.). About half of the species have been surveyed for sucking lice, which prove to be parasitized only by species of *Hoplopleura* and *Polyplax* (table 18). In concert with their endemic hosts, the species of *Hoplopleura* and *Polyplax* have not been recorded from murid hosts native to regions outside of Sulawesi. The sucking louse associated with *Echiothrix centrosa* is no exception. As with the endemic hoplopleurid sucking lice that parasitize endemic sciurids on Sulawesi (Musser et al. 2010), there has probably been much phyletic tracking of murid hosts by sucking lice in Sulawesi as ancestral murids diverged into new taxa. With respect to the current study, *Polyplax melasmothrxi*, which uniquely parasitizes *Melasmothrix naso* on Sulawesi, has distinct morphological similarities with two undescribed species of *Polyplax* that parasitize the two species of *Tateomys* listed in table 18. This reinforces the close phyletic relationship between *Melasmothrix* and *Tateomys*. Although *Polyplax beaucournui* shares a few of these characters (such as the stout DPHS and DAChS borne on small tubercles), it is otherwise morphologically fairly distinct from the lice of *Melasmothrix* and *Tateomys*. If these lice have phyletically tracked their hosts, as has been reported previously for other groups of sucking lice and their mammalian hosts (Kim, 1985; Light and Hafner, 2007; Smith et al., 2008), this would suggest that *Echiothrix* is not as closely related to *Melasmothrix* and *Tateomys* as the host analyses indicate. However, these louse data should be viewed with some caution because lice do not always phyletically track the evolution of their hosts. For example, Lyal (1987) showed that about 21% of the known taxa of trichodectid chewing lice have not phyletically tracked their mammalian hosts. In the exceptions, host switching (nonphyletic tracking) had evidently occurred. Therefore, *P. beaucournui* could reflect a historical case of host switching by an ancestral sucking louse from another species of murid with which it is not

TABLE 18  
Sucking Lice (Anoplura) Recorded From Native Sulawesi Murids

Host species	Louse species	Reference
<i>Bunomys chrysocomus</i>	<i>Hoplopleura chrysocomi</i>	Durden, 1990
	<i>Polyplax wallacei</i>	Durden, 1987
<i>Bunomys fratrorum</i>	<i>Hoplopleura sembeli</i>	Durden, 1990
	<i>Polyplax wallacei</i>	Durden, 1987
<i>Bunomys andrewsi</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Echiothrix centroso</i>	<i>Polyplax beaucournui</i>	Present report
<i>Eropeplus canus</i>	<i>Polyplax eropepli</i>	Durden, 1987
<i>Haeromys</i> n. sp.	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Margaretamys beccarii</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Margaretamys elegans</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Margaretamys parvus</i>	<i>Polyplax</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Maxomys dollmani</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Maxomys hellwaldii</i>	<i>Hoplopleura sembeli</i>	Durden, 1990
<i>Maxomys musschenbroekii</i>	<i>Hoplopleura musseri</i>	Durden, 1990
<i>Maxomys wattsi</i>	<i>Hoplopleura traubi</i>	Durden and Musser, 1991
<i>Maxomys</i> , n. sp.	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Melasmothrix naso</i>	<i>Polyplax melasmothrxi</i>	Durden and Musser, 1992
<i>Rattus bontanus</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Rattus facetus</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Rattus hoffmanni</i>	<i>Hoplopleura sembeli</i>	Durden, 1990
<i>Rattus mollicomulus</i>	<i>Polyplax</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Sommeromys macrorhinos</i>	<i>Hoplopleura sommeri</i>	Musser and Durden, 2002
<i>Taeromys callitrichus</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Taeromys hamatus</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Taeromys punicans</i>	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Taeromys</i> , n. sp.	<i>Hoplopleura</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Tateomys macrocercus</i>	<i>Polyplax</i> , n. sp.	Durden and Musser, ms. in prep.
<i>Tateomys rhinogradoides</i>	<i>Polyplax</i> , n. sp.	Durden and Musser, ms. in prep.

taxonomically closely related. In cases of host-switching, it appears that the ectoparasites that switch to a different host species are tracking similar morphological resources of their hosts such as skin or hair type (Lyal, 1987).

Another case of resource tracking is evident in the three undescribed species of sucking lice that parasitize three species of *Margaretamys* on Sulawesi (table 18). *Margaretamys beccarii* and *M. elegans* are each parasitized by a different undescribed species of *Hoplopleura* whereas *M. parvus* is parasitized by an undescribed species of *Polyplax*. We have collections of lice from multiple specimens of these three species of *Margaretamys*, so this does not represent a collecting artifact. In this case, the most likely explanation is that the two undescribed *Hoplopleura* species are exhibiting phyletic host tracking and that the *Polyplax* louse represents a

historical host-switching event. As an aside, *Margaretamys beccarii* and *M. elegans* are more similar to each other in cranial and dental traits than either is to the morphologically divergent *M. parvus* (Musser, 1981). Additional collecting from other endemic species of murids together with molecular analyses of sucking lice and hosts should assist in unraveling these intimate host-parasite relationships.

*Polyplax* attracts our attention within a broader zoogeographical context. While the many species in *Hoplopleura* parasitize species of native rats and mice occurring throughout the continents and archipelagos stretching from peninsular Malaysia to Australia (Durden and Musser, 1991; Musser and Durden, 2002), *Polyplax* displays, as explained by Durden and Musser (1991: 8), an interesting geographical distribution in the Indo-Australian region where

*Polyplax* is well represented in mainland Southeast Asia, the Greater Sunda islands, Sulawesi, and the Philippines but is unknown (except as parasites of introduced commensal rats and mice) further eastward, despite the presence of numerous species of seemingly suitable native murine hosts [see Musser and Carleton, 2005]. Apparently, *Polyplax* failed to accompany the ancestral murids that progressively colonized islands southeastward from mainland Southeast Asia across the Moluccas to New Guinea and Australia.

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