

A NEW SPECIES OF GYMNURE, *PODOGYMNURA*,
(MAMMALIA: ERINACEIDAE) FROM
DINAGAT ISLAND, PHILIPPINES

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Abstract.—A new species, *Podogymnura aureospinula*, of Philippine gymnure is described from Dinagat, a small island off the northeast coast of Mindanao in the southern Philippines. This species is distinguished from other members of the subfamily by the possession of spiny pelage, inflation of the frontal region, and presence of a distinct cusp at the base of the talonid notch. This new species is second in size among the living Echinoricinae only to *Echinosorex gymnurus*. The relationship of *Podogymnura* to the other extant genera of echinosoricines is discussed. Based on these comparisons, *Podogymnura* and *Echinosorex* are shown to share a number of cranial and dental characters and are considered to be more closely related to one another than either is to *Hylomys* or *Neotetracus*.

In 1972 and 1975, Dioscoro S. Rabor and a field party from Mindanao State University collected mammals and birds on Dinagat and Siargao islands, which are located off the northeast coast of Mindanao in the southern Philippines. The itinerary, habitat descriptions, and a report on the birds from the 1972 trip may be found in duPont and Rabor (1973), and a report on the mammals in Heaney and Rabor (1982). Specimens from this collection are housed in the Delaware Museum of Natural History, University of the Philippines at Los Banos, and the U.S. National Museum of Natural History. Among the mammals collected on Dinagat are four specimens of a unique member of the family Erinaceidae. In this paper, we describe these specimens as a new species and discuss the relationships of the Philippine gymnures, *Podogymnura*, within the erinaceid subfamily Echinoricinae.

Methods

External measurements were taken from collector's labels. Cranial measurements (Table 1) were taken by Heaney with dial calipers graduated to 0.1 mm. Dental measurements (Table 2) were taken by Morgan using an Anderson craniometer attached to a Bausch and Lomb binocular microscope (Anderson 1968). All cranial measurements are as defined in DeBlase and Martin (1974) except the following: rostral length, from midline at anterior tip of nasals to orbital margin of infraorbital canal; rostral breadth, taken at labial edge of premaxillae just posterior to I³; post-palatal depth, depth of cranium measured at the point just posterior of palate to point above at 90° to occlusal plane of molars; I¹ to M³, maximum labial length from anterior edge of I¹ alveolus to posterior edge of M³ at alveolus; M² to M², greatest width of palate taken at labial margin of alveoli; palatal width at M³, alveolar distance between lingual margins; height of coronoid, maximum vertical height from ventral edge of mandible to tip of coronoid process; depth of mandible, vertical height from ventral edge of mandible to alveolar

surface between M_1 and M_2 ; thickness of mandible, distance from lingual to labial edge of mandible taken between M_1 and M_2 . All dental measurements in Table 1 are dimensions of the teeth, not their alveoli, and represent the maximum length and/or width of a specified tooth or of a series of teeth. Dental nomenclature follows Szalay (1969:202). Specimens from the following museums were used in this study (standard acronym follows in parentheses): Delaware Museum of Natural History (DMNH), Field Museum of Natural History (FMNH), University of the Philippines at Los Baños, Museum of Natural History (UPLB), and the U.S. National Museum of Natural History (USNM).

Podogymnura aureospinula, new species

Holotype.—DMNH 4386, adult female, skin and skull. Obtained 23 April 1972 by Dioscoro S. Rabor (original number 259) at Plaridel, Albor Municipality, Dinagat Island, Surigao del Norte Province, Republic of the Philippines. Skin well prepared and in good condition. Skull complete except for zygomatic arches, both of which are broken (Figs. 1, 2).

Referred specimens.—The holotype and one adult male from Balitbiton, Loreto Municipality, Dinagat (UPLB 3753) were examined and measured. Two additional specimens (one male, one female) from Kambinlio, Loreto Municipality, Dinagat, are in the collection at UPLB, but were not examined.

Diagnosis.—Size large; dorsal pelage short and spinous, golden brown color overall; temporal, sagittal, and nuchal crests prominent; frontal region conspicuously inflated; interorbital region strongly constricted; external pterygoid processes large and separated at base from internal pterygoid processes by deep groove; mandibular rami robust; P^2 large; P^4 broad lingually; metaconule prominent on M^1 and M^2 ; metacone present on M^3 ; P_4 with small, but distinct, metaconid; distinct cusp at base of talonid notch between metaconid and entoconid on M_1 – M_3 .

Description.—Size (Tables 1 and 2) large for extant members of subfamily. Dorsal pelage composed of three types of hairs: slate-gray underfur ca. 5 mm in length; stiff, bristly, or spiny hairs, black at base and remainder golden yellow, many with black tips, ca. 15 mm in length; black, spiny hairs, ca. 12 mm in length. Golden spines twice as abundant as black hairs in middle of back. Black spines densest at mid-dorsum, decreasing in abundance laterally, disappearing on sides. Black-tipped golden spines especially common at mid-dorsum, also disappearing on sides. Only golden spines present on sides. Overall color of dorsum golden-brown, with black spines and black-tipped golden spines adding a black speckling. On holotype, golden color distinctly metallic when viewed at proper angle. Other specimens somewhat faded, not as metallic. Ventral pelage lacks spines, grades evenly from dorsal color to brownish-gray over most of venter; throat darker on some specimens. Ventral hairs of two types: soft, gray underfur ca. 5 mm in length, and slightly coarser guard hairs ca. 9 mm in length, gray at base and tipped with light brown. Pelage of rostrum and around eyes short, dense, and spiny. Upper and lower lips clothed in very short, moderately dense, white or light brown fur. Vibrissae dark at base, very light for most of length, up to 55 mm. Rhinarium long, naked, and distinctly bilobed, with nostrils opening laterally. Ears relatively large, appearing naked, but with sparse covering of extremely

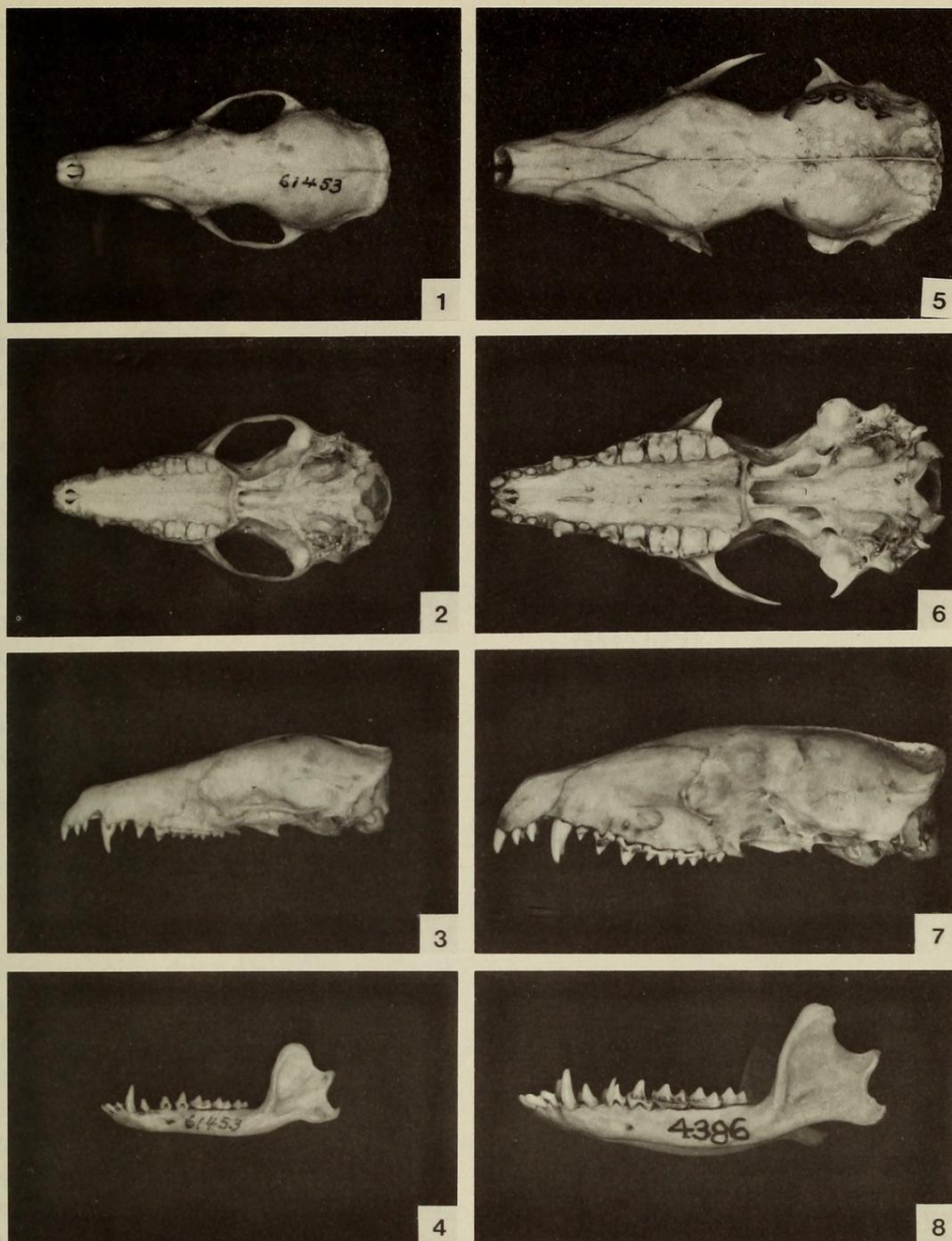


Fig. 1. From top to bottom—dorsal, ventral, and left lateral views of cranium and lateral view of mandible of *Podogymnura truei truei* (FMNH 61453) from Mt. Apo, Davao Prov., Mindanao (1–4) and *Podogymnura aureospinula* (DMNH 4386), holotype, from Plaridel, Dinagat, Surigao del Norte Prov. (5–8). Actual size.

short, white hairs. Fore and hind feet with moderate covering of short, white or light brown hairs dorsally, nearly naked ventrally. Hind legs appear almost naked distal to knee joint. Dorsal base of tail with area sparsely furred, nearly naked, 15 mm in diameter. Tail with sparse covering of short hairs. Two pairs of mammae, one pair pectoral, one pair inguinal.

Skull large and robust. Temporal crests converge at or slightly anterior to

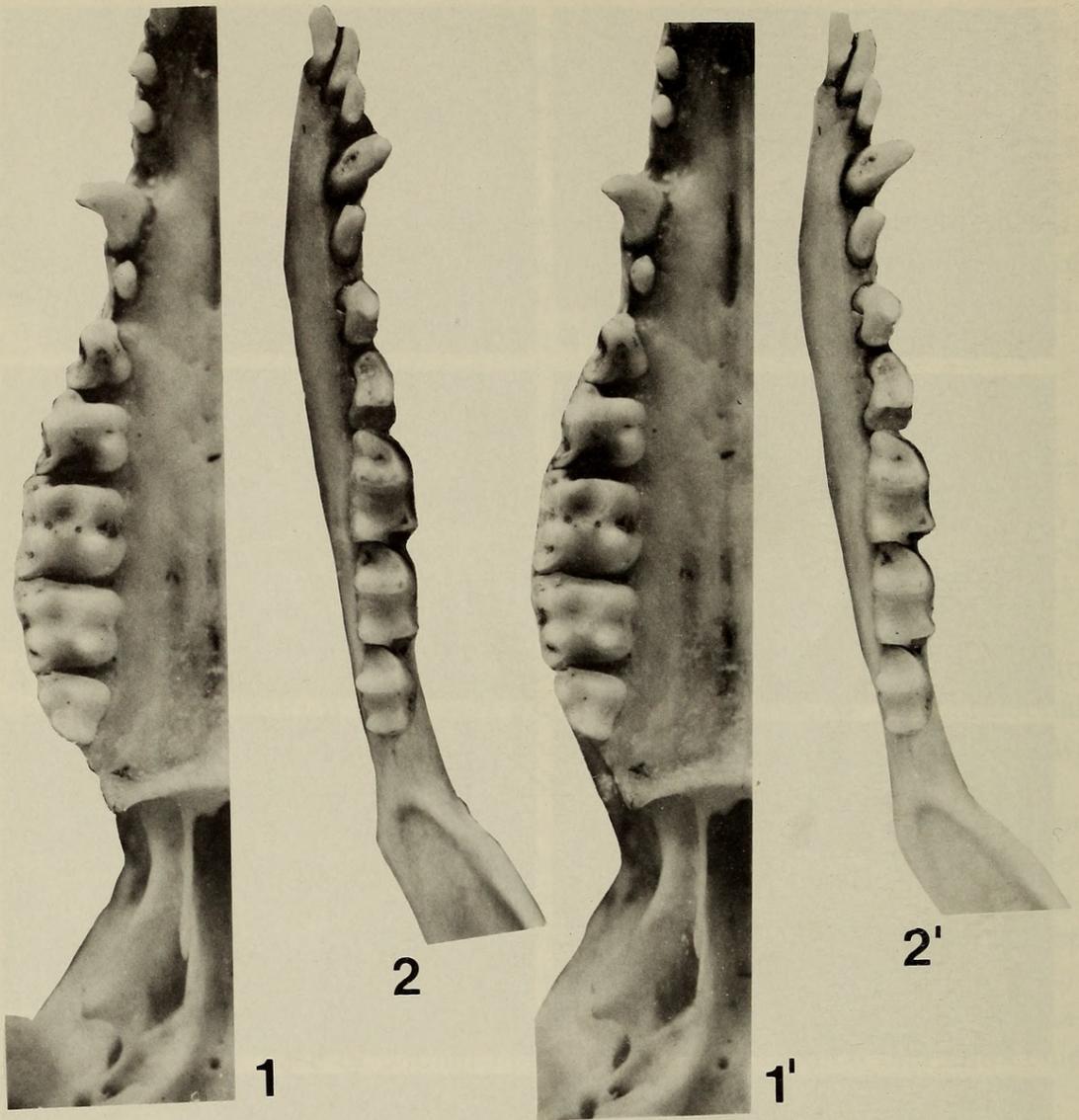


Fig. 2. Stereophotographs of upper (1, 1') and lower (2, 2') dentitions of *Podogymnura aureospinula* (DMNH 4836), holotype. $\times 3$.

interorbital constriction to form sagittal crest. Sagittal crest prominent, 0.5 to 1.0 mm in height anteriorly to 2.5 mm in height posteriorly where it meets nuchal crest. Nuchal crest well developed. Frontal region conspicuously inflated. Frontals expanded laterally into orbital fossa. Rostrum relatively broad posteriorly, resulting from inflation of posterodorsal portion of maxilla. Inflation causing convexity in dorsal profile of skull, beginning at anterior edge of frontals, approximately dorsal to P^3 , and extending posteriorly to interorbital constriction. Highest point on skull dorsal to orbits. Interorbital region constricted. Braincase relatively long and not noticeably inflated. Paroccipital and mastoid processes prominent. Mastoid exposure on ventrolateral corner of skull gently concave and composed of thick bone. Post-tympanic process of squamosal large, broad posteriorly, and with well developed epitympanic sinus. Periotic not inflated. Periotic component of bulla reduced, having a distinct, rounded emargination in ventromedial edge. Basisphenoid component of bulla more vertically oriented, projecting ventral to

level of occipital condyles. Tympanic cavity broadly open ventrally. External pterygoid processes large, triangular-shaped, and separated at base from internal pterygoid processes by deep groove. Mandibular rami relatively thick.

All incisors single-rooted, I^1 enlarged. I^2 and I^3 much smaller, nearly identical in size. Canine double-rooted, long, and flared laterally. P^2 single-rooted, small compared to other premolars. P^3 three-rooted, some specimens with slight lingual expansion and small, but distinct, hypocone. P^4 broad lingually, with hypocone and protocone parallel to palatal midline. Metaconule prominent on M^2 and M^3 , protoconule absent. M^3 relatively large, with small, but distinct metacone. I_1 and I_2 approximately same size, spatulate, and procumbent. I_3 considerably smaller. Canine large and vertical, highest tooth in lower tooth row. P_2 and P_3 comparatively robust, P_2 one-half the size of P_3 . P_4 large, talonid basin moderately to well developed, and distinct metaconid present. Lower molars with small cusp at base of talonid notch between entoconid and metaconid, sometimes absent on M_3 . Postcristid on M_1 and M_2 slopes lingually at hypoconulid to meet moderately to strongly developed postcingulid.

Etymology.—*L. aureus*, golden; *L. spinula*, diminutive of thorn. The specific name refers to the golden spines which characterize the dorsal pelage of this species. We suggest "golden-spined gymnure" as an English name.

Comparisons.—*Podogymnura aureospinula* is more closely related to *Podogymnura truei* than to any other species in the Echinisoricinae as judged by the combination of the following characters: long rostrum, absence of postorbital processes, constricted interorbital region, extreme anterior placement of upper molariform teeth relative to orbit and infraorbital foramen, relatively small I^1 , I^2 and I^3 equal in size, large laterally flaring upper canines, loss of P_1^1 , comparatively large P^3 , and M^1 and M^2 square in outline. On the other hand, *P. aureospinula* possesses at least three derived characters that are unique among the Echinisoricinae: spiny dorsal pelage, conspicuously inflated frontal region, and presence of a cusp at base of talonid notch on lower molars. These characters might justify generic distinction for *P. aureospinula*; however, rather than erect a monotypic genus, we choose to place this new species in the genus *Podogymnura* to indicate the presumed monophyletic nature of the two endemic Philippine erinaceids.

Podogymnura truei is the only echinosoricine which requires detailed comparison with *P. aureospinula*. The other extant echinosoricine genera are compared to *Podogymnura* in more general terms in the Discussion section. *Podogymnura aureospinula* and *P. truei* are quite different in external appearance. Besides its smaller size, *P. truei* has a longer, softer pelage, with no indication of spines, or even coarse hairs. Its underfur is particularly long, about twice as long as that of *P. aureospinula*. The dorsal surfaces of the fore and hind feet of *P. truei* have longer, darker hairs. The overall color of the pelage is darker in *P. truei*; dorsally it varies from reddish to chestnut brown compared to the golden brown color of the large species, and ventrally it is a medium brown, whereas the venter of *P. aureospinula* is gray, with a brownish tinge.

The most obvious difference between the skulls of *Podogymnura aureospinula* and *P. truei* is greater size of the former, its skull being 20% longer than the largest skull of *P. truei* measured (Table 1). Perhaps as a result of allometric changes correlated with increasing skull size, the temporal, sagittal, and nuchal crests and paroccipital and mastoid processes are more prominent in *P. aureo-*

Table 1.—Selected cranial and external measurements of echinosoricines.

Measurements	<i>Podogymnura aureospinula</i> holotype, UPLB 3753	<i>Podogymnura trueti</i> holotype	<i>Podogymnura trueti trueti</i> (N = 5)	<i>Podogymnura trueti minima</i> (N = 3-5)	<i>Echinosorex gymnaurus albus</i> (N = 4-5)	<i>Hylomys suillus dorsalis</i> (N = 8-11)	<i>Neotetracus sinensis</i> (N = 4-7)
Condylobasal length	53.5, 52.2		40.1 ± 1.31 (38.8-42.2)	38.1 (37.2-38.7)	86.9 ± 4.23 (81.6-91.4)	36.1 ± 0.58 (35.1-36.8)	30.2 ± 1.38 (28.4-31.4)
Braincase breadth	18.9, 18.9		16.5 ± 0.57 (16.0-17.4)	15.7 ± 0.06 (15.6-15.7)	26.9 ± 0.13 (26.7-27.0)	15.5 ± 0.39 (15.0-16.2)	13.7 ± 0.28 (13.3-14.0)
Interorbital breadth	11.5, 11.3	9.0	9.5 ± 0.23 (9.3-9.8)	9.3 ± 0.27 (8.9-9.6)	14.1 ± 0.29 (13.7-14.4)	9.6 ± 0.15 (9.5-9.9)	7.6 ± 0.07 (7.5-7.7)
Rostral length	22.5, 21.8	16.3	17.0 ± 0.26 (16.7-17.5)	16.4 ± 0.59 (15.7-16.9)	33.9 ± 4.30 (30.5-41.3)	16.1 ± 0.40 (15.5-16.7)	12.8 ± 0.61 (11.8-13.4)
Post-palatal depth	14.8, 14.6		10.6 ± 0.26 (10.2-10.8)	10.1 ± 0.43 (9.5-10.7)	24.3 ± 1.44 (23.0-26.3)	9.2 ± 0.24 (8.9-9.7)	8.6 ± 0.21 (8.3-8.9)
Rostral width	7.5, 7.8	5.4	5.6 ± 0.11 (5.6-5.8)	5.5 ± 0.21 (5.3-5.7)	13.0 ± 0.43 (12.6-13.6)	5.3 ± 0.16 (4.9-5.5)	5.4 ± 0.18 (5.1-5.6)
Post-palatal length	19.7, 18.5		14.4 ± 0.48 (13.9-15.5)	14.4 ± 0.53 (13.7-14.9)	28.2 ± 0.86 (27.1-29.4)	13.2 ± 0.34 (12.7-13.7)	10.8 ± 0.33 (10.5-11.2)
Mastoid breadth	21.0, 20.2		16.3 ± 0.77 (15.6-17.4)	15.0 ± 0.27 (14.8-15.4)	31.6 ± 1.36 (30.4-32.8)	15.1 ± 0.35 (14.4-15.6)	12.9 ± 0.42 (12.3-13.3)
I ¹ to M ³	27.7, 26.6	19.8	20.5 ± 0.58 (19.9-21.3)	19.8 ± 0.68 (19.1-20.7)	47.1 ± 1.98 (44.9-49.5)	18.7 ± 0.34 (18.3-19.2)	15.7 ± 0.65 (14.6-16.3)

Table 1.—Continued.

Measurements	<i>Podogymnura aureospinula</i> holotype, UPLB 3753	<i>Podogymnura truei truei</i> holotype	<i>Podogymnura truei truei</i> (N = 5)	<i>Podogymnura truei minima</i> (N = 3-5)	<i>Echinosorex gymmnurus albus</i> (N = 4-5)	<i>Hylomys suillus dorsalis</i> (N = 8-11)	<i>Neotetracus sinensis</i> (N = 4-7)
P ¹ to M ³	13.0, 12.6	8.9	9.3 ± 0.29 (9.1-9.7)	9.1 ± 0.39 (8.8-9.8)	22.5 ± 0.79 (21.3-23.1)	8.1 ± 0.15 (7.8-8.4)	7.0 ± 0.15 (6.8-7.2)
M ² to M ² (labial)	15.2, 14.0	10.1	11.0 ± 0.16 (10.8-11.2)	10.6 ± 0.41 (10.1-11.2)	25.1 ± 0.49 (24.5-25.7)	10.8 ± 0.20 (10.6-11.3)	9.8 ± 0.18 (9.6-10.1)
Palatal width (M ³)	8.4, 7.9	5.9	6.5 ± 0.18 (6.3-6.7)	6.2 ± 0.41 (5.7-6.8)	13.6 ± 0.65 (12.7-14.1)	6.8 ± 0.28 (6.5-7.5)	5.7 ± 0.26 (5.4-6.1)
Total length	284, 249	210	201.8 ± 5.2 (196-210)	193.0 ± 16.0 (179-216)	667.4 ± 48.0 (582-695)	165.0 ± 4.1 (157-170)	163.2 ± 8.8 (152-174)
Length of head and body	211, 190	148	143.0 ± 7.1 (134-154)	136.0 ± 11.2 (124-151)	414.4 ± 19.9 (392-445)	143.8 ± 4.0 (134-150)	107.2 ± 4.1 (101-111)
Tail	73, 59	62	58.8 ± 2.6 (56-62)	57.0 ± 5.4 (53-65)	253.0 ± 37.8 (190-285)	21.6 ± 2.8 (17-26)	54.0 ± 8.1 (43-63)
Hind foot	42, 39	36	33.2 ± 0.4 (33-34)	31.5 ± 2.1 (29-34)	72.2 ± 2.6 (69-75)	28.3 ± 1.0 (27-30)	24.0 ± 1.2 (22-25)
Ear	26, 22	19	21.2 ± 0.4 (21-22)	20.1 ± 0.60 (19.5-21)		17.3 ± 0.7 (16-18)	

Table 2.—Selected dental and mandibular measurements (mm) of *Podogymnura* species.

Measurement	<i>Podogymnura aureospinula</i> holotype, UPLB 3753	<i>Podogymnura truei truei</i> holotype	<i>Podogymnura truei truei</i> (N = 5)	<i>Podogymnura truei minima</i> (N = 4-5)
Length of maxillary tooth row	20.6, 20.4	15.2	15.5 ± 0.44 (15.1–16.2)	15.0 ± 0.65 (14.4–15.9)
Length from M ¹ to M ³	9.8, 9.6	6.7	7.1 ± 0.21 (6.9–7.4)	7.0 ± 0.33 (6.6–7.5)
Length of P ³	2.7, 2.5	1.8	1.9 ± 0.11 (1.8–2.1)	1.8 ± 0.08 (1.7–1.9)
Width of P ³	2.4, 1.7	1.1	1.3 ± 0.17 (1.2–1.6)	1.4 ± 0.07 (1.3–1.5)
Length of P ⁴	3.2, 3.0	2.2	2.4 ± 0.05 (2.3–2.4)	2.4 ± 0.11 (2.3–2.6)
Width of P ⁴	3.2, 3.0	2.1	2.4 ± 0.10 (2.3–2.5)	2.4 ± 1.54 (2.2–2.5)
Length of M ¹	3.8, 3.8	2.6	2.9 ± 0.04 (2.8–2.9)	2.8 ± 0.11 (2.6–2.9)
Width of M ¹	3.7, 3.4	2.3	2.7 ± 0.12 (2.6–2.9)	2.6 ± 0.08 (2.5–2.7)
Length of M ²	3.5, 3.5	2.4	2.5 ± 0.11 (2.4–2.7)	2.5 ± 0.16 (2.3–2.7)
Width of M ²	3.7, 3.3	2.4	2.6 ± 0.05 (2.6–2.7)	2.6 ± 0.11 (2.5–2.7)
Length of M ³	2.7, 2.6	1.7	1.9 ± 0.15 (1.7–2.1)	1.8 ± 0.09 (1.7–1.9)
Width of M ³	2.8, 2.8	1.8	2.1 ± 0.08 (2.0–2.2)	2.0 ± 0.11 (1.9–2.1)
Total length of mandible	41.2, 40.8		30.1 ± 0.77 (29.6–31.5)	28.8 ± 0.58 (28.2–29.6)
Height of coronoid	13.9, 13.4	9.2	9.7 ± 0.50 (9.0–10.4)	9.3 ± 0.59 (8.6–10.0)
Depth of ramus between M ₁ and M ₂	4.7, 4.8	3.1	3.3 ± 0.22 (3.0–3.6)	3.2 ± 0.25 (2.8–3.5)
Breadth of ramus between M ₁ and M ₂	2.6, 2.8	1.6	1.8 ± 0.05 (1.7–1.8)	1.7 ± 0.07 (1.6–1.8)
Length of mandibular toothrow	21.4, 20.7	15.8	16.2 ± 0.54 (15.7–17.1)	15.7 ± 0.64 (15.1–16.6)
Length from M ₁ to M ₃	11.2, 10.5	7.8	8.0 ± 0.26 (7.6–8.2)	7.8 ± 0.31 (7.5–8.3)
Length of P ₄	3.0, 2.6	1.9	2.0 ± 0.10 (1.9–2.1)	2.0 ± 0.19 (1.8–2.3)
Width of P ₄	1.8, 1.7	1.1	1.3 ± 0.04 (1.2–1.3)	1.2 ± 0.08 (1.1–1.3)
Length of M ₁	4.3, 4.1	3.0	3.1 ± 0.11 (2.9–3.2)	2.9 ± 0.09 (2.9–3.2)
Width of M ₁	2.5, 2.5	1.7	1.9 ± 0.13 (1.7–2.0)	1.8 ± 0.04 (1.8–1.9)

Table 2.—Continued.

Measurement	<i>Podogymnura aureospinula</i> holotype, UPLB 3753	<i>Podogymnura truei truei</i> holotype	<i>Podogymnura truei truei</i> (N = 5)	<i>Podogymnura truei minima</i> (N = 4-5)
Length of M ₂	4.0, 3.7	2.7	2.8 ± 0.13 (2.6-2.9)	2.7 ± 0.08 (2.6-2.8)
Width of M ₂	2.4, 2.4	1.6	1.8 ± 0.11 (1.7-1.9)	1.8 ± 0.09 (1.7-1.9)
Length of M ₃	3.3, 3.1	2.3	2.3 ± 0.11 (2.2-2.4)	2.3 ± 0.15 (2.1-2.5)
Width of M ₃	2.1, 2.0	1.4	1.5 ± 0.05 (1.5-1.6)	1.5 ± 0.16 (1.3-1.7)

spinula, approaching the condition seen in the much larger *Echinosorex*. In most skulls of *P. truei*, the weak temporal crests meet near the anterior edge of the interparietal, forming a short, weak sagittal crest, while in larger skulls of the same species, the temporal crests meet somewhat farther forward. The temporal crests of *P. aureospinula* converge at or slightly anterior to the interorbital constriction to form the strong sagittal crest, which is particularly high posteriorly where it bisects the interparietal. The nuchal crest of *P. aureospinula* is more strongly developed than in *P. truei*.

Podogymnura truei shows no evidence of the frontal inflation characteristic of *P. aureospinula*. The dorsal margin of the skull of *P. truei* rises in a nearly straight line to reach a maximum height above the glenoid region, rather than dorsal to the orbits as in *P. aureospinula*. The inflation of the frontals and posterodorsal portion of the maxilla of *P. aureospinula* is not characteristic of any other modern echinosoricine, although some erinaceines (e.g. *Paraechinus*) have moderately inflated frontals. The interorbital region appears to be more constricted in *P. aureospinula*, although this feature is certainly enhanced by the inflation anterior to the constriction. The more prominent development of the sagittal and nuchal crests gives the braincase of *P. aureospinula* the appearance of being longer, whereas the braincase of the smaller species appears shorter, broader, and more bulbous, particularly in smaller specimens.

The mastoid exposure on the posterolateral corner of the skull is inflated in *Podogymnura truei* and the bone is thin and nearly transparent. The mastoids of *P. aureospinula* are gently concave and composed of thicker bone. The periotic of *P. truei* is also inflated. The periotic is not inflated in *P. aureospinula* and the periotic component of the bulla has a small, rounded emargination in its ventromedial edge which is lacking in the smaller species. The basisphenoid portion of the bulla of *P. aureospinula* is more vertically oriented, projecting ventral to the occipital condyles, whereas the basisphenoid bulla of *P. truei* is more horizontal, tending to enclose the tympanic cavity. Coupling the more vertical orientation of the basisphenoid bulla with the reduced periotic portion of the bulla, the tympanic cavity is more open ventrally in *P. aureospinula*. The post-tympanic process of the squamosal is relatively larger in *P. aureospinula* than in any other modern echinosoricine. Its external pterygoid processes are also relatively large, but these are smaller in *P. truei*. *Podogymnura aureospinula* has a deep groove at the base

of the external pterygoid processes which separates them from the internal pterygoid processes. There is no evidence of this groove in any specimen of *P. truei* examined. As with the skull, the mandible of *P. aureospinula* is larger and more robust than that of its smaller counterpart. The mandibular rami are particularly thickened in *P. aureospinula*.

The upper incisors and canines of *Podogymnura aureospinula* and *P. truei* are similar in morphology. The P² is somewhat longer and broader in *P. aureospinula*; it is more conical in *P. truei*. In most specimens of *P. truei*, the P³ is two-rooted, thin, and blade-like, with no indication of a protocone or hypocone. Butler (1948) stated that the P³ of *Podogymnura* had only two roots; however, the larger series of specimens now available shows this character to be variable. Most specimens of *P. truei* have a two-rooted P³, but the few that have a slight lingual expansion of P³ have three roots. The P³ of *P. aureospinula* is three-rooted, and bears a small hypocone. The P⁴ of *P. aureospinula* is broader lingually, the hypocone is larger, and the protocone is higher and more lingually placed. In comparison, the P⁴ in the smaller species is rather narrow lingually, the hypocone is small, and the protocone is located closer to the paracone. The M¹ and M² are similar in the two species, except for the more prominent metaconule and cingula in *P. aureospinula*. The M³ of *P. aureospinula* is larger and bears a small metacone, the latter being absent on the M³ of *P. truei*.

As in the upper dentition, the P₂ and P₃ are relatively larger and more robust in *P. aureospinula* than in *P. truei*. The talonid basin is reduced on P₄ in *P. truei* and a metaconid is absent or tiny. The P₄ of *P. aureospinula* has a moderately to well developed talonid basin and the metaconid is distinct. The morphology of the lower molars is similar in the two species. *P. aureospinula* has a small, distinct cusp located at the base of the talonid notch between the entoconid and metaconid on M₁, M₂, and sometimes M₃. The entoconulid is normally located slightly anterior to, but close to the entoconid, and therefore this cusp does not appear to be homologous with an entoconulid. This cusp is absent in *P. truei* and seems to be unique among modern echinosoricines.

Ecology.—Virtually nothing is known of the natural history of *Podogymnura aureospinula*. The vicinity where the holotype of *P. aureospinula* was taken was described by duPont and Rabor (1973:4) as “. . . a logged area in rolling country and low hills where there were still many patches of remnant dipterocarp forests in the surrounding localities.” These forests are dominated by *Dipterocarpus*, *Shorea*, *Hopea*, *Anisoptera*, and *Pentacme* among the Dipterocarpaceae, and include members of at least eleven other plant families. Undergrowth consists mainly of rattan and ferns. Other terrestrial mammals taken at the type locality of *P. aureospinula* include *Urogale everetti*, *Tarsius syrichta*, *Cynocephalus volans*, *Sundasciurus mindanensis*, *Exilisciurus surrutilus*, *Batomys* sp., *Rattus everetti*, and *Rattus rattus* (Heaney and Rabor 1981).

Additional specimens examined.—*Podogymnura truei truei* (2 ♂♂, 4 ♀♀). PHILIPPINES, Mindanao, Davao Province: E slope of Mt. McKinley, 5800 ft. elev., FMNH 56129, 56172, 56181; N slope of Mt. Apo, Lake Linau, 7800 ft. elev., FMNH 61435; E slope of Mt. Apo, Baclayan, 5400 ft. elev., FMNH 61453; Mt. Apo, 6000 ft. elev., USNM 125286 (holotype).

Podogymnura truei minima (2 ♂♂, 3 ♀♀). PHILIPPINES, Mindanao, Bukidnon Province: Mt. Katanglad, near Malay Balay, DMNH 5949-5953.

Echinosorex gymnurus albus (1 ♂, 4 ♀♀). INDONESIA, Borneo, Sempang River: USNM 145581–582, 145584–586.

Hylomys suillus dorsalis (10 ♂♂, 1 ♀). MALAYSIA, Borneo, Sabah, Mt. Kinabalu, Bundu Tuhan: USNM 292337–339, 292341–342, 292350–354, 292356.

Neotetracus sinensis (1 ♂, 2 ♀♀, 4?). CHINA: Yunnan, Ho mu shu Pass, USNM 241402; Szechuan, Kwan Shien, 3000 ft. elev., USNM 258124–129.

Discussion

The genus *Podogymnura* and its type species, *P. truei*, were described by Mearns (1905) from a single specimen collected on Mount Apo, south-central Mindanao, in the Philippines. Until the late 1940's, this specimen, an adult female consisting of a complete body in alcohol and a skull lacking the zygomatic arches and braincase, was the only known specimen of the genus. Mearns provided a detailed description of the external characters of *P. truei* but he did not illustrate the cranium or mandible and his description of them was brief. He described the dentition of *P. truei*, comparing it with that of *Hylomys*, but his descriptions and comparisons are so general that they are of little use. Lyon (1909) noted that although *Podogymnura* and *Hylomys* appeared to be closely related with respect to size and external characters, they were distinct dentally. Cabrera (1925) provided a key to the living echinosoricine genera in which he distinguished *Podogymnura* by the combination of loss of P_1^1 , P^3 larger than P^2 , and larger upper canines. Butler (1948) regarded *Podogymnura* as intermediate between *Echinosorex* and the smaller *Hylomys* and *Neotetracus*, although he pointed out that in the enlargement of the canines, relatively large P^3 , length of the rostrum, and position of P^4 and M^1 relative to the orbit and infraorbital foramen, *Podogymnura* is similar to *Echinosorex*.

Sanborn (1952) reported on 64 specimens of *Podogymnura truei* collected on Mount Apo and Mount McKinley on Mindanao. He compared *Podogymnura* to the other genera of modern echinosoricines, reaching the same general conclusion as did Butler. Sanborn (1953) described a new subspecies of *Podogymnura truei*, *P. t. minima*, from four specimens collected on Mount Katanglad, Bukidnon Province, north-central Mindanao. His diagnosis was based exclusively on the smaller size of *P. t. minima*. Detailed cranial and dental measurements of *P. t. truei* (including the type) and topotypic specimens of *P. t. minima* (Tables 1 and 2) indicate that, on the whole, the available specimens from Mount Katanglad are slightly smaller than specimens from Mount Apo and Mount McKinley, but there is broad overlap in size between them, especially in dental measurements. In fact, the teeth of the type specimen of *P. t. truei* from Mount Apo are actually smaller in many dental measurements than the teeth of the topotypic specimens of *P. t. minima*. Sanborn specifically noted that there was no difference in color between his series of *P. t. minima* and the nominate form. The DMNH specimens of *P. t. minima*, however, are lighter in color than topotypic specimens of *P. t. truei*, being slightly more reddish brown and having the tail uniformly lighter. Besides the references cited above, Hollister (1913), Taylor (1934), and Alcasid (1970) mentioned *Podogymnura*, but provided no new information.

Comparison of Podogymnura with other living echinosoricines.—Butler (1948) made exhaustive comparisons of three of the five extant genera of echinosori-

cines: *Hylomys*, *Neotetracus*, and *Echinosorex*. His comparisons of *Podogymnura* were general, as they were based solely on published descriptions and figures of the type of *P. truei*, the only specimen of the genus known at that time. The fifth living genus of echinosoricine, *Neohylomys*, was not described until 1959. Since 1948 many specimens of *Podogymnura* have been collected, but the genus has not been adequately compared with the other members of its subfamily. Our description of a new species of *Podogymnura*, which in some characters appears to bridge the morphological gap between *Podogymnura* and *Echinosorex*, calls for fuller comparisons and a reassessment of the phylogenetic relationships of the Philippine gymnures.

As Butler (1948) and others have noted, *Hylomys* and *Neotetracus* are closely related forms, although in our opinion they do represent distinct genera, contrary to Van Valen (1967). The status of *Neohylomys* is uncertain; the only specimens are in China, and unavailable for study. Many of the characters unique to *Hylomys* and *Neotetracus*, such as the reduced antemolar dentition, the palatal perforations, the presence of posterior processes of the maxillae and anterior processes of the parietals which extend across the frontals and meet or nearly meet dorsal to the orbits, the prominent flange on the anterior edge of the orbit, and the strongly concave anterior portion of the zygomatic arch for attachment of the lateral snout muscles, are derived characters which demonstrate a close phylogenetic relationship between the two genera. Conversely, many of the characters that are shared by *Podogymnura* and *Echinosorex*, but are not present in the other two genera, appear to be primitive for the Echinosoricinae. Of these characters, the longer rostrum, better developed maxillary dentition anterior to P⁴, widely separated maxillae and parietals dorsal to the orbits, and the nonperforated palate are certainly primitive. In the remaining characters shared by *Podogymnura* and *Echinosorex*, it is difficult to determine the primitive character state for the Echinosoricinae because no appropriate outgroup exists. Butler (1948) felt that the two distinct groups of living echinosoricines represented two separate specialized offshoots from the primitive condition. Suffice it to say that *Podogymnura* and *Echinosorex* share so many cranial and dental features that they undoubtedly represent closely related genera.

Although they share many cranial characters, *Podogymnura* and *Echinosorex* are extremely different externally. *Echinosorex* is a larger animal with a tail equal to about 60% of the length of head and body. *Podogymnura* is medium-sized (*P. aureospinula*) or small (*P. truei*) and has a tail equal to about 35% of the length of head and body. *Podogymnura* is a chestnut brown (*P. truei*) to golden brown (*P. aureospinula*) color and has relatively short pelage. *Echinosorex* is either pure white (*E. gymnurus albus*) or predominantly black with white markings on the neck and face (all other forms of the species) and has long, coarse guard hairs on the dorsum. Based on its external appearance, especially its small size and short tail, *Podogymnura truei* more closely resembles *Hylomys* and *Neotetracus* than *Echinosorex*.

Additional cranial characters shared by *Podogymnura* and *Echinosorex* not listed above include: well developed canines and P³, small supraorbital crests, presence of two longitudinal grooves in maxillary component of hard palate which extend from incisive foramina to small foramina located medial to P² or P³, pres-

ence of a ventral process on maxillary portion of zygomatic arch, and more anterior placement of upper cheek teeth relative to orbit and infraorbital foramen. The tympanic bone is slender and not firmly attached to the bulla in *Podogymnura* and *Echinosorex*, whereas in *Hylomys* and *Podogymnura* the tympanic is broader and is firmly attached to the edge of the bulla, contributing to its formation and restricting the size of the opening of the tympanic cavity. Although Butler (1948) stated that *Echinosorex* lacked the anterior process of the tympanic, the large series of echinosoricines at our disposal reveals that both *Echinosorex* and *Podogymnura* definitely have an anterior process, but it is smaller than that of *Hylomys* and *Neotetracus*.

In addition to the differences in external morphology cited above, there are a number of cranial and dental characters that are diagnostic of *Podogymnura* and distinguish it readily from *Echinosorex*. These include: less prominent temporal, sagittal, and nuchal crests and mastoid and paroccipital processes; more concave maxillary portion of zygomatic arch; broader, more inflated braincase; more anterior placement of upper molars relative to orbit and infraorbital foramen (M^2 is anterior to front edge of orbit and M^1 is below infraorbital foramen); smaller I^1 ; I^2 and I^3 equal in size; canines relatively larger and flared laterally; loss of P_1^1 ; M^1 square in outline; absence of protoconule on M^1 ; smaller metaconule on M^1 and M^2 ; reduced posterolingual apex of M^3 .

Podogymnura aureospinula is intermediate between *Echinosorex* and *P. truei* in many characters, although some of the characters on which this observation is based are probably related to its intermediate size. The more prominent temporal, sagittal, and nuchal crests and mastoid and paroccipital processes of *P. aureospinula* relative to *P. truei* are almost certainly correlated with its greater size. These features of the bony crests and processes are best developed in *Echinosorex*, the largest genus among living echinosoricines, and are likely to be allometric changes associated with increasing skull size. Other intermediate characters of *P. aureospinula* which are more difficult to ascribe to allometry are the larger P^3 , more prominent metaconule on M^1 and M^2 , the presence of a metacone on M^3 , and the deep groove separating the bases of the external and internal pterygoid processes. Whether these are derived characters indicating a closer relationship between *Echinosorex* and *P. aureospinula* or whether these represent primitive characters shared by *Echinosorex* and *P. aureospinula* and lost by *P. truei* cannot be determined from available data. Regardless of the similarities between *P. aureospinula* and *Echinosorex*, the two species of *Podogymnura* are certainly more closely related to one another than either is to *Echinosorex* and have probably been isolated in the Philippines for a considerable period of time.

Acknowledgments

We wish to thank M. D. Carleton, P. Myers, and R. W. Thorington for valuable comments on the manuscript, and G. Lake and S. F. Campbell for assistance in preparation of the manuscript and tables. Photographic assistance was provided by D. Bay and V. Krantz. We thank P. Freeman, D. Niles, D. S. Rabor, R. W. Thorington, and R. M. Timm for permission to examine specimens under their care.

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