Original investigation

Integrated systematic reevaluation of the Amazonian genus *Scolomys* (Rodentia: Sigmodontinae)

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Abstract

Qualitative, mensural, genetic, and phylogenetic analyses were conducted to clarify species limits, distributions, and relationships in the poorly known Amazonian rodent genus *Scolomys*. *Scolomys melanops* is characterized by consistent differences in comparison with all other samples of the genus. However, our data do not support the recognition of *S. juruaense* as a valid species, but rather as a synonym of *S. ucayalensis*. Only minimal differences in Cyt-b sequences were present between *S. juruaense* and *S. ucayalensis*, and phylogenetic analyses consistently retrieved a monophyletic genus *Scolomys* with the relationship ((*S. juruaense* + *S. ucayalensis*) + *S. melanops*). The apparent morphological distinctiveness of *S. juruaense* in the original description was due to small sample sizes and comparisons of adult specimens from Brazil with the juvenal type material of *S. ucayalensis* from Peru. The two species that we recognize, *S. melanops* and *S. ucayalensis,* can be separated by the short, relatively wide rostrum and wide zygomatic arches of *S. melanops* versus the longer, relatively thinner rostrum and absolutely narrower zygomatic arches of *S. ucayalensis*. *Scolomys melanops* ranges from the eastern slopes of the Andes in Ecuador to near Iquitos in Amazonian Peru, and we document the presence of *S. ucayalensis* in western Brazil, northern Peru, and southern Colombia.

Key words: Muridae, Cyt-b, mitochondrial DNA, morphology, morphometrics

Introduction

Although many new mammalian species have been described from the Amazon in recent years (e. g., Patterson 2000; Patton et al. 2000; Voss et al. 2002 b), the majority of small mammals of this region remain unrevised and poorly known both in their systematics and distribution. *Scolomys* (Muridae: Sigmodontinae sensu Musser and Carleton 1993) constitutes an enig- matic genus of Amazonian rodent. Although these spiny, small-bodied, short-tailed mice are generally considered to belong to the tribe Oryzomyini (Reig 1986; Voss and Carleton 1993), they do not show all the morphological synapomorphies of the tribe (Patton and da Silva 1995; Steppan 1995). Among sigmodontine genera, *Scolomys* shows external resem-

blance only to *Neacomys* – which also is small and spiny – but the two are quite distinctive cranially (Anthony 1924; Patton and da Silva 1995).

For most of the past century, *Scolomys* was known by only a few scattered specimens. The type species of the genus, *S. melanops,* was described on the basis of six individuals from Mera, Ecuador, on the Amazon-facing slopes of the Andes (Anthony 1924). No further specimens of the genus were reported for more than 60 years, until Albuja-V. (1991) noted an unspecified number of *S. melanops* from Huamaní on the slopes of Volcán Sumaco (also along the eastern versant of the Ecuadorian Andes). In the same year, Pacheco (1991) described a new species, *S. ucayalensis*, based on two specimens from Jenaro Herrera on the Río Ucayali (in Amazonian Peru), and mentioned three additional individuals of *S. melanops* (from Limoncocha in Amazonian Ecuador). Soon thereafter, Sokolov and Malygin (1994) noted two further topotypic specimens of *S. ucayalensis,* and Rageot and Albuja (1994) reported three topotypes of *S. melanops.*

The genus was then revised by Patton and da Silva (1995), who named a new species, *S. juruaense*, based on 23 specimens from four localities along the Rio Juruá in western Brazil. Morphologically, *S. melanops* is highly distinctive in cranial proportions compared with the other two species they recognized (e. g., wider and shorter rostrum, wider zygomatic arches, and more-inflated nasolacrimal capsules). In addition, the karyotype of *S. melanops* (2n = 60) differs from that of *S. juruaense* (2n = 50), but the chromosomal makeup of *S. ucayalensis* remains unknown (Patton and da Silva 1995). In contrast, *S. juruaense* and *S. ucayalensis* are similar cranially. Patton and da Silva (1995) considered that those two species differ in dorsal coloration (pale reddish brown to reddish black in *S. juruaense* while uniformly dark gray to brownish black in *S. ucayalensis*), in size (*S. juruaense* larger), and in a few discrete cranial characters. However, due to the small sample sizes available at the time, it was impossible for

them to evaluate age-based variation or dental characters fully.

Subsequent to that revision, many new specimens of *Scolomys* have been collected in Ecuador, Peru, and – for the first time – Colombia. Hice (2001) reported a large series of *S. melanops* from the Allpahuayo Reserve near Iquitos, Peru, extending the species' distribution far into the Amazonian lowlands. Fleck and Harder (2000) noted one individual of *S. ucayalensis* from the Río Gálvez in northern Peru, and Castro-Revelo and Zapata-Ríos (2001) mentioned the collection of several specimens from the Yasuní National Park in Amazonian Ecuador, which they considered *S. juruaense.* Additionally, an age series of *S. ucayalensis* from close to the type locality was collected recently, and other smaller, unreported collections from various localities now exist in several museums. The material presently available to us allows for assessing nongeographic (especially ontogenetic) variation and reevaluating species limits and geographic distributions in the genus. Moreover, we use mtDNA sequences from newly collected specimens to determine genetic relationships among samples of three critical populations and compare with selected oryzomyine and thomasomyine taxa.

Material and methods

Museum collections and specimens examined

Voucher specimens are deposited in the following institutional collections: AMNH, American Museum of Natural History (New York, U.S.A.); IAvH, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (Villa de Leiva, Colombia); ICN, Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia (Bogotá, Colombia); KU, University of Kansas Natural History Museum (Lawrence, U.S.A.); MPEG, Museu Paraense Emílio Goeldi (Belém, Brazil); MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Lima, Peru); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley, U.S.A.); TTU, Museum of Texas Tech University (Lubbock, U.S.A.); and USNM, National Museum of Natural History (Washington,

D.C., U.S.A.). We examined the specimens listed below, including the holotype of *Scolomys melanops* and topotypes of *S. ucayalensis* and *S. juruaense* (see also Fig. 1 and Tab. 1. for geographic placement of these localities). In our general morphological examinations, we assessed the diagnostic characters mentioned by PATTON and DA SILVA (1995) as well as others currently used in sigmodontine systematics. Information not provided by the original collector appears in brackets.

Scolomys melanops (total = 33). ECUADOR (*n* = 12). Provincia Napo: Limoncocha, 250 m [0°25′ S, 76°38′ W, PAYNTER 1993], USNM 513581–513583. Provincia Pastaza: Mera, [3 800 ft (= 1 160 m), ANTHONY 1924; 1°28′ S, 78°08′ W, PAYNTER 1993], AMNH 67518, 67520–67523, 67524 [holotype]; USNM 399936–399937, 548381. PERU (*n* = 21). Departamento Loreto: Iquitos, 25 km S, Allpahuayo Reserve, [110–180 m, 3°28′ S, 73°25′ W, HICE 2001], TTU 85486–85490, 85492–85497, 85499–85502, 85504; San Jacinto, 175–190 m, [2°19′ S, 75°52′ W, DUELLMAN and MENDELSON 1995], KU 158212; 1.5 km N of Teniente López, 175–190 m, [2°36′ S, 76°07′ W, DUELLMAN and MENDELSON 1995, for camp], KU 158213–158216.

Scolomys juruaense (sensu PATTON and DA SILVA 1995; total = 8). BRAZIL (*n* = 8). Estado do Acre: Sobral, left bank Rio Juruá [8°22′ S, 72°49′ W, PATTON and DA SILVA 1995], MVZ 183172. Estado do Amazonas: Barro Vermelho, left bank Rio Juruá [6°28′ S, 68°46′ W, PATTON and DA SILVA 1995], MVZ 183169–183171; Penedo, right bank Rio Juruá [6°50′ S, 70°45′ W, PATTON and DA SILVA 1995], MVZ 183165–183166; Seringal Condor, left bank Rio Juruá, [6°45′ S, 70°51′ W, PATTON and DA SILVA 1995], MPEG 23824 [holotype; voucher specimen not examined; tissue sample sequenced]; MVZ 183167–183168.

Scolomys ucayalensis (total = 20). COLOMBIA (*n* = 6). Departamento Amazonas: Municipio Leticia, Corregimiento Puerto Santander, cerca de la Quebrada Bocaduché, margen sur Río Caquetá, 150 m, 0°40′ S, 72°08′ W, ICN 16233. Departamento Nariño: Municipio Ipiales, cuenca alta del Río Rumiyaco, 755 m, 0°30′ N, 77°14′ W, IAvH 6206–6207; Municipio Ipiales, cuenca alta del Río Rumiyaco, 780 m, 0°29′ N, 77°15′ W, IAvH 6203–6205. PERU (*n* = 14). Departamento Loreto: Centro de Investigaciones Jenaro Herrera, 2.8 km E of Jenaro Herrera, right bank of the Río Ucayali, 135 m [4°52′ S, 73°39′ W, PACHECO 1991], MUSM 5460, 5474 [holotype reexamined by V. PACHECO]; Nuevo San Juan, Río Gálvez, 148 m, [5°15′ S, 73°10′ W, SIMMONS et al. 2002], AMNH 272668, 272686, 272697, 272706, 272708, 272721; MUSM 13356–13361.

Measurements

The following cranial measurements were taken with digital calipers to the nearest 0.01 mm (modified from PATTON et al. 2000): CIL, condyloincisive length (greatest length from anteriormost margins of upper incisors to posteriormost margins of occipital condyles); ZB, zygomatic breadth (greatest breadth across zygomatic arches); BB, braincase breadth (greatest breadth across lateral walls of braincase); IOC, least interorbital constriction (least distance across roof of skull between orbits); RL-1, rostral length-1 (taken diagonally from anteriormost internal margin of orbit to anteriormost margins of nasal bones); RL-2, rostral length-2 (taken diagonally from anteriormost internal margin of orbit to anterior border of alveolus of corresponding incisor); NL, nasal length (maximum midline length of nasal bones); RW-1, rostral width-1 (maximum rostral width across lateral margins of nasolacrimal capsules); RW-2, rostral width-2 (rostral width taken immediately anterior to nasolacrimal capsules); OL, orbital length (taken diagonally from anteriormost internal margin to posteriormost internal margin of orbit); DL, diastema length (from posteriormost face of base of one upper incisor to anteriormost edge of M1 on same side of cranium); MTRL, maxillary molar tooth row length (maximum crown length of a maxillary tooth row); IFL, incisive foramen length (maximum internal length of one incisive foramen); IFW, incisive foramina width (internal maximum width across both incisive foramina); PBL, palatal bridge length (taken from posterior margin of upper incisors to anteriormost margin of mesopterygoid fossa); AW, alveolar width (maximum distance across labial margin of M1s); OCW, occipital condyle width (maximum distance across lateral margins of occipital condyles); MB, mastoid breadth (greatest breadth across mastoid processes); BOL, basioccipital length (distance from anteriormost margin of foramen magnum to basioccipital-basisphenoid suture); MPFL, mesopterygoid fossa length (distance from anteriormost margin of mesopterygoid fossa to posterior tip of hamular processes of pterygoids, along major axis of skull); MPFW, mesopterygoid fossa width (maximum internal width of mesopterygoid fossa); ZPW, zygomatic plate width (minimum width of zygomatic plate at midheight from anterior to posterior margins of plate); CD, cranial depth (vertical distance from plane determined by incisor tips and ventral borders of bullae, to top of cranial vault; measured by placing skull on glass microscope slide and subtracting slide thickness).
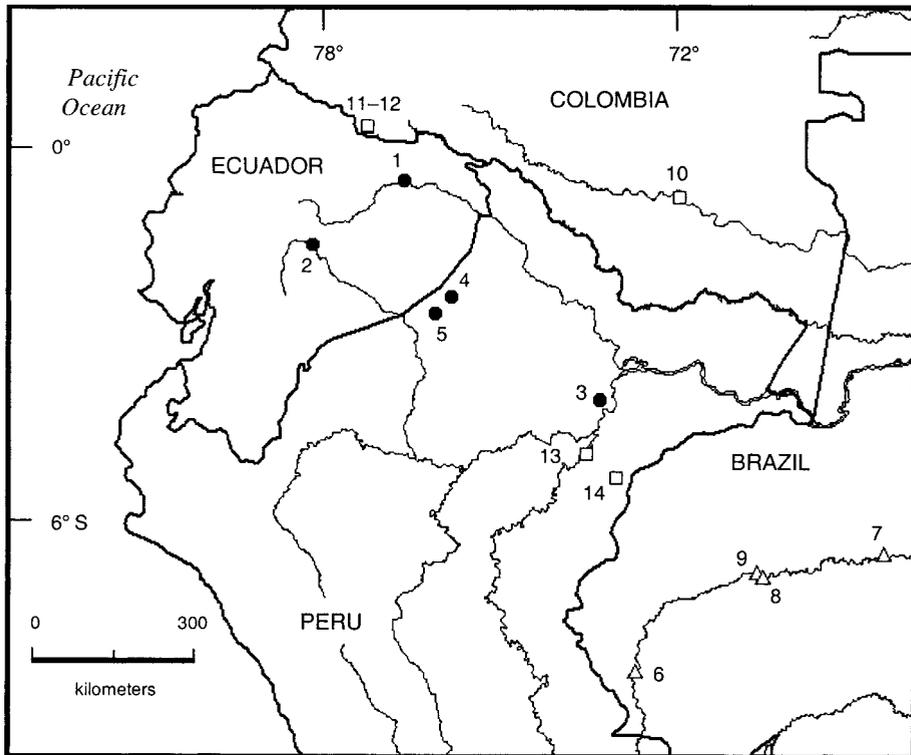
Fig. 1. Documented collection localities for species of *Scolomys*. Closed circles denote *S. melanops*; open squares *S. ucayalensis*; and open triangles *S. juruaense* sensu Patton and da Silva (1995). Numbers correspond to abbreviated localities as provided in Tab. 1 and used throughout the text. See Material and methods for museum catalog numbers and full provenience of specimens.

Molar toothwear classes

Seven toothwear classes were established for *Scolomys*, based primarily on the Río Gálvez age series (molar terminology of Reig 1977). Class 1, M3 incompletely erupted (m3 either fully erupted or not). Class 2, both M3 and m3 fully erupted, at same level as other molars; upper labial cusps and lower lingual cusps unworn, sharp. Class 3, most upper labial and lower lingual cusps with moderate wear, rounded; upper lingual and lower labial cusps well-worn, very smooth but still distinguishable as independent entities. Class 4, upper lingual and lower lingual cusps worn, flat and evident only as undulations on lateral border of molars; in M1 and M2, paraflexus, mesoflexus, and metaflexus open; mesoflexid of m1 open; most other flexids closed in m1 and m2. Class 5, M1 and M2 with paraflexus, mesoflexus, and metaflexus closed, creating interior enamel fossettes; all flexids of m1 and m2 closed (including meso-

flexid of m1); large interior fossettes still present in M1, M2, m1, and m2. Class 6, molars beginning to appear dished-out; most details of occlusal topography obliterated and only small interior fossettes present in upper and lower molars; internal fossette (formed from mesoflexus) clearly present in M1 and internal fossette (formed from mesoflexid) clearly present in m1. Class 7, no internal fossettes present in M1 or m1.

Statistical analyses

All statistical analyses were performed with Mini-tab (1998; Release 12.1), with probabilities compared to a significance level of $\alpha = 0.05$. Males and females (typically not strongly size-dimorphic in sigmodontine rodents; e. g., Voss and Marcus 1992) were pooled in all analyses because of small sample sizes. Series from Río Gálvez and Allpahuayo were used to assess age-related variation.

Table 1. Abbreviated locality names used in the text. Numbers correspond to sites plotted on the map (Fig. 1). See Material and methods for full provenience and museum catalog numbers.

Scolomys melanops
1   Limoncocha
2   Mera
3   Allpahuayo
4   San Jacinto
5   Teniente López

Scolomys juruaense
6   Sobral, Rio Juruá
7   Barro Vermelho, Rio Juruá
8   Penedo, Rio Juruá
9   Seringal Condor, Rio Juruá

Scolomys ucayalensis
10   Río Caquetá
11   Río Rumiyaco, 755 m
12   Río Rumiyaco, 780 m
13   Río Ucayali
14   Río Gálvez

These two localities offer moderate numbers of intact crania from a variety of toothwear classes ($n = 14$ for Allpahuayo; 9 for Río Gálvez). For both localities separately, we plotted each variable versus toothwear class to determine if individuals continued to grow throughout the observed range of toothwear classes.

We calculated a series of descriptive statistics and univariate tests for measured adult specimens of *Scolomys* (Classes 4–7). First, we calculated descriptive statistics of cranial measurements and one derived ratio (RL-1/ZB) for the two groups considered clearly morphologically distinct by PATTON and DA SILVA (1995; *S. melanops* and [*S. ucayalensis* + *S. juruaense*]). Additionally, we conducted two-tailed t-tests comparing means of those groups for each measurement or ratio. Next, we assessed mensural variation among adult specimens of *S. ucayalensis* and *S. juruaense* with the following geographic groupings: Amazon-facing slopes of the Andes in Colombia (Río Rumiyaco); Peruvian Amazon (Río Gálvez); and Brazilian Amazon (Rio Juruá). First, we calculated univariate descriptive statistics for each group. Then, we performed a one-way ANOVA on each cranial measurement and conducted Tukey's tests of pairwise comparisons between means of the three groups.

We then conducted a principal components analysis (PCA) based on the covariance matrix of $\log_e$-transformed cranial measurements of all adult specimens (Classes 4–7). In the PCA, we did not include MFL or MFW, which were missing for many specimens. PCA is a multivariate ordination technique that extracts axes of maximum dispersion among specimens without regard to the group (e.g., locality) to which the specimens belong. However, for the plot of specimen scores on the first two principal components (and for an additional bivariate plot), distinct symbols were used for the three currently accepted species.

Molecular data

Fragments of the mitochondrial gene Cytochrome b (Cyt-b) were sequenced for individuals of *Scolomys melanops* (KU 158213, from San Jacinto, Peru), *S. ucayalensis* (MUSM 13356, from Río Gálvez, Peru), and *S. juruaense* (MPEG 23824, the holotype from Seringal Condor, Brazil). Whole genomic DNA was extracted from frozen or ethanol-preserved tissue with Chelex (WALSH et al. 1991). The two primers used for amplification of Cyt-b (MVZ 05 and MVZ 16; SMITH and PATTON 1993) bracket an 801-bp fragment. The same primers were used for direct sequencing except when heavy-strand sequences (MVZ 16) were not readable; in that case, we used primer MVZ 45, which is located halfway downstream the light strand (SMITH and PATTON 1993). We purified double-stranded PCR products using the QIAquick PCR Purification Kit (QUIAGEN[TM] Inc., Chatsworth, CA) and sequenced directly from the purified PCR products on an ABI 377[TM] automatic sequencer, following the d-Rhodamine Terminator Sequencing Kit (Applied Biosystems[TM]) protocol.

Using Cyt-b sequences, we performed phylogenetic analyses to assess relationships within *Scolomys* and compare with selected oryzomyine and thomasomyine taxa from PATTON and DA SILVA (1995). *Peromyscus truei* and *Neotoma albigula* were used as outgroups (peromyscine and neotomine sigmodontines; GenBank Accession Numbers AF108703 and AF108704, respectively). Sequences were aligned by eye and transferred into PAUP* (SWOFFORD 2002; Version 4.0b10). To obtain overall phenetic measures of similarity between pairs of *Scolomys* taxa, we determined both uncorrected and corrected (TAMURA and NEI 1993 substitution model) genetic distances. Then, we performed two different suites of maximum parsimony analyses: one including all nucleotide changes and a second one excluding third-position transitions (saturated at levels higher than 12% divergence; GARCÍA, unpubl. data). Informative characters were treated as unordered and equally weighted. For both sets of analyses,

we used a heuristic search of 300 random-addition replicates with TBR branch swapping. Bootstrap values (with 300 pseudoreplicates; Felsenstein 1985) and decay indices (Bremer 1994; using TreeRot, Sorenson 1996) were then calculated and placed on the corresponding nodes of the respective strict-consensus tree of each prior analysis. Bootstrap analyses were performed using heuristic searches employed within each pseudoreplicate (10 random-addition replicates; TBR branch swapping). Bremer (1994) values were calculated based on the strict-consensus tree of each parsimony analysis, using a heuristic search of 10 random-addition replicates with TBR branch swapping. Finally, we performed a maximum likelihood analysis under a heuristic search with the 2-parameter HKY85 + G + I model (Hasegawa et al. 1985), in which we estimated nucleotide frequencies, transition-to-transversion ratio, proportion of invariable sites, and shape (α) of the gamma distribution of rate change at different sites (Yang 1996).

We also mapped character changes onto the two strict-consensus cladograms obtained by maximum parsimony and onto the maximum likelihood tree using MacClade (Maddison and Maddison 1999; Version 3.08a). We determined uniquely derived, unambiguously mapped, and unreversed base changes for *Scolomys* taxa and then used Sequence Navigator™ to translate sequences and determine whether or not these base substitutions led to amino acid changes.

Results

External coloration

The variation in external coloration present among specimens from single localities encompasses the entire range of colors formerly considered diagnostic of different species. For example, specimens of *Scolomys ucayalensis* from Río Gálvez range in dorsal coloration from dark gray to reddish or yellowish brown, and this variation appears to be correlated with our toothwear categories. Whereas the youngest individuals (e. g., Classes 1–2) are grayish dorsally with a pelage dominated by dark spines, those in Classes 4–7 are almost always more richly colored (brown or reddish to yellowish brown) due to a stronger infusion of thinner, cinnamon-colored hairs that more completely cover the darker spines. Simi-

larly, in the Río Rumiyaco sample of *S. ucayalensis* (composed of only adults), the dorsal coloration ranges from orange-brown to reddish brown; in contrast to the coloration of those adults, the only juvenal specimen of *S. ucayalensis* from Colombia (Río Caquetá) is dull grayish brown. Likewise, the few skins of *S. melanops* we examined from Allpahuayo and Teniente López include adult specimens that are paler (infused with cinnamon-brown) than the grayish juveniles (see also Anthony 1924 for similar variation in the type series from Mera). These age-related changes in coloration do not represent an abrupt transition from juvenal to adult pelage, but rather a transition that continues throughout adulthood.

In contrast to general changes in dorsal appearance correlated with ontogeny, a few differences in external morphology correspond to geography. For example, despite the great age-related variation in dorsal coloration at single sites, we note that adults of *S. ucayalensis* from the Río Gálvez series show slightly paler dorsal coloration than any *S. melanops* from Allpahuayo. In addition, the color of the plantar surface and pads of the hind foot is distinctive at the Río Rumiyaco (a peculiar bluish gray not found in specimens from any other series, which instead have brownish or whitish plantar surfaces and pads). Furthermore, some animals from Río Rumiyaco show a unique salmon-colored lateral line separating the dorsal and ventral pelage. Finally, whereas the tails of specimens from the Rio Juruá are nearly naked (Patton and da Silva 1995), those of individuals from Río Rumiyaco are well haired.

Cranial morphology

Clear cranial differences exist between *Scolomys melanops* and all other congeneric specimens examined, as previously reported by Pacheco (1991) and Patton and da Silva (1995). First and most notably, the zygomatic arches of *S. melanops* are robust, distinctly rounded, and laterally expanded (= wide, rounded orbital openings of Patton

and DA SILVA 1995), whereas all other series have narrow, subparallel zygomatic arches (Fig. 2). Secondly, the rostrum of *S. melanops* is consistently short (and thus relatively wide), in contrast to the longer (and relatively more slender) rostrum of all specimens of *S. ucayalensis* and *S. juruaense*.

Several additional characters mentioned by PATTON and DA SILVA (1995) serve to separate *S. melanops* on the one hand from *S. ucayalensis* and *S. juruaense* on the other as general tendencies, but not absolutely. First, the incisive foramina are wider overall in *S. melanops* (especially in the Teniente López series). Second, the nasolacrimal capsules are more inflated. Third, the subsquamosal foramen is generally more constricted (or even closed) in *S. ucayalensis* and *S. juruaense* than in *S. melanops*. For example, all specimens of *S. melanops* from Allpahuayo have open subsquamosal foramina, but the foramen is very narrow or almost closed in approximately half the series of *S. ucayalensis* from Río Gálvez and Río Rumiyaco (but clearly open in the remaining specimens of those series). Fourth, although the coronoid process of the mandible is generally longer and more curved in *S. ucayalensis* and *S. juruaense*, some specimens from the two large ontogenetic series (*S. melanops* from Allpahuayo and *S. ucayalensis* from Río Gálvez) overlap in this character. Finally, the difference in opisthodonty-proodonty of the incisors mentioned by PATTON and DA SILVA (1995) is not clear in our examinations; the species overlap in this character when large series are compared.

In contrast to the morphological distinctiveness of *S. melanops*, we found no consistent qualitative difference between *S. ucayalensis* (samples from Peru and Colombia) versus specimens currently assigned to *S. juruaense* (from Brazil). PATTON and DA SILVA (1995) considered that *S. juruaense* possessed a squared anterior margin of the mesopterygoid fossa (rather than rounded, as in *S. ucayalensis*). The anterior margin of the mesopterygoid fossa is indeed rounded (with hardly any medial spine) in most specimens of both *S. melanops* and *S. ucayalen-*

sis, but a few individuals of each have a weakly squared fossa. Similarly, PATTON and DA SILVA (1995) noted that the lateral margins of the incisive foramina of *S. juruaense* are distinctly stepped, while those of the type of *S. ucayalensis* are smoothly tapering. Our examinations show that this character can vary within a single locality. A few specimens of *S. ucayalensis* from Río Gálvez are abruptly constricted in the anterior portion (= stepped of PATTON and DA SILVA 1995). Some specimens of *S. melanops* from Allpahuayo (and all from Teniente López) show a similar trend.

Molar morphology

Our examinations of the two available age series show that S*colomys melanops* (Allpahuayo) and *S. ucayalensis* (Río Gálvez) share the same basic molar morphology. As a general characterization, *Scolomys* molars are pentalophodont with well-developed mesolophs and mesolophids, and undivided anterior margins of M1 and m1 (anterocone and anteroconid entire, without anteromedian flexus or flexid). Based on these two age series, both species possess (on the lingual side) a protoflexus and hypoflexus on M1, a hypoflexus on M2, and an incipient hypoflexus on M3. On the labial side of the upper molars, both species have a paraflexus, mesoflexus, and metaflexus on M1. The anteroflexus is usually separated as an enamel fossette in the Río Gálvez sample of *S. ucayalensis* (with a strongly developed anteroloph present); in contrast, the anteroloph is poorly developed in *S. melanops* from Allpahuayo, with a very short anteroflexus. Tiny fossettes are usually present in the posterolabial region of M1, probably indicating the former presence of a posteroflexus (before significant toothwear). In M2, a paraflexus, mesoflexus, and metaflexus are present, as well as a fossette indicative of a posteroflexus. In M3, a mesoflexus and paraflexus are present, but the metaflexus is absent. In all three upper molars, the interior extension of the paraflexus, mesoflexus, and metaflexus (when present) are commonly iso-
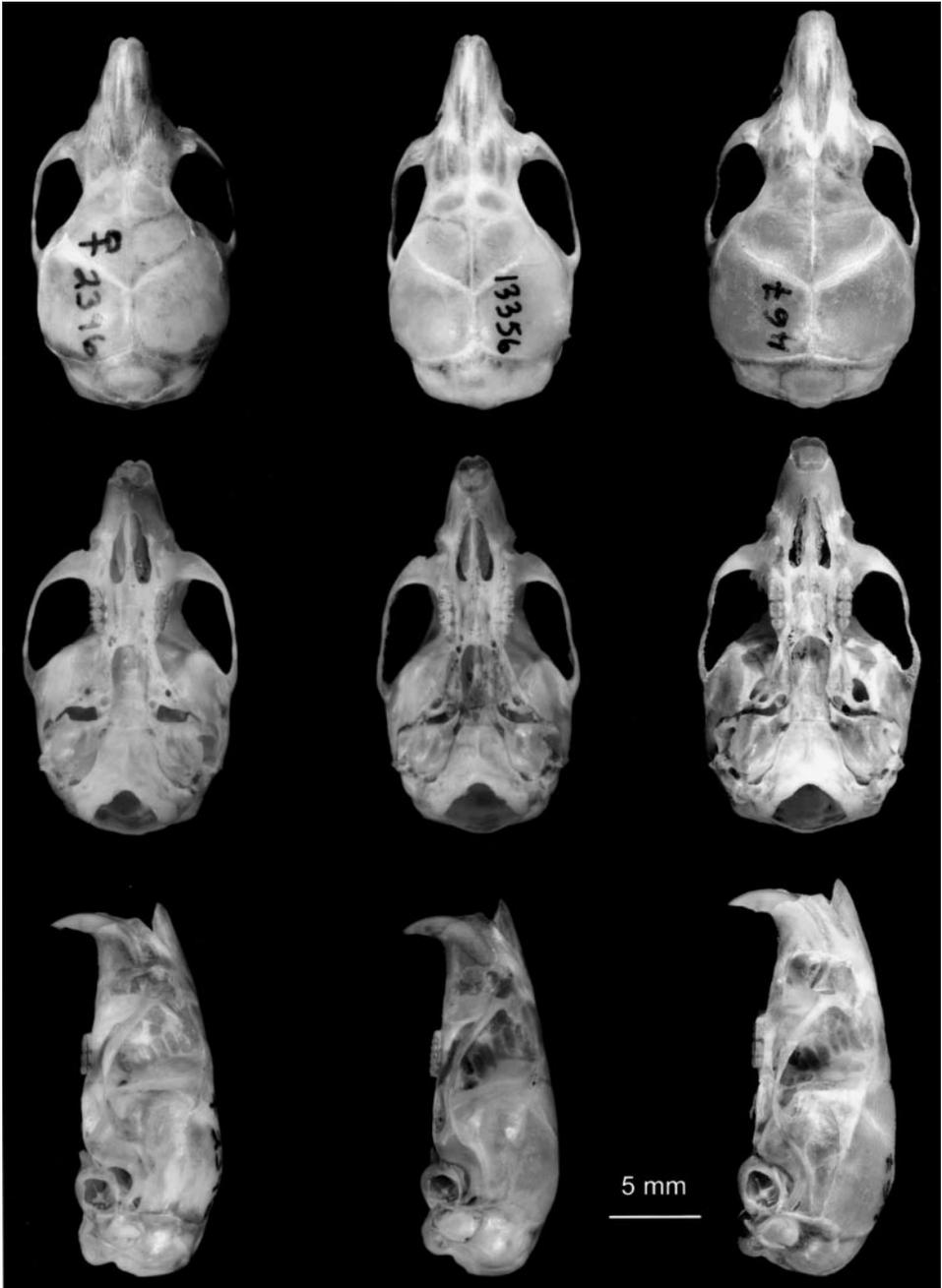
Fig. 2. Dorsal, ventral and lateral views of the crania of *Scolomys melanops* (left, TTU 85501, Allpahuayo, Peru) and *S. ucayalensis* (center, MUSM 13356, Río Gálvez, Peru; and right, IAvH 6205, Río Rumiyaco, Colombia), all adults in toothwear Class 4.

lated as internal fossettes. These flexi are generally deeper in the Río Gálvez series of *S. ucayalensis* than in the Allpahuayo sample of *S. melanops*. On the labial side, the lower molars show flexids corresponding to the flexi present on the lingual side of the upper molars, with the addition of a small protoflexid in m3. On the lingual side, m1 has a metaflexid, mesoflexid, posteroflexid, and weakly developed entoflexid. In overall size, m1 is shorter than M1, due to the reduced development of the procingulum of m1. In m2, a mesoflexid, entoflexid, posteroflexid, and sometimes metaflexid are present. Likewise, m3 has a mesoflexid, posteroflexid, and (in some cases) a minuscule metaflexid. In the lower molars, the entolophid, mesolophid, and posterolophid are often isolated as internal fossettes.

Although age series were not available at other sites, we did note one possible molar difference between Colombian specimens and individuals of *S. ucayalensis* and *S. juruaense* from farther south. Specimens from Río Gálvez and the Rio Juruá show a well-developed anteroloph and deep anteroflexus (often isolated as an internal fossette) in M1. In contrast, the anteroloph is poorly developed in the Colombian Río Caquetá specimen. Similarly, when present, the enamel fossette (remnant of the anteroflexus) is extremely shallow in specimens from Río Rumiyaco.

Statistical analyses

For almost all variables, measurements were smaller for individuals in toothwear Classes 1 and 2 than for those in Classes 4–7 (by visual inspection of plots). In *Scolomys melanops* (from Allpahuayo), growth appeared to plateau by Class 4. In the largest series of *S. ucayalensis* (Río Gálvez), a similar plateau was apparent, but beginning at Class 3. The only measurement that did not follow this general pattern was maxillary molar tooth row length, where the youngest individuals had generally larger measurements (due to wear on the molars in older individuals, reducing the crown measurement).

The principal components analysis showed clear separation between *S. melanops* and all other specimens of both *S. ucayalensis* and *S. juruaense* (Fig. 3 A). Neither PCI nor PCII can be interpreted as a size factor, as both include some variables with positive coefficients and others with negative ones (Tab. 2). In contrast to the multivariate distinctiveness of *S. melanops*, no apparent separation existed between *S. ucayalensis* and *S. juruaense*. Specimens of *S. juruaense* from Brazil spanned the extent of the data swarm of *S. ucayalensis* from Peru and Colombia. The two complete adult specimens from Colombia clearly fell with *S. ucayalensis* from Peru, although they lay toward one end of that data swarm.

Descriptive statistics and associated t-tests comparing means of *S. melanops* and (*S. ucayalensis* + *S. juruaense*) showed differences in cranial proportions but not in overall size (Tab. 3). Only nine of the 23 measurements were significantly different in mean between the two groupings. Interestingly, CIL, MB, CD, and BB – measurements reflecting basic dimensions of overall skull size – were not significantly different in mean. *Scolomys melanops* was significantly larger in mean only for ZB and IFW. In contrast, *S. ucayalensis* + *S. juruaense* showed larger means for IOC, RL-1, RL-2, NL, RW-2, MTRL, and ZPW. A plot of RL-1 versus ZB (for all age classes) reflected a clear shape difference between the two groups, except for in the very youngest specimens (Fig. 3 B). Likewise, although the observed values for adults overlapped for those two measurements, they did not overlap for the derived ratio of RL-1/ZB (Tab. 3).

The three available, although small, series of adult *S. ucayalensis* (Río Rumiyaco and Río Gálvez) and *S. juruaense* (Rio Juruá) showed similar means for almost all measurements (Tab. 4). Differences in mean were significant in only two of the univariate ANOVAs: BB and MB. Tukey's comparisons showed that the series from Río Rumiyaco averaged larger than the other two in MB, and larger than Rio Juruá in BB.
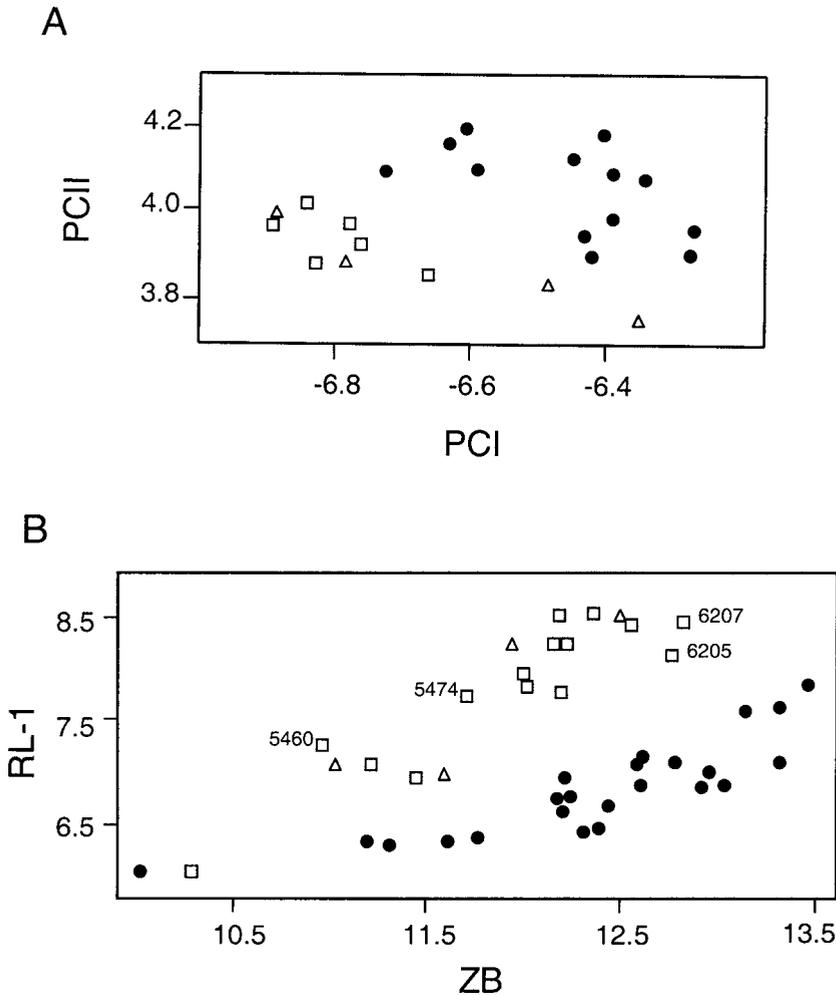
A

B

Fig. 3. Graphical results from mensural analyses. (A): Plot of specimen scores on the first two axes of the principal components analysis (PCA) based on the covariance matrix of $\log_e$-transformed cranial measurements of adult *Scolomys* specimens in toothwear classes 4–7. (B): Plot of RL-1 versus ZB of *Scolomys* specimens in all age classes; numbers indicate the holotype (MUSM 5474) and paratype (MUSM 5460) of *S. ucayalensis* and the two complete specimens of that species from Río Rumiyaco (IAvH 6205 and 6207). In both plots: solid circles indicate *S. melanops*; open squares *S. ucayalensis*; and open triangles *S. juruaense* sensu Patton and da Silva (1995).

Molecular data

We obtained Cyt-b fragments of 776 bp for *Scolomys melanops*, 748 bp for *S. ucayalensis*, and 801 bp for *S. juruaense* (GenBank Accession Numbers AF527419–AF527421). The sequence divergence between *S. ucayalensis* (Río Gálvez) and the holotype of *S. juruaense* (Seringal Condor, Rio Juruá)

was only 1% (for both uncorrected and Tamura-Nei distances). On the contrary, both the Rio Juruá and Río Gálvez samples were 14% (uncorrected) to 17% (Tamura-Nei distance) divergent from the individual of *S. melanops* (Teniente López).

All three phylogenetic analyses retrieved a monophyletic genus *Scolomys* with the ((*S. juruaense* + *S. ucayalensis*) + *S. melanops*)

Table 2. Results of the principal components analysis (PCA) of cranial measurements for *Scolomys* adults in toothwear classes 4–6. Principal components were extracted from the covariance matrix of measurements transformed to their natural logarithms. Elements of the unit eigenvector, eigenvalues, and percentage of variation are given for the first three axes.

	PCI	PCII	PCIII
ln-Condyloincisive length	−0.165	0.156	0.131
ln-Zygomatic breadth	−0.037	0.316	0.135
ln-Braincase breadth	−0.095	0.095	0.074
ln-Least interorbital constriction	−0.294	−0.157	0.093
ln-Rostral length-1	−0.434	−0.110	0.021
ln-Rostral length-2	−0.371	0.010	−0.079
ln-Nasal length	−0.399	−0.100	0.217
ln-Rostral width–1	−0.112	0.308	0.150
ln-Rostral width-2	−0.237	0.039	−0.264
ln-Orbital length	−0.180	0.108	−0.024
ln-Diastemal length	−0.217	0.189	0.001
ln-Maxillary molar tooth row length	−0.158	−0.240	−0.035
ln-Incisive foramen length	−0.109	0.272	−0.639
ln-Incisive foramina width	0.175	0.658	−0.011
ln-Palatal bridge length	−0.183	0.091	0.062
ln-Alveolar width	−0.093	0.174	−0.009
ln-Occipital condyle width	−0.088	0.092	0.212
ln-Mastoid breadth	−0.064	0.119	0.117
ln-Basioccipital length	−0.221	0.203	0.265
ln-Zygomatic plate width	−0.249	0.002	−0.475
ln-Cranial depth	−0.098	0.093	0.190
Eigenvalue	**0.039**	**0.015**	**0.006**
and % variation	49.7%	18.8%	7.9%

Table 3. Descriptive statistics and results of t-tests comparing cranial measurements (mm) and the derived ratio (RL-1/ZB) for adults in age classes 4–7 of *Scolomys melanops* and the pooled sample of (*S. ucayalensis* + *S. juruaense*). Statistics are given as mean ± standard error, sample size, and range (minimum–maximum). Significance is indicated as follows: * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$; n. s. = $P > 0.05$.

	S. melanops	*S. ucayalensis* + *S. juruaense*
Condyloincisive length (n. s.)	20.44 ± 0.22, 16 (18.43–21.75)	20.81 ± 0.28, 11 (18.78–21.76)
Zygomatic breadth *	12.65 ± 0.12, 18 (11.34–13.45)	12.13 ± 0.17, 10 (11.06–12.80)
Braincase breadth (n. s.)	11.24 ± 0.07, 19 (10.63–11.84)	11.40 ± 0.12, 11 (10.85–12.21)
Least interorbital constriction ****	5.14 ± 0.06, 21 (4.76–5.75)	5.71 ± 0.07, 11 (5.37–6.08)
Rostral length-1 ***	7.05 ± 0.10, 18 (6.28–7.83)	8.03 ± 0.18, 10 (6.97–8.51)
Rostral length-2 **	6.20 ± 0.09, 18 (5.54–6.86)	6.80 ± 0.12, 11 (6.10–7.31)
Nasal length **	7.72 ± 0.08, 18 (7.29–8.46)	8.64 ± 0.26, 10 (7.03–9.66)

Table 3. (continued)

	S. melanops	*S. ucayalensis + S. juruaense*
Rostral width-1 (n.s.)	4.82 ± 0.07, 17 (4.30–5.28)	4.69 ± 0.08, 11 (4.28–5.22)
Rostral width-2 **	3.66 ± 0.05, 17 (3.31–3.99)	3.90 ± 0.06, 11 (3.51–4.22)
Orbital length (n.s.)	7.04 ± 0.06, 19 (6.38–7.49)	7.27 ± 0.10, 11 (6.56–7.66)
Diastema length (n.s.)	6.08 ± 0.09, 17 (5.62–6.55)	6.28 ± 0.12, 11 (5.70–7.15)
Maxillary molar tooth row length ***	2.54 ± 0.03, 19 (2.30–2.92)	2.73 ± 0.03, 11 (2.60–3.00)
Incisive foramen length (n.s.)	3.86 ± 0.07, 19 (3.09–4.21)	3.91 ± 0.07, 11 (3.68–4.48)
Incisive foramina width **	2.40 ± 0.06, 17 (1.88–2.72)	2.16 ± 0.03, 11 (2.04–2.35)
Palatal bridge length (n.s.)	9.11 ± 0.11, 15 (8.53–9.80)	9.28 ± 0.11, 11 (8.62–9.70)
Alveolar width (n.s.)	4.64 ± 0.06, 17 (4.20–5.06)	4.67 ± 0.05, 11 (4.44–4.94)
Occipital condyle width (n.s.)	5.99 ± 0.05, 19 (5.62–6.33)	6.06 ± 0.08, 11 (5.76–6.58)
Mastoid breadth (n.s.)	10.30 ± 0.07, 18 (9.88–10.88)	10.40 ± 0.10, 11 (9.93–10.92)
Basioccipital length (n.s.)	3.25 ± 0.03, 18 (3.06–3.57)	3.33 ± 0.08, 11 (2.73–3.63)
Mesopterygoid fossa length (n.s.)	3.87 ± 0.15, 5 (3.38–4.23)	3.76 ± 0.10, 8 (3.24–4.24)
Mesopterygoid fossa width (n.s.)	1.79 ± 0.06, 13 (1.32–2.06)	1.90 ± 0.04, 11 (1.68–2.14)
Zygomatic plate width *	1.67 ± 0.03, 20 (1.47–1.87)	1.79 ± 0.04, 11 (1.65–1.96)
Cranial depth (n.s.)	8.83 ± 0.10, 16 (8.0–9.69)	8.93 ± 0.09, 11 (8.51–9.58)
RL-1/ZB ***	0.55 ± 0.01, 15 (0.52–0.58)	0.66 ± 0.01, 10 (0.60–0.70)

Table 4. Descriptive statistics for adult specimens of *Scolomys* from the Peruvian Amazon (Río Gálvez; *S. ucayalensis*), Brazilian Amazon (Rio Juruá; type series of *S. juruaense*), and eastern-facing slopes of the Andes in Colombia (Río Rumiyaco; *S. ucayalensis*). Statistics are given as mean ± standard error, sample size, and range (minimum–maximum). Asterisks (*) denote measurements for which ANOVAs indicated significant differences in mean among samples. See text for results of Tukey's tests of pairwise comparisons.

	Río Gálvez	Rio Juruá	Río Rumiyaco
Condyloincisive length (n.s.)	21.15 ± 0.22, 4 (20.51–21.54)	20.21 ± 0.55, 4 (18.78–21.20)	21.16 ± 0.58, 3 (20.00–21.76)
Zygomatic breadth (n.s.)	12.16 ± 0.05, 4 (12.02–12.24)	11.79 ± 0.30, 4 (11.06–12.50)	12.78 ± 0.02, 2 (12.76–12.80)

Table 4. (continued)

	Río Gálvez	Rio Juruá	Río Rumiyaco
Braincase breadth *	11.41 ± 0.12, 4 (11.10–11.68)	11.07 ± 0.10, 4 (10.85–11.27)	11.81 ± 0.20, 3 (11.61–12.21)
Least interorbital constriction (n. s.)	5.86 ± 0.10, 4 (5.62–6.08)	5.69 ± 0.11, 4 (5.48–5.89)	5.55 ± 0.10, 3 (5.37–5.72)
Rostral length-1 (n. s.)	8.23 ± 0.12, 4 (7.94–8.51)	7.70 ± 0.40, 4 (6.97–8.51)	8.29 ± 0.14, 2 (8.15–8.43)
Rostral length-2 (n. s.)	6.91 ± 0.05, 4 (6.77–7.00)	6.60 ± 0.28, 4 (6.10–7.31)	6.91 ± 0.25, 3 (6.42–7.24)
Nasal length (n. s.)	8.55 ± 0.38, 4 (7.98–9.66)	8.48 ± 0.55, 4 (7.03–9.45)	9.16 ± 0.06, 2 (9.10–9.21)
Rostral width-1 (n. s.)	4.70 ± 0.04, 4 (4.59–4.78)	4.63 ± 0.20, 4 (4.28–5.22)	4.75 ± 0.19, 3 (4.37–5.00)
Rostral width-2 (n. s.)	3.96 ± 0.05, 4 (3.82–4.04)	3.88 ± 0.11, 4 (3.75–4.22)	3.84 ± 0.16, 3 (3.51–4.02)
Orbital length (n. s.)	7.46 ± 0.07, 4 (7.28–7.56)	7.04 ± 0.19, 4 (6.56–7.50)	7.33 ± 0.18, 3 (7.04–7.66)
Diastema length (n. s.)	6.23 ± 0.11, 4 (5.96–6.46)	6.35 ± 0.32, 4 (5.70–7.15)	6.24 ± 0.19, 3 (5.87–6.46)
Maxillary molar tooth row length (n. s.)	2.69 ± 0.05, 4 (2.60–2.81)	2.70 ± 0.02, 4 (2.64–2.74)	2.84 ± 0.08, 3 (2.72–3.00)
Incisive foramen length (n. s.)	3.78 ± 0.03, 4 (3.68–3.83)	3.92 ± 0.11, 4 (3.76–4.24)	4.08 ± 0.21, 3 (3.76–4.48)
Incisive foramina width (n. s.)	2.17 ± 0.06, 4 (2.08–2.35)	2.16 ± 0.04, 4 (2.09–2.28)	2.14 ± 0.10, 3 (2.04–2.33)
Palatal bridge length (n. s.)	9.32 ± 0.14, 4 (8.95–9.62)	9.18 ± 0.24, 4 (8.62–9.70)	9.36 ± 0.19, 3 (8.98–9.55)
Alveolar width (n. s.)	4.63 ± 0.08, 4 (4.44–4.79)	4.63 ± 0.07, 4 (4.51–4.81)	4.77 ± 0.13, 3 (4.52–4.94)
Occipital condyle width (n. s.)	6.14 ± 0.11, 4 (5.93–6.39)	5.86 ± 0.05, 4 (5.76–5.96)	6.22 ± 0.19, 3 (5.93–6.58)
Mastoid breadth *	10.31 ± 0.13, 4 (9.99–10.59)	10.19 ± 0.10, 4 (9.93–10.43)	10.81 ± 0.09, 3 (10.63–10.92)
Basioccipital length (n. s.)	3.45 ± 0.07, 4 (3.30–3.63)	3.12 ± 0.14, 4 (2.73–3.40)	3.46 ± 0.15, 3 (3.16–3.62)
Mesopterygoid fossa length (n. s.)	3.93 ± 0.13, 4 (3.62–4.24)	3.59 ± 0.12, 4 (3.24–3.75)	– –
Mesopterygoid fossa width (n. s.)	1.81 ± 0.06, 4 (1.68–1.91)	1.93 ± 0.08, 4 (1.76–2.13)	1.99 ± 0.07, 3 (1.90–2.14)
Zygomatic plate width (n. s.)	1.83 ± 0.07, 4 (1.65–1.96)	1.75 ± 0.07, 4 (1.66–1.95)	1.79 ± 0.09, 3 (1.70–1.96)
Cranial depth (n. s.)	8.98 ± 0.13, 4 (8.59–9.15)	8.78 ± 0.10, 4 (8.51–8.98)	9.08 ± 0.25, 3 (8.82–9.5)

relationship consistent. The parsimony analysis using all characters resulted in two equally most-parsimonious cladograms (CI = 0.458; RI = 0.414; 1064 steps; 272 parsimony-informative characters). In the strict-consensus tree, *S. ucayalensis* was sister to *S. juruaense* (100% bootstrap value and decay index of 29), with *S. melanops* sister to them (97% bootstrap support and decay index of 8; Fig. 4 A). The second analysis with third-position transitions removed also yielded two equally most-parsimonious cladograms (CI = 0.478; RI = 0.485; 534 steps). The resulting strict-consensus tree showed identical topology regarding the genus *Scolomys* (again with strong bootstrap support and high decay indices) and improved the resolution and support for other genera (Fig. 4 B). Finally, the maximum likelihood analysis resulted in a tree showing the same relationships among the *Scolomys* samples (Fig. 5; ln-likelihood value 5150.026, empirical base frequencies A = 0.335; C = 0.332; G = 0.060, and T = 0.273; transition-to-transversion ratio = 5.152; value of the gamma shape parameter, $\alpha = 0.557$; and proportion of invariable sites 0.468).
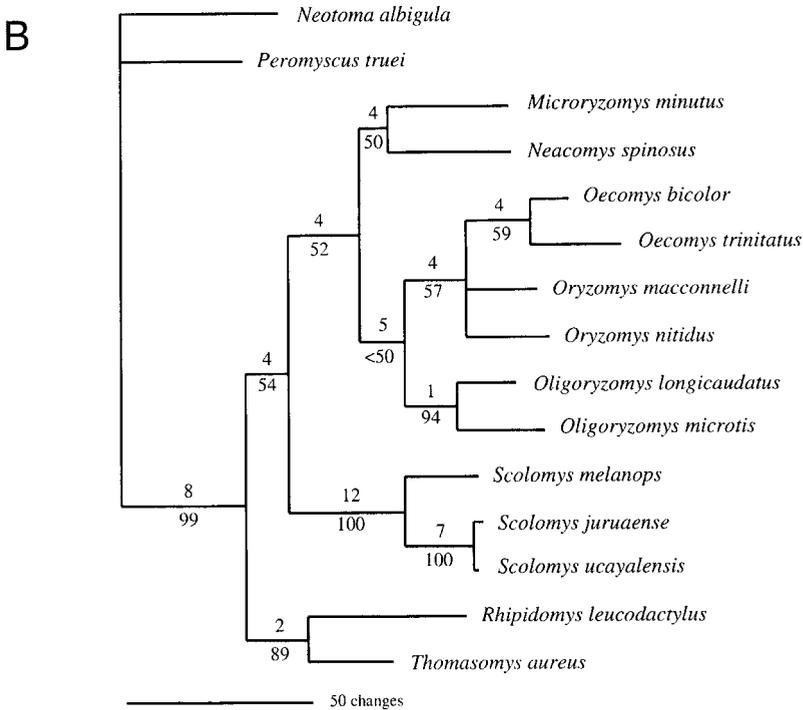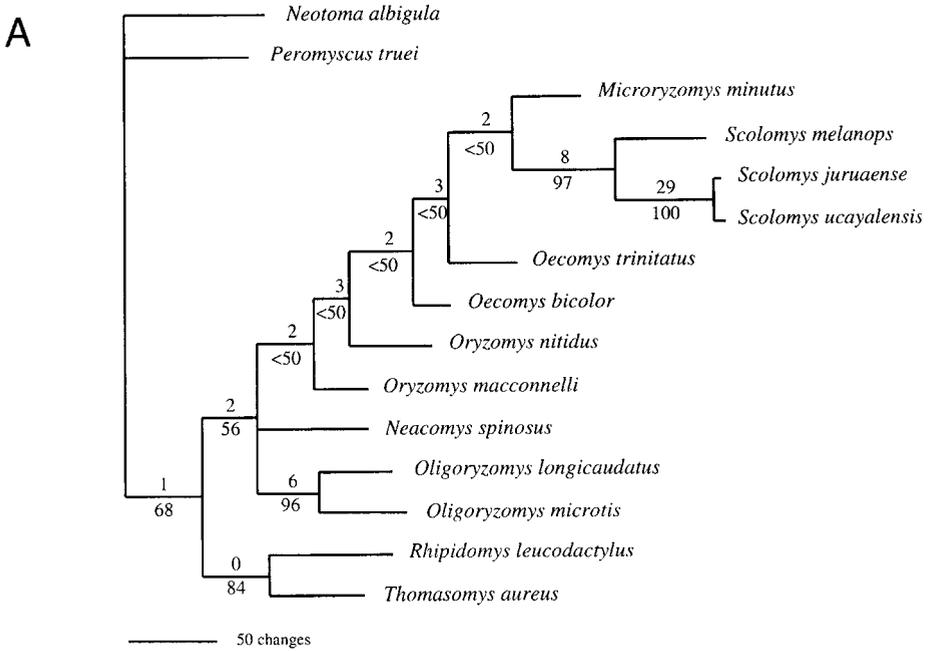
Of the 23 character-state changes associated with the *Scolomys* taxa, 12 were unambiguously mapped onto the respective trees obtained by the parsimony and likelihood analyses. All these nucleotide changes were unreversed and uniquely derived for the *Scolomys* samples. Two were autapomorphies of *S. melanops*; the *S. juruaense* + *S. ucayalensis* clade shared five synapomorphies; and five synapomorphies united the entire *Scolomys* clade. These nucleotide changes included both transitions and transversions, as well as silent and non-silent substitutions (Tab. 5).

Discussion

Alpha-systematic conclusions

Based on similarity of qualitative morphological features, lack of morphometric discrimination, and nearly identical sequences for the mitochondrial gene Cyt-b, we consider *Scolomys juruaense* Patton and da Silva 1995 a synonym of *Scolomys ucayalensis* Pacheco 1991. The apparent distinctiveness of *S. juruaense* in size with respect to *S. ucayalensis* found by Patton and da Silva (1995) was due to comparison of adult specimens of *S. juruaense* with the juvenal holotype (considered adult in the original description) and paratype of *S. ucayalensis*. In *Scolomys*, disappearance of occlusal pattern in the molars due to toothwear occurs faster than in most oryzomyine genera, making aging of specimens problematic before collection of age series at Allpahuayo and Río Gálvez. The holotype of *S. ucayalensis* falls within Class 2 (V. Pacheco in litt.). The paratype, which we examined, also represents an animal in Class 2 and agrees in cranial morphology with the nearby series from Río Gálvez. Patton and da Silva (1995) compared measurements from those two specimens with measurements of Brazilian individuals that they considered adults, yielding an ostensible difference in size. Other differences between *S. ucayalensis* and *S. juruaense* noted by those authors – i. e., in addition to size – can be attributed to ontogenetic changes (coloration) or other intrapopulational variation (stepped versus smoothly tapered lateral margin of incisive foramina; form of mesopterygoid fossa). The Cyt-b sequence from the type specimen of *S. juruaense* is only slightly different from that of *S. ucayalensis* from Río Gálvez (very near the type locality of

▶

Fig. 4. Results of phylogenetic analyses of Cyt-b sequences using maximum parsimony for three samples of the genus *Scolomys* and 10 species of oryzomyine and thomasomyine rodents, with *Neotoma albigula* and *Peromyscus truei* used as outgroups. (A): Strict-consensus tree for analysis including all nucleotide changes. (B): Strict-consensus tree for analysis excluding third-position transitions. Bremer decay indices and Bootstrap support values for nodes are shown above and below each leading branch, respectively.
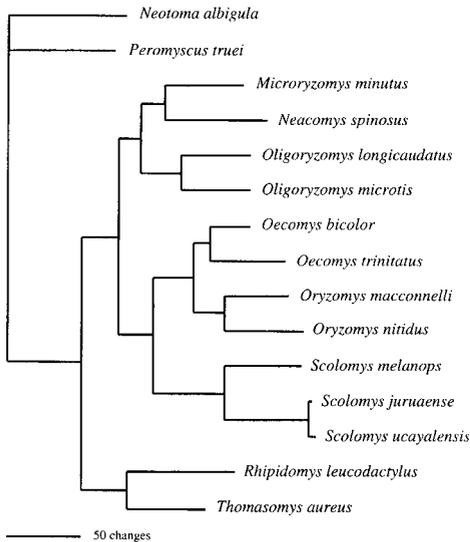
A

Neotoma albigula

Peromyscus truei

Microryzomys minutus

2
<50

8
97

Scolomys melanops

3
<50

29
100

Scolomys juruaense

Scolomys ucayalensis

2
<50

Oecomys trinitatus

3
<50

Oecomys bicolor

2
<50

Oryzomys nitidus

Oryzomys macconnelli

2
56

Neacomys spinosus

6
96

Oligoryzomys longicaudatus

Oligoryzomys microtis

1
68

0
84

Rhipidomys leucodactylus

Thomasomys aureus

50 changes

B

Neotoma albigula

Peromyscus truei

4
50

Microryzomys minutus

Neacomys spinosus

4
52

4
59

Oecomys bicolor

Oecomys trinitatus

4
57

Oryzomys macconnelli

5
<50

Oryzomys nitidus

1
94

Oligoryzomys longicaudatus

Oligoryzomys microtis

4
54

12
100

Scolomys melanops

7
100

Scolomys juruaense

Scolomys ucayalensis

8
99

2
89

Rhipidomys leucodactylus

Thomasomys aureus

50 changes

Fig. 5. Maximum likelihood tree obtained for three samples of the genus *Scolomys* and 10 species of oryzomyine and thomasomyine rodents, with *Neotoma albigula* and *Peromyscus truei* used as outgroups.

S. ucayalensis). Finally, whereas we did not find any unreversed nucleotide change unique to either *S. ucayalensis* or *S. juruaense*, five such base changes are shared between them. These five synapomorphies of the two previously recognized species should now be considered autapomorphies of *S. ucayalensis*.

Conversely, *S. melanops* is morphologically, karyologically, and genetically well differentiated from *S. ucayalensis* (now including *S. juruaense*). The most salient morphological differences between the two species are in cranial proportions. The rostrum of *S. melanops* is extremely short and wide, in contrast to the longer, relatively thinner rostrum of *S. ucayalensis* (all *Scolomys* have a distinctively blunt rostrum when compared with other oryzomyines). Additionally, its zygomatic arches are distinctly wider and more rounded than the narrow, straight ones of *S. ucayalensis*. Indeed, adults of the two species do not overlap in the derived ratio of RL-1/ZB. Although clear proportional differences exist between the two species, they are generally similar in

overall cranial size (e. g., CIL, MB, CD, BB). Most other diagnostic characters of *S. melanops* listed by PATTON and DA SILVA (1995) serve as general tendencies, but not as absolute differences. Finally, *S. melanops* (from Teniente López) is 17% (Tamura-Nei distance) divergent from samples of *S. ucayalensis* from Peru and Brazil for Cyt-b and shows two unique nucleotide changes.

Phylogenetic affinities

The placement of *Scolomys* in the tribe Oryzomyini is controversial. Voss and CARLETON (1993) provided a diagnosis of the tribe based on five morphological characters, one of which was the possession of four or more pairs of mammae. Although Voss and CARLETON (1993) included *Scolomys* in the 15 genera that they placed in the tribe, PATTON and DA SILVA (1995) correctly noted that *Scolomys* lacks a pectoral pair of mammae and thus shows only four of the five synapomorphies of the tribe. Recently, Voss et al. (2002 a) noted the presence of only six mammae in a new oryzomyine genus, *Handleyomys*. All other genera in the tribe evidently possess at least eight mammae.

In addition to the previous five synapomorphies, STEPPAN (1995) proposed the presence of hemal arches associated with caudal vertebrae (typically between the second and third) as a putative synapomorphy for oryzomyines. He examined 11 of the 15 genera assigned to the Oryzomyini by Voss and CARLETON (1993); of those 11, all but *Nesoryzomys* possess hemal arches (STEPPAN 1995). We note that *Sigmodontomys* and *Lundomys* (two of the oryzomyine genera not considered by STEPPAN 1995) also have hemal arches (based on our examination of *S. alfari*, ICN 12157 from Colombia, and *L. molitor*, AMNH 206363, 206368, 206392–206393 from Uruguay). Voss et al. (2002 a) also reported the presence of hemal arches in *H. fuscatus*. In contrast, *Scolomys* lacks hemal arches (based on three examined specimens of *S. ucayalensis* with postcranial skeletons: AMNH 272721, IAvH 6205, and ICN

Table 5. Unique and unreversed autapomorphies and synapomorphies for *Scolomys*, with their effect on the resulting amino acid. TI, transition; TV, transversion.

Position	Change	Type	Codon position	Final codon	Amino acid	Effect
Autapomorphies of *S. melanops*						
39	T → C	TI	3	ATC	Ile	silent
375	A → C	TV	3	GCC	Ala	silent
Synapomorphies of *S. juruaense* + *S. ucayalensis*						
52	T → C	TI	1	CTC	Phe → Leu	non-silent
375	A → T	TV	3	GCT	Ala	silent
705	A → T	TV	3	CTT	Leu	silent
709[a]	A → C	TV	1	CTT	Ile → Leu[b]	non-silent
	A → C	TV	1	CGT	Ser → Arg[c]	non-silent
711[a]	A → T	TV	3	CGT	Arg[b]	silent
	A → T	TV	3	CTT	Leu[c]	silent
Synapomorphies of *S. juruaense* + *S. ucayalensis* + *S. melanops*						
186	A → C	TV	3	GCC	Ala	silent
466	A → G	TI	1	GTA	Met → Val	non-silent
609	A → T	TV	3	ACT	Thr	silent
642	C → T	TI	3	AAT	Asn	silent
700[a]	C → A	TV	1	ATT	Leu → Ile[d]	non-silent
	C → A	TV	1	ATA	Leu → Met[e]	non-silent

[a] nucleotide change is the same for all the taxa involved, but the amino acid translated from the codon is different for the respective taxa because of differences in the composition of one of the two other bases of the codon.
[b] In *S. juruaense*
[c] In *S. ucayalensis*
[d] In *S. melanops*
[e] In *S. juruaense* and *S. ucayalensis*

16233). Thus, of the oryzomyine genera in which the character has been examined, *Scolomys* and *Nesoryzomys* constitute the only ones lacking hemal arches.

Despite its possession of four of the six synapomorphies of the Oryzomyini, the inclusion of *Scolomys* in that tribe has not yet been conclusively demonstrated in a phylogenetic analysis. Its position was unstable in a recent molecular phylogenetic study of sigmodontine genera using Cyt-b, never appearing within oryzomyines (SMITH and PATTON 1999). Lacking strong support for its inclusion in the tribe, those authors conservatively considered *Scolomys* a unique lineage among sigmodontines. However, because support for deeper nodes of the analyses of SMITH and PATTON (1999) is

weak, firm evidence against the placement of *Scolomys* as an oryzomyine is also lacking. The ingroup and outgroup assumptions of Voss (1993) would indicate that the lack of hemal arches and the possession of only six mammae are plesiomorphic character states. Thus, if *Scolomys* represents a basal lineage within the Oryzomyini (see Voss et al. 2002 a), the possession of eight or more mammae and the presence of hemal arches would then represent synapomorphies not of the tribe, but rather of less-inclusive clades within it. Further phylogenetic studies with extensive taxon sampling are necessary to assess the placement of *Scolomys* and the relevance of these morphological characters fully.

Natural history and distributions

Based on information provided by collectors, both species of *Scolomys* occupy terrestrial habitats within both intact and disturbed forests and other secondary vegetation. Although the precise habitat in which the type series of *S. melanops* was taken at Mera is unknown (Anthony 1924; see also Musser et al. 1998), topotypic specimens were later taken in traps placed both in cultivated fields and at the edge of a mature forest (see Rageot and Albuja 1994, who also described nests of the species). At Limoncocha, three individuals of *S. melanops* were collected in Sherman live traps in a small patch of remnant forest (A. L. Gardner in litt.). All specimens from San Jacinto and Teniente López were obtained only in pitfall traps placed in disturbed habitats, although Sherman traps and Victor snap traps were set both in the trees and on the ground (R. M. Timm pers. com.; N. Woodman in litt.). At Allpahuayo, individuals were captured in pitfall, Sherman, and Victor traps in several classes of selectively logged forest. Most were caught on the ground, but two were taken on fallen logs about 1 m above the forest floor. There, *Scolomys* was encountered in all months of the wet season, but never in the four drier months (Hice 2001; C. L. Hice in litt.).

Similar information exists for *S. ucayalensis*. Both individuals from the type series taken on the Río Ucayali (Jenaro Herrera) were captured in edge habitat, one near a stream and the other adjacent to a patch of forest (Pacheco 1991); two additional specimens from the type locality were captured in pitfall traps in forest (Jsaev 1994). All individuals of that species trapped at Río Gálvez were found in primary forest (both upland and valley-bottom terra firma forest, not seasonally flooded). Most were obtained in Sherman traps placed on the ground, but one was captured on a fallen tree approximately 70 cm above the ground. Nevertheless, none was encountered in traps placed in trees higher above the forest floor (R. S. Voss in litt.; see also Fleck and

Harder 2000). Animals from Río Rumiyaco were taken in Sherman traps on the ground in both primary forest and small plots ("chagras") of manioc within the forest (Y. Muñoz-Saba pers. com.). The specimen from Río Caquetá was captured in a Sherman trap placed on the forest floor in primary habitat; none entered traps set high in the trees at 22–25 m (P. Rivas-Pava in litt.). Along the Río Juruá, specimens were captured in primary terra firma forest in Sherman traps on the ground; none was encountered in an equal number of traps set in trees at 10–15 m (Patton and da Silva 1995; Patton et al. 2000) or in Victor rat traps or Sherman traps placed in vine tangles within 1–3 m of the ground (J. L. Patton in litt.).

The genus *Scolomys* is now known from 16 localities: the 14 from which we have examined specimens and confirmed specific identification, plus Huamaní in the on the eastern versant of the Andes in Ecuador (Albuja-V. 1991) and Yasuní National Park in Amazonian Ecuador (Castro-Revelo and Zapata-Ríos 2001). Based on our confirmed material, *S. melanops* has a moderately restricted distribution and little geographic variation, with localities on the slopes of the Andes in Ecuador and in Amazonian regions of Ecuador and Peru. Given the distributional and natural history information now available, *S. melanops* is probably not endangered (contra Tirira-S. 1999). In contrast, *S. ucayalensis* shows a puzzling distribution and considerable geographic variation. Most (six) localities lie south of the Amazonas river, but three sites are present far to the north in Colombia. Genetic divergence among examined southern samples of *S. ucayalensis* in Peru and Brazil is low. Although morphological data (composition of anteroloph/anteroflexus, coloration of plantar pads, hairiness of tail, and braincase size) insinuate a moderate level of differentiation between northern and southern populations of the species, mtDNA sequence data from northern populations are currently lacking. Despite these reservations, all populations that we ascribe to *S. ucayalensis* share a consistent

general morphology and indicate a much more extensive distribution for the species than previously suggested. The proximity of the locality of *S. melanops* at Allpahuayo just north of the Amazonas-Marañón to Peruvian localites of *S. ucayalensis* south of that river raises the possibility that it serves as a distributional barrier for the two species there. The Rio Juruá does not constitute a significant historical barrier to non-volant small mammals (Patton et al. 1997; Gascon et al. 2000; Patton et al. 2000), but other rivers in the region are larger and may do so (da Silva and Patton 1998).

Future studies should add to our understanding of the distributions and evolutionary relationships of the species and populations of *Scolomys*. We have not examined material from Ecuador reported as *S. melanops* from Huamaní (Albuja-V. 1991) and

S. juruaense from the Yasuní National Park (Castro-Revelo and Zapata-Ríos 2001). In addition, numerous specimens of the genus are present in the Escuela Politécnica Nacional in Quito (L. Albuja-V. pers. com.). If specimens from Yasuní truly represent *S. ucayalensis* (including *S. juruaense*), that would reveal another region where the distributions of *S. melanops* and *S. ucayalensis* come into close contact. Clearly, larger and better-preserved series, karyotypes, and DNA-sequence data are necessary for northern samples of *S. ucayalensis* to characterize populations there adequately and further examine levels of differentiation from southern populations of the species. In general, more collection effort throughout the region is essential to fill large gaps in the known distributions of *Scolomys*.

Acknowledgements

Zusammenfassung

Erneute integrierte, systematische Auswertung der amazonischen Gattung *Scolomys* (Rodentia: Sigmodontinae)

Wir haben qualitative, quantitative und genetische Analysen durchgeführt, um die Grenzen und Aufteilung von *Scolomys*, einer wenig bekannten Gattung amazonischer Nagetiere, aufzuklären. *S. melanops* ist charakterisiert durch die konsistenten proportionalen Unterschiede in der Schädelform im Vergleich zu allen anderen Gruppen dieser Gattung. Unsere Daten unterstützen nicht die Anerkennung von *S. juraense* als gültige Art; vielmehr belegen sie, daß es sich um ein Synonym von *S. ucayalensis* handelt. Nur minimale Unterschiede in den Gensequenzen Cyt-b von *S. juruaense*

und *S. ucayalensis* sind vorhanden. Die phylogenetischen Analysen lassen erneut auf *Scolomys* als monophyletische Gattung mit dem Verhältnis ((*S. juruaense* + *S. ucayalensis*) + *S. melanops*) schließen. Der scheinbare Unterschied laut der Originalbeschreibung des *S. juruaense* kam zustande, weil die untersuchte Anzahl zu klein war und auch, weil ein Vergleich zwischen brasilianischen ausgewachsenen Tieren und dem Typusmaterial aus jungen Exemplaren von *S. ucayalensis* aus Peru angestellt wurde. *S. melanops* und *S. ucayalensis* können, an Hand des relativ kurzen und breiten Rostrums und der breiten Jochbögen von *S. melanops* getrennt werden. Dagegen hat *S. ucayalensis* ein langes und relativ dünnes Rostrum und absolut enge Jochbögen. *Scolomys melanops* ist von den Osthängen der Anden in Ekuador bis in die Nähe von Iquitos im Amazonasgebiet von Perú angesiedelt. Die Anwesenheit von *S. ucayalensis* im Westen Brasiliens, im Norden Perus und im Süden Kolumbiens können wir belegen.

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