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Sulawesi Rodents: Species Traits and Chromosomes of *Haeromys minahassae* and *Echiothrix leucura* (Muridae: Murinae)

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ABSTRACT

Results from analyses of chromosomal spreads of a male tree mouse, *Haeromys minahassae,* and a male shrew rat, *Echiothrix leucura,* are described and illustrated. A 2N of 48, FN of 54, autosomes consisting of 21 pairs of telocentric chromosomes and two pairs of small metacentrics, and sex chromosomes made up of a large submetacentric X and smaller submetacentric Y characterize the karyotype of *H. minahassae.* The chromosomal set of *E. leucura* encompasses a 2N of 40; FN of 75; an autosomal component of 14 submetacentric pairs, two telocentric pairs, and three small metacentric pairs; a small submetacentric X chromosome; and small telocentric Y. Although the karyotypes constitute additional sets of data to that provided by morphology of skins, skulls, and teeth (also briefly described here), the information they provide on the phylogenetic relationships of either species is ambiguous. Rather than indicating closest relatives, these chromosomes may contribute more to polarizing karyotypic characters in certain groups of Indo-Australian murids.

INTRODUCTION

The small tree mouse, *Haeromys minahassae* (fig. 1), and large shrew rat, *Echiothrix leucura* (fig. 3), are among the more than 40 species of murid rodents which occur on Sulawesi and nowhere else. Both species are represented by samples collected only in the northern and central parts of the island, have been found only in tropical lowland evergreen rain forest, and are infrequently encountered by collectors—a reflection of the arboreal life style and spotty distribution of the granivorous tree mouse, and the specialized and secretive habits of the vermivorous shrew rat.

Phylogenetic relationships of each species have yet to be determined. *Haeromys minahassae* is related to other species of *Haeromys* which are found on the Sundaic is-

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lands of Palawan and Borneo. The genus is characterized by retention of many primitive morphological traits and a few derived features. Some of these specializations are also shared by species of *Chiropodomys,* arboreal mice indigenous to Indochina and islands on the Sunda Shelf (Musser, 1979; Musser and Newcomb, 1983), but this link is weak and whether or not it reflects close relationship has to be tested with additional data. In what has been documented of its morphology based on museum study skins, crania and mandibles, and dentitions, *E. leucura* retains some primitive characters but most of its diagnostic traits are derived. Its closest relative is unknown, and the species seems as isolated within a phylogenetic framework as it is in its geographic distribution (Misonne, 1969; Musser, 1969).

I will try to clarify these muddled views in a systematic revision of *Haeromys* (Musser, in prep.) and a morphological analysis of the specialized traits peculiar to *Echiothrix* (Musser and Sawitzke, in prep.). Here I present results from analyses of a different data set—chromosomal number and morphology—and discuss its significance for inferring phylogenetic relationships between these two Sulawesian endemics and other elements of the murine fauna native to the Indo-Australian region. First, I will introduce the rodents by presenting brief descriptions of their insular distributions, morphological characteristics, forest habitats, and habits.

Specimens and Methods

Specimens cited here are in collections of the American Museum of Natural History, New York (AMNH); the British Museum (Natural History), London (BM); the Museum Zoologicum Bogoriense, Bogor (MZB); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); and the National Museum of Natural History of the Smithsonian Institution, Washington, D.C. (USNM).

I measured external dimensions—total, tail, hind foot, and ear lengths—and took weights shortly after the animals were captured; length of head and body was derived by subtracting tail length from total length. Crania and molar rows were measured by me in the laboratory.

Karyotypes were prepared and stained in the field from chromosomes of bone marrow, and processed by employing colchicine, hypotonic citrate, and flame-drying, procedures that were described by Patton (1967).

I use four terms to describe the shape of each chromosome relative to position of the centromere: **metacentric** (the chromosome is biarmed, one arm being about the same length as the other); **submetacentric** (one arm is shorter than the other, about a third of its length); **subtelocentric** (one arm is very short relative to the long arm on the other side of the centromere); and **telocentric** (the centromere is at the tip of the chromosome or near enough that any portion on the other side of the centromere is so short as to be indistinguishable or nearly so).

Acknowledgments

Curators at the institutions cited above allowed me access to collections under their care and loaned me specimens; I appreciate their generous help.

I am grateful to Charles J. Cole and Carol Townsend who taught me the techniques required to obtain and preserve chromosome spreads, procedures I could use in isolated forest camps. When I returned with my boxes of slides, Jay allowed full access to equipment and supplies in his laboratory; he and Carol tutored me in the craft of extracting the significant data pressed between glass slide and cover slip. The chromosomal spreads were photographed by Cameron Newcomb.

The manuscript has been strengthened by the intelligent criticisms and contributions of Audrone Biknevicius, Charles J. Cole, Lawrence R. Heaney, and James L. Patton; I thank them for their time and effort.

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ANIMALS AND HABITATS

Haeromys minahassae is the smallest native murid living on Sulawesi (fig. 1; table 1). Its short head and body—about as long and thick as my thumb—is clothed by a soft tawny brown dorsal coat, a white or whitish gray ventral coat, and counterbalanced by a long and brown whiplike tail.

The tree mouse has a gracile cranium (fig. 5) in which the rostrum is short and wide; the zygomatic plates are narrow, and the zygomatic notches very shallow; the interorbit is wide; the braincase is globular, its dorsolateral margins weakly defined by indistinct ridges; the zygomatic arches are slender and delicate; the incisive foramina are short, as is the wide bony palate; the sphenopalatine vacuities are small, set in a wide mesopterygoid fossa; the pterygoid plates are wide; and the auditory bullae are small. The mandible is stocky, and the ramus is nearly square in side view; the coronoid is a low projection, as are the condylar and angular processes.

Incisors are short and orange, the molars low-crowned and white. Coronal cusp patterns are simple. A cusp is retained on the anterolabial corner of each second and third upper molar, a prominent posterior cingulum forms the back of each first and second upper tooth, an anterocentral cusp connects large anterolingual and anterolabial cusps at the front of each first lower molar, and labial cusplets are few (fig. 7). Three roots anchor each upper molar, two roots each lower tooth, which is a primitive condition (Musser and Newcomb, 1983).

Characteristics of the Sulawesian tree rat are generally representative of the genus *Haeromys*. Morphological aspects of the group are a composite of many retained primitive traits and a few derived ones (three pairs of mammae, whiplike tail, large opening between bullae and squamosal, spacious sphenopterygoid vacuities, a ridge bounding the pterygoid bridge between foramen ovale and bulla, and cusplets on anterior margins of first molars are derived examples; Musser and Newcomb, 1983).

The specimen of *H. minahassae* from which the chromosomal spreads were obtained is part of a sample (table 1) collected from the forested slopes above Kuala Navusu between 250 and 500 ft in the Malakosa region of central Sulawesi (see the map in Musser and Dagosto, 1987: 30). Two specimens from forest along the Sungai Sadaunta (1°22′S, 119°59′E) at 3050 and 3300 ft (AMNH 226817 and 226816) constitute the only other records from the central part of the island.

Elsewhere in Sulawesi, *H. minahassae* has been collected in the northeastern arm, but nowhere else. One example, the holotype (BM 97.1.2.39), comes from Rurukan (1°21′N, 124°52′E); two others (RMNH 21159 and 21160) were taken near Tumaratus (1°09′N, 124°48′E) at 700–800 m; and another (MZB 4840) was obtained from 700–800 m near Tomohon (1°19′N, 124°49′E).

Haeromys minahassae is rarely encountered by biologists and infrequently collected, possibly because of its arboreal habits and patchy distribution within the forest. As indicated by specimens I have studied, the altitudinal distribution of the tree mouse extends from 250 to 3300 ft, a range contained within the elevational brackets of tropical lowland evergreen rain forest on Sulawesi. In this type of forest along Kuala Navusu, relative humidity is about 100 percent and ambient air temperatures are moderately high. For example, during 95 days in 1975, the period when the mice were collected, the average minimum air temperature was 73.6°F (range, 72–76°) and the average maximum temperature was 80.9°F (range, 74–87°). The canopy is 20–40 m high, with emergent trees reaching 50–70 m. The high diversity of species includes not only the tall canopy-formers but understory trees, shrubs, palms, and woody vines as well; Musser and Dagosto (1987: 41–44) provided a fuller description.

Haeromys minahassae was collected during the night in traps set above ground on woody vines in tangles like those shown in figure 2. The scansorial facility of this tree mouse (fig. 1)—its ability to climb and scamper along vines and other cylindrical substrates above ground—is impressive. In this understory beneath the canopy, the mice have access to fruits of herau palms (*Areca vestiaria*) and species of figs (*Ficus*), which form a large part of their diet. The pulp of the herau fruit is consumed, but pulp of figs is discarded and only the seeds are eaten. Other frugivorous species of rats living on Sulawesi also

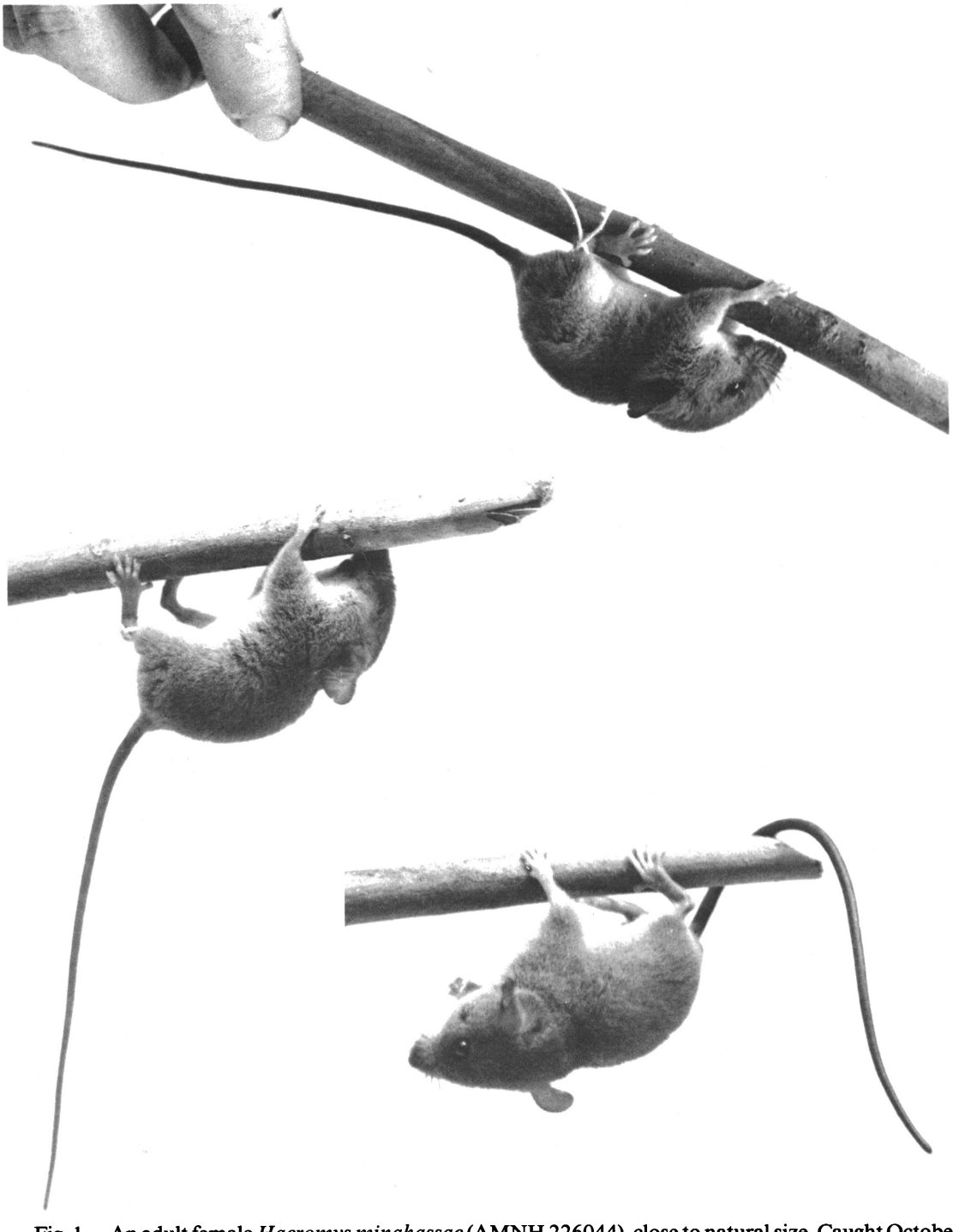

Fig. 1. An adult female *Haeromys minahassae* (AMNH 226044), close to natural size. Caught October 17, 1975, at 250 ft along Kuala Navusu, central Sulawesi. The long, flexible tail is a scansorial specialization.

Fig. 2. Woody vines on which *Haeromys minahassae* were caught (arrows) in the understory of tropical lowland evergreen rain forest along Kuala Navusu, 500 ft. The tangles are loosely coiled about trunks of fig trees (*Ficus* spp.) and hang from their crowns by viney suspensions. Seeds from fig fruit are a primary dietary component of the tree mouse. Photographed October, 1975.

Fig. 3. A young adult male *Echiothrix leucura* (AMNH 225682), about two-thirds natural size. Caught October 15, 1975, at 400 ft above Kuala Navusu, central Sulawesi. The elongate head, large eyes, long and pointed ears, spiny fur, delicate front feet, long and robust hind feet, and long sturdy tail are distinctive characteristics.

eat figs, but they digest the pulp and pass the intact seeds in their feces; *H. minahassae* is distinguished from those fig consumers as the only seed predator (Musser, personal obs. and fieldnotes).

The range in variation of morphological and chromatic traits that characterize the samples from the Malakosa region and Sungai Sadaunta includes the features described for the holotype of *Mus minahassae* (Thomas, 1896). I compared specimens from my series directly with the holotype of *minahassae* and found their characteristics to be similar. Venter coloration is the only conspicu-

Fig. 4. Tropical lowland evergreen rain forest above Kuala Navusu, 400 ft, the habitat of *Echiothrix leucura*. The broad leaves of a young palm, *Livistona rotundifolia,* partially shade the leaf-covered forest floor. Photographed November, 1975.

Fig. 5. Cranium and mandible of an adult *Haeromys minahassae* (AMNH 226047) from Kuala Navusu in the Malakosa region of central Sulawesi. About ×3.

ous difference between the samples from central Sulawesi and those from the northeastern arm: chest and abdomen of the latter are whitish gray rather than white. Evidence from museum skins and skulls convinces me that the samples from these two regions of the island represent the same species.

Echiothrix leucura is one of the large-bodied species which is native to Sulawesi (fig. 3; table 1). Its elongate head and body are covered by a bristly, variegated gray and brown dorsal pelage, and a white (stained with russet in some individuals) semispinous ventral coat. The dark brown of its very large and soft ears contrasts with the predominantly gray and spiny pelage. Its front legs

Fig. 6. Cranium and mandible of an adult *Echiothrix leucura* (AMNH 225681) from Kuala Navusu. About ×2.

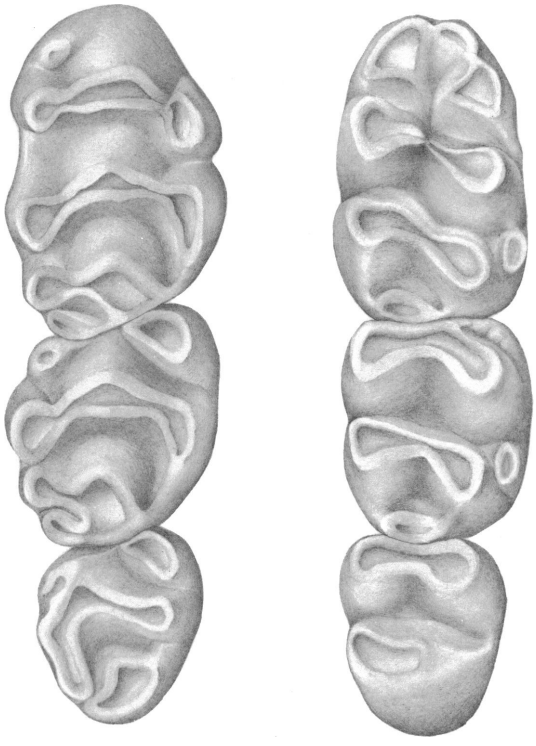

Fig. 7. Occlusal views of right upper (left) and lower (right) molar rows of *Haeromys minahassae* (AMNH 226048; CLM1–3 = 3.3 mm, clm1–3 = 3.4 mm) from Kuala Navusu.

Fig. 8. Occlusal views of right upper and lower molar rows of *Echiothrix leucura* (AMNH 225681; CLM1–3 and clm1–3 each = 6.5 mm) from Kuala Navusu.

are thin and the feet small and delicate. The hind legs are short and strong, the feet very large and very long, with short outer digits and long central ones. Its thick tail is longer than the head and body and white everywhere except for the proximal one-third to one-half, which is dark gray on dorsal and ventral surfaces. Females have two pairs of inguinal teats, no more, no less.

The distinctive cranium of the shrew rat (fig. 6) has a high, squarish, and slightly ridged braincase; a wide interorbit; graceful, elongate rostrum with stretched incisive foramina; gracile zygomatic arches; a long palatal bridge; moderately large sphenopalatine vacuities; a simplified pterygoid region in which much of the pterygoid shelf is gone, and the surfaces for muscle attachment significantly reduced; and moderately large auditory bullae. The elongate and gracile mandible, with its low coronoid projection and caudally directed condylar and angular processes, reflects the protracted configuration of the cranium.

Teeth are unique. The cream-colored upper incisors are short and delicate, and their front faces are scored by either one or two shallow grooves. Lower incisors are also cream colored, very long and thin, and very sharp. Molars are very small in relation to the surface areas of bony palate and dentaries. Their crowns are low and the coronal cusp patterns simple (fig. 8). The low cusps are discrete in young animals but wear quickly with advancing age to form basined occlusal surfaces. Upper molars are anchored by three roots under each tooth, lowers by two.

Chromosomal spreads were obtained from a specimen in a sample of eight individuals collected in the Malakosa area between 100 and 400 ft along the Kuala Navusu (table 1).

TABLE 1

Selected Measurements (in millimeters) and Weight (in grams) from Samples of *Haeromys minahassae* and *Echiothrix leucura* Collected Along Kuala Navusu in the Malakosa Region of Central Sulawesi[a]

Species and individual	Sex	Age	LHB	LT	LHF	LE	WT	GLS	CLM1–3
H. minahassae									
AMNH 226043[b]	M	A	78	131	21	15	14	—	—
AMNH 226047	F	A	70	125	20	15	13	23.4	3.1
AMNH 226051	F	A	75	128	19	15	15	23.7	3.1
AMNH 226050	M	A	74	133	19	16	15	23.5	3.1
AMNH 226045	F	A	76	127	19	15	13	23.3	3.1
AMNH 226044	F	A	75	120	19	16	12	22.7	3.1
AMNH 226048	F	YA	70	120	20	15	11	22.9	3.3
AMNH 226049	F	J	64	111	19	14	10	21.1	3.1
AMNH 226046	M	J	62	104	18	14	7	20.1	3.1
E. leucura									
AMNH 225684	M	OA	225	258	53	33	310	54.1	6.0
AMNH 225681	M	A	219	242	51	34	290	53.6	6.2
AMNH 225683	F	A	221	245	52	34	275	52.8	6.4
AMNH 225685	F	A	221	241	53	34	293	54.2	—
AMNH 225682[b]	M	A	227	—	53	33	—	—	—
AMNH 225679	F	YA	208	247	52	33	248	51.5	6.4
AMNH 225678	M	YA	213	253	53	32	235	52.4	6.3
AMNH 225680	M	YA	200	235	52	33	220	50.2	6.4

[a] Abbreviations: M, male; F, female; OA, old adult; A, adult; YA, young adult; J, juvenile; LHB, length of head and body; LT, length of tail; LHF, length of hind foot; LE, length of ear; WT, weight; GLS, greatest length of skull; CLM1–3, crown length of maxillary molar row.

[b] Karyotyped.

Morphology of skins and skulls in this series is like that described for specimens diagnosed and named *Echiothrix brevicula* by Miller and Hollister (1921). The 13 individuals upon which this taxon was based were collected at Pinedapa (1°25′S, 120°35′E), 100 ft, which is south of the Malakosa region and in the same forest formation (see the map in Musser and Dagosto, 1987: 30). My comparison of the rats from Kuala Navusu with the holotype of *brevicula* (USNM 219744) and the rest of the Pinedapa series confirms this identity.

In contrast to the meager samples of *Haeromys minahassae,* the shrew rat is represented in museums by larger series collected at more places. Still, all the localities are only in the northern arm and central core of Sulawesi. Sufficient geographic variation in cranial and chromatic characters exists, enough to have stimulated Miller and Hollister (1921) to not only name *E. brevicula,* but also *E. centrosa,* which was founded on specimens from higher elevations in central Sulawesi. The distinctions between those two forms, and between them and *leucura* from the northeastern arm of the island (east of Bumbulan, 0°29′N, 122°53′E), involve size and pelage coloration. These differences have not always been interpreted as those which delimit species, for in their list of Indo-Australian mammals, Laurie and Hill (1954) regarded *brevicula* and *centrosa* as subspecies of *Echiothrix leucura.* In identifying the sample from Kuala Navusu as *E. leucura,* I have followed their arrangement. Whether or not the morphological differences among samples represent geographic variation within one species or define limits of more than one reproductively isolated entity cannot be determined without a rigorous systematic revision of the genus.

Echiothrix leucura is another inhabitant of tropical lowland evergreen rain forest; all specimens I have studied come from locales between 100 and 3600 ft. The shrew rat is terrestrial and nocturnal. I trapped it on the forest floor (fig. 4), in runs alongside fallen tree trunks, and on rotting limbs and trunks

that lay across ravines and streams. Earthworms are the primary dietary component of *E. leucura*. The morphological specializations in the body conformation, as well as in skull and teeth, reflect its ability to forage for earthworms, run along substrates, leap away from predators, and consume soft-bodied invertebrates.

CHROMOSOMES

Haeromys minahassae. – Chromosomal spreads were obtained from a male (AMNH 226043) collected in the Malakosa area of central Sulawesi along the Kuala Navusu at 250 ft (0°58'S, 120°27'E). Twenty-five cells were studied. The diploid number is 48; the fundamental number is 54 (fig. 9). The autosomal set consists of 21 pairs of telocentric chromosomes that range in size from a large first pair to succeeding smaller pairs in a graded series, and two pairs of small metacentrics. The presumed X chromosome (largest chromosome of the heteromorphic pair) is submetacentric and also the largest chromosome in the karyotype; the Y chromosome is a smaller submetacentric.

Echiothrix leucura. – Spreads were obtained from a male (AMNH 225682) trapped along the Kuala Navusu at 400 ft. Twenty cells were examined. The diploid number is 40; the fundamental number is 75 (presumably 76 in females; fig. 10). The autosomes consist of 14 pairs of submetacentrics in which the first pair is the largest and the others range in size from moderately large to small, two pairs of small telocentrics, and three pairs of small metacentrics. The presumed X chromosome is a small submetacentric; the Y a small telocentric.

SIGNIFICANCE

The chromosomal data provide another set of characters that might point to the closest phylogenetic relatives of *H. minahassae* and *E. leucura*. But do they?

Morphology of museum skins and associated skulls and dentitions of the Sulawesian *Haeromys* clearly tie it to the Bornean *H. pusillus* and *H. margaretae* as well as a Palawan species, which together form a monophyletic group (Musser, in prep.). The phylogenetic relationships between this cluster and other genera are unclear. Tate (1936) suggested that *Haeromys* was a derivative of the *Rattus cremoriventer* group. Initially, Ellerman (1941, 1949) had also allied *Haeromys* with *Rattus* but later considered it to be more closely related to *Lorentzimys* of New Guinea. Misonne (1969) was unsure about the affinities of *Haeromys* but included it within his *Lenothrix-Parapodemus* Division which, in the context of his inquiry, meant that *Haeromys* was not closely allied to *Rattus* or the *cremoriventer* group or any other cluster, only "that it was one of those genera that are relict in some way, arboreal to some degree, lives in high mountains or are isolated on islands, and dwell in deep forest" (Musser and Newcomb, 1983: 559).

In a study of relationships among Sundaic murines that was based on morphological characters derived from skins, skulls, and teeth, Musser and Newcomb (1983: 557) rejected any close ties between *Haeromys* and either *Rattus* or *Niviventer* (which contains the *cremoriventer* group). Among the rats and mice known to occur on the Sunda Shelf, *Haeromys,* they suggested, may be more closely related to *Chiropodomys* than to any other genus. Even between those two the link was weak, as the hypothesized phylogenetic alliances need to be further tested with data from other characters and *Haeromys* should be compared with species occurring outside the Sundaic region. What may have been Musser and Newcomb's primary contribution was demonstrating that the very ambiguity characterizing *Haeromys*'s phylogenetic position stemmed from its retention of so many primitive characters. Of all the traits associated with skins, skulls, and dentitions to which polarities could be hypothesized, the fewest derived features of any Sundaic species are possessed by *Haeromys*. The many primitive traits retained by species of *Haeromys* are shared by other species that are native not only to the Sunda Shelf but also to archipelagos and continents outside that area. It was this primitive suite that formed the foundation upon which the conflicting statements of relationships were constructed by Tate (1936), Ellerman (1941, 1949), and Misonne (1969). Shared specializations suggest *Haeromys* to be phylogenetically closer

to *Chiropodomys* than to any other Sundaic murid (Musser and Newcomb, 1983).

If the karyotype derived from one specimen of *H. minahassae* is even generally representative of the genus, the chromosomal information—at the level of gross morphology as well as diploid and fundamental numbers—does not sharpen the resolution of *Haeromys*'s position within the diversity of Asian murines, and only reinforces the view that it is characterized by the retention of many primitive traits and few derived ones. In its high diploid number, low fundamental number, and its composition of basically telocentric pairs of chromosomes, the karyotype represents what is likely a primitive chromosomal condition, assuming that high number of telocentrics and low number of biarmed elements is more primitive than a complement characterized by mostly biarmed elements (for example, see Viegas-Péuignot et al., 1983).

This presumed primitive state defined by a high number of acrocentric autosomes is the primary karyotypic feature that is shared by *Haeromys,* as represented by the Sulawesian *H. minahassae,* and *Chiropodomys,* as sampled by Thai and Malay specimens of *C. gliroides.* Chromosomal spreads of Thai *C. gliroides* consist of 21 pairs of telocentric chromosomes that grade in size from large to small; sex chromosomes have not been identified; and both diploid and fundamental numbers are the same, 42 (Marshall, 1977; Tsuchiya et al., 1979). In samples of *C. gliroides* from the Malay Peninsula, spreads contain a diploid number of 42, a fundamental number of 48, 18 pairs of telocentric chromosomes, one pair of small metacentrics, one pair of small submetacentrics, a large metacentric X chromosome, and a medium-size submetacentric Y (Yong, 1973, 1983). *Haeromys* and the Malayan *Chiropodomys* also share a large biarmed X chromosome, which is the largest in the complement. But it is metacentric in *Chiropodomys* (a "duplicate-type X chromosome," as Yong, 1973: 61, described it) and unlike the biarmed configuration of the X chromosome in *H. minahassae.*

The karyotype of *Margaretamys beccarii* (Musser, 1981: 288), a tree rat endemic to Sulawesi, also resembles that of *Haeromys minahassae.* The diploid number is 42 and the fundamental number is 46 for *M. beccarii,* and its chromosomal package consists of 19 pairs of telocentric chromosomes and two pairs of small metacentrics (sex chromosomes have yet to be identified). The first pair of telocentrics is the largest in the karyotype and the others decrease in size with pair 19 the smallest. Aside from the differences in diploid and fundamental numbers (48 and 54, respectively, in *H. minahassae*), and a possible difference in conformation of sex chromosomes, the combination of all telocentric and two small metacentric pairs in *M. beccarii* is morphologically more reminiscent of *H. minahassae* than is the karyotype of *Chiropodomys gliroides,* which has telocentric autosomes but either no small metacentric pairs (Thailand) or small metacentric and submetacentric pairs (Malay Peninsula).

However, except for being arboreal and indigenous to Sulawesi, *M. beccarii* and *H. minahassae* are not especially closely related. No derived morphological traits (as seen in skins, skulls, and dentitions) are shared by the two species, and the characters which are held in common are primitive ones (compare table 11 in Musser, 1981: 324, with table 38 in Musser and Newcomb, 1983: 536). A karyotype in which all but two pairs are telocentric, which is common to the two species, is possibly another shared primitive feature.

In its diploid number and gross morphology of chromosomes, the autosomal complement of *H. minahassae* appears more similar to the non-*Rattus* native Australian murines than to *Chiropodomys* or any other murine indigenous to Indochina, the Sunda Shelf, or Sulawesi. The euchromatic autosomal complements of species of *Pseudomys, Leggadina, Notomys, Melomys,* and *Hydromys,* as shown by Baverstock et al. (1977), have four characteristics in common: (1) a diploid number of 48, (2) the first telocentric pair is "distinguishably" larger than any of the other pairs, (3) autosomal pairs 2–21 are telocentric and grade in size from large to small, and (4) there are two pairs of small metacentric autosomes (pairs 22 and 23).

The chromosomal characteristics shared among the Australian species could "be due to karyotypic convergence," according to

Fig. 9. Karyotype from a male *Haeromys minahassae* AMNH 226043): 2N = 48, FN = 54. The first autosomal pair is the largest of the telocentrics, and pairs 22 and 23 are small metacentrics. Additional explanation is provided in the text.

Baverstock et al. (1977: 115), but that seemed unlikely to them and they argued "that the common and widespread occurrence of such a distinctive karyotype in the same zoogeographic region (Australasia) emphasizes homology." Furthermore, the species "appear to have a common phyletic origin in Australasia, and there seems little doubt that a similar karyotype must have been present in the ancestor of the entire group." Some of the other Australian species (excluding *Rattus*) that were sampled exhibited karyotypes that Baverstock and his colleagues suggested were modified from this presumed ancestral configuration by what they believed to be fixed pericentric inversions.

Haeromys minahassae has a diploid number of 48, the first pair of telocentrics appear slightly larger than the others, autosomal pairs 2 through 21 are telocentric and form a graded series of decreasing size, and pairs 22 and 23 are small metacentrics. The resemblance between *Haeromys* and the Australian cluster seems impressive if possession of identical diploid numbers is significant. If such an identity is not especially significant, then the resemblance between karyotypes of *Margaretamys beccarii* and *H. minahassae* (2N of 42 versus 2N of 48) is just as noteworthy.

Do the karyotypic similarities between *Haeromys minahassae* and the Australian species indicate close relationship and common phyletic origin? Possibly. However, an explanation more plausible to me is that the karyotype of *H. minahassae* is conservative, retaining primitive characteristics which are also found in most of the indigenous Australian rats and mice. If a diploid number of 48 and a set of chromosomes consisting of mostly telocentrics and two pairs of small metacentrics is primitive for Indo-Australian murines, it would not be surprising to find such a karyotype shared among different species scattered throughout the region from Southeast Asia to New Guinea and Australia. A similar karyotype characterizes *Hapalomys longicaudatus* from the Malay Peninsula (Yong et al., 1982), for example. And it may not be a surprise to find it in at least one species of *Haeromys,* a genus with a relictual distribution in tropical forests on the Sunda Shelf and Sulawesi and one that is characterized by few specialized features (Musser and Newcomb, 1983).

Chromosomal data turn out to be ambiguous in detecting the nearest phylogenetic relative of *Haeromys.* But the information from the one specimen of *H. minahassae* does point to the next set of inquiries necessary to determine the real significance of the kary-

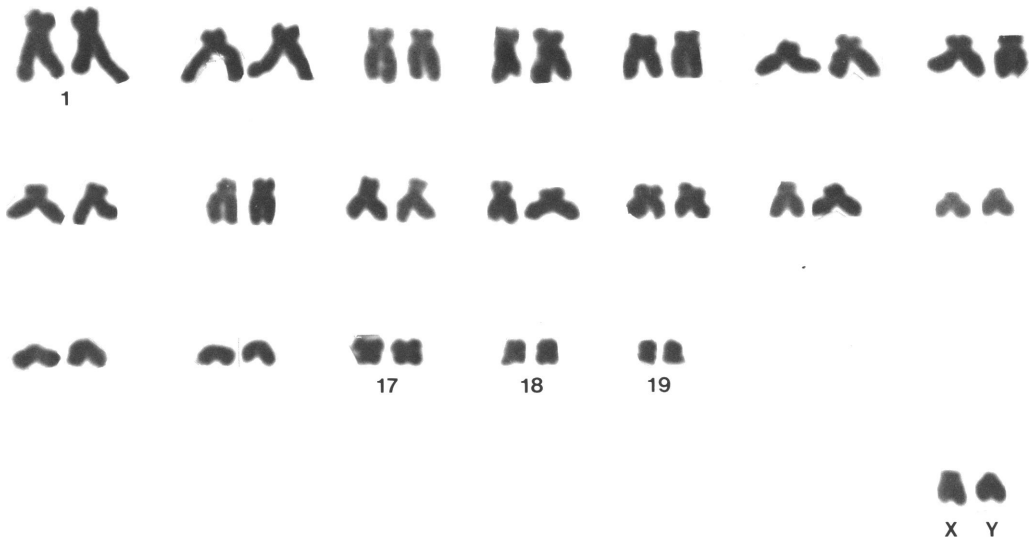

Fig. 10. Karyotype of a male *Echiothrix leucura* (AMNH 225682): 2N = 40, FN = 75. All autosomes are submetacentric except pairs 15 and 16, which are telocentric, and the small metacentric pairs 17–19. See text for additional discussion.

otype. First, the other species of *Haeromys* should be sampled to discover the range in chromosomal morphology and number within the genus. Second, banding techniques should be used to elucidate the amount and distribution of constitutive heterochromatin in the karyotypes of *Haeromys,* and to determine whether or not the autosomal chromosomes are homologous with those in some species of *Chiropodomys, Margaretamys,* or the Australian group. For example, after processing chromosomes in a sample of *C. gliroides* from the Malay Peninsula through G- and C-banding, Yong (1983) discovered that one arm of the metacentric and the short arm of the submetacentric autosomes are heterochromatic, as is the entire Y-chromosome. Finally, the morphological traits of *Haeromys* need to be compared with those of the Australian cluster as well as Sulawesian *Margaretamys* to discover if there are shared derivations by which a phylogenetic relationship could be inferred indicating that the species of *Haeromys* and those in Australia share a more recent common ancestor that was different from the one shared by other Indochinese, Sundaic, and Sulawesian species, especially those in *Chiropodomys* and *Margaretamys.* Such an inquiry would indicate the significance of the resemblance between *Haeromys* and the Australian murids which is now seen in gross chromosomal structure. My preliminary studies, however, suggest the chromosomal resemblances between *Haeromys* and the Australian genera to reflect shared primitive traits.

In contrast to *Haeromys,* the shrew rat, *Echiothrix,* has not been found anyplace outside mainland Sulawesi. Data derived from museum study skins, skulls, and teeth have yielded different interpretations of the phylogenetic relationship between *Echiothrix* and other Indo-Australian murids. Thomas (1898) regarded *Rhynchomys,* a large-bodied shrew rat known only from the Philippine island of Luzon (Musser, 1969), to be the closest relative of *Echiothrix* and even suggested that the two be placed in the same subfamily. Writing in 1936, Tate disagreed with Thomas and put forth the opinion that *Echiothrix* is a specialized derivative of the *Rattus xanthurus* group, which is a cluster of species endemic to Sulawesi. Ellerman (1941), believing that Tate completely misjudged the distinctive and specialized features of the Sulawesian shrew rat, considered *Echiothrix* to be morphologically far removed from any species of *Rattus.*

A study of molar occlusal patterns undertaken by Misonne (1969) could not identify the closest relative of *Echiothrix*. He included the genus in a division basically defined by one characteristic: occlusal surfaces of molars become basined—not cuspidate—after only a little wear. To Misonne, the group consists of some members of the Murinae (the New Guinea *Macruromys* and Philippine *Crunomys*) and all of the Hydromyinae (the Australian and New Guinea *Leptomys, Paraleptomys, Xeromys, Hydromys, Pseudohydromys, Microhydromys, Neohydromys, Parahydromys, Crossomys, Mayermys,* and Philippine *Chrotomys, Celaenomys,* and *Rhynchomys*). Misonne concluded that *Echiothrix* belongs in the Murinae, but is not dentally close to any of the other genera he considered members of that group; noted that its "common trend towards a basin-shaped molar structure, a character not met with in any other Murinae, allows a classification closer to the Hydromyinae" (p. 159); and even suggested that the shrew rat, along with *Macruromys* and *Crunomys,* could be "an example of possible transition" between the two subfamilies "but this cannot be clearly shown now" (p. 159). Clearly, his results are equivocal and he was really left in a quandry about the place of *Echiothrix* in the evolution of the morphological and cladistic diversity of murines endemic to the archipelagos and continents from Indochina to Australia.

Chromosomal data are currently unrevealing about phylogenetic relationships between *Echiothrix* and other murids. Karyotypes have not been published for *Macruromys, Crunomys,* or any of the Philippine shrew rats (*Chrotomys, Celaenomys,* and *Rhynchomys*) so chromosomal comparisons between them and *Echiothrix* are not yet possible. Of the other genera that Misonne (1969) grouped within the Hydromyinae, only the Australian *Hydromys chrysogaster* is represented by karyotypes (Baverstock et al., 1977). It has a diploid number of 48, 22 pairs of telocentric autosomes, and two small pairs of metacentric autosomes, a set of chromosomes that is strikingly unlike *Echiothrix* with its diploid number of 40, 14 pairs of submetacentric autosomes, two pairs of small telocentrics, and three pairs of small metacentrics. The Sulawesi animal possesses a derived chromosomal configuration compared with what I interpret to be a primitive karyotype that is retained by the Australian rat. No chromosomal evidence suggests a close phylogenetic relationship between *Hydromys* and *Echiothrix.*

Among the other Indo-Australian murids—aside from *Hydromys*—whose karyotypes have been described and published, the only ones with chromosomal compositions remotely similar to that possessed by *Echiothrix* are three species of *Maxomys.* A diploid number of 36, fundamental number of 71 (72 in females), autosomal set of all biarmed chromosomes, metacentric X chromosome, and telocentric Y characterize *M. whiteheadi* from the Malay Peninsula (Yong, 1969). *Maxomys inas,* also from the Peninsula, has a diploid number of 42, fundamental number of 83 (84 in females), 20 autosomal pairs of biarmed chromosomes (10 metacentrics and 10 submetacentrics), metacentric X chromosome, and telocentric Y (Yong, 1969). The Sulawesian *M. hellwaldii* has a diploid number of 34, a fundamental number of 61 (62 in females); an autosomal cluster consisting of four pairs of metacentrics, seven pairs of submetacentrics, two pairs of subtelocentrics, and three pairs of telocentrics; a subtelocentric X chromosome and telocentric Y (Musser, in prep.). In all the other species of *Maxomys* sampled to date (*M. bartelsii, M. moi, M. rajah,* and *M. surifer*), telocentric chromosomes form a significant portion of the autosomal karyotype (Yong, 1969; Duncan and Van Peenen, 1971; Van Peenen et al., 1974; Markvong et al., 1973).

These chromosomal resemblances between *Echiothrix* and *Maxomys* are gross; at more refined levels the similarities vanish. No species of *Maxomys,* for example, has an autosomal composition of mostly submetacentric chromosomes. Homologies among chromosomes of the two groups are just a guess without banding patterns, and it is unknown if the biarmed elements result from fusion of telocentric chromosomes, the addition of heterochromatin, or a combination of both processes. Without further information, the karyotypic resemblances between *Echiothrix* and *Maxomys* are interesting but essentially uninformative; the chromosomal

composition of *E. leucura* remains distinctive, possibly highly derived, and enigmatic in the context of its significance for phylogenetic inference.

Karyotypes of the two endemic Sulawesian murids reported here provide a window through which we can view possible phylogenetic relationships between them and other species, those indigenous to Sulawesi and those occurring elsewhere. But the window is small and the view cramped. In its low diploid number (40), high fundamental number (75), and autosomal component of mostly biarmed chromosomes, the karyotype of *Echiothrix leucura* is strikingly different from that of *Haeromys minahassae,* which is characterized by a higher diploid number (48), lower fundamental number (54), and predominantly uniarmed autosomes. The two karyotypes share only the metaphorical similarity of being mirrors, one reflecting the specialized essence of the shrew rat, the other the primitive nature of the tree mouse. Images of their closest relatives and their evolutionary histories remain unformed and cloudy.

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