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SYSTEMATICS OF ARGENTINEAN, PARAGUAYAN, AND URUGUAYAN SWAMP RATS OF THE GENUS *SCAPTEROMYS* (RODENTIA, CRICETIDAE, SIGMODONTINAE)

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We present a systematic study of *Scapteromys* populations from Argentina, Paraguay, and Uruguay, based on molecular and morphological evidence. First, based on DNA sequences (801 base pairs) from the mitochondrial cytochrome-*b* gene, we found that *Scapteromys* populations fall into 2 main clades; 1 formed by Argentinean and Paraguayan populations together with 1 population from western Uruguay, and the other constituted by the remaining Uruguayan populations. Analysis of molecular variance showed that 86.93% of the genetic variation uncovered in *Scapteromys* is explained by differences between clades. Morphological analyses corroborated the existence of 2 main morphotypes among *Scapteromys* specimens. The phylogeographic break identified is mostly congruent with patterns of morphological and chromosomic variation. In light of these results, we propose that *S. aquaticus* be elevated to the rank of species, we redefine the known distributions of *S. aquaticus* and *S. tumidus*, and we provide a list of character states that allow an unambiguously diagnosis of both species.

Key words: phylogeography, *Scapteromys*, South America, species limits, swamp rats

The genus of swamp rats, *Scapteromys*, belongs to Sigmodontinae, a New World subfamily of cricetid rodents. *Scapteromys* is distributed through part of the Río de la Plata basin and some adjacent areas in east-central Argentina, south coastal Brazil, southern Paraguay, and Uruguay. It occupies habitats near watercourses, including large rivers, small creeks, ponds, and swamps. Darwin, who collected a specimen that later became the type of *Scapteromys tumidus*, wrote, "This rat was caught in so wet a place amongst the flags bordering a lake, that it must certainly be partly aquatic in its habits" (Waterhouse 1839:58). In fact, *Scapteromys* is an excellent swimmer; it propels itself by horizontal undulations of the tail and by rowing and paddling with the hind and fore feet, respectively (Massoia and Fornes 1964). *Scapteromys* also is able to climb trees, a behavior reported as an adaptation to living in flooded areas (Barlow 1969; Sierra de Soriano 1969). *Scapteromys* is mainly nocturnal and feeds primarily on insects and oligochaetes but also hirudines and vegetation (Barlow 1969; Massoia 1961).

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Phylogenetic analyses of nuclear and mitochondrial DNA sequences indicate that this genus is part of the tribe Akodontini (D'Elía 2003; Smith and Patton 1999). Hershkovitz (1966) and Massoia (1980) established the basis of the current contents of *Scapteromys* by removing some species previously allocated to the genus and placing them into new genera, *Kunsia* and *Bibimys*. Massoia and Fornes (1964) considered *Scapteromys aquaticus*, a taxon described by Thomas (1920), to be a subspecies of *S. tumidus*, whereas Hershkovitz (1966) recognized only *S. tumidus* without any internal division.

With the advent of cytogenetic studies of sigmodontine rodents, it was shown that *Scapteromys* has a large amount of chromosomal variation. Further, this variation appeared to be geographically structured. A diploid number (2n) of 32 occurred in populations from Argentina (Brum et al. 1986; Fronza et al. 1976) and Paraguay (P. Myers, pers. comm.), whereas populations in Uruguay had 2n = 24 (Brum 1965; Brum et al. 1972, 1986). Three karyomorphs have been reported from Brazilian populations: 2n = 24, 34, and 36 (Freitas et al. 1984). In parallel, our knowledge of *Scapteromys* also increased directly from fieldwork, which extended the known distribution of the genus. Myers and Wetzel (1979) obtained *Scapteromys* in Paraguay, and Contreras (1966, 1982), Freitas et al. (1984), and González

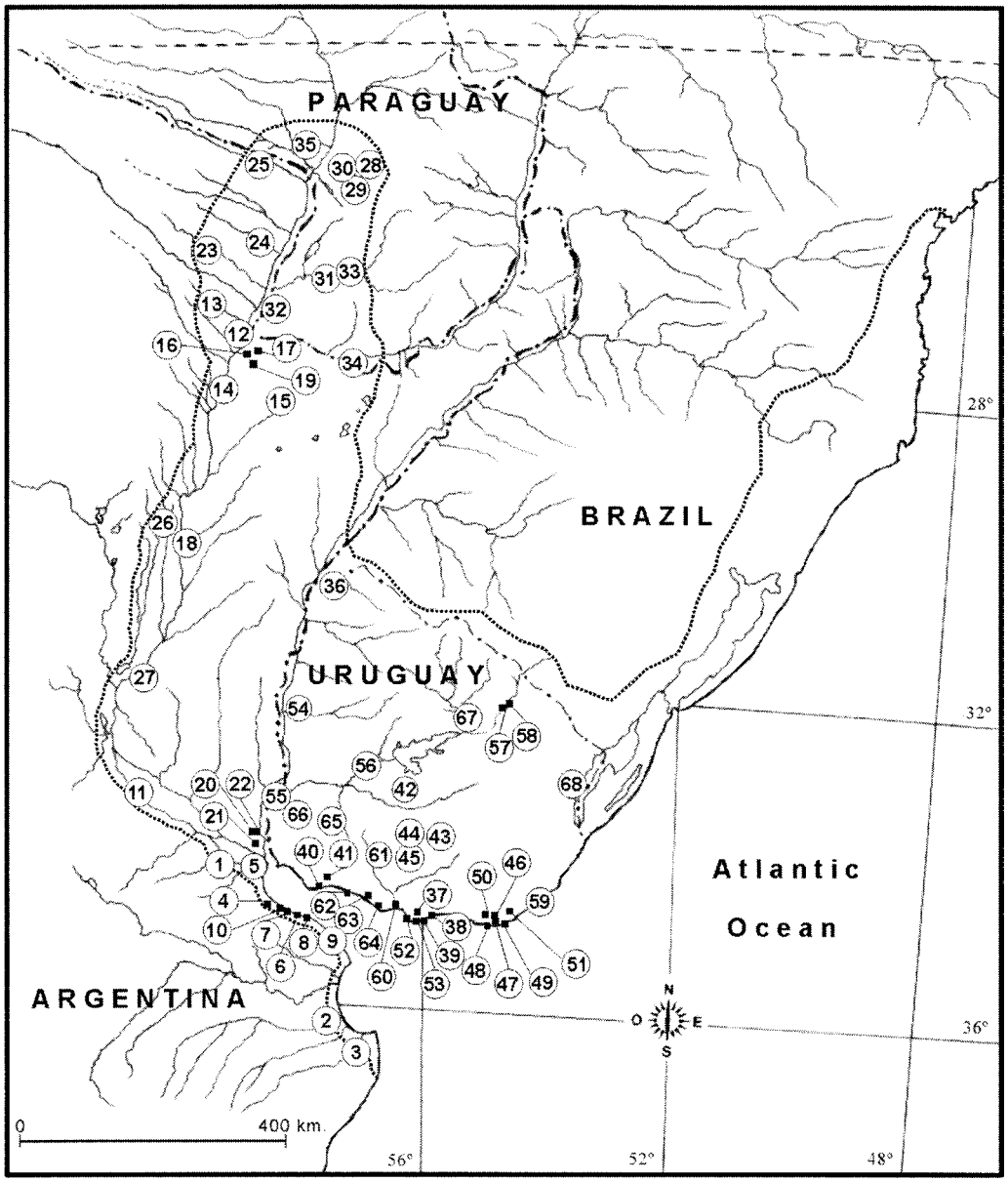

FIG. 1.—Map of a portion of the southern cone of South America showing collecting localities of *Scapteromys* specimens included in this study. Numbers refer to sites listed in Appendix I. Dotted line encloses the approximate known distribution of the genus (compiled from several sources). See Appendix I for population names and specimens included.

(1994) reported it from several new Argentinean, Brazilian, and Uruguayan localities, respectively. In addition, Reig (1994) described the 1st known fossil species of the genus, *S. hershkovitzii*, from Pliocene deposits of southeastern Buenos Aires province, Argentina.

In this study we present a systematic study of *Scapteromys* populations from Argentina, Paraguay, and Uruguay based on molecular and morphological evidence. First, we analyze the phylogeographic structure (Avise et al. 1987) based on mitochondrial DNA (mtDNA) sequences obtained from the cytochrome-*b* gene. Second, we evaluate the agreement among the uncovered phylogeographic pattern and morphological and karyotypic variation. Third, we consider the taxonomic rank of the phylogeographic units found within *Scapteromys*.

MATERIALS AND METHODS

Molecular data analyses.—Phylogeographic analysis was based on the first 801 base pairs (bp) of the cytochrome-*b* gene of 47 specimens of *Scapteromys* belonging to 16 populations from Argentina, Paraguay, and Uruguay (Fig. 1; Appendix I). Sequences of 4 specimens were obtained from Smith and Patton (1999) and D'Elía (2003). Cytochrome-*b* gene sequences generated in this study were amplified and sequenced from a single fragment using primers located in 1 flanking region of the gene and approximately 801 bp toward the 3′ end of the gene (MVZ 05–MVZ 16—see da Silva and Patton [1993] for primer sequences and positions). Amplifications via polymerase chain reaction (PCR) were as follows: 94°C for 3 min; 33 cycles of denaturation at 94°C for 20 s, annealing at 48°C for 15 s and extension at 72°C for 60 s; 72°C for 7 min. Negative controls were included in all

experiments. Double-stranded DNA products were dye-labeled (Big Dye Reaction Kit, Applied Biosystems, Inc., Foster City, California) in a 2nd PCR reaction (95°C for 3 min; 30 cycles of 95°C for 10 s; 50°C for 5 s; 60°C for 4 min). The products were sequenced using an ABI 377 automatic sequencer (Applied Biosystems). In all cases, both heavy and light DNA strands were sequenced and compared. Sequences were visualized, reconciled, and translated to proteins to proof for stop codons using Sequence Navigator version 1.0.1 (Applied Biosystems). All sequences were deposited in GenBank (accession numbers AY445526–AY445553 and AY445555–AY445570).

Sequence alignment was done with the program Clustal X (Thompson et al. 1997) using the default costs. Descriptive analyses assessment of base composition, number of variable characters by codon position, observed number of differences between all haplotype pairs, and differences between pairs of populations of the cytochrome-*b* gene sequences were completed with the program MEGA 2.0 (Kumar et al. 2001).

Aligned sequences were subjected to maximum parsimony analysis (Farris 1982; Kluge and Farris 1969) using PAUP* 4 (Swofford 2000) to generate cladograms. The search strategy used consisted of 200 heuristic replicates with tree bisection and reconnection and random addition of taxa. Based on the results of D'Elía (2003), samples of *Kunsia* and *Blarinomys* (Appendix I) were used as outgroups (Nixon and Carpenter 1993) to polarize character state changes. Characters were treated as unordered and equally weighted. Relative support of the recovered clades was assessed by performing 1,000 jackknife replications (Farris et al. 1996) with 5 addition sequence replicate each and the random deletion of one-third of the data. Branches with <50% support were allowed to collapse. In addition, Bremer support values (Bremer 1994) were computed for those nodes that originate from branches longer than 1 or 2 steps. Molecular synapomorphies were documented by examining PAUP* outputs and visualized using MacClade 3.05 (Maddison and Maddison 1992). Only those changes unambiguously optimized regardless of the kind of character transformation used (i.e., accelerated or delayed) were included.

A hierarchical analysis of the distribution of genetic diversity was conducted in the form of an analysis of molecular variance (AMOVA—Excoffier et al. 1992) using Arlequin version 2.000 (Schneider et al. 2000). Hierarchical levels were defined on the basis of sampling localities and major clades found in the maximum parsimony analysis.

Morphologic data analyses.—Five hundred sixty-four *Scapteromys* specimens belonging to 68 populations were examined (see Appendix I). Locality and sex information were recorded as given on specimen tags and collection catalogs. Skulls were segregated into 5 age classes based on molar wear following Barlow's (1969) classification. Examples of the molar occlusal morphology variation related to wear can be consulted in Massoia (1981; figure 1). A subset of 443 skulls (in general, adult individuals) were qualitatively scored for those skull features (i.e., shape of the frontoparietal suture and mesopterygoid fossa) discussed by Massoia and Fornes (1964) as relevant to diagnosing *Scapteromys* forms. In addition, molar morphology and other cranial characters also were evaluated. Holotypes of *S. aquaticus* and *S. tumidus* were not directly examined; their morphological character states were obtained through examination of high-quality photographs.

Morphometric analyses included only adult specimens (age classes 3–5, $n = 229$) and were based on the following 18 cranial and dental dimensions: condyloincisive length (CIL), palatilar length (PL), upper diastema length (DL), greatest zygomatic breadth (ZB), least interorbital breadth (IOB), breadth of braincase (BB), breadth of rostrum (RB), nasal length (NL), greatest nasal breadth (GNB), incisive foramen length (IFL), incisive foramen breadth (IFB), breadth of mesopterygoid fossa (BMF), alveolar length of maxillary toothrow (LM1–3), width of upper 1st molar (WM1), length of upper 1st molar (LM1), mandible length without incisor (ML), dentary depth (DH), and alveolar length of mandibular toothrow (Lm1–3). Measurements were taken according to definitions provided by Myers et al. (1990) and Hershkovitz (1990; figure 15), except DH, which corresponds to the dimension between the mandible angular and condyloid processes. Descriptive statistics (mean, standard deviation, and range) were derived for locality samples with 5 or more adult individuals (11 samples). Effect of gender on the 18 recorded variables was examined through 1-way analysis of variance (ANOVA) in the largest study sample ($n = 51$, females = 23; La Balandra population from Argentina). To increase sample sizes for the multivariate analyses of craniodental dimensions, variables that showed significant intersexual differences were discarded and sexes pooled. A subset of 130 intact skulls (without missing measurements) was used in multivariate analyses. This sample was constituted only of specimens from age class 3 because 1-way ANOVA revealed significant differences in most of the variables among adult age classes (results not shown). Multiple analysis of variance (MANOVA) was used to test for significant differences between groups defined on the basis of sampling localities and major clades found in the maximum parsimony analysis. Principal components were extracted from a variance–covariance matrix and computed using the craniodental variables after transformation to their natural logarithms. Statistics analyses used the program Statistica (StatSoft, Inc. 2001).

RESULTS

Molecular based analyses.—Twenty-one cytochrome-*b* haplotypes were found among the 47 sequenced specimens of *Scapteromys* (Table 1). These haplotypes present a strong base compositional bias, with a marked deficit of guanine, especially in 3rd codon positions. The mean base percentages across all *Scapteromys* haplotypes and across all base positions are A = 27.7, C = 32.2, T = 27.3, and G = 12.8. The 21 haplotypes are defined by 55 variables sites of which 10 correspond to 1st codon positions, 7 to 2nd positions, and 38 to 3rd positions. These 55 nucleotide substitutions implied 11 amino acid differences. Intrapopulation divergence was low, ranging from 0 to 5 observed substitutions (0–0.6%). Four of the 11 populations from which >1 specimen was sequenced showed no variation (Table 1). Intrapopulation divergence accounts for only 2.06% of the total uncovered genetic variation. Values of divergence between haplotype pairs from different populations show a large range of variation, from 0 to 38 observed substitutions (0.0–4.7%). Only 3 of the 21 recovered haplotypes are found in >1 population (Table 1). Moreover, all studied specimens from Estancia La Quemada 1 ($n = 4$) and Estancia La Quemada 2 ($n = 3$) shared the same haplotype.

Maximum parsimony analysis of *Scapteromys* haplotypes yielded 22 most parsimonious trees of 245 steps (consistency index [CI] = 0.898, retention index [RI] = 0.970). A strict consensus analysis of these trees (Fig. 2A) revealed 2 main clades that are reciprocally monophyletic. One clade (the western clade) includes all Argentinean and Paraguayan populations together with a population from western Uruguay (Las Cañas); the 2nd (the eastern clade) has a more restricted

TABLE 1.—Distribution of the 21 cytochrome-*b* haplotypes uncovered in the phylogeographic analysis of population of *Scapteromys*. Population numbers are those of Fig. 1 and Appendix I. Haplotype numbers correspond to those listed in Fig. 2.

	Haplotype number																				
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
6 La Balandra	1	4																			
9 Punta de Indio		1																			
11 Ramallo				3																	
13 Selvas del Río de Oro					1	1	1														
18 Río Paraná, 0.5 km W Esquina								1													
23 17 km W Villafañe									1	1											
30 Estancia Ype Kua											1										
32 Estancia Yacaré												1									
33 C. del Río Tebicuary													4								
46 Arroyo el Renegado														2	1						
50 Las Flores																1	2			1	
55 Las Cañas			6																		
57 Estancia La Quemada 1																					4
58 Estancia La Quemada 2																					3
59 Arroyo La Palma																		2	3		
63 Kiyú																				1	

distribution and includes the remaining Uruguayan populations (Fig. 2B). Support for both clades was high: jackknife = 100% and Bremer support = 6 and 12 for the western clade and the eastern clade, respectively. AMOVA indicates that most (86.93%) of the uncovered genetic divergence of *Scapteromys* is explained by the divergence between these 2 main clades. Observed substitutions among populations of both clades ranges from 3.6% to 4.7%. Relationships among haplotypes within each of the main clades are poorly resolved. Only 2 of the 6 populations from which >1 haplotype was recovered appeared as monophyletic. AMOVA indicated that only 11.01% of the total genetic variation of *Scapteromys* was explained by differences among populations within each main clade. Observed substitutions among populations within each clade ranges from 0.0% to 1.0%.

Morphological analysis.—Two main morphological types exist among *Scapteromys* individuals. The 1st morphotype is characterized by a frontoparietal suture that more or less resembles an open U or V, and it is often associated with a quadrate mesopterygoid fossa that has a bluntly pointed median palatine process (Fig. 3A). This morphotype characterized all Argentinean and Paraguayan populations as well as 1 from Uruguay (Las Cañas) and is present in the holotype of *S. aquaticus* (BMNH 17.6.1.6). A more or less pronounced frontoparietal suture resembling a W, often associated with a rounded mesopterygoid fossa that lacks a median palatine process, characterized the other morphotype (Fig. 3B). This morphotype is common in all but 1 of the Uruguayan populations, and it is represented by the holotype of *S. tumidus* (BMNH 55.12.24.18). However, there is some degree of variability in these characters. There are, for example, individuals whose frontoparietal sutures are irregular and cannot be scored as either of the 2 morphotypes. The correspondence between morphotypes and geography also is obscured by the fact that at most of the eastern clade localities and at 2 southern populations of the western clade, both main morphs occur in sympatry (Table 2). In these polymorphic populations, however, 1 of the morphotypes is always predominant.

Sexual dimorphism in craniodental measurements was significant in only 1 (breadth of the braincase; $F = 4.95, P \leq 0.05$) of the 18 dimensions examined. This variable was excluded from the subsequent ordination analyses. Descriptive statistics (available on request) showed that populations from the eastern clade are slightly larger than those from western clade. This observation was noted by Massoia and Fornes (1964), although later minimized by Hershkovitz (1966). Crania in eastern clade populations generally are larger and more robust than those in the western clade. In general, eastern clade specimens have, on average, slightly larger cranium, upper diastema, zygomatic breadth, braincase breadth, palatal length, mandible length, dentary depth, incisive foramina length, upper and lower toothrows, and upper first molar width than western clade specimens.

In the principal component analysis, the 130 specimens clustered into 2 groups (Fig. 4) that correspond to the eastern and western clades. These groups overlap moderately. Principal component 1 explains 39.7% of the variance and has a high correlation with most of the length dimensions (e.g., CIL, ML, IFL, Lm1–3, LM1–3). This fact suggests a general size factor for the 1st component (Table 3). The 2nd and 3rd principal components, which explain 18.3% and 10.4% of the total variation, correlate with breadth measurements (IOB, IFB, BMF). Dispersion of scores along the 1st principal component indicates a moderate distinction in size of most craniodental variables between eastern clade and western clade specimens. Variation in IOB, BMF, and IFB contributes to the dispersion of scores along the 2nd principal component. In general, western clade specimens are characterized by smaller skulls and dentitions in length dimensions but with broader interorbit, incisive foramina, and mesopterygoid fossa than the eastern clade counterparts. MANOVA revealed significant differences between the eastern and western groups (Wilks' lambda = 0.2368, $F = 21.23$, $P < 0.0001$, $d.f. = 112$).

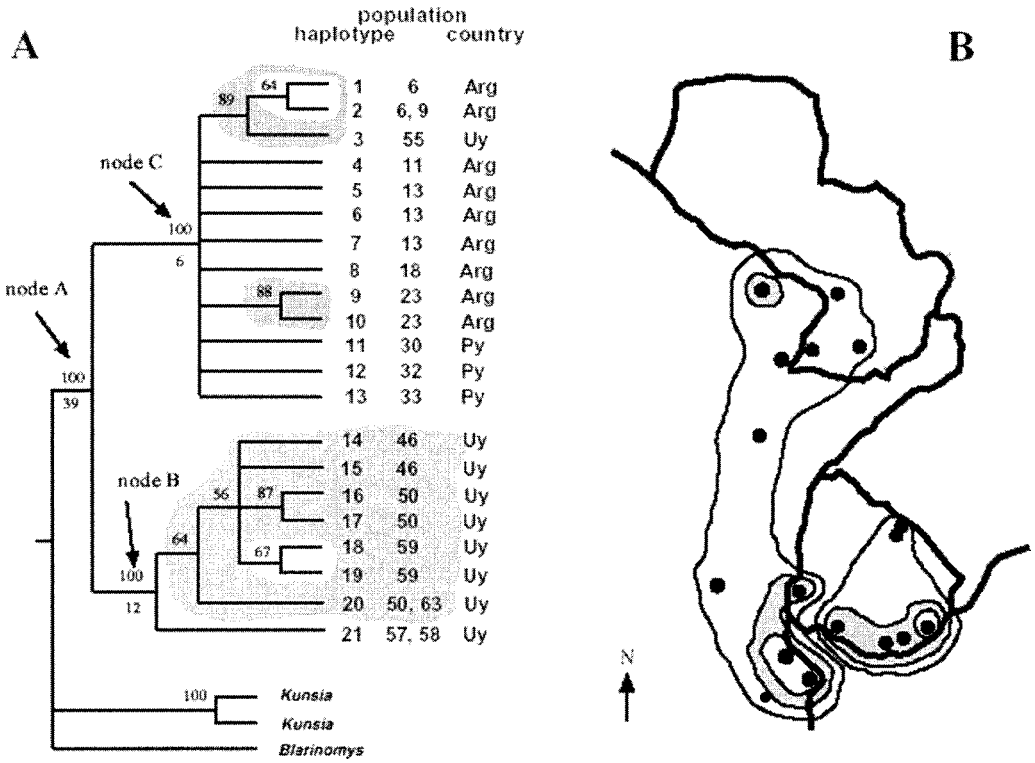

FIG. 2.—Strict consensus cladogram (22 shortest trees of 245 steps, $CI = 0.898$, $RI = 0.970$) of the 21 *Scapteromys* cytochrome-*b* haplotypes found in this study. Haplotypes recovered from *Kunsia* and *Blarinomys* specimens were used as outgroups. A) Numbers above and below branches correspond to parsimony jackknife and Bremer support values, respectively, of the nodes at their right. Numbers at the right of haplotype numbers identify populations as detailed in Fig. 1 and Appendix I. Nodes A, B, and C are discussed in the text. Py = Paraguay, Arg = Argentina, Uy = Uruguay. B) The same consensus tree superimposed onto the distribution map of *Scapteromys* populations studied (Fig. 1). Wider lines indicate boundaries of countries. Shaded areas correspond with the clades depicted in the tree.

DISCUSSION

Taxonomy of the genus *Scapteromys* as it currently is understood remains controversial. Waterhouse (1837) described *Mus tumidus* from Maldonado, Uruguay, and erected *Scapteromys* as a new subgenus of *Mus*. Waterhouse (1839) further described *tumidus* and included it in his new comprehensive genus *Hesperomys*, ignoring *Scapteromys*. Thirty years later, Fitzinger (1867) elevated *Scapteromys* to genus, although some later authors continued to use *Scapteromys* as a subgenus of *Hesperomys* (e.g., Thomas 1884). Thomas (1917) referred a series of *Scapteromys* collected on Isla Ella, Argentina, to the species *S. tomentosus* (a species currently allocated to the genus *Kunsia*) with the observation that those specimens differed from *S. tumidus* only in color. Three years later, Thomas (1920) noticed that his previous assignment of the specimens from Isla Ella to *tomentosus* was wrong and described a new species, *S. aquaticus*, on the basis of that material. Remarkably, Thomas made no comment regarding his previous note about the similarity of *aquaticus* and *tumidus*. During the following four decades, taxonomic references to *Scapteromys* sensu stricto were limited to a handful of references in general treatises of taxonomy (e.g., Cabrera 1961; Devicenzi 1935; Ellerman 1941; Gyldenstolpe 1932) or taxonomic historical accounts (e.g., Tate 1932).

Massoia and Fornes (1964) published a study that 4 decades later remains the most significant contribution of *Scapteromys* taxonomy and natural history. In regard to the distinction between *tumidus* and *aquaticus*, these authors assessed variation of skull, teeth, and external morphology within and among Argentinean and Uruguayan populations. They documented that morphological differences between the forms are minor and basically limited to the shape of the frontoparietal suture and the width of the mesopterygoid fossa. These authors also mentioned that individuals of *S. tumidus* are brownish and seem to be slightly larger than those of *S. aquaticus*, which are blackish. As individuals showing intermediate phenotypes were also found, Massoia and Fornes (1964) considered both forms as subspecies. Accordingly, *S. t. tumidus* is distributed across Uruguay, and *S. t. aquaticus* has a disjunct distribution in Argentina, northeast of Buenos Aires and south of Entre Ríos provinces and southeast of Chaco province. An isolated record from Santa Fe province, however, began to fill in this geographic gap (Contreras 1966). Later, Myers and Wetzel (1979) extended *Scapteromys* range northward, reporting specimens from Paraguay. Importantly, Massoia and Fornes (1964) indicated that the correspondence between geographic distribution of the trenchant characters they used to define and diagnose both subspecies and the suggested geographic distributions of the taxa is not absolute. Later, Hershkovitz (1966) stated that the characters enumerated by Massoia and Fornes (1964) are highly variable and then dismissed the formal recognition of 2 different taxa.

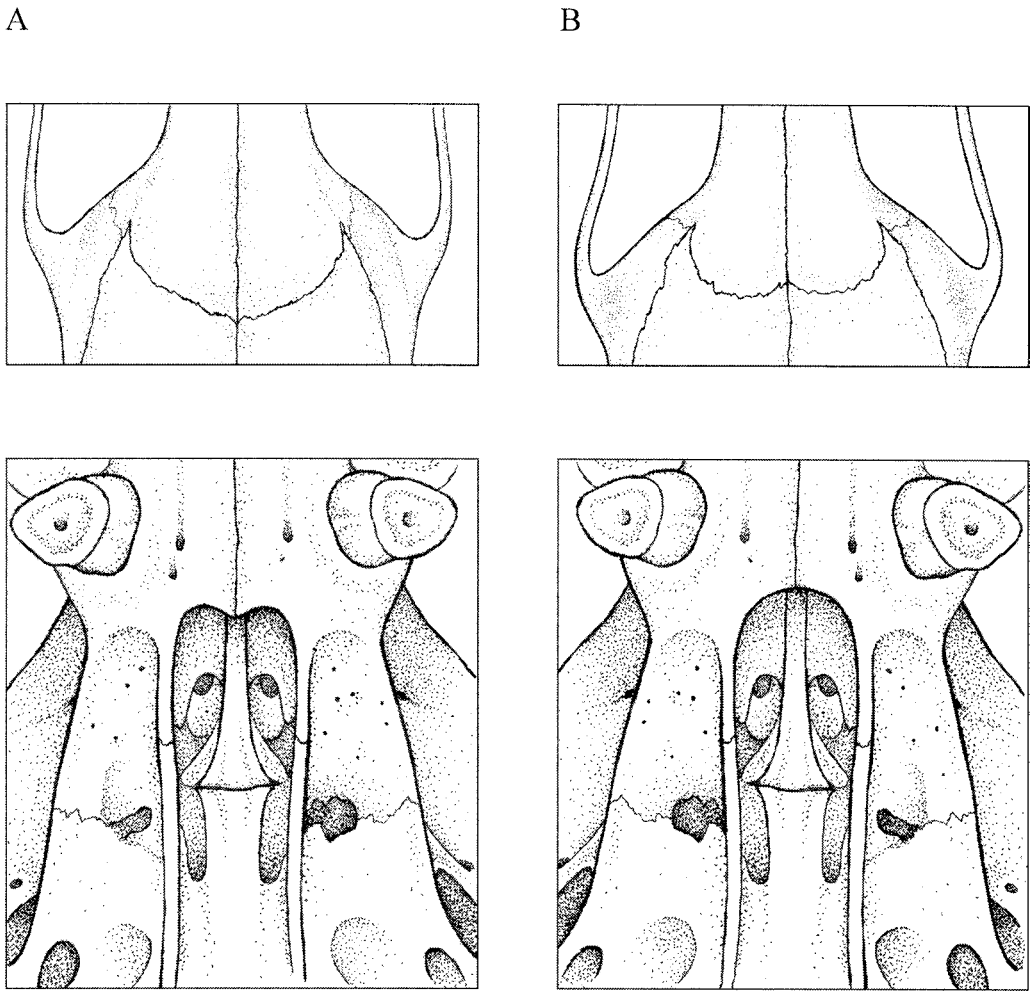

FIG. 3.—Dorsal views of *Scapteromys* skulls (anterior at top, posterior at bottom) showing different type of frontoparietal suture (above) and mesopterygoid fossa (below). A) U- (or V-) type suture and quadrate mesopterygoid fossa with a median palatine process (specimen GD 334 from Ype Kua, Paraguay). B) W-type suture and rounded mesopterygoid fossa lacking a median palatine process (specimen MNHNM 4266 from La Paloma, Uruguay).

Cytogenetic studies showed that *Scapteromys* exhibit a large amount of chromosomal variation that appears to be geographically structured. Argentinean and Paraguayan populations have a 2n = 32 (Brum et al. 1986; Fronza et al. 1976; P. Myers, pers. comm.), whereas populations in Uruguay have 2n = 24 (Brum 1965; Brum et al. 1972, 1986). Finally, 3 karyomorphs, 2n = 24, 34 and 36, have been reported from Brazilian populations (Freitas et al. 1984). With this evidence at hand, the previously mentioned authors tried to match available names with the karyomorphs recovered. Brum et al. (1972, 1986) proposed that the 2n = 32 corresponded to *S. aquaticus* (distributed in Argentina) and the 2n = 24 to *S. tumidus* (distributed in Uruguay). In addition, Freitas et al. (1984) suggested the existence of an undescribed species in Brazil. In spite of these assertions, which are repeated in the most recent comprehensive treatise of mammal taxonomy (Musser and Carleton 1993), Hershkovitz's (1966) views prevailed, and only *S. tumidus* currently is recognized (but see Galliari et al. 1996; Pardiñas 1996).

The major phylogeographic break identified in this study (Fig. 2B) largely matches the geographic patterns of morphologic and karyotypic (Brum et al. 1986; Fronza et al. 1976; P. Myers, pers. comm.) variation. This finding provides support to the traditional view (Massoia and Fornes 1964) about the geographic distribution of *aquaticus* and *tumidus*. Moreover, this view also is extended since the present analysis constitutes the 1st study of *Scapteromys* systematics to include specimens from Paraguay as well as from several Argentinean and some Uruguayan localities. However, 2 issues must be considered when interpreting the biological meaning of this congruence. First, this congruity is not absolute, as discussed later in this article. Second, the phylogeographic pattern was uncovered on the basis of a marker that is maternally inherited (Gyllensten et al. 1985; but see also Gyllensten et al. 1991; Zouros et al. 1992) and therefore reveals geographic structure due to female dynamics but not that of males. At the same time, the following aspects, which are inherent to the design of this study, hamper the interpretation of the congruence mentioned previously: only a small fraction of the specimens morphologically studied were sequenced (47 of 443); none of the karyotyped specimens was sequenced; karyotyped specimens come from few populations, and in several cases no specimens from those localities were sequenced; and the morphology of some karyotyped specimens

could not be assessed because neither museum nor field numbers were provided in the original publications (e.g., Brum et al. 1986; Fronza 1970).

As mentioned previously, chromosomal, morphological, and mtDNA data sets are largely but not fully concordant. The main discrepancy arises with respect to the population at Las Cañas, in western Uruguay (Fig. 2B). Haplotypes recovered from that population are of the *aquaticus* type and as such fall in the western clade containing all haplotypes recovered from Argentinean and Paraguayan specimens. Ten additional steps are needed to recover a clade formed by all Uruguayan haplotypes. The apparent discrepancy arises because the single individual karyotyped from Las Cañas showed the presumed *tumidus* diploid complement (i.e., 2n = 24—Brum et al. 1972). Unfortunately, this specimen (MNHN 1957) was unavailable to sequence, and, further, its mesopterygoid fossa is quadrate in shape but lacks the palatine median process, and its frontoparietal suture displays an irregular pattern. The morphological material ($n = 11$) from Las Cañas, which includes 6 individuals that were sequenced, shows that 8 are of the *aquaticus* morphotype (Table 2). The specimen MNHN 1979 (not sequenced) shows a suture of the W type.

In summary, the evidence at hand indicates that, from mitochondrial DNA and for the most part from morphology, the population of Las Cañas belongs to the *aquaticus* form, whereas what has been called a *tumidus* diploid complement has been reported for 1 specimen from that locality. Different explanations may account for this mismatch in the patterns of geographic variation. It is possible that the karyomorphs are not monophyletic, that the ''*aquaticus* karyomorph'' is present but so far undiscovered in the area of Las Cañas, or that individuals bearing ''*tumidus* haplotypes'' inhabit the area of Las Cañas but so far have not been discovered. It also is possible that there is a disagreement between the inferred gene tree and the species tree for the population of Las Cañas. Random fixation of alternative haplotypes via lineage sorting may cause a pattern like this (Neigel and Avise 1986). More interesting from a biological point of view would be a case of introgression via hybridization. A scenario like this, well known in geomyid rodents (Patton and Smith 1994; Ruedi et al. 1997), has not been yet reported for any sigmodontine group, but it should be noted that only a small number of studies have used molecular evidence to assess sigmodontine variation at the population level. With the data at hand, it is not possible to choose among these alternatives to explain the apparent discrepancy among data sets at Las Cañas.

Currently there is no reason to assume that the recovered gene tree does not reflect the organism history. This is simply because there is not a 2nd data set amenable to comparison with the mitochondrial based tree; that is, no other *Scapteromys* data set has been analyzed with an explicit historical approach. Therefore, the apparent incongruence between mtDNA variation and karyotype distributions should be taken only as a guide to direct future research, whereas the gene tree should be accepted as the best available hypothesis of taxonomic relationships (Brower et al. 1996).

Here we suggest that at least 2 different *Scapteromys* forms exist in nature. These forms can be differentiated because they have unique combinations of derived features not present in the other (i.e., they are diagnosable). We suggest that the rank of species should be given to each. The names to apply to these taxa are *S. tumidus* (Waterhouse 1837) and *S. aquaticus* Thomas 1920. This hypothesis states that both species are distributed allopatrically. Populations from northern, southern, and eastern Uruguay are assigned to *S. tumidus*. Tentatively, populations from central Uruguay are also allocated to this species. Future studies will clarify the taxonomic status of Brazilian populations. *S. aquaticus* inhabits Argentina, Paraguay, and the Uruguayan area of Las Cañas in the Department of Río Negro. Under this arrangement the Uruguayan sigmodontine fauna is increased from 14 to 15 species (González 2001). Future studies will provide further testing of the hypothesis here advanced.

The present study reveals several synapomorphies of the cytochrome-*b* gene that allow diagnosis of *S. tumidus* and *S. aquaticus* (Table 4). Seventeen character-state transformations occurred along the line leading from the *Scapteromys* common ancestor (node A in Fig. 2A) to the common ancestor of *S. tumidus* haplotypes (node B in Fig. 2A). However, 1 of the *S. tumidus* synapomorphies (an A-to-G change in position 693) is obscured by the fact that this character-state transformation also evolved in parallel in 2 haplotypes recovered from 6 specimens of *S. aquaticus*. Eight nucleotide characters have changed state along the line leading from the *Scapteromys* common ancestor to the common ancestor of *S. aquaticus* haplotypes (node C in Fig. 2A). None of these character-state transformations has evolved independently in any of the recovered *S. tumidus* haplotypes. This fact is not unexpected given the low amount of homoplasy ($CI = 0.898$) of the data set. In addition to the synapomorphies, there are several other derived character states that evolved only within the *S. tumidus* and *S. aquaticus* clades. These substitutions (data not shown, available on request) are mainly autopomorphic changes and also may be used to assign individuals to 1 of the 2 species. When DNA sequences are translated to amino acids (data not shown, available on request), 1 and 3 character transformations occur along the lines leading from the *Scapteromys* common ancestor to the *S. aquaticus* clade and the *S. tumidus* clades, respectively. It must be noted that the sequencing of more specimens could potentially decrease these numbers by uncovering more homoplasy.

Under this scheme karyomorphs do not match species boundaries and therefore should not be used to diagnose *Scapteromys* species. This assertion goes contrary to the idea of karyotypes being species specific. This line of thinking has resulted in the description of several putative species based primarily or exclusively on chromosomal differences (e.g., Fagundes et al. 2000; Silva and Yonenaga-Yassuda 1998; Silva et al. 2000; Spotorno et al. 1998). However, there are numerous cases of chromosomal polymorphisms and polytypisms within and between sigmodontine populations (Fagundes et al. 1998; Fernandez-Donoso et al. 2001; Sbalqueiro and Nascimento 1996), and chromosomal hybrids have been reported in natural

Table 2.—Type of frontoparietal suture, mesopterygoid fossa, and presence or absence of median palatine process scored in 443 *Scapteromys* specimens from 68 populations. An asterisk indicates that for a population at least 1 of the individuals morphologically studied also was included in the phylogeographic analysis. Suture types are explained in the text and shown in Fig. 3. See Appendix I for locality details. I = irregular; R = rounded; Q = quadrate; P = present; A = absent.

		Frontoparietal suture			Mesopterygoid fossa		Median palatine process	
Population sample	*n*	U type	W type	I	R	Q	P	A
1 Estación Experimental INTA Canal 6, Argentina	7	7				6	6	
2 Estancias La Porteña y San Antonio, Argentina	2	1		1		2	2	
3 General Lavalle, Argentina	1	1				1	1	
4 Hudson, Argentina	9	9			2	7	7	2
5 Isla Ella, Argentina	2	2				1	1	
6 La Balandra, Argentina*	78	72		5	1	71	59	14
7 Los Talas, Argentina	29	22		7	3	23	21	5
8 Palo Blanco, Argentina	13	12		1		12	12	
9 Punta de Indio, Argentina*	2	1		1		2	2	
10 Punta Lara, Argentina	53	46	1		2	45	44	5
11 Ramallo, Argentina*	5	5				5	5	
12 Desembocadura Río de Oro, Argentina	2	2				2	2	
13 Selvas del Río de Oro, Argentina*	4	4				4	4	
14 Ahoma Sur, Argentina	1	1				1	1	
15 Caa Guazú, Argentina	1	1				1	1	
16 Estero Valenzuela, Argentina	2	2				2	2	
17 Laguna Paiva y Laguna Pampín, Argentina	22	22				22	22	
18 Río Paraná, 0.5 km W Esquina, Argentina*	1	1						
19 San Cayetano, Argentina	1	1				1	1	
20 Arroyo San Felipe, Argentina	1	1				1	1	
21 Brazo Largo, Argentina	1	1				1	1	
22 Pasaje Talavera, Argentina	2	2				2	2	
23 17 km W Colonia Villafañe, Argentina*	2	2				2	1	1
24 Estancia Guaycolec, Argentina	1	1				1	1	
25 Parque Nacional Río Pilcomayo, Argentina	5	5				5	5	
26 Alejandra, Argentina	1	1				1	1	
27 Puerto Ocampo, Argentina	1	1				1	1	
28 Estancia San Ignacio, Paraguay	1	1				1	1	
29 1.6 km S Tobati, Paraguay	5	5				5	5	5
30 Estancia Ype kua, Paraguay*	1	1				1	1	
31 Costa del río Tebicuary, Misiones, Paraguay	2	2			1	1		2
32 Estancia Yacaré, Paraguay*	1	1				1	1	
33 Costa del río Tebicuary, Paraguari, Paraguay*	7	7				7	6	1
34 Isla Yacyretá, Paraguay	4	4				4	4	
35 24 km NW Villa Hayes, Paraguay	1	1				1	1	
36 La Isleta, Uruguay	2	1	1		1	1		2
37 Arroyo Frasquito, Uruguay	4	2	2			4	3	1
38 Arroyo y Balneario Salinas, Uruguay	4		3		1	2	1	2
39 Bañado Tropa Vieja, Uruguay	3		3		3			3
40 Arroyo Artilleros, Uruguay	4		4			4	3	1
41 La Paz, Uruguay	1		1			1	1	
42 Estancia del Medio, Uruguay	4	2	1	1	3	1		4
43 Barra del Arroyo Mansavillagra, Uruguay	1		1		1			1
44 Paso de Pache, Uruguay	6	2	3	1		4	3	3
45 Puntas de Maciel, Uruguay	3		2	1	1	2	2	1
46 Arroyo El Renegado, Uruguay*	3	1	2		1	2	1	1
47 Arroyo Pan de Azúcar, Uruguay	3		2		1	1	1	1
48 Balneario Solís, Uruguay	1	1			1			1
49 Barra del Arroyo Maldonado, Uruguay	16		15	1	7	7	5	9
50 Las Flores, Uruguay*	7	1	5		2	3	2	3
51 San Carlos, Uruguay	8	2	4	2	6	2	2	6
52 Parque Lecoq, Uruguay	24	2	21	1	15	8	5	18
53 Bañados de Carrasco, Uruguay	2		2			2	1	1
54 Arroyo Negro, Uruguay	1			1	1			1
55 Las Cañas, Uruguay*	11	8	1	2	2	6	4	5
56 Rincón de Baygorria, Uruguay	1		1		1			1
57 Estancia La Quemada 1, Uruguay*	5		5		5		4	1
58 Estancia La Quemada 2, Uruguay*	3	1	1	1	3		2	1
59 Arroyo La Palma, Uruguay*	7	1	6		4	3	3	4

TABLE 2.—Continued.

Population sample	*n*	Frontoparietal suture			Mesopterygoid fossa		Median palatine process	
		U type	W type	I	R	Q	P	A
60 Barra Santa Lucía-Delta del Tigre, Uruguay	15	6	7	2	10	5	5	10
61 Estancia Santa Clara, Uruguay	4		4		2	2	2	2
63 Estancia Voulminot, Uruguay	1		1		1			1
63 Kiyú, Uruguay*	1		1			1		1
64 Km 37.5 Ruta 1, Uruguay	2	1	1		1	1	1	1
65 3 km S Cardona, Uruguay	21	5	13	1	17	3	1	19
66 Arroyo Perdido, Uruguay	2		1	1		2	1	1
67 7 km E Barra Tacuarembó, Uruguay	1		1			1	1	
68 Arroyo Avestruz, Uruguay	1	1			1			1
Total	443	285	116	30	100	311	279	142

populations (Yonenaga et al. 1975). Moreover, Nachman and Myers (1989), by means of laboratory breeding, showed that chromosomally heterozygous individuals of *Holochilus* do not experience a detectable decrease in fitness. Cytogenetic studies of *Scapteromys* were not designed to assess intrapopulation variation. Reported variation within each karyomorph limits polymorphism to the morphology of the Y chromosome (Brum et al. 1986; Freitas et al. 1984; Fronza et al. 1976).

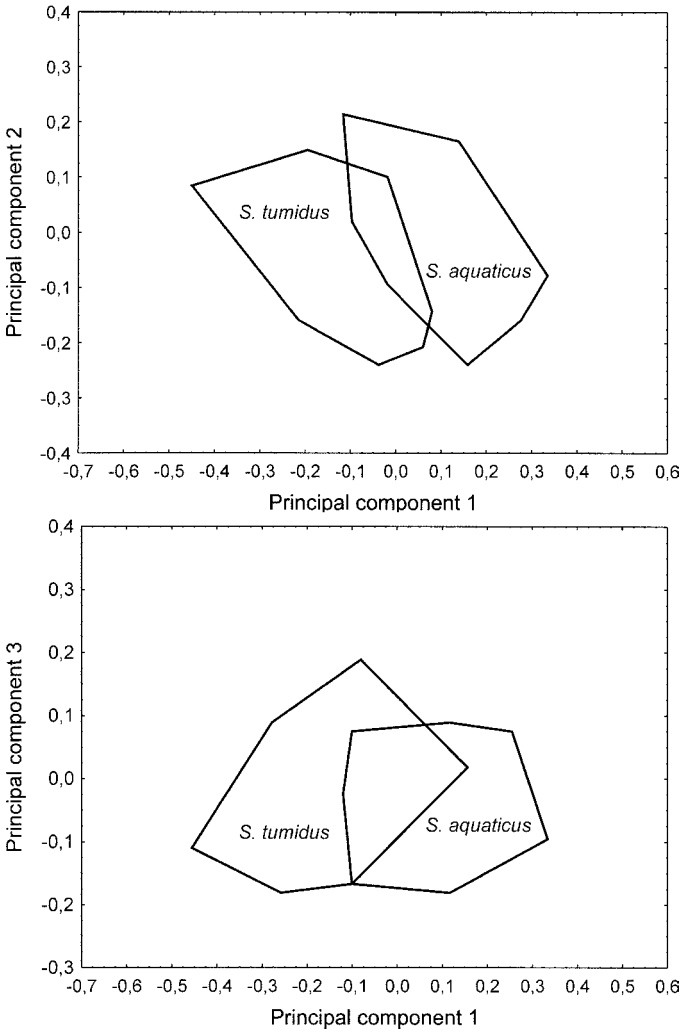

FIG. 4.—Specimen scores of western clade (*Scapteromys aquaticus*, $n = 67$) and eastern clade individuals (*S. tumidus*, $n = 63$) on the principal components 1 and 2 (top) and 1 and 3 (bottom) extracted from the variance–covariance matrix of 17 craniodental measurements (see text and Table 3).

Both *Scapteromys* species are morphologically differentiable; statistical analyses showed that in general *S. tumidus* is slightly larger than *S. aquaticus*. No craniodental qualitative character state considered herein allows unambiguous diagnosing of *Scapteromys* species (Table 2). Both *S. aquaticus* and *S. tumidus* are polymorphic regarding these qualitative characters. However, in both species, 1 morphotype is clearly predominant; the U- or V-shaped suture is predominant in *S. aquaticus* and the W suture in *S. tumidus*. Interestingly, *S. aquaticus* is far more nearly homogeneous than *S. tumidus* in relation to these characters (Table 2). For example, only 2 of 282 (0.71%) specimens of *S. aquaticus* presented a W suture, whereas 29 of 161 (18.01%) specimens of *S. tumidus* showed a U suture. The biological meaning of this difference is unclear

TABLE 3.—Results of principal component (PC) analysis of craniodental measurements of adult *Scapteromys* specimens (age class 3, $n = 130$). Abbreviations for variable names are described in the text.

Variable	Pearson correlations		
	PC1	PC2	PC3
CIL	−0.88	0.28	0.03
LD	−0.72	0.50	−0.07
IOB	0.06	0.36	−0.14
ZB	−0.86	0.00	0.12
RB	−0.70	0.32	−0.22
PL	−0.81	0.37	−0.01
ML	−0.85	0.28	0.12
DH	−0.75	0.29	−0.01
NL	−0.74	0.25	0.01
GNB	−0.58	0.10	−0.13
IFL	−0.74	0.23	0.08
IFB	0.22	0.81	−0.37
BMF	0.37	0.56	0.74
LM1−3	−0.63	−0.20	0.21
Lm1−3	−0.51	−0.24	0.22
BM1	−0.75	−0.27	0.21
LM1	−0.63	−0.21	0.09
Eigenvalue	0.02	0.009	0.005
% of variance	39.7	18.3	10.42

Table 4.—Molecular synapomorphies of *Scapteromys tumidus* (synapomorphy 1 to synapomorphy 17) and *S. aquaticus* (synapomorphy 18 to synapomorphy 25) as revealed by maximum parsimony analysis of cytochrome-*b* gene sequences (801 base pairs). One of the character transformations (indicated by an asterisk) defining the synapomorphies of *S. tumidus* also has evolved in parallel in 2 haplotypes of *S. aquaticus*. Other characters have a consistency index <1 because the character state present in 1 *Scapteromys* species also has evolved independently in 1 of the 3 outgroup specimens.

		Character state			
	Nucleotide position/codon position	*Scapteromys* common ancestor	*S. tumidus* common ancestor	*S. aquaticus* common ancestor	Character consistency index
1	6/3	a	t		1
2	40/1	a	g		1
3	189/3	c	t		1
4	312/3	c	t		0.50
5	447/3	c	t		1
6	466/1	a	g		1
7	476/2	c	t		1
8	478/1	c	t		0.50
9	483/3	t	c		1
10	522/3	a	g		0.67
11	597/3	c	t		1
12	693/3*	a	g		0.67
13	710/2	c	t		0.50
14	711/3	a	g		0.67
15	732/3	a	g		1
16	753/3	a	g		1
17	780/3	c	t		1
18	48/3	c		t	0.50
19	174/3	c		t	1
20	192/3	c		t	1
21	285/3	c		t	1
22	294/3	c		t	1
23	321/3	c		t	1
24	336/3	c		t	1
25	549/3	c		t	1

so far. In addition, the same haplotype was found in specimens showing different morphological types (all specimens from Estancia La Quemada 2, a population showing both suture types, share the same haplotype), indicating that morphological evolution is not coupled with the evolution of the mitochondrial genome.

Resumen

Presentamos un estudio sistemático, basado en evidencia molecular y morfológica, de poblaciones argentinas, paraguayas, y uruguayas de *Scapteromys*. En primer lugar, basado en secuencias de ADN (801 pb) del gen mitocondrial que codifica para el citocromo *b*, encontramos que las poblaciones de *Scapteromys* forman dos clados principales; uno constituido por poblaciones argentinas y paraguayas junto a una población del oeste de Uruguay, y el otro integrado por las demás poblaciones de Uruguay. Análisis de varianza molecular muestran que el 86,93% de la variación genética encontrada en *Scapteromys* se debe a diferencias entre estos dos clados. Análisis morfológicos corroboran la existencia de 2 morfotipos principales entre especímenes de *Scapteromys*. El quiebre filogeográfico encontrado es mayoritariamente congruente con los patrones de variación morfológica y cromosómica. A la luz de estos resultados, proponemos que *S. aquaticus* sea elevado al rango de especie, redefinimos la distribución conocida de *S. aquaticus* y *S. tumidus* y proveemos una lista de estados de carácter que permiten la diagnosis precisa de ambas especies.

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APPENDIX I

Specimens examined.—The *Scapteromys*, *Kunsia*, and *Blarinomys* specimens used in this study are listed here. All *Scapteromys* specimens were used in morphological analysis; specimens used in molecular and multivariate analyses (age class 3 only) are indicated by superscripts m and p, respectively. Accession numbers are indicated for those specimens whose sequences were retrieved from GenBank. See Fig. 1 for locality numbers and locations of sites. Museum and collection acronyms and personal field numbers are as follows. Argentina: Colección Félix de Azara, Corrientes (CAF); Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn (CNP); Instituto de Limnología "Raúl Ringuelet," Buenos Aires (ILPLA); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN); Museo de La Plata, La Plata (MLP); Museo de Ciencias Naturales y Tradicional de Mar del Plata, Mar del Plata (MMP); field number of Ulyses Pardiñas (UP, vouchers will be deposited in Museo de La Plata, La Plata, Argentina). Brazil: field number of Alexandra Bezerra (ARB, voucher will be deposited at the Museu Nacional, Rio de Janeiro, Brazil); field number of the Laboratório de Citogenética de Vertebrados, Departamento de Biologia, Universidade de São Paulo (CIT, vouchers will be deposited at the Museu de Zoologia da Universidade de Sao Paulo, Sao Paulo). Paraguay: Museo Nacional de Historia Natural del Paraguay, Asunción (MNHNP); field number of Guillermo D'Elía (GD [GD 029, GD 053, GD 087, GD 267, GD 290, and GD 310], vouchers will be deposited in the Nacional de Historia Natural del Paraguay, Asunción). United Kingdom: The Natural History Museum, London (BMNH). Uruguay: Museo Nacional de Historia Natural, Montevideo (MNHN); field number of Guillermo D'Elía (GD, vouchers will be deposited at Museo Nacional de Historia Natural, Montevideo); field numbers of the Laboratorio de Evolución, Facultad de Ciencias, Universidad de la República (CA and EV, vouchers will be deposited at Nacional de Historia Natural, Montevideo). United States: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago, Illinois (FMNH); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); field number of Louise Emmons (LHE, vouchers will be deposited at the National Museum of Natural History, Washington, D.C.).

Scapteromys.—The following 564 *Scapteromys* specimens belonging to 68 populations were examined. Localities are shown in Fig. 1.

ARGENTINA, Buenos Aires Province: (1) Estación Experimental INTA Canal 6, Campana, 34°10′S, 58°57′W (MACN 15675, MACN 18670^{p}, MACN 18671, MACN 20331, MACN 20332, MMP 1143, MLP 30.X.95.10); (2) Estancias La Porteña y San Antonio, 36°01′S, 57°26′W (MLP 4.IV.00.5, MLP 11.VIII.99.43^{p}); (3) General Lavalle, 36°25′S, 56°57′W (MLP 1675^{p}); (4) Hudson, 34°47′S, 58°10′W (MLP 5.XII.01.37, MLP 8.IV.97.3, MLP 8.IV.97.10^{p}, MLP 8.IV.97.11^{p}, MLP 8.IV.97.12, MLP 8.IV.97.13, MLP 8.VIII.00.1, MLP 8.VIII.00.6, MLP 15.X.01.7, MLP 17.XII.01.1); (5) Isla Ella,

Delta del Paraná, exact location not recorded (BMNH 17.6.1.6 [holotype of *Scapteromys aquaticus*], FMNH 29160); (6) La Balandra, 34°56′S, 57°43′W (CNP 718, CNP 719, CNP 720, CNP 721[p], CNP 724, CNP 725, CNP 726, CNP 727, CNP 728, CNP 729[p], ILPLA 45[p], ILPLA 52[p], ILPLA 97, ILPLA 98, ILPLA 99, ILPLA 100[p], ILPLA 101, ILPLA 102, ILPLA 103, ILPLA 104, ILPLA 105, ILPLA 106, ILPLA 108, ILPLA 109, ILPLA 172, ILPLA 188[p], ILPLA 189, ILPLA 233, ILPLA 234[p], ILPLA 235[p], ILPLA 236, ILPLA 237[p], ILPLA 238[p], ILPLA 239[p], ILPLA 240, ILPLA 241, ILPLA 242, ILPLA 243, ILPLA 245, ILPLA 246[p], ILPLA 247[p], ILPLA 248, ILPLA 249, ILPLA 250, ILPLA 252, ILPLA 253, MLP 08.IV.97.5, MLP 1.VIII.00.17, MLP 1.VIII.00.19, MLP 1.VIII.00.20[p], MLP 15.X.01.1[p], MLP 15.X.01.2, MLP 15.X.01.3, MLP 15.X.01.4, MLP 15.X.01.5[p], MLP 15.X.01.6[mp] AY275131, MLP 25.IV.01.8[p], MLP 25.IV.01.9[p], MLP 25.IV.01.10[p], MLP 25.IV.01.11, MLP 26.V.99.9[p], MLP 27.XI.01.5, MLP 27.XI.01.6, MLP 27.XII.01.1[p], MLP 27.XII.01.2[p], MLP 27.XII.01.3, MLP 27.XII.01.4, MLP 29.XII.00.10, MLP 29.XII.00.11, MLP 29.XII.00.4, MLP 29.XII.00.5, MLP 29.XII.00.6, MLP 29.XII.00.7, MLP 29.XII.00.8, MLP 29.XII.00.9[p], MLP 5.VIII.98.5, MLP 5.VIII.98.6[p], MLP s/n[p], UP-BAL 503[m], UP-BAL 510[m], UP-BAL 513[m], UP-BAL 514[m], UP-BAL 002[p], UP-BAL 019[p], UP-BAL 040[p]); (7) Los Talas, 34°53′S, 57°53′W (MLP 1.VIII.00.16, MLP 1.VIII.00.18, MLP 1.VIII.00.24, MLP 8.IV.97.6[p], MLP 8.IV.97.7[p], MLP 8.IV.97.8, MLP 8.IV.97.22, MLP 9.V.01.1, MLP 9.V.01.2, MLP 9.V.01.3, MLP 9.V.01.4, MLP 9.V.01.5, MLP 9.V.01.6, MLP 15.X.01.10, MLP 15.X.01.11, MLP 15.X.01.12, MLP 15.X.01.13[p], MLP 15.X.01.14, MLP 20.XII.00.14, MLP 25.IV.01.12, MLP 25.IV.01.13, MLP 25.IV.01.14, MLP 25.IV.01.15, MLP 25.IV.01.16, MLP 25.IV.01.17[p], MLP 25.IV.01.18, MLP 25.IV.01.29, MLP 25.IV.01.30, MLP 25.IV.01.31, MLP 25.IV.01.5, MLP T03); (8) Palo Blanco, 34°55′S, 57°45′W (MLP 1.VIII.00.21, MLP 1.VIII.00.22, MLP 1.VIII.00.23, MLP 1.VIII.00.25, MLP 1.VIII.00.26, MLP 8.IV.97.2[p], MLP 8.IV.97.14, MLP 8.IV.97.15, MLP 8.IV.97.17[p], MLP 8.IV.97.18[p], MLP 8.IV.97.19, MLP 8.IV.97.20, MLP 8.IV.97.21, MLP 25.IV.01.4); (9) Punta de Indio, 35°16′S, 57°15′W (CNP 715[mp], CNP 717); (10) Punta Lara, 34°49′S, 57°59′W (FMNH 98286, FMNH 98287, FMNH 98288, FMNH 98289, MACN 13318, MACN 13444, MACN 13445, MACN 14022[p], MACN 14023[p], MACN 14428, MACN 14429[p], MACN 14431, MACN 14432, MACN 14452[p], MACN 15391, MACN 15404, MACN 15405, MACN 15411, MACN 15412, MACN 15413, MACN 15414, MACN 15416, MACN 15418, MACN 19198, MLP 1.XII.76.1, MLP 1.XII.76.2, MLP 10.VIII.00.2, MLP 10.VIII.00.4, MLP 10.VIII.00.5, MLP 16.V.01.8, MLP 20.XII.00.13, MLP 20.XII.00.17, MLP 20.XII.00.18, MLP 31.X.80.4, MMP 183, MMP 315, MMP 356, MMP 358, MMP 359[p], MMP 489, MMP 490, MMP 491, MMP 494, MMP 497, MMP 500, MMP 596, MNHN 859, MNHN 860[p], MNHN 863, MNHN 906, MNHN 907[p], UMMZ 111005, UMMZ 111006, UMMZ 115509); (11) Ramallo, 33°28′S, 60°01′W (CNP 722, CNP 723, CNP 732[m], MLP 12.XI.02.19[m], MLP 12.XI.02.20[m]); Chaco Province: (12) Desembocadura Río de Oro, 27°03′S, 58°33′W (MACN 14337, MACN 14364[p]); (13) Selvas del Río de Oro, 26°47′S, 58°57′W (CNP 712[m], CNP 713[m], CNP 714[mp], CNP 716); Corrientes Province: (14) Ahoma Sur, Empedrado, 27°57′S, 58°48′W (CAF 02606[p]); (15) Caa Guazú, 28°52′S, 58°35′W (MLP 2.IV.02.6); (16) Estero Valenzuela, 27°28′S, 58°49′W (CAF 04839[p], CAF 05082); (17) Laguna Paiva y Laguna Pampín, 27°30′S, 58°50′W (CAF 01655, CAF 01657, CAF 01662, CAF 03950, CAF 03982, CAF 03984, CAF 04084, CAF 04109, CAF 04171, CAF 04205[p], CAF 04206, CAF 04238, CAF 04244, CAF 04245, CAF 04257, CAF 04280, CAF 04308[p], CAF 04351, CAF 04523, CAF 04669, CAF 04757, CAF 04851); (18) Río Paraná, 0.5 km W Esquina, 30°00′S 59°35′W (UMMZ 166640[mp]); (19) San Cayetano, 27°34′S, 58°44′W (CAF 01689[p]); Entre Ríos Province: (20) Arroyo San Felipe, Delta del Paraná, location not recorded (MMP 416); (21) Brazo Largo, 33°51′S, 58°53′W (MACN 17753); (22) Pasaje Talavera, 33°58′S, 58°20′W (MMP 414, MMP 472); Formosa Province: (23) 17 km W Colonia Villafañe, 26°11′S, 59°15′W (CNP 710[m], CNP 711[m]); (24) Estancia Guaycolec, 25°47′S, 58°01′W (CAF 02596); (25) Parque Nacional Río Pilcomayo, 25°10′S, 58°09′W (MACN 20774, MACN 20775, MACN 20776, MACN 20777[p], MACN 20778); Santa Fe Province: (26) Alejandra, 29°54′S, 59°50′W (MMP 1511); (27) Puerto Ocampo, 28°31′S, 59°08′W (MLP s/n[p]).

PARAGUAY, Caaguazu Department: (28) Estancia San Ignacio, 24 km NNW Carayao, 25°05′S, 56°36′W (UMMZ 133931[p]); Cordillera Department: (29) 1.6 km S Tobatí, 25°16′S, 57°04′W (UMMZ 125954[p], UMMZ 125955, UMMZ 125956, UMMZ 133932, UMMZ 133933); (30) Estancia Ype kua, 25°15.04′S, 57°19.02′W (GD 334[m]); Misiones Department: (31) Costa del río Tebicuary, 26°31′S, 57°14′W (GD 549[p], GD 550[p]); Ñeembucu Department: (32) Estancia Yacaré, 0.87 km WNW of Puesto San Fernando, 26°35.03′S, 58°08.70′W (GD 087[m]); Paraguari Department: (33) Costa del río Tebicuary, 26°24′S, 57°02′W (GD 029, GD 053, GD 267, GD 269[p], GD 290[m], GD 317, UMMZ 174882[m], UMMZ 174991[mp] AY275132, UMMZ 174884[m]); (34) Isla Yaciretá, 27°24′S, 56°45′W (MNHNP 1082, MNHNP 1084, MNHNP 1086, MNHNP 1088); Presidente Hayes Department: (35) 24 km W Villa Hayes, 25°05′S, 57°46′W (UMMZ 133936[p]).

URUGUAY, Artigas Department: (36) La Isleta, Colonia Artigas, location not recorded (MNHN 556[p], MNHN 558[p]), Canelones Department: (37) Arroyo Frasquito, Pando, 34°43′S, 55°57′W (MNHN 561[p], MNHN 1484[p], MNHN 1485[p], MNHN 1488[p]); (38) Arroyo y Balneario Salinas, Salinas, 34°46′S, 55°46′W (FMNH 122712, FMNH 122713, MNHN 514, MNHN 515); (39) Bañado Tropa Vieja, 34°47′S, 55°48′W (MNHN 1040, MNHN 1047, MNHN 1048); Colonia Department: (40) Arroyo Artilleros, Santa Ana, 34°23′S, 57°33′W (MNHN 530[p], MNHN 531, MNHN 536[p], MNHN 2359[p]); (41) La Paz, Colonia Valdense, 34°21′S, 57°18′W (MNHN 560[p]); Durazno Department: (42) Estancia del Medio, La Paloma, 32°43′S, 55°36′W (MNHN 1476[p], MNHN 1490, MNHN 1492, MNHN 1496[p]); Florida Department: (43) Barra del Arroyo Mansavillagra, location not recorded (MNHN 1504[p]); (44) Paso de Pache, km 64 Ruta 5, 34°23′S, 56°17′W (MNHN 1820, MNHN 1821[p], MNHN 1823[p], MNHN 1859, MNHN 1899[p], MNHN 1910); (45) Puntas de Maciel, 34°37′S, 56°22′W (MNHN 511, MNHN 512, MNHN 513[p]); Maldonado Department: (46) Arroyo El Renegado, 3 km W Pan de Azúcar, 34°47′S, 55°16′W (MNHN 3844[m], CA 682[m], MVZ 183267[mp]); (47) Arroyo Pan de Azúcar, 34°47′S, 55°14′W (MNHN 1437[p], MNHN 1862, MNHN 1865[p]); (48) Balneario Solís, 34°48′S, 55°22′W (MNHN 1861[p]); (49) Barra del Arroyo Maldonado, 34°55′S, 54°51′W (AMNH 206246, AMNH 206247[p], AMNH 206248[p], AMNH 206249, AMNH 206250, AMNH 206252, AMNH 206253, AMNH 206254, AMNH 206255, AMNH 206256[p], AMNH 206257, BMNH 55.12.24.180 [holotype of *Scapteromys tumidus*], MMP 335, MNHN 643[p], MNHN 730, MNHN 732[p]); (50) Las Flores, margen oeste del Arroyo Tarariras, location not recorded (MNHN 3858, MNHN 3859, MNHN 4285[p], MNHN 4286, MNHN 4287[m], MNHN 4288[m], MVZ 183268[m] AF108669, MVZ 183269[m] AY275133); (51) San Carlos, 34°48′S, 54°55′W (MMP 1550[p], MMP 1552[p], MMP 1557[p], MMP 1560, MMP 1561, MMP 1562, MMP 1571[p], MMP 1580[p]); Montevideo Department: (52) Parque Lecoq, 34°49′S, 56°21′W (AMNH 206208, AMNH 206209, AMNH 206210, AMNH 206216, AMNH 206217, AMNH 206218, AMNH

206219, AMNH 206220[p], AMNH 206221, AMNH 206222, AMNH 206223, AMNH 206224, AMNH 206225, MACN 13229, MNHN 649, MNHN 968, MNHN 1433, MNHN 1434, MNHN 1438[p], MNHN 1439, MNHN 1440[p], MNHN 1866[p], MNHN 1926, MNHN 2459[p]); (53) Bañados de Carrasco, 34°53′S, 56°03′W (MNHN 1435[p], MNHN 1509); Paysandú Department: (54) Arroyo Negro, 15 km S Paysandú, 32°28′S, 58°09′W (MNHN 1853); Río Negro Department: (55) Las Cañas, 33°10.28′S, 58°21.06′W (EV 1110[mp], GD 600[m], GD 601[m], GD 602[m], GD 603[m], GD 609[m], GD 656, MNHN 1876, MNHN 1957, MNHN 1976, MNHN 1979[p]); (56) Rincón de Baygorria, 32°53′S, 56°48′W (MNHN 2364[p]); Rivera Department: (57) Estancia La Quemada 1, 32°01.20′S, 54°34.22′W (GD 639[m], GD 640[m], GD 643[mp], GD 644[m], GD 664[mp]); (58) Estancia La Quemada 2, 32°01.83′S, 54°37.04′W (GD 638[m], GD 649[mp], GD 650[m]); Rocha Department: (59) Arroyo La Palma, Ruta 15 km 10, La Paloma, 34°35.18′S, 54°10.71′W (CA 628[m], MNHN 4263[mp], MNHN 4264[m], MNHN 4265, MNHN 4266[m], MNHN 4267, MNHN 4269[m]); San José Department: (60) Barra del Río Santa Lucía-Delta del Tigre, 34°44′S, 56°24′W (FMNH 122714[p], MLP 30.IX.96.3, MNHN 493[p], MNHN 494[p], MNHN 499, MNHN 503, MNHN 505, MNHN 506, MNHN 507, MNHN 508[p], MNHN 1494[p], MNHN 1495, MNHN 1499[p], MNHN 1506[p], MNHN 1511[p]); (61) Estancia Santa Clara, Chamizo, 34°10′S, 56°41′W (MNHN 741, MNHN 742, MNHN 1497[p], MNHN 1498[p]); (62) Estancia Voulminot, Puerto Arazatí, 34°31′S, 57°04′W (MNHN 522); (63) Kiyú, 34°39′S, 56°45′W (GD 326[mp]); (64) km 37.5, Ruta 1, 34°46′S, 56°31′W (MNHN 960, MNHN 961); Soriano Department: (65) 3 km S of Cardona, 33°56′S, 57°22′W (AMNH 206271, AMNH 206272, AMNH 206273[p], AMNH 206274[p], AMNH 206275, AMNH 206276, AMNH 206277, AMNH 206278[p], AMNH 206279, AMNH 206280[p], AMNH 206281, AMNH 206290, AMNH 206298, AMNH 206299, AMNH 206300, AMNH 206301[p], AMNH 206302, AMNH 206309, AMNH 206310, AMNH 206311, AMNH 206312[p]); (66) Arroyo Perdido, Santa Elena, location not recorded (MNHN 552[p], MNHN 553[p]); Tacuarembo Department: (67) 7 km E Barra Tacuarembó, location not recorded (MNHN 2361); Treinta y Tres Department: (68) Arroyo Avestruz, location not recorded (MNHN 1505).

Kunsia tomentosus.—BOLIVIA, Santa Cruz Department: Margabalito (LHE 1619[m] AY275120). BRAZIL, Goiás State: Parque Nacional das Emas (ARB 140[m]).

Blarinomys breviceps.—BRAZIL, São Paulo State: Serra da Cantareira (CIT 1391[m] AY275112).