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A review of the spiny mouse genus *Scolomys* (Rodentia: Muridae: Sigmodontinae) with the description of a new species from the western Amazon of Brazil

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Abstract.—Included within a collection of mammals assembled during a year-long vertebrate survey of the Rio Juruá in the western Amazon Basin of Brazil is a series of specimens of a new spiny mouse of the genus *Scolomys*. This genus is one of the more highly-localized and poorly-known murid rodents of the neotropical forests. Prior to the collection reported here, there were two recognized species known from a total of 15 specimens. One of these, *S. melanops* Anthony, 1924, is known only from three closely spaced localities in eastern Ecuador; the second, *S. ucayalensis* Pacheco, 1991, is known from only one locality in north-central Perú. We provide a revised diagnosis and description of the genus while describing the third species, suggest phylogenetic affinities of the genus within the tribe Oryzomyini, and summarize aspects of the ecology and life history of the new species.

Resumo.—Um novo catito de espinho (gênero *Scolomys*) foi coletado durante um levantamento da fauna de vertebrados realizado no rio Juruá, no oeste da Amazônia brasileira. Este gênero de roedores murídeos neotropicais foi pouco estudado e possui uma distribuição geográfica muito restrita. Somente duas espécies eram até então conhecidas: uma do leste do Equador (*S. melanops* Anthony, 1924; 13 espécimes provenientes de três localidades) e outra do norte do Peru (*S. ucayalensis* Pacheco, 1991; dois espécimes provenientes de uma localidade). Neste estudo nós descrevemos uma terceira espécie e apresentamos uma revisão aumentada da diagnose e descrição do gênero. Também sugerimos afinidades filogenéticas dentro da tribo Oryzomyini, além de sumarizarmos pela primeira vez aspectos da ecologia e história natural desses animais.

The genus *Scolomys* contains small-bodied and strongly spinose mice of the tribe Oryzomyini Vorontsov, 1959 (sensu Voss & Carleton 1993) of the South American Sigmodontinae (Muridae) rodents. Each of the two known species has a very localized distribution in the forests of western Amazonia. The genus was described in 1924 by H. E. Anthony and the type species, *S. melanops*, is known from a total 13 specimens from three nearby localities in east-central Ecuador. A second species, *S. ucayalensis*, was recently described by Pacheco (1991) based on two specimens from a single locality in north-central Perú.

We have obtained a series of 23 specimens from four localities along the Rio Juruá in the lowland Amazonian forest of western Brazil (states of Amazonas and Acre) that represents a third species of this poorly-

known genus. Based on these new materials and an examination of most other specimens, we provide an expanded diagnosis and description of the genus and describe the new species here. We also compare *Scolomys* to the sympatric and superficially similar oryzomyine genus *Neacomys* as well as to other oryzomyine genera, provide remarks on phyletic relationships based on morphological characters and comparative DNA sequences, and summarize what few facts are available on life history and ecology.

Scolomys Anthony, 1924

Type species.—*Scolomys melanops* Anthony (1924:2).

Emended diagnosis.—Members of the tribe Oryzomyini (sensu Voss & Carleton 1993) of the murid rodent subfamily Sigmodontinae (sensu Carleton & Musser 1984) with 3 pairs of mammae (1 thoracic, 1 abdominal, and 1 inguinal [following position designations given by Voss & Carleton 1993; Anthony (1924) recorded mammae as 1 pectoral, 2 inguinal]). Pelage comprised of short, stiff spines on both dorsum and venter with equal-length normal hairs interspersed throughout, giving general spiny appearance over entire body. Skull with short and blunt rostrum flanked by shallow zygomatic notches; supraorbital margins rounded, forming a moderately-developed shelf overhanging posterior half of orbit, and extending onto braincase as ridges; braincase rather globular in shape; interparietal large and well-developed; palate long and wide, with well-developed and complex posterolateral pits, but with rather short and posteriorly broadened incisive foramina; alisphenoid strut absent; carotid arterial circulation of Pattern 3 (of Voss 1988); subsquamosal fenestra reduced to totally occluded, tegmen tympani either not in contact with or only touches, but does not overlap, squamosal; incisors small, narrow, proodont to orthodont; upper and lower molars small, pentalophodont, but with low cusps that wear quickly with age; procingulum of M1 undivided by anteromedial flexus; labial flexi deeply penetrating in all molars; lingual flexi reduced in size in M1 and M2 and obsolete in M3; upper and lower molars with well-developed mesoloph(id)s; stomach unilocular and hemiglandular; male phallus cylindrical with incomplete crater rim, terminally exposed urethral flaps, lateral mounds of distal baculum hidden by tissue of crater rim, and an epidermis with small and widely-spaced spines.

Description.—Body pelage short and close, with texture markedly spinose both above and below; color ranges from grizzled pale reddish-black to nearly totally black dorsally and gray ventrally; dorsal hairs of two types: (1) long (averaging 12 mm), stout, flat, and broad (averaging 0.6 mm) spines with a medial trough on both surfaces, with the terminal ⅓ to ¼ increasingly dark to the tip and proximal portion clear; and (2) long, thin hairs of length equal to spines and with tips reddish or blackish; ventral hairs of both types uniformly gray from base to tip. Mystacial, superciliary, genal I, submental, interramal, and carpal vibrissae present. Pinnae small, appearing somewhat thickened and thus stiff, and, while appearing naked from a distance, are clothed externally and internally with short reddish-brown hairs. Manus with five large, fleshy plantar pads (two carpal and three interdigital); toes pale in color; digit I reduced but with a small nail, digits II through V long and well-developed with short, stout, and curved claws. Pes rather short and broad, although metatarsus is nearly twice as long as digit III; the heel is haired and the naked sole begins at about ¼ the length of the plantar surface (not including the digits); outer digits shorter than the middle three (with the claw of I extending to or just past the base of II and that of V to the proximal phalax of IV); conspicuous tufts of long, silvery hairs present at dorsal bases of claws extending past the tips, but the claw is visible from above;

Fig. 1. Photograph of a living *Scolomys juruaense,* new species (INPA 2490, Barro Vermelho, left bank Rio Juruá, Amazonas, Brazil).

claws short, stout (about twice as long as deep) and strongly curved along their dorsal surface; plantar pads five to six (thenar and four interdigital pads large, fleshy, and always present; hypothenar pad either absent or only weakly developed). Tail shorter than head-and-body, appearing sparsely haired, without a terminal tuft or pencil of long hairs; 15–18 scale annuli per cm at mid-length; annular hairs broad, blackish, and 2.5–4 scale rows in length, but sparsely distributed so that the tail scales are conspicuous. The overall impression is of a small-bodied, short-tailed, and short-eared mouse with a broad head, but short and pointed rostrum and very spiny fur (Fig. 1).

Skull, in dorsal view, with short and broad or tapering rostrum flanked by shallow, barely perceptible zygomatic notches; nasolacrimal capsules expanded (especially so in *S. melanops,* Fig. 2); interorbital region broad and hourglass-shaped, with well-defined beaded ledges overhanging margins from middle of frontals, continuing along posterior margins of orbit and onto braincase just above the squamoso-parietal suture as weakly to moderately-developed temporal ridges. Braincase distinctly rounded and globular in appearance, dominating dorsal aspect of skull (length of braincase ½ length of skull). Nasals somewhat expanded and taper posteriorly to a median point that terminates well behind the premaxillary-frontal sutures. Interparietal large, ½ to ⅓ as deep as wide.

In lateral view, nasals extend only to or just barely beyond anterior curvature of incisors. Zygomatic plate narrow, vertical to slightly angled posteriorly from base, and without distinct, free dorsal edge (thus, the zygomatic notch is shallow when viewed from above). Zygomatic arch thin with jugal reduced. Postglenoid foramen moderate to small; hamular process of squamosal stout;

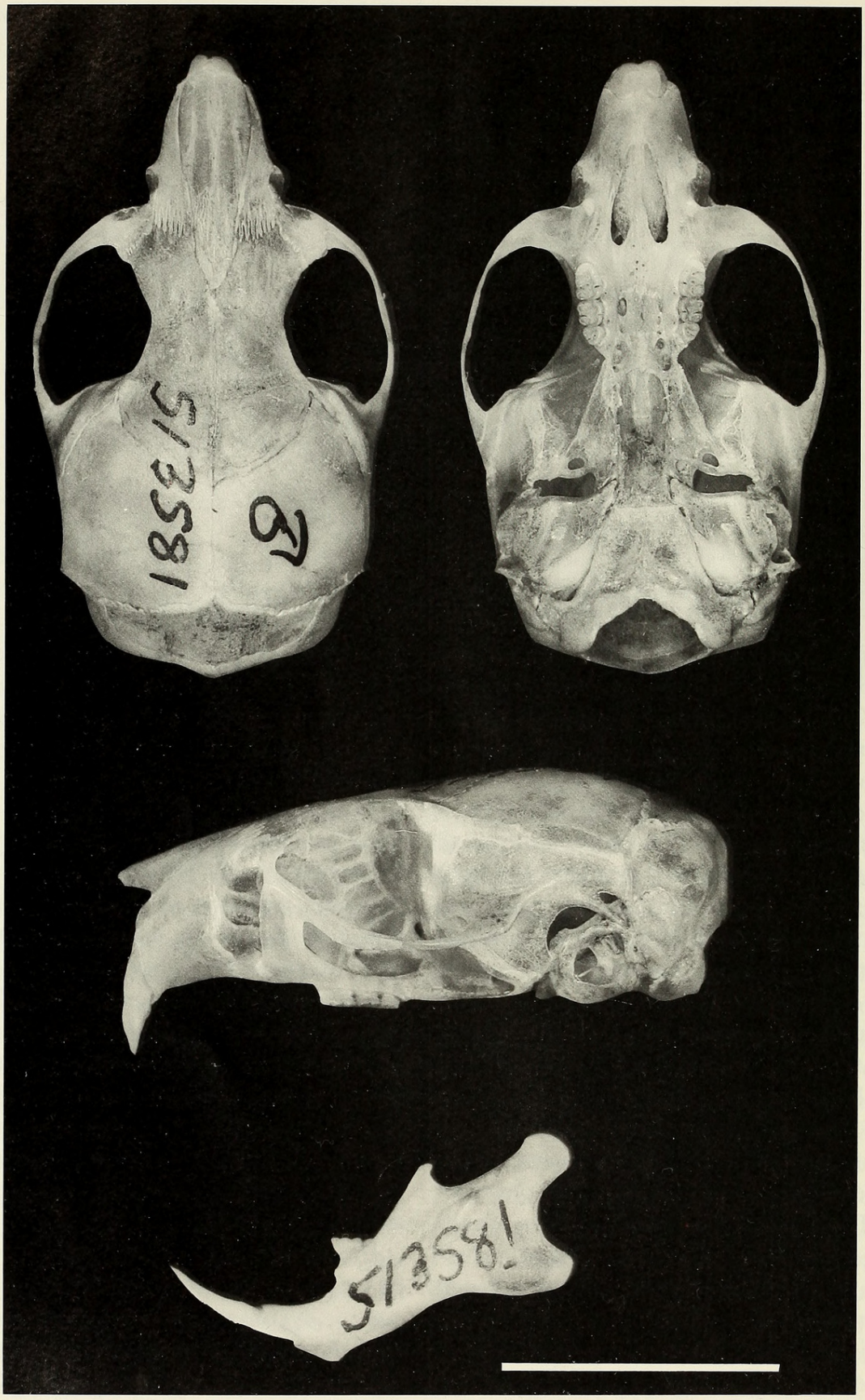

Fig. 2. Dorsal, ventral, and lateral views of cranium, lateral view of left mandible of *Scolomys melanops* Anthony, USNM 513581, adult male. Scale bar equals 10 mm.

subsquamosal foramen reduced to totally occluded; mastoid fenestra very small to lacking. Tegmen tympani of periotic either does not contact or abuts, but does not overlap, the squamosal. Tympanic bullae small and inflated ventrally only to level of molar series.

In ventral view, incisive foramina moderate in size (occupying about 60% of diastemal distance) and distinctly tear-drop in shape, pointed anteriorly with diverging sides and expanded, rounded posterior margins; premaxillary-vomerine septum greatly swollen and nearly filling the entire cavity when viewed ventrally. Bony palate long and wide (sensu Hershkovitz 1962), without a medial ridge or palatal excrescences, with only weakly evident lateral folds, but with large and complex posterolateral pits. The mesopterygoid fossa wide with parallel sides and a rounded or squared anterior margin, ending well behind the third molars; bony roof of fossa complete, or perforated only by barely perceptible sphenopalatine vacuities along the presphenoid. Parapterygoid fossae well developed, with lateral margins straight to slightly convex and strongly divergent towards the bullae, devoid of vacuities except for a small foramen ovale, and moderately excavated, certainly not flat in appearance. Alisphenoid strut absent, but only foramen ovale is present laterally; without anterior opening of alisphenoid canal. A shallow trough where the masticatory-buccinator branch of the maxillary nerve courses visible; it emanates from anterior margin of the foramen ovale and obliquely crosses the alisphenoid onto the squamosal. Facial circulation apparently derived only from the internal carotid artery (Pattern 3, of Voss, 1988), as indicated by a greatly reduced to absent stapedial foramen, no squamoso-alisphenoid groove along interno-lateral wall of braincase, and no sphenofrontal foramen (signs of supraorbital branch of stapedial artery).

Mandible short and stout; coronoid process short with a weakly to moderately-curved posterior projection; capsular processes of lower incisor alveoli weakly developed; lower incisors thin, elongate, with enamel essentially devoid of pigment. Upper incisors ungrooved, with yellow to pale yellow enamel; small, deeper than wide, and proodont (*S. melanops,* Fig. 2) to orthodont (*S. ucayalensis* and the new species described below).

Maxillary tooth rows slightly convergent posteriorly, and angled obliquely downward and outward at about a 40 degree angle. Teeth of nearly all known specimens moderately to well-worn, and, as the cusps are low, even a little wear obscures surface topography. Molars small, always longer (anteriorly–posteriorly) than wide, and forming a graded series with the third molar greatly simplified. Upper teeth pentalophodont with principal cusps arranged transversely and slightly obliquely; labial and lingual reentrant folds do not interdigitate, or contact, with major labial folds of M1 and M2 (paraflexus and metaflexus) deep, extending at least ⅔ across the tooth, lingual folds reduced, with protoflexus only evident as a shallow lateral indentation in M1 and not visible at all in M2. Procingulum of M1 and m1 well-developed but not divided into separate anterolabial and anterolingual conules (no anteromedial flexus [-id]); anteroflexus on M1 absent so that anteroloph not separated from labial anteroconule; anteroloph of M2 well developed; distinct mesolophs present and extending to labial margin of all three molars; posteroloph well developed on M1 but barely perceptible on M2 and absent on M3. Paracone and metacone of M1 and M2 tall and well developed with protocone and hypocone proportionately reduced in size and much lower in topography; only paracone and weakly-developed protocone present on M3.

Content and distribution.—The genus *Scolomys* comprises two described species, the known ranges of which are geographically restricted within the western Amazon Basin (Fig. 3). The type species, *S. melan-*

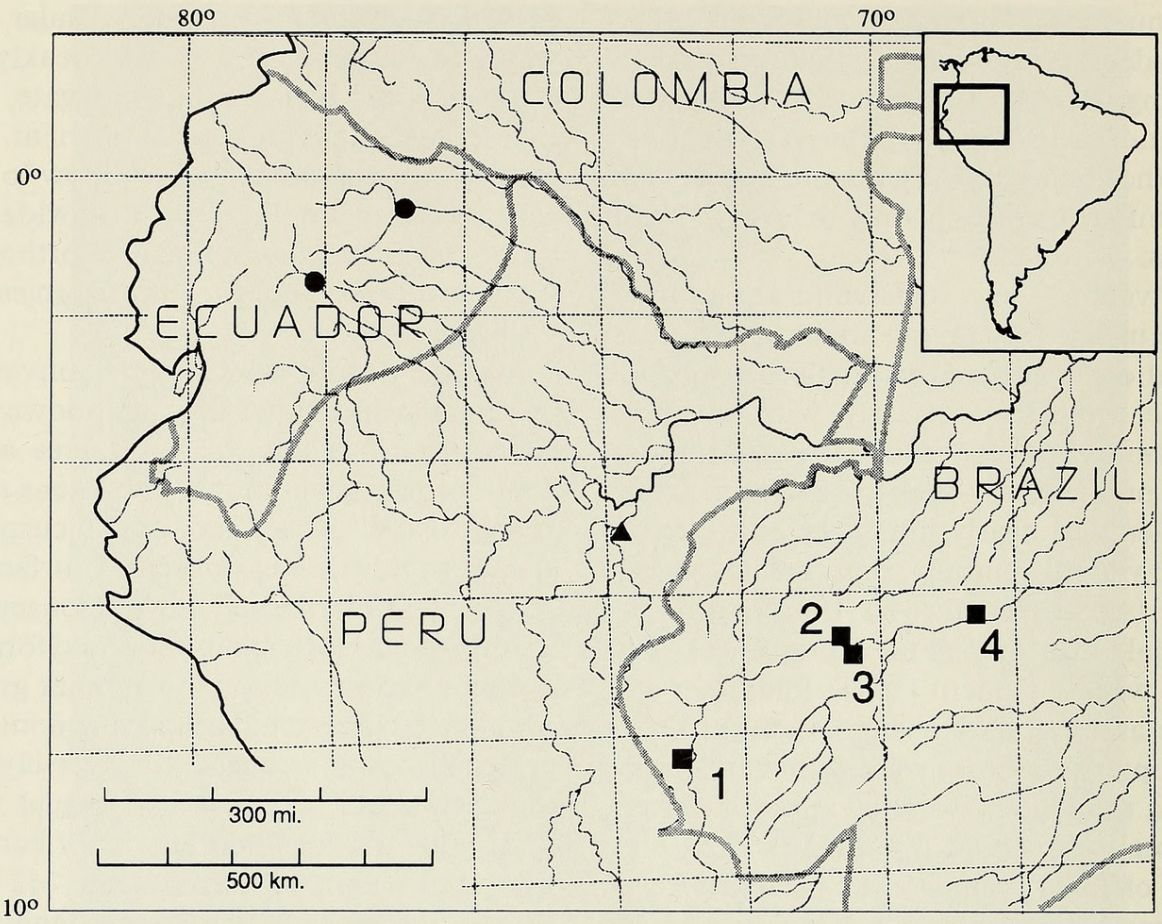

Fig. 3. Distributional records of spiny mice, genus *Scolomys*. Circles = *S. melanops* Anthony, triangle = *S. ucayalensis* Pacheco, and squares = *S. juruaense* new species (numbered as in list of specimens; see text).

ops, is known from three localities in eastern Ecuador: the type locality at Mera, 1160 m, Pastaza Province (holotype and five paratypes in the American Museum of Natural History, New York [AMNH], and three topotypes in the Natural Museum of Natural History, Washington D.C. [USNM]); Huamaní, Volcán Sumaco, Napo Province (above Mera, one specimen in the collection of the Escuela Politécnica Nacional, Quito [Albuja, 1991]), and Limoncocho, 250 m, Napo Province (3 specimens in USNM). *Scolomys ucayalensis* Pacheco is known from two specimens from its type locality, Centro de Investigaciones "Jenaro Herrera," 2.8 km E Jenaro Herrera, Depto. Loreto, right bank of Río Ucayali, Perú, 135 m. A third species from four localities in western Amazonia of Brazil is described here; it may be known as

Scolomys juruaense, new species

Holotype.—MPEG 23824 (Museo Paraense Emilio Goeldi, Belém, Pará, Brazil), adult female, collected on 19 September 1991 by J. L. Patton (original number 15570); skin with skull and mandibles, in good condition, plus liver tissue preserved both deep frozen and in ethyl alcohol. Tissues are maintained in the collections of the Museum of Vertebrate Zoology, University of California, Berkeley.

Type locality.—Seringal Condor, left bank Rio Juruá, Amazonas, Brazil 70°51′W, 6°45′S. Obtained in tree-fall slash disturbance in otherwise primary terra firme (or upland, non-seasonally flooded) forest.

Paratypes.—The total known sample of *S. juruaense* consists of the holotype and 22 additional specimens that are deposited in

the Coleção de Mamíferos, Instituto Nacional de Pesquisas da Amazônia (INPA); Museu Paraense Emilio Goeldi (MPEG); and Museum of Vertebrate Zoology, University of California at Berkeley (MVZ), listed here by locality (numbered as in the map, Fig. 3): Brazil—Acre: (1) Sobral, left bank Rio Juruá, 72°49′W, 8°22′S—INPA 2485, adult female, skin with skull, carcass in fluid plus karyotype; INPA 2486, adult male, in fluid plus karyotype; MPEG 24023, adult female, skin with skull, carcass in fluid plus karyotype; MPEG 24024, adult female, in fluid plus karyotype; MVZ 183172, juvenile female, in fluid plus karyotype. Amazonas: (2) type locality—MPEG 24019, adult male, skin and skull; MPEG 24020, adult male, skin and skull plus karyotype; MVZ 183167, adult female, skin and skull; MVZ 183168, adult male, skin and skull plus karyotype; (3) Penedo, right bank Rio Juruá, 70°45′W, 6°50′S—INPA 2487, adult male, skin and skull; INPA 2488, adult male, body in fluid with skull extracted; MPEG 24022, adult female, body in fluid with skull extracted; MVZ 183165, adult male, body in fluid with skull extracted; MVZ 183166, adult female, skin and skull; and (4) Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S—INPA 2489, subadult male, skin and skull plus karyotype; INPA 2490, adult female, skin and skull plus karyotype; INPA 2491, adult female, skin and skull plus karyotype; INPA 2492, adult male, skin and skull, karyotype; MPEG 24021, adult male, skin and skull plus karyotype; MVZ 183169, subadult male, skin and skull plus karyotype; MVZ 183170, adult male, in fluid plus karyotype; and MVZ 183171, adult male, in fluid. Liver tissues preserved in 95% ethyl alcohol and frozen at −76°C are available for all specimens and are deposited in the Museum of Vertebrate Zoology, as are chromosome slides for all karyotyped specimens.

Distribution.—Known from three localities on the left and one on the right bank in the central and upper reaches of the Rio Juruá in the Brazilian states of Acre and Amazones (Fig. 3); all localities are below 400 m in elevation.

Etymology.—The name refers to the known distribution along the Rio Juruá, the largest white-water tributary of the Rio Amazonas with an origin extralimital to the Andean cordillera.

Diagnosis.—A small-bodied mouse (Table 1) with short, nearly naked tail (83% of body length); short, broad head with pointed snout (Fig. 1); short and relatively broad hindfeet; hypothenar pad greatly reduced to absent (minutely present in 15 of 23 specimens) but thenar and interdigital pads well-developed; small and rounded ears; dorsal color varying from a grizzled pale reddish-brown (Sudan Brown to Antique Brown; capitalized color terms from Ridgway 1912) to dark reddish-black (Raw Umber) finely streaked with black; with rounded and inflated braincase; short, basally-broad rostrum that tapers distally; narrowed and straight zygomatic arches; narrow but long orbital openings; subsquamosal fenestra totally occluded by stout hamular process of squamosal; short and distally broad incisive foramina with sides distinctly 'stepped'; wide mesopterygoid fossa with parallel sides and squared, as opposed to rounded, anterior margin (Fig. 4); and 2N = 50. Other characteristics are as listed above for the genus.

Measurements of holotype.—Measurements are in millimeters and weight (mass) in grams; external measurements are those recorded on the specimen label and bilateral measurements were taken on the right side with digital calipers: Total length, 160; head and body, 86; tail, 76; hind foot (with claws), 21; ear (from notch), 16; condyloincisive length (CIL), 21.21; zygomatic breadth (ZB), 12.42; braincase breadth (BB), 11.59; least interorbital breadth (IOC), 5.84; rostral length (RL, taken from anterior orbit to tip of nasals), 7.98; nasal length (NL), 8.60; rostral width-1 (RW-1, across nasolacrimal capsules), 4.86; rostral width-2 (RW-2, at premaxillo-maxillary suture), 3.61; orbital

Table 1.—Selected measurements of spiny mice of the genus *Scolomys* (mean ± one standard error and range, with sample size).

Variable	*S. melanops*	*S. ucayalensis*	*S. juruaense*
Total length	153.9 ± 3.01 (138–167) $n = 10$	144.0 $n = 1$	152.4 ± 1.9 (142–163) $n = 11$
Tail length	62.8 ± 2.06 (55–77) $n = 10$	60.0 $n = 1$	69.0 ± 1.50 (26–76) $n = 11$
Hind foot length	20.9 ± 0.31 (20–23) $n = 10$	18.0 $n = 1$	20.6 ± 0.20 (19–22) $n = 16$
Ear height	15.0 $n = 3$	13.0 $n = 1$	15.6 ± 0.18 (15–17) $n = 16$
Condyloincisive length	19.87 ± 0.30 (18.51–20.67) $n = 7$	19.41 ± 0.47 (18.94–19.89) $n = 2$	20.43 ± 0.22 (18.60–21.97) $n = 16$
Zygomatic breadth	12.42 ± 0.18 (11.37–12.90) $n = 8$	11.52 ± 0.25 (11.27–11.77) $n = 2$	12.13 ± 0.13 (11.18–13.30) $n = 16$
Braincase breadth	11.12 ± 0.07 (10.82–11.41) $n = 8$	11.41 ± 0.13 (11.29–11.54) $n = 2$	11.39 ± 0.11 (10.54–12.33) $n = 16$
Least interorbital constriction	4.96 ± 0.07 (4.77–5.45) $n = 9$	5.58 ± 0.09 (5.49–5.68) $n = 2$	5.59 ± 0.09 (4.55–6.13) $n = 16$
Rostral length	6.92 ± 0.16 (6.34–7.78) $n = 9$		7.86 ± 0.11 (6.93–8.48) $n = 15$
Nasal length	7.64 ± 0.10 (7.16–8.14) $n = 9$	7.69 ± 0.27 (7.42–7.96) $n = 2$	8.31 ± 0.11 (7.83–9.34) $n = 15$
Rostral width—1	4.78 ± 0.07 (4.47–5.10) $n = 9$		4.81 ± 0.07 (4.36–5.40) $n = 16$
Rostral width—2	3.48 ± 0.08 (3.21–3.84) $n = 9$		3.64 ± 0.06 (2.79–4.05) $n = 16$
Orbital length	6.90 ± 0.10 (6.45–7.21) $n = 8$		7.38 ± 0.09 (6.67–7.89) $n = 16$
Diastema length	5.84 ± 0.09 (5.50–6.34) $n = 9$	5.59 ± 0.21 (5.38–5.80) $n = 2$	6.23 ± 0.09 (5.73–6.75) $n = 16$
Maxillary tooth row length	2.70 ± 0.05 (2.49–2.93) $n = 9$	2.81 ± 0.13 (2.69–2.94) $n = 2$	2.66 ± 0.04 (2.31–2.88) $n = 16$

Table 1.—Continued.

Variable	*S. melanops*	*S. ucayalensis*	*S. juruaense*
Incisive foramen length	3.76 ± 0.09 (3.31–4.19) *n* = 9	3.765 ± 0.001 (3.76–3.77) *n* = 2	3.94 ± 0.07 (3.17–4.32) *n* = 16
Palatal bridge length	9.03 ± 0.19 (8.42–9.69) *n* = 6	8.65 ± 0.05 (8.60–8.70) *n* = 2	9.14 ± 0.12 (8.28–9.87) *n* = 16
Alveolar width	4.41 ± 0.07 (4.15–4.74) *n* = 8	4.475 ± 0.001 (4.47–4.48) *n* = 2	4.62 ± 0.05 (4.29–4.96) *n* = 16
Occipital condyle width	5.82 ± 0.07 (5.54–6.14) *n* = 7		6.01 ± 0.06 (5.64–6.46) *n* = 16
Mastoid breadth	10.28 ± 0.15 (9.67–10.70) *n* = 7		10.29 ± 0.08 (9.70–10.73) *n* = 16
Basioccipital length	3.19 ± 0.06 (2.98–3.38) *n* = 7		3.23 ± 0.05 (2.83–3.60) *n* = 16
Mesopterygoid fossa length	3.30 ± 0.18 (2.98–3.68) *n* = 4		3.61 ± 0.05 (3.35–3.92) *n* = 16
Mesopterygoid fossa width	1.79 ± 0.09 (1.38–2.15) *n* = 7		1.97 ± 0.03 (1.78–2.20) *n* = 16
Zygomatic plate width	1.59 ± 0.06 (1.42–1.81) *n* = 7		1.71 ± 0.03 (1.54–1.93) *n* = 16
Cranial depth	8.32 ± 0.12 (7.87–8.72) *n* = 7		8.89 ± 0.09 (8.18–9.49) *n* = 16

length (OL), 7.74; maxillary diastema length (D), 6.43; maxillary tooth row length (MTRL), 2.82; incisive foramen length (IFL), 4.00; palatal bridge length (PBL), 9.68; alveolar width (AW, outside of M1), 4.58; occipital condyle width (OCW), 6.46; mastoid breadth (MB), 10.73; basioccipital length (BOL), 3.44; mesopterygoid fossa length (MPFL), 3.48; mesopterygoid fossa width (MPFW), 2.13; zygomatic plate width (ZPW), 1.66; cranial depth (CD), 8.97; mass, 26 grams.

Additional measurements.—See Table 1 for additional measurements of adult specimens of *S. juruaense* and of *S. melanops* and *S. ucayalensis.*

Description.—Dorsal coloration uniform from snout to rump, but individuals vary both within and among localities from grizzled pale reddish-brown to dark reddish-black; ventral coloration uniformly clear gray. Fore and hindfeet clothed dorsally with stiff white hairs; ungual tufts of thin, silvery hairs extend to or just beyond tip of claws. Otherwise as described for the genus, above.

Most features of cranial morphology (Fig. 4 and Table 1) are given above in the diagnosis, or detailed under the extended de-

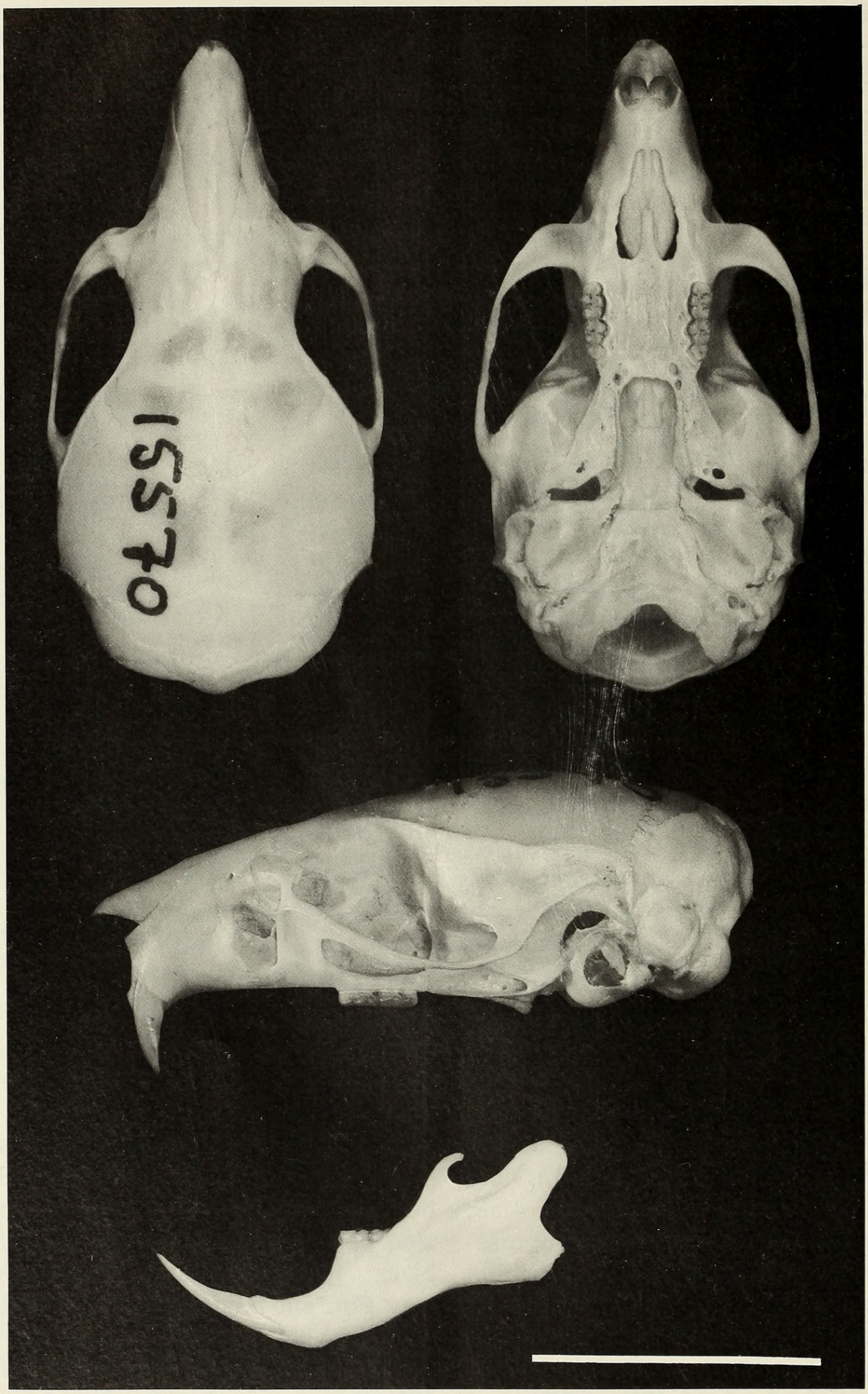

Fig. 4. Dorsal, ventral, and lateral views of cranium, lateral view of left mandible of the holotype of *Scolomys juruaense*, new species, MPEG 23824, adult female (original number JLP 15570). Scale bar equals 10 mm.

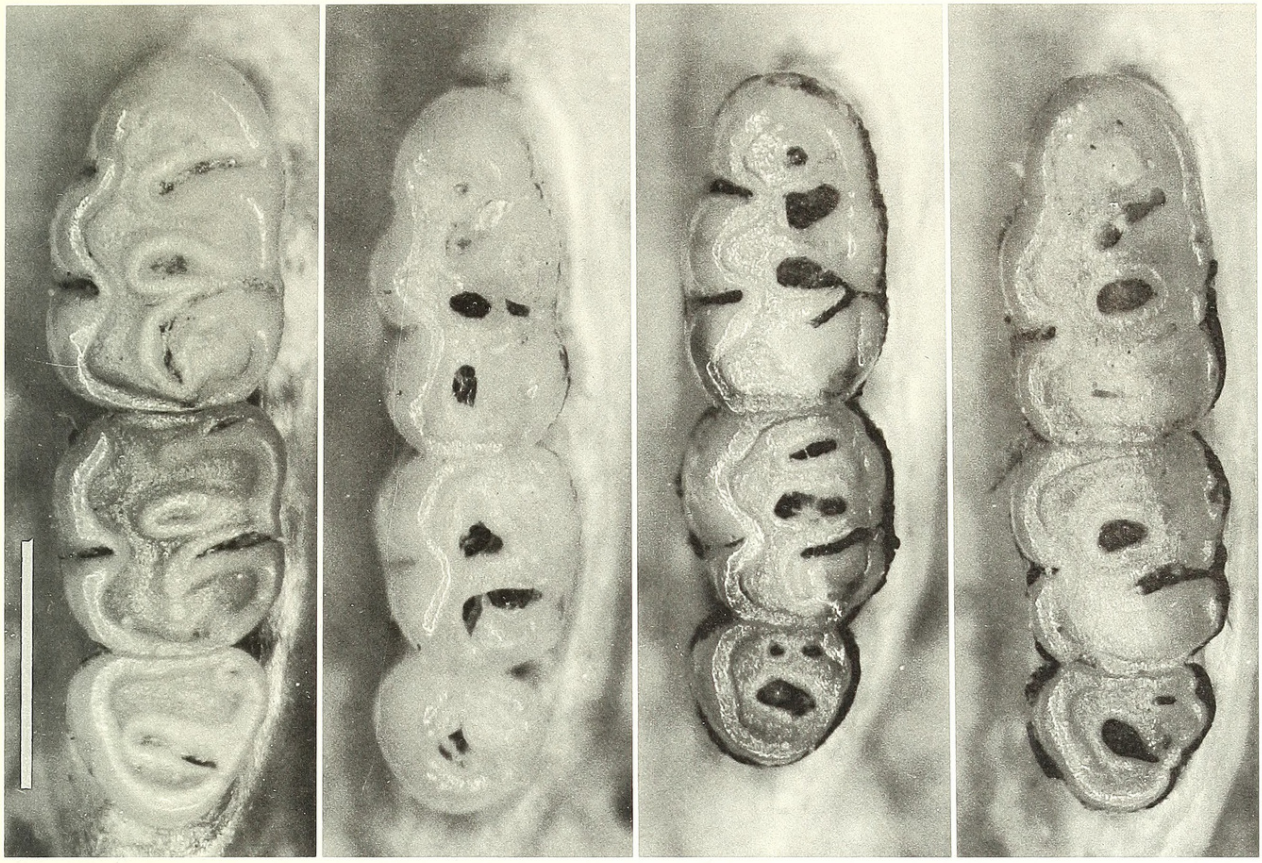

Fig. 5. Occlusal views of left upper maxillary tooth row (from left to right) of *S. melanops,* USNM 513581 and *S. juruaense,* new species, MVZ 183169, INPA 2487, INPA 2485. Scale bar equals 1 mm.

scription of the genus above. Features of particular note include a short rostrum distally tapering from a broad base; relatively long nasals; shallow zygomatic notches; wide interorbital region with well-developed ledges extending posteriorly as ridges onto temporal region; narrow, rather straight, and nearly parallel zygomatic arches with reduced jugals; elongated and narrow orbital openings; short (about ⅔ diastemal length) but posteriorly-widened incisive foramen with distinctly "stepped" lateral margins; broad mesopterygoid fossa with parallel sides and a flat, squared anterior margin; orthodont upper incisors; and short and stout hamular process of squamosal totally occluding subsquamosal fenestra.

Maxillary and mandibular molar teeth are as described above for the genus (Fig. 5). The general lack of specimens with unworn molars precludes the determination of structural differences in occlusal morphology that may characterize each of the three recognized species.

Phallus (Fig. 6) small, elongated, and narrow (averaging 4.2 mm in length and 1.6 mm in width), with a distinctly cylindrical shape and straight sides. External surface of the glans rugose, sparsely covered with small spines (averaging 7 per mm) buried in irregular pits from the lip of the terminal crater (excluding a narrow non-spinous rim) to the prepuce; without a dorsal groove or lateral notches, but with a thickened, spine-free midventral ridge extending from prepuce to crater rim. A distinct, corrugated and non-spinous crater rim present, low in profile ventrally, enlarged laterally, but incomplete at dorsal midline and not circumscribing entire crater; crater rim distinctly separated from spinous epithelium of proximal glans by a distinct fold or groove. Medial bacular mound visible distally beyond the crater rim; distinctly shorter and round-

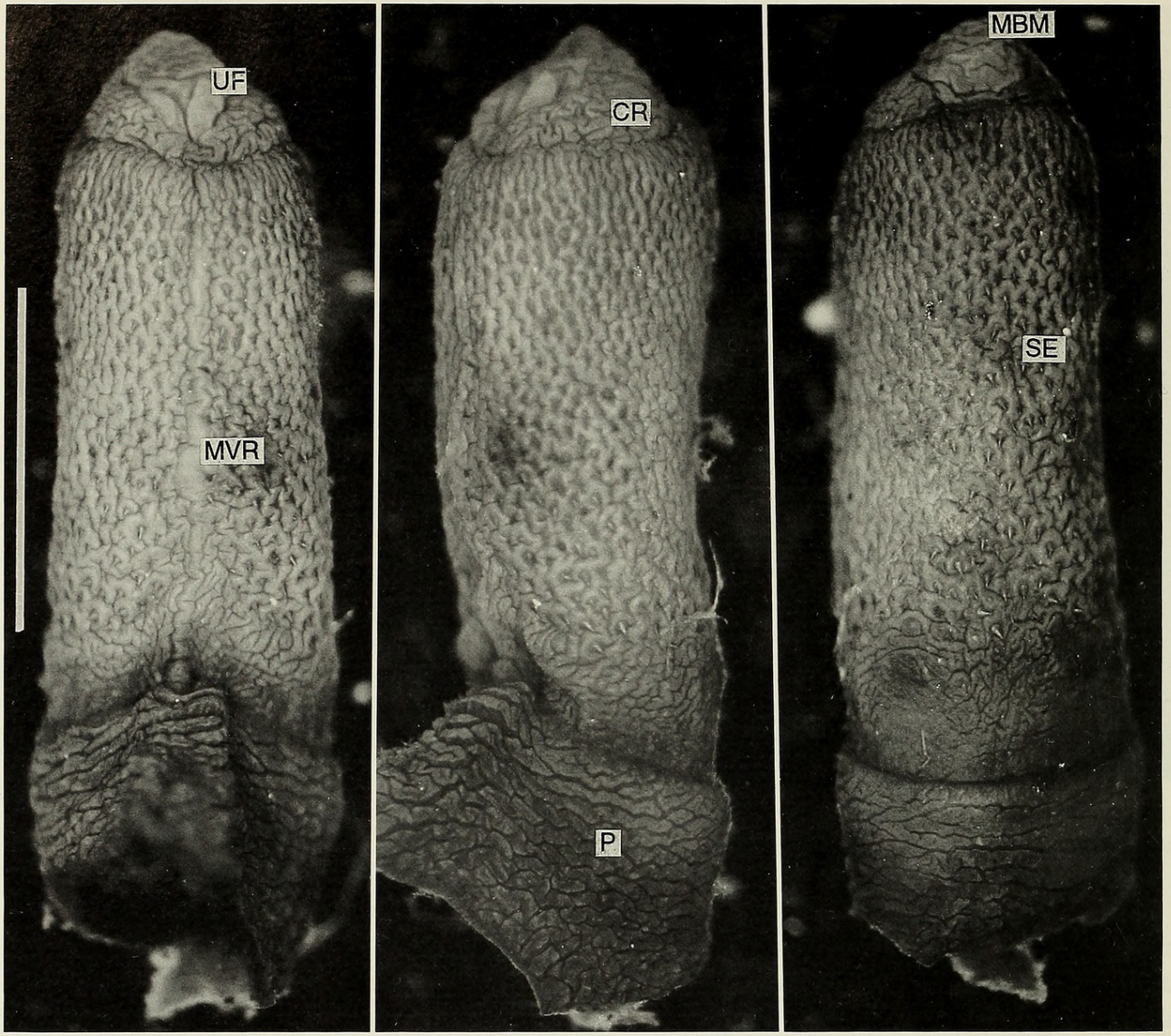

Fig. 6. Ventral, lateral, and dorsal views of the male phallus of *S. juruaense,* new species (MVZ 183171). CR, crater rim; MBM, medial bacular mound; MVR, midventral ridge; P, prepuce; SE, spinous epithelium; UF, urethral flaps. Scale bar equals 2 mm.

ed lateral mounds buried under laterally expanded crater rim. Dorsal papilla lacking spines and thickened, spatulate, and triangular in shape, with its tip extending just above crater rim. Urethral flaps lacking spines, but well developed, tapering distally, and varying in length but always visible above crater rim at ventral base of medial bacular mound. Distal baculum cartilaginous and tridigitate; proximal baculum with a stout straight shaft and laterally flared base.

Stomach unilocular and hemiglandular, with a moderately deep incisura angularis (extending about one-third the depth of the corpus and antrum), with rather short but thick bordering fold, and an expanded corpus with a moderately small antrum (terms from Carleton 1973).

Chromosome preparations are available from nine males and five females (see specimens examined above). The diploid number is 50 and the fundamental number is 68. The karyotype (Fig. 7A) is comprised of an acrocentric X-chromosome, the largest element of the complement, a small acrocentric Y-chromosome, and 24 pairs of autosomes of the following size and morphology: 2 pairs of large subtelocentric

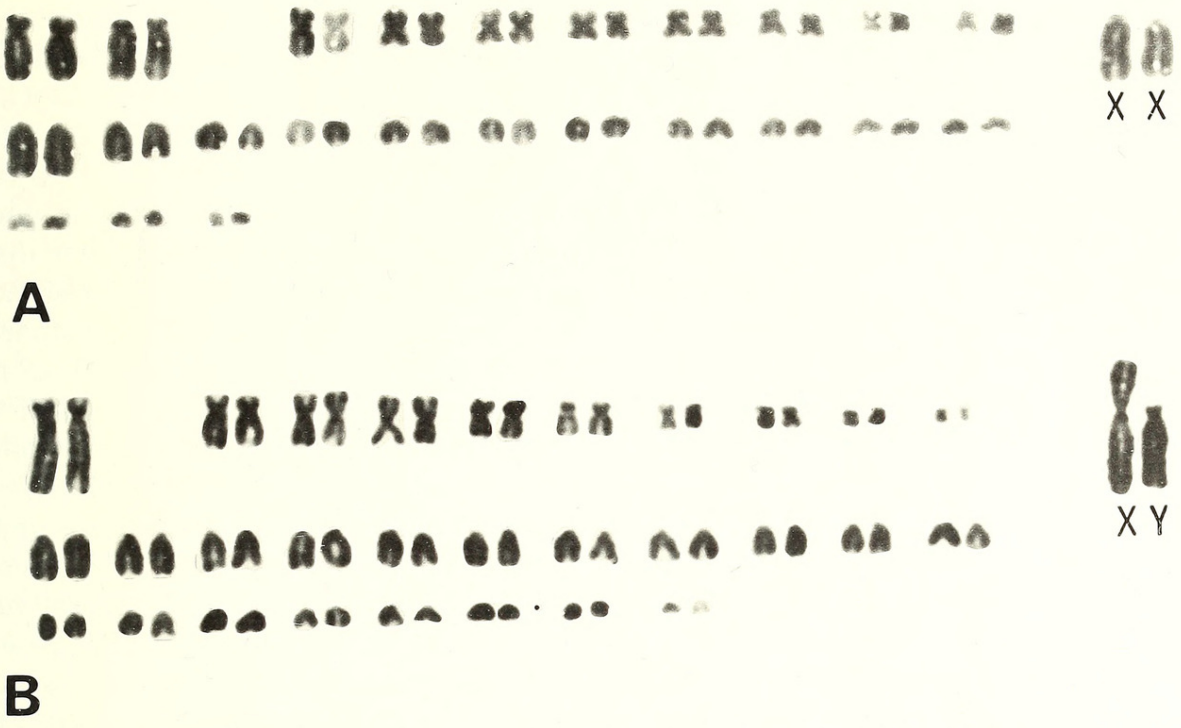

Fig. 7. Karyotypes of (A) *S. juruaense,* new species (MVZ 183172; female, 2N = 50, FN = 68) and (B) *S. melanops* (USNM 513583; male, 2N = 60, FN = 78).

chromosomes, 8 pairs of meta-submetacentric chromosomes grading in size from medium to small, and one large and 13 medium to small pairs of acrocentric chromosomes.

Comparisons.—From *S. melanops* (see Table 1 and Figs. 2 and 4), *S. juruaense* averages larger in all cranial dimensions except maxillary tooth row length and zygomatic breadth; and it differs by virtue of orthodont versus proodont upper incisors; longer and distally tapering rostrum; less expanded nasolacrymal capsules when viewed from above; narrow, rather straight, and nearly parallel zygomatic arches enclosing a narrow and elongated orbital opening; occluded as opposed to open subsquamosal fenestra; more gracile mandible with longer, more curved, and narrower coronoid process; usually present but minute hypothenar pad on sole of hind foot; and 2N = 50 rather than 2N = 60 karyotype. *Scolomys juruaense* is also larger in all cranial dimensions (except maxillary tooth row length, least interorbital constriction, and braincase breadth) than *S. ucayalensis,* although proportionally their skulls are more similar to one another than either is to *S. melanops* (ratio diagram, Fig. 8). These two species can be distinguished by the following combination of characters: pale reddish-brown to reddish-black dorsal coloration as opposed to uniformly dark gray to brownish-black (Pacheco 1991), longer hind foot, longer ear, greater breadth across the zygomatic arches, longer nasals, longer diastema, "stepped" lateral margins of the incisive foramen, and squared (rather than distinctly rounded) anterior margin of the mesopterygoid fossa. The karyotype of *S. ucayalensis* is not known.

Little comparison can be made in relation to the occlusal surfaces of the cheek teeth. These details are not given in the original description of *S. ucayalensis* and the teeth are too worn in most available specimens of both *S. melanops* and *S. juruaense* (Fig. 5). Similarly, no comparison can be made in soft anatomical structures, as none have been described for species other than what we provide here for *S. juruaense.* The karyotype of *S. melanops* (Fig. 7B) is grossly sim-

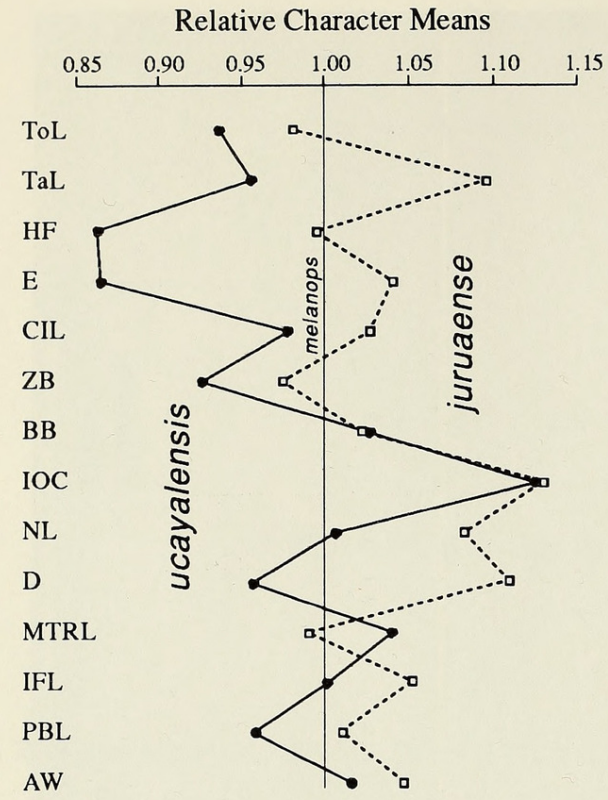

Fig. 8. Ratio diagram comparing averages of external and cranial dimensions for *Scolomys ucayalensis* (solid circles) and *S. juruaense* (open squares) in relation to those of *S. melanops* (vertical line).

ilar to that of *S. juruaense* (Fig. 7A), with a diploid number of 60 and fundamental number of 78. Its karyotype is composed of one pair of large subtelocentric, 9 pairs of medium-sized to minute meta-and submetacentric, and 19 pairs of acrocentric autosomes grading evenly from medium-sized to small. The X is a large submetacentric chromosome, the largest element of the complement, and the Y is a subtelocentric element as large as the autosomal pair.

The phenotypic similarity (especially orthodont incisors, distally tapering rostrum, less-flared and parallel zygomatic arches, long and narrow orbital openings, and more elongated braincase) of *S. juruaense* and *S. ucayalensis* suggest a closer genetic relationship between them relative to *S. melanops*. This hypothesis remains to be tested, however.

Habitat.—All specimens of *S. juruaense* were obtained in primary terra firme (upland, non-seasonally flooded) forest in Sherman live traps placed on the ground and baited with a combination of ground whole oats, raisins, and peanuts. As all individuals were live-trapped, stomach contents consisted only of the bait used (ground whole oats, raisins, and peanuts) and a few insect parts which may have been ingested accidentally. An equal number of Sherman traps placed in the trees at heights of 10–15 meters failed to secure any specimens of this species, although species of the sigmodontine genera *Oecomys* and *Rhipidomys* were taken. Other sigmodontines found sympatric with *S. juruaense* include *Oryzomys capito, Oryzomys yunganus, Oryzomys macconnelli, Neacomys spinosus, Neacomys* sp. (a smaller-bodied form sympatric with *N. spinosus,* with proportionally longer tail, shorter tooth row, and 2N = 35/36 as opposed to 2N = 64 karyotype), *Nectomys squamipes, Oecomys trinitatus, Oecomys roberti, Oecomys superans, Oecomys bicolor,* and *Rhipidomys leucodactylus.*

Reproduction.—*Scolomys juruaense* apparently breeds in both wet and dry seasons as pregnant or perforate females were taken in March (wet season), and in August, September, and October (dry season). Two of the three female specimens of *S. melanops* from the type locality were pregnant when collected in March. Litter sizes (maximum number of embryos 3 in both *melanops* [Anthony 1924] and *juruaense* [range 1–3]) are somewhat low in comparison to other sympatric small-bodied oryzomyines, notably *Oligoryzomys microtis* (modal litter size 5, range 2–8) and *Neacomys spinosus* (modal litter size 3, range 2–4).

Phylogenetic Affinities

Voss & Carleton (1993) provided a phylogenetic diagnosis of the Oryzomyini Vorontsov, 1959, defining the tribe by the following combination of characters: (1) a pectoral pair of mammae (with mammary counts of eight or more); (2) a long palate

with prominent posterolateral pits; (3) no alisphenoid strut separating the buccinator-masticatory and accessory oval foramina; (4) no posterior suspensory process of the squamosal attached to the tegmen tympani; and (5) no gall bladder. They included one extinct and 14 Recent genera within this diagnosed unit: *Scolomys* along with *Holochilus, Lundomys, †Megalomys, Melanomys, Microryzomys, Neacomys, Nectomys, Nesoryzomys, Oecomys, Oligoryzomys, Oryzomys, Pseudoryzomys, Sigmodontomys,* and *Zygodontomys.* While the placement of *Scolomys* within the Oryzomyini has never been challenged, to our knowledge, this genus possesses only four of these five diagnostic characters. Among oryzomyines, *Scolomys* apparently is unique with a reduced mammary count, lacking both pectoral and postaxial pairs.

No hypothesis of phylogenetic relationships among the member genera of the Oryzomyini has as yet been proposed and a sufficient understanding of character variation in the soft and hard anatomy within the tribe is, at present, too limited for such to be developed here. *Scolomys* and *Neacomys* are the only neotropical sigmodontines with strongly spinose fur, and they are superficially similar in overall small size, relatively short and naked-appearing tail, and apparently strictly terrestrial habits as well. This resemblance is apparently not due to immediate common ancestry, however. For example, we could score 21 of the 25 characters listed by Voss & Carleton (1993: 23–27) in both genera. Of these, the two differ in mammary count (6 in *Scolomys,* the presumptive ancestral state of 8 in *Neacomys*), carotid circulation (*Scolomys* has the derived Pattern 3, *Neacomys* the ancestral Pattern 1), anteroloph on M1 (present [=ancestral state] in *Neacomys,* confluent with anterolabial conule in *Scolomys*), and protoflexus of M2 (absent in *Scolomys,* present [=ancestral state] in *Neacomys*). The two genera do share 17 characters in common, but all are apparently shared-primitive traits either for sigmodontines as a whole (11 characters; numbers 1, 2, 3, 4, 6, 9, 13, 14, 15, 16, and 24 of Voss & Carleton 1993) or for oryzomyines in particular (6 are shared broadly by other genera in the tribe; characters 7, 8, 10, 12, 21, and 25). *Scolomys* does share the derived carotid circulation pattern with *Oligoryzomys* (Carleton & Musser 1989), some but not all *Oryzomys* (Gardner & Patton 1976), *Nectomys,* and *Holochilus* (Voss & Carleton 1993), which might suggest a relationship among this group of genera.

As a means to assess relationships within the Oryzomyini, we examined the sequence of 801 base pairs (267 codons) of the mitochondrial cytochrome-b gene for 17 species of seven oryzomyine genera (*Microryzomys minutus*; *Neacomys spinosus* and two undetermined species; *Nectomys squamipes*; *Oecomys bicolor, roberti, superans, trinitatus,* and an undetermined species; *Oligoryzomys longicaudatus* and *microtis*; *Oryzomys capito, macconnelli, nitidus,* and *yunganus*; and *Scolomys juruaense*). The thomasomyine taxa *Thomasomys aureus* and *Rhipidomys leucodactylus* were used as out-groups. Methods for DNA extraction, amplification by the polymerase chain reaction (PCR), and sequencing, as well as oligonucleotide primers used in the PCR reactions follow those given in Smith & Patton (1993). All sequences are available in GenBank; those for *Nectomys squamipes, Oligoryzomys longicaudatus, Oryzomys capito,* and the two thomasomyine outgroups were presented in Smith & Patton (1993). Table 2 provides a matrix of average sequence divergence distances, corrected for multiple replacements (Brown et al. 1982), and of the average number of transversions at the 3rd position of codons. Distances between these genera of oryzomyines are substantial, averaging 33.99% in corrected sequence divergence (range 25.6% [*Oecomys* versus *Oryzomys*] to 40.8% [*Microryzomys* versus *Scolomys*]). Moreover, *Scolomys* is consistently the most divergent, with an av-

Table 2.—Above the diagonal: average pair-wise divergence estimates of 801 base pairs of the mitochondrial cytochrome-b gene among seven genera of oryzomyine rodents, and between them and two thomasomyine out-group taxa, corrected for multiple hits by the method of Brown et al. (1982). Below the diagonal: average number of 3rd position transversions (with estimates of times of divergence, in millions of years, in parentheses). Averages for both sequence divergence and numbers of 3rd position transversions among species within a given genus are given on the diagonal.

Taxon[a]	*Microryzomys*	*Neacomys*	*Nectomys*	*Oecomys*	*Oligoryzomys*	*Oryzomys*	*Scolomys*	*Thomasomys*	*Rhipidomys*
Microryzomys	—	29.6	28.5	30.3	34.0	36.4	40.8	40.5	44.4
Neacomys	46.0 (7.5)	22.4/25.0	31.2	35.6	35.4	37.3	38.5	43.4	44.3
Nectomys	36.3 (5.9)	39.0 (6.4)	—	31.1	33.6	30.7	36.9	43.7	40.4
Oecomys	34.5 (5.6)	41.2 (6.7)	38.4 (6.3)	14.8/18.0	32.4	25.6	38.5	37.7	42.3
Oligoryzomys	45.0 (7.3)	44.8 (7.3)	42.5 (6.9)	37.8 (6.2)	17.5/20.0	30.0	39.3	37.2	36.0
Oryzomys	43.3 (7.1)	44.5 (7.3)	39.0 (6.4)	31.1 (5.1)	34.9 (5.7)	24.9/30.0	38.0	36.9	41.2
Scolomys	35.0 (5.7)	43.3 (7.1)	45.0 (7.3)	44.6 (7.3)	44.5 (7.3)	46.0 (7.5)	—	48.6	41.7

[a] *Microryzomys minutus* (Peru: MVZ 173957), *Neacomys spinosus* (Brazil: MNFS 1262), *Neacomys* sp. 1 (Brazil: MNFS 1395), *Neacomys* sp. 2 (Brazil: JLP 15365), *Nectomys squamipes* (Peru: MVZ 166700), *Oecomys bicolor* (Brazil: MNFS 1499), *Oecomys* sp. (Brazil: J354), *Oecomys roberti* (Brazil: JLP 15241), *Oecomys superans* (Brazil: JLP 15517), *Oecomys trinitatus* (Brazil: MNFS 1250), *Oligoryzomys longicaudatus* (Argentina: MVZ 155842), *Oligoryzomys microtis* (Brazil: MNFS 1321), *Oryzomys capito* (Peru: MVZ 166676), *Oryzomys macconnelli* (Brazil: MNFS 156), *Oryzomys nitidus* (Brazil: MNFS 1419), *Oryzomys yunganus* (Brazil: MNFS 1101), *Scolomys juruaense* (holotype, MPEG 23824), *Thomasomys aureus* (Peru: MVZ 170076), and *Rhipidomys leucodactylus* (Peru: MVZ 168938).

erage of 38.67% divergence in all pair-wise comparisons.

The mtDNA sequences were analyzed both by the minimum evolution tree estimate (using the METREE version 1.2 program; Rzhetsky & Nei 1992), based on Kimura 2-parameter molecular distance matrices (Kimura 1980), and maximum parsimony (using PAUP 3.1.1; Swofford 1993). While both approaches provide strong support for the monophyly of the oryzomyine genera examined (at a confidence limit value of 99% in the distance phenogram [Fig. 9A] and a bootstrap value of 95% in the parsimony cladogram [Fig. 9B]) relative to the thomasomyine out-group genera, neither view provides much resolution among the oryzomyine genera or in the specific placement of *Scolomys* among them. All terminal branches are very long and internodal distances are short. As a result, nearly all internodes linking the oryzomyine genera have either confidence limits (Fig. 9A) or bootstrap values (Fig. 9B) below 50%. However, with the exception of *Oryzomys,* both measures are above 90% in the linkage of species within polytypic genera. *Scolomys* appears as a weakly supported sister taxon to a clade composed of *Nectomys, Oryzomys,* and *Oecomys* (with a confidence of only 46%) in the distance tree and to *Nectomys* in the parsimony tree (but at a bootstrap value <50%).

While the mtDNA sequence data do not provide strong support for relationships among this group of oryzomyine genera, these data are significant for two reasons. For one, the very short internodal distances suggest that divergence among taxa was nearly simultaneous and that, as a consequence, resolution of relationships by any set of characters is likely to be difficult. It may not be surpising, therefore, that *Scolomys* combines a few uniquely derived morphological characters with others that are apparently primitive for the tribe. This general lack of resolution is opposite to that observed among members of the tribe Akodontini of the South American sigmodontines, based on variation over the same sequence of cytochrome-b (Smith & Patton 1993). Consequently, difficulties in resolv-

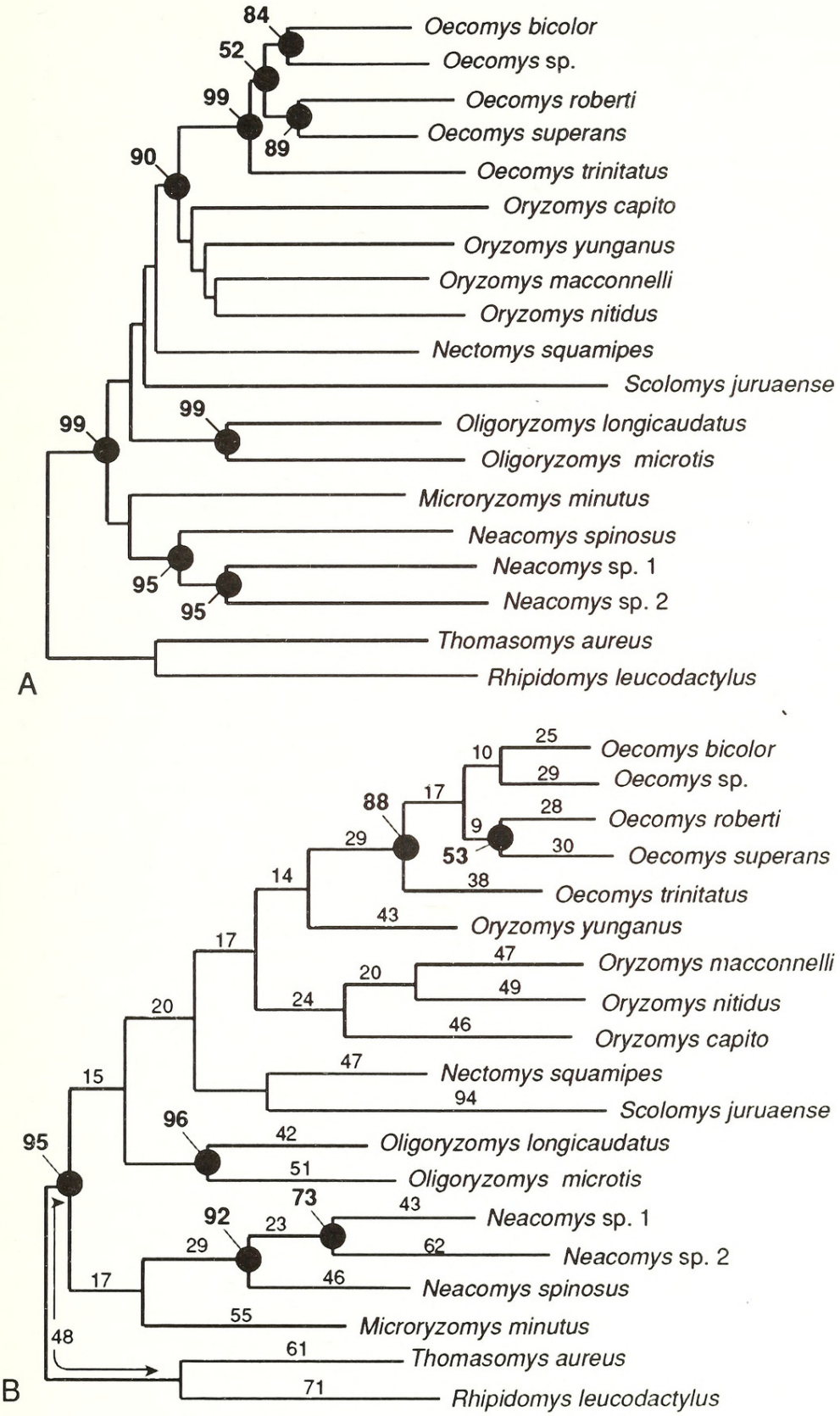

Fig. 9. Hypotheses of phyletic relationship between exemplar species of seven genera of the tribe Oryzomyini, with the thomasomyine genera *Thomasomys* and *Rhipidomys* as out-groups, based on 801 base pairs of the mitochondrial cytochrome-b gene. (A) Minimum evolution tree based on a Kimura 2-parameter distance matrix (METREE version 1.2; Rzhetsky & Nei 1992); branch lengths are proportional and circled numbers at each node are confidence limits. (B) Maximum parsimony cladogram, excluding 3rd position transitions (PAUP version 3.1.1; Swofford 1993); the number of character changes along each branch is indicated and circled numbers at specific nodes are bootstrap values (based on 500 iterations) above 50%.

ing relationships among oryzomyine genera are likely to reflect true patterns and timing of diversification rather than inadequacies of the sequence used in comparisons. Secondly, the long terminal branches and overall extensive degree of sequence divergence suggest that divergence times within the oryzomyines are deep. Based on the rate estimate of 2.3% per million years for third position transversions of the cytochrome-b gene (Table 2; rate calculation from Smith & Patton [1993] for the Akodontini), times of divergence among the examined genera of oryzomyines average about 6.6 million years (range 5.1 to 7.5). These numbers are in general accordance with estimates of times of divergence for the Sigmodontinae as a monophyletic lineage, based on DNA-DNA hybridization analyses (reviewed in Catzeflis et al. 1993). However, they also suggest that divergences within the oryzomyines were nearly simultaneous with the divergence between members of that tribe and at least the Akodontini (Catzeflis et al. 1993: their fig. 12.4), if not for other sigmodontines as well.

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