An Introduction to the Genus *Bibimys* (Rodentia: Sigmodontinae): Phylogenetic Position and Alpha Taxonomy

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Bibimys is an exceptionally poorly understood genus of sigmodontine rodents. It is known from both fossil and recent specimens. Currently, *Bibimys*, with three species, is placed with the genera *Kunsia* and *Scapteromys* in the tribe Scapteromyini. This study is the first to examine the phylogenetic position of *Bibimys* within the Sigmodontinae and, in particular, to examine its purported close relationship with *Kunsia* and *Scapteromys*. It is the first study to include samples of all three of the currently recognized species of *Bibimys*. We found that *Bibimys*, *Kunsia* and *Scapteromys* do not form a monophyletic group and that all three genera seem to be part of the akodont radiation. We present an amended diagnosis of the genus. Our analyses cast doubt on the distinctiveness of the three forms currently included within *Bibimys*. A gazetteer of *Bibimys* localities is presented. Finally, we suggest future research directions that should shed new light on the evolutionary history of this little-known genus.

SYSTEMATICS OF *BIBIMYS* AND THE SCAPTERMYINI

Sigmodontine rodents traditionally have been arranged in groups of genera based on morphological similarity. Some of these groups have received the formal rank of tribes (e.g., McKenna and Bell, 1997). Few, however, have been examined from a formal phylogenetic perspective. One of the proposed groups is the tribe Scapteromyini, which was informally described by Hershkovitz (1966) and later formally introduced by Massoia (1979) although without a diagnosis. The scapteromyines are one of the smallest of the sigmodontine tribes, consisting of only three genera: *Bibimys* (3 recent species currently recognized), *Kunsia* (2 recent species) and *Scapteromys* (2 recent species). For convenience, we shall informally refer to these three genera as the scapteromyine genera, but testing the phylogenetic validity of the tribe Scapteromyini and determining its evolutionary position within the Sigmodontinae is one of our goals in this paper.

Few studies deal with the scapteromyine genera. In part, this is because scapteromyine rodents, with the exception of *Scapteromys*, are known from very few specimens. Some of the type specimens are badly preserved (e.g., *Bibimys labiosus*, *Kunsia fronto chacoensis*) or were described from fossil material (e.g., *Kunsia fronto fronto*). In addition, these rodents are mainly distributed in the Río de la Plata basin, which traditionally has not been the main focus of authorities working on

sigmodontine evolutionary history. As a result of the limited number of studies dealing with these genera, our knowledge of scapteromyine systematics is exceptionally poor even in such basic aspects as alpha taxonomy, patterns of diversification, and place within the sigmodontine radiation. Only after these fundamental issues are clarified will we be able to investigate the processes by which the diversity of the group arose, its biogeographic history, and its conservation status.

The present contribution is part of a revisionary study of the scapteromyine rodents. It is based on both morphological and molecular evidence. New material from the genus *Bibimys* has recently become available as the result of fieldwork in Argentina, Brazil, and Paraguay. Here, we examine the genus *Bibimys* at two hierarchical levels. First, we analyze the phylogenetic position of *Bibimys* within the sigmodontine radiation and, in particular, its relationships with the other scapteromyine genera. Second, we provide an emended diagnosis of the genus *Bibimys* and present new evidence concerning the validity of its three species.

PHYLOGENETIC ANALYSIS

Mice and rats of the subfamily Sigmodontinae (*sensu* Reig, 1980) constitute one of the most diverse components of the Neotropical mammal fauna. Further, current and past sigmodontine diversity is still being characterized with the continuing description of both extant and fossil genera and species (e.g., González et al., 1998; Ortiz et al., 2000). Recently, the widespread adoption of a cladistic approach (e.g., Engel et al., 1998; Smith and Patton, 1999; Steppan, 1995) has lead to substantial progress in clarifying the phylogenetic relationships of the numerous sigmodontine taxa. However, our understanding of sigmodontine evolutionary history is far from complete (D'Elía, 2000), in part because large and/or relevant components of the sigmodontine radiation have not yet been included in any phylogenetic analysis.

The taxonomic history of the scapteromyine group is brief and relatively simple. A scapteromyine concept can be traced back to Peters (1860), who placed *Mus tomentosus* together with *Hesperomys* (*Scapteromys*) *tumidus* in *Scapteromys*. Thirty years after its original description, Fitzinger (1867) elevated *Scapteromys* to generic status, although some authors continued to use *Scapteromys* as a subgenus of *Hesperomys* (e.g., Thomas, 1884). In the following years, more fossil and recent species were added to *Scapteromys* (Gyldenstolpe, 1932; Miranda-Ribeiro, 1914; Winge, 1887). Hershkovitz (1966) removed taxa previously assigned to *Scapteromys* (e.g., *S. tomentosus*) to create the genus *Kunsia* and suggested that both genera be combined into an informal group known as the scapteromyines. He further suggested that the scapteromyines were part of the akodont radiation. At the same time, he called into question the scapteromyine condition of three other taxa, including *B. labiosus* (at that time *Scapteromys labiosus*). Avila-Pires (1972) described a new subspecies of *Kunsia fronto*. Later, Massoia (1979), the first author to use the name Scapteromyini, expanded the group with the description of a new species and

genus, *Bibimys torresi*. One year later, Massoia (1980a) allocated two species - *Akodon chacoensis* and *Scapteromys labiosus* – to *Bibimys*. More recently, as result of a broad phylogenetic study, Smith and Patton (1999) found that the scapteromyine genera *Kunsia* and *Scapteromys* formed a clade that fell within their akodont lineage, and therefore they did not recognize the Scapteromyini as a tribe separate from the Akodontini. These authors suggested that analysis of *Bibimys* DNA sequences would shed new light on the relationships of their expanded Akodontini.

Materials and Methods

Voucher specimens for the individuals sequenced in this study are or will be deposited in the following collections: Argentina - Centro Nacional Patagónico Colección Mamíferos (CNP) and Museo de Mar del Plata Colección Mamíferos (MMP-Ma); Brazil - Museu Nacional do Rio do Janeiro (MN); Paraguay - Museo Nacional de Historia Natural del Paraguay (MNHNP; GD: field number of Guillermo D'Elía); and United States of America - Museum of Vertebrate Zoology (MVZ) and The University of Michigan Museum of Zoology (UMMZ). Complete cytochrome *b* gene sequences from specimens belonging to the three recognized species of *Bibimys* were studied as follows. *B. chacoensis* (*n* = 2): CNP 756 (Argentina, Province of Chaco, Department of Bermejo, Cancha Larga, S 27° 04 W 58° 43) and GD 153 (Paraguay, Myers et al., *in prep.*). *B. labiosus* (*n* = 2): MN 62062 and MN 62063 (Brazil, State of Minas Gerais, Viçosa, S 20º 45' W 42º 53'). *B. torresi* (*n* = 1): MMP-Ma 3620 (Argentina, Province of Buenos Aires, Canal 6, S 34º 09' W 58º 57'). The specimens from *B. chacoensis* and *B. labiosus* are from localities close to the type localities for each form and agree morphologically with the descriptions of the corresponding holotypes (pers. obs. and Gonçalves et al., this volume). The specimen of *B. torresi* comes from the type locality of the species. In addition we sequenced one specimen of each of the following species: *Akodon montensis* (MNHNP 2910: Paraguay, Department of Itapua, Estancia San Isidro, S 26º 29' W 55º 54'), *A. azarae* (GD 264: Paraguay, Department of Paraguari, Cost of the Tebicuary River, S 26º 24' W 57º 02'), *Scapteromys aquaticus* (UMMZ 17499: Paraguay, Department of Paraguari, Cost of the Tebicuary River, S 26º 24' W 57º 02') and *S. tumidus* (MVZ 183269: Uruguay, Department of Maldonado, Las Flores, S 34º 49' W 55º 19'). We completed our sigmodontine dataset with sequences available through GENBANK as of May 2001, and with new sequences kindly provided by J. L. Patton and M. F. Smith (Museum of Vertebrate Zoology).

Although sigmodontine (*sensu* Reig, 1980) monophyly is well corroborated (Engel et al., 1998; but see also Steppan, 1995) the identity of the sister group of sigmodontines is not clear. The subfamily Sigmodontinae falls in a large cricetid clade composed of other main branches of the muroid radiation (see D'Elía, 2000). Currently, the relationships among those groups are not understood. Therefore, to polarize sigmodontine character states, we have included as outgroups (Nixon and Carpenter, 1993) representatives of the other primary clades that make up the large

cricetid clade. These are the arvicolines, the cricetines, the neotomines, the peromyscines and the tylomyines. Outgroup sequences were retrieved from GENBANK, with the exception of that for *Tylomys*, which was generated in this study. A total of 115 taxa were included in our phylogenetic analysis, of which 93 belong to the ingroup and 22 belong to the outgroup. All taxa analyzed as well as the sources of their cytochrome *b* sequences are listed in Appendix 1.

The cytochrome *b* gene sequences reported in this study were amplified and sequenced in two fragments using primers located both internally and in the flanking regions of the gene (MVZ 05–MVZ 16 and MVZ 103-MVZ 14, Smith and Patton, 1993; Smith *pers. com.*). Negative controls were included in all experiments. Dye-labeled PCR products were sequenced using an ABI 377 automated sequencer. In all cases both heavy and light DNA strands were sequenced and compared.

Sequence alignment was done with the program Clustal X (Thompson et al., 1997) using the default values for all alignment parameters. Cytochrome *b* sequences of sigmodontine taxa reported in GENBANK vary from 1140 to 1144 base pairs. From the alignment it was clear that the position of the indel responsible for the difference is at the very end of the sequence, but it was impossible to determine unambiguously its exact position (i.e, if it corresponds to the codon number 380 or 381). To avoid this problem, we chose to work with the first 1134 bases of the sequences.

Aligned sequences were subjected to maximum parsimony analysis (MP; Kluge and Farris, 1969; Farris, 1982). In all cases, characters were treated as unordered and equally weighted. We employed two strategies to search for the most parsimonious tree(s). First, PAUP* 4 (Swofford, 2000) was used to perform 200 replicates of traditional heuristic searches with random addition of sequences and tree bisection-reconnection branch swapping. Second, two batches of parsimony ratchet (Nixon, 1999) were performed in PAUP* using command files written in PAUPRat (Sikes and Lewis, 2001). The difference between the two ratchet batches was the percentage of perturbed characters, which were 15% and 25%, respectively. Each ratchet batch consisted of 20 series of 200 iterations. For each series a different command file was used. Two measures of clade support were calculated. First, 500 bootstrap replications with 3 addition sequence replicates each were executed. Second, we performed 500 parsimony jackknife replications with 3 addition sequence replicates each and the deletion of one-third of the character data. In both bootstrap and jackknife searches, the branches with less than 50 % of support were allowed to collapse.

Results and Discussion

Four different cytochrome *b* haplotypes were found among the five specimens of *Bibimys* that were sequenced. Both individuals from Viçosa (Minas Gerais, Brazil) shared the same haplotype. Therefore, only one specimen from that locality was considered in the phylogenetic analyses. The cytochrome *b* gene of *Bibimys* had a

length of 1141 base pairs. *Bibimys* cytochrome *b* haplotypes showed a strong base compositional bias (Table 1), with a marked deficit of guanine (12.27 % of all positions, 3.68 % in third positions). Similar compositional biases are common in sigmodontine rodents (e.g., our complete dataset; Myers et al., 1995; Smith and Patton, 1993, 1999) and in mammals in general (Irwin et al., 1991).

Our total dataset had 677 variable characters, of which 570 were parsimony-informative. The 200 replicates of heuristic search found 48 shortest trees, while the parsimony ratchets recovered those 48 trees plus 107 additional shortest trees, totaling 155 shortest trees. A final TBR swapping of those 155 trees performed in PAUP* 4 (Swofford, 2000) found an additional shortest tree not originally recovered by either the replicated heuristic searches or the parsimony ratchets. In total, we recovered 156 most parsimonious trees of 10280 steps (CI = 0.120, RI = 0.474). The strict consensus of those trees is shown in Figure 1.

Table 1. Base composition of *Bibimys* cytochrome *b* haplotypes (1141 bases). Haplotype data from four specimens are presented; each specimen is identified by its museum record number (e.g., MN 62062).

	A	C	G	T
MN 62062[a]	0.29448	0.30149	0.12445	0.27958
CNP 756[a]	0.29886	0.30061	0.12182	0.27870
GD 153[a]	0.29886	0.29886	0.12182	0.28046
MMP 3620[a]	0.29798	0.30149	0.12270	0.27783
Mean across haplotypes[b]	0.29755	0.30061	0.12270	0.27914
1st position[c]	0.30577	0.23950	0.20997	0.24475
2nd position[c]	0.21053	0.25263	0.12105	0.41579
3rd poition[c]	0.37632	0.40987	0.03684	0.17697

[a] The mean frequency of each base, averaged across all codon positions.

[b] The mean frequency of each base, averaged across all haplotypes.

[c] The mean frequency of each base, averaged across all haplotypes and listed by codon position.

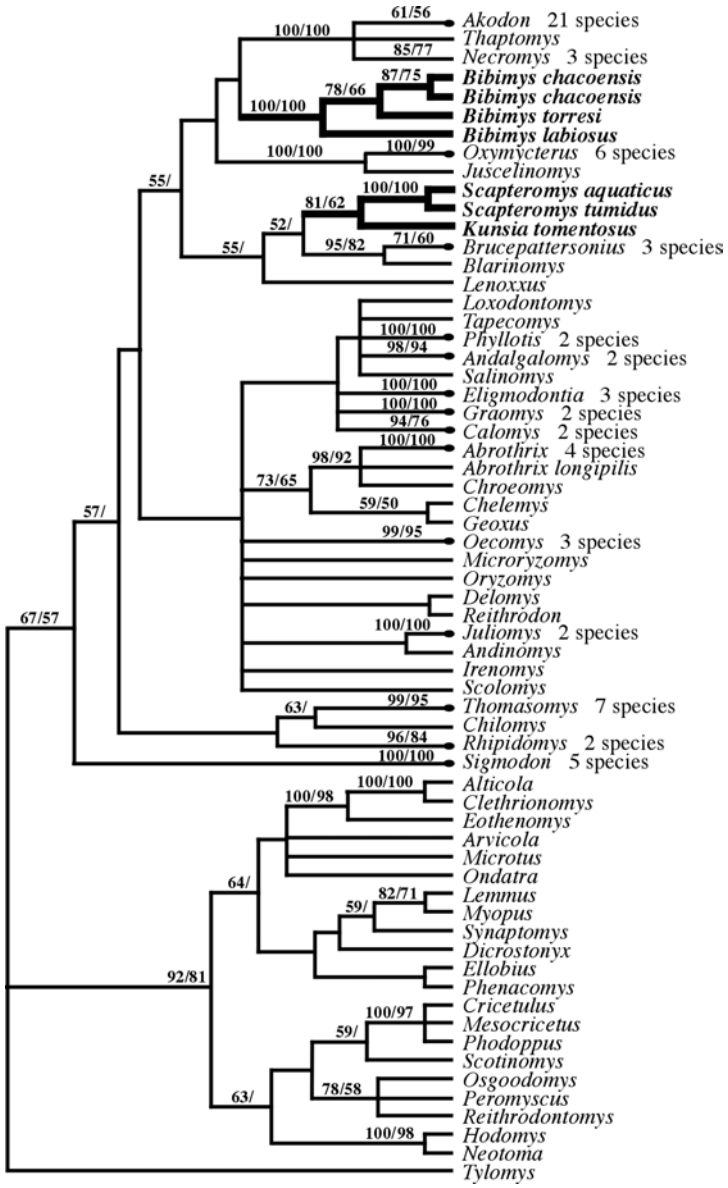

Figure 1. Strict consensus of the 156 most-parsimonious trees (length 10280, CI = 0.120, RI = 0.474) obtained by maximum parsimony analyses (i.e., heuristic searches and parsimony ratchets) of 93 sigmodontine and 22 outgroup taxa. More than one species of several non-scapteromyine genera were included in the analyses (see Appendix 1). To simplify the figure, only genera are shown as terminal taxa. Exceptions are the scapteromyine taxa and the genus *Abrothrix*, which was not monophyletic. Numbers above branches indicate parsimony jackknife (right of the diagonal) and bootstrap (left of the diagonal). Only values above 50 % are shown. For technical details of the analyses, refer to the text.

In the most recent treatise of mammal classification (McKenna and Bell, 1997) the Scapteromyini is listed as a sigmodontine tribe, implying that these rodents constitute a monophyletic group. However, the results obtained here (Figure 1) do not support the grouping of *Bibimys*, *Kunsia* and *Scapteromys* as a natural group. *Bibimys* is the sister group of a clade containing *Akodon*, *Necromys* and *Thaptomys*, whereas *Kunsia* and *Scapteromys* are sister to each other in a clade also containing *Brucepattersonius*, *Blarinomys* and *Lenoxus*. Both clades are part of the tribe Akodontini as defined by Smith and Patton (1999). However, the two clades containing the scapteromyine genera, as well as the whole akodont clade, have low levels of support (<50%) as measured by bootstrap values (Figure 1). When only those clades with bootstrap values $\geq$ 50 % are retained, *Bibimys* and the clade *Kunsia-Scapteromys* fall into a basal polytomy involving several sigmodontine lineages. Although parsimony jackknife values are in general somewhat higher than bootstrap values, they are also low. This lack of support for most sigmodontine suprageneric groups (in analyses based on cytochrome *b* gene sequences) was earlier documented by Smith and Patton (1999). Currently, it is unclear if the lack of resolution of suprageneric sigmodontine groups is the result of the limited resolving power of the cytochrome *b* gene at that taxonomic level or the result of an explosive radiation of the group following its entry into the South American continent.

These results indicate that one must be cautious with the interpretation of scapteromyine relationships. Clearly, phylogenetic analyses of other data sets are needed to evaluate hypotheses about the phylogenetic relationships of *Bibimys* with respect to *Kunsia* and *Scapteromys* in particular, and with the rest of the sigmodontines in general. Of those possible data sets, the study of more slowly evolving nuclear DNA sequences, as well as a broad morphological analyses not limited to craniodental features, are promising. We are currently working in both directions.

Given the lack of support for a scapteromyine clade at the molecular (cytochrome *b*) level, it is interesting to explore the reasons why *Bibimys* has traditionally been considered related to *Scapteromys* and *Kunsia*. As noted above, few authors have analyzed the phylogenetic relationships of *Bibimys*. Massoia (1979), when including *Bibimys* in the tribe Scapteromyini, implied a close phyletic relationship of this genus with *Kunsia* and *Scapteromys*. This evolutionary hypothesis was based exclusively on similarities in molar morphology, including the presence of a slender mesoloph in M1 and M2, a cylindromorphic M3, and reduced posterolophids on m1 and m2. Pardiñas (1996), who studied dental and jaw morphology of both extant and extinct specimens, later reinforced Massoia's hypothesis. However, Hershkovitz (1966) explicitly excluded *Bibimys* (*Scapteromys labiosus* at that time) from his concept of a scapteromyine group, stating that it morphologically resembled *Akodon azarae*. His conclusions were based mainly on the cranial and molar morphology of *B. labiosus* as portrayed in Winge's (1887) description of that species. Thus, different authors reached strikingly different

conclusions from the study of the same characters. This situation, common in rodent systematics, is due in part to the difficulty of establishing homologies among dental features such as cusps, lophs, etc., as well as the relatively small number of characters provided by molar morphology. Recent progress in the study of molar development (see Jernvall and Jung, 2000; Jernvall. at al., 2000; Peters and Balling, 1999) should improve our ability to determine the homologies of these traits.

In addition to the small set of craniodental characters mentioned above and the DNA sequence data presented here, two other types of data have been used to explore the phylogenetic affinities of *Bibimys*. Gonçalves et al. (this volume), based on a phenetic comparison of phallic and karyotypic data, cast doubt on the affinity of *Bibimys* to *Kunsia* and *Scapteromys*. Unfortunately, as those authors indicate, their results are difficult to interpret because these characters were not analyzed in a cladistic framework and the taxonomic coverage of the study was limited to scapteromyine genera. As a result, it is not possible to determine if suggested shared character states are synapomorphies or plesiomorphies, or if they evolved independently.

Interestingly, a new species of sucking lice has recently been recorded from *Bibimys* specimens (Castro and Gonzalez, 2003). This parasite seems to belong to the *aitkeni* species group of the genus *Hoplopleura*. The other species of this group are parasites of mice of the genera *Akodon* and *Necromys*. In contrast, *H. scapteromydis*, recorded from *Scapteromys*, does not belong to the *aitkeni* group (Castro and Gonzalez, 2003). The relationships among these parasites have not been analyzed phylogenetically, however, and this evidence should be interpreted with caution.

Our analysis supports the inclusion of *Bibimys*, *Kunsia* and *Scapteromys* in the akodontine tribe as defined by Smith and Patton (1999). This result is an extension of analyses presented by Smith and Patton (1999), who found evidence for the placement of the clade *Kunsia-Scapteromys* within the akodont radiation. This finding is important because it implies that the akodont rodents are both morphologically and ecologically more diverse than traditionally recognized, including cursorial akodon-like mice and long nosed mice, as well as the crimson nosed *Bibimys*, the semiaquatic *Scapteromys* and the largest sigmodontine rat, the fossorial *Kunsia*. Hershkovitz (1966), who suggested an akodont origin for his scapteromyine group (*Kunsia* plus *Scapteromys*), was the first to point out the akodont condition of the scapteromyines. Nevertheless, one must be cautious in expanding the akodont tribe to include the scapteromyines due to the low levels of support found for this hypothesis (Figure 1). In addition, it is worth noting that the akodont tribe, as currently defined, lacks a formal diagnosis. Overall, in the light of these results and other sigmodontine phylogenetic studies, it is clear that the sigmodontine tree is far from resolved. Future cladistic analyses of morphological characters along with new DNA sequences are needed to provide a set of derived character states useful for defining the limits and contents of the akodonts and other related groups.

BIBIMYS ALPHA TAXONOMY

Currently, three species of *Bibimys* are recognized. The genus was erected by Massoia in 1979, with the type species *B. torresi* Massoia, 1979. Later, Massoia (1980a) referred *Scapteromys labiosus* Winge, 1887, and *Akodon chacoensis* Shamel, 1931, to *Bibimys* but did not critically review the genus or provide diagnostic characters. *Bibimys* has a large distribution in tropical and subtropical lowlands of eastern Argentina, east-central Brazil, and eastern Paraguay (Myers et al., *in prep.*), although records are scattered and include very few known localities. Interestingly, there are specimens of *Bibimys* in Argentinean and Brazilian Late Pleistocene-Holocene deposits (Pardiñas, 1996; Pardiñas et al., 2004; Winge, 1887).

The existence of three species in the genus *Bibimys* has never been questioned. The genus, however, has never been critically revised. Trapping members of the genus is difficult and, as a result, few specimens are available (see notes in Dyzenchauz and Massarini, 1999). The type localities of *Bibimys* are separated by considerable distances (Figure 2), which we suspect has supported the common assumption of the existence of significant differences among these three forms. Pardiñas (1996), based on craniodental characters, suggested that *B. chacoensis* (there referred to as *B. labiosus* following Massoia, 1988) and *B. torresi* were conspecific. In contrast, Gonçalves et al. (this volume), based on geographic distances between known populations and differences in the number of autosomal arms of *B. torresi* and *B. labiosus*, argued for the validity of both species. The present contribution is the first attempt to evaluate the alpha taxonomy of *Bibimys* that includes material referred to all recognized forms.

Materials and methods

Morphological analyses of *Bibimys* were based on fossil and recent specimens (Appendix 2). The recent specimens included here were live trapped by us, recovered from owl pellets, or borrowed from museum collections. All specimens are or will be housed in the following collections: Argentina - Museo de La Plata Colección Mamíferos (MLP), Centro Nacional Patagónico Colección Mamíferos (CNP), Colección Elio Massoia (CEM), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN Zoología), Museo de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" (MMP-Ma), and Colección Felix de

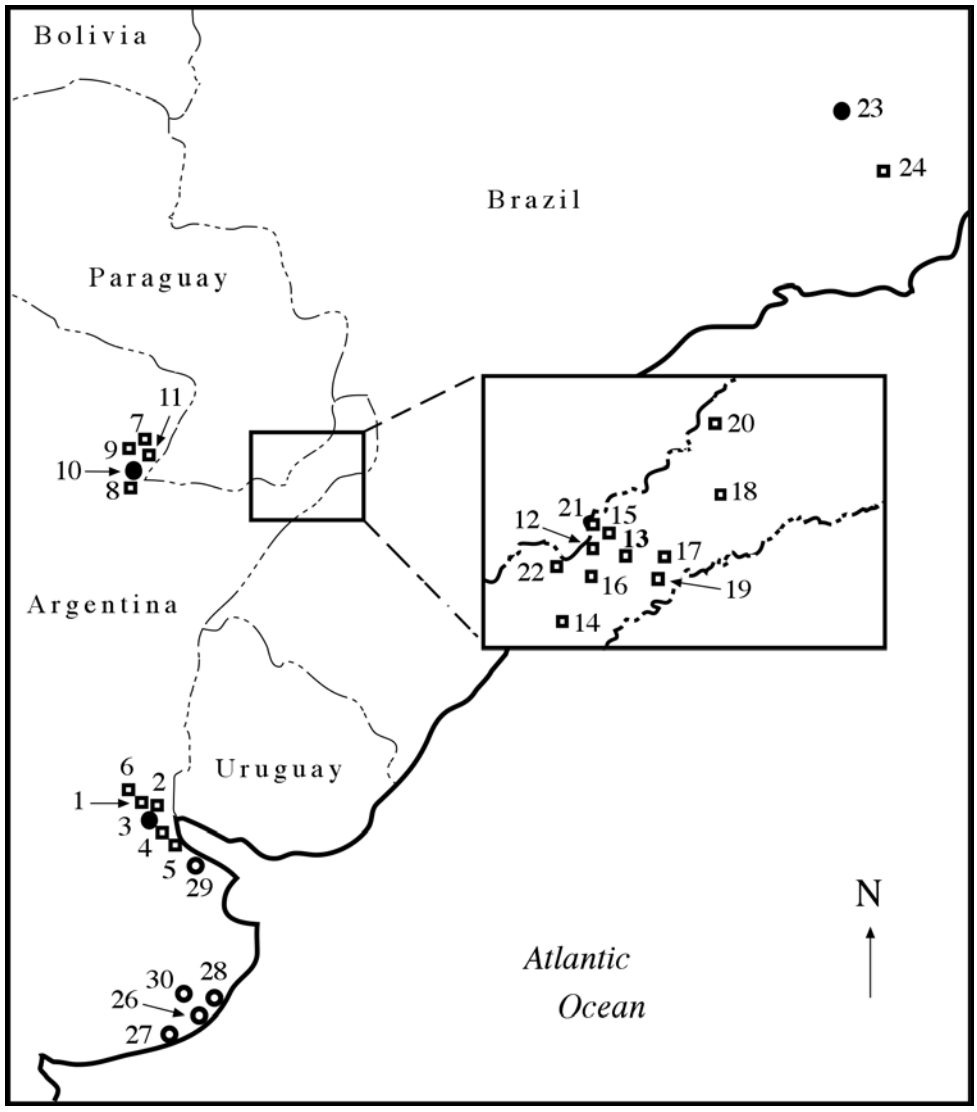

Figure 2. Map showing all recorded localities for *Bibimys*. Black circles indicate type localities. Open squares indicate recent localities. Open circles indicate fossil localities. Both fossil and recent specimens have been taken from locality 23, the type locality of *B. labiosus*. Localities 10 and 3 (recent) are the type localities of *B. chacoensis* and *B. torresi*, respectively. The Brazilian (Minas Gerais) locality number 31 is not mapped because it is not specified in its museum record. For details on locality names, reference sources, as well the specimens analyzed in this contribution, see Appendix 2. For details on the Paraguayan locality number 25 see Myers et al. (in prep.).

Azara (CFA); Denmark - Universitets Zoologiske Museum (ZMC); Paraguay, Museo Nacional de Historia Natural del Paraguay (GD, field number of Guillermo D'Elía); United Kingdom, Natural History Museum (BMNH); United States of America - National Museum of Natural History (USNM), and University of Michigan Museum of Zoology (UMMZ). Craniodental measurements were taken with digital calipers following Myers et al. (1990). Terminology for molar structures follows Reig (1977). External measurements were obtained from the specimen labels and field catalogues. In addition, information about *B. labiosus* was obtained from Gonçalves et al. (this volume). Genetic variation in *Bibimys* was assessed from the specimens reported in the phylogenetic analysis (see above).

Results and discussion

We have put together by far the largest series of *Bibimys* specimens to date, and the only one that includes specimens from all three recognized species. Although this series is not adequate to address some issues (see below), it allows us to evaluate the taxonomic utility of some characters mentioned in the literature and to evaluate for the first time other characters in the context of *Bibimys* taxonomy. In the light of this new information we present the following emended diagnosis of the genus *Bibimys*.

Bibimys Massoia, 1979

Type species: *Bibimys torresi* Massoia, 1979

Species included:

Bibimys labiosus (Winge, 1887)
Bibimys chacoensis (Shamel, 1931)
Bibimys torresi Massoia, 1979.

Emended diagnosis: Sigmodontine rodents (*sensu* Reig 1980) with the following combination of characters (Figure 3): small size (head-body length < 130 mm); gnathic process of the premaxilla well developed and forming a sharply projecting plate anterior to the incisors; anterior part of nasals inflected dorsally; sides of interorbital region squared, not beaded or ledged; interorbital region hour-glass shaped; zygomatic notches moderately deep and broad; anterior margin of zygomatic plate approximately vertical; anterior half of the zygomatic arch flattened and expanded dorsal-ventrally; braincase inflated and slightly narrower than the zygomatic breadth; upper incisors strongly opisthodont; molars terraced and moderately hypsodont; M1/m1 with anteromedian flexus/xid present; M1-2/m1-2 with mesolophs/phids fused with paralophule/entolophulid; M3 with cylindrical outline and two persistent enamel islands but no evidence of a hypoflexus; m3 rectangular with large oblique hypoflexid; length of m3 slightly

shorter than that of m2; mesopterygoid fossae narrower than parapterygoid plates; anterior margin of mesopterygoid fossa squared and lacking a median spine; alisphenoid strut present; squamosal root of the zygomatic arch connected to a slender hamular process by a crest; small subsquamosal fenestra above large postglenoid foramen; tegmen tympani anteriorly enlarged and reaching the squamosal; stapedial foramen and posterior opening of alisphenoid canal large; squamosal-alisphenoid groove and sphenofrontal foramen absent; gall bladder present; stomach unilocular and hemiglandular; anterior part of snout, from just below the external nares to the opening of the mouth, strikingly swollen, appearing bulbous; entire area from just dorsal to the rhinarium to the lower lips covered with remarkable short, bristle-like, all-white hairs that run stiffly outward from (i.e., perpendicular to the surface of) the lips, skin underlying the hairs distinctively reddish in living specimens (color is lost in both skins and formalin-preserved specimens).

Distribution: Late Pleistocene-Late Holocene of Argentina: Buenos Aires Province. Late Pleistocene-Holocene of Brazil: Minas Gerais State. Recent Argentina: Buenos Aires, Chaco, Entre Ríos, and Misiones Provinces; Brazil: Minas Gerais State, and Paraguay (Myers et al., *in prep*.). See Figure 2 and Appendix 2 for details.

Species boundaries: As stated above, the validity of the three species currently assigned to *Bibimys* has never been critically assessed. Previous studies such as Pardiñas (1996) and Gonçalves et al. (this volume) limited their comparisons to two forms. The only qualitative morphologic character proposed to date to distinguish among *Bibimys* species was the number of roots of M3. Pardiñas (1996) reported that the M3 of *B. chacoensis* (referred to as *B. labiosus* in that paper) had three roots whereas that of *B. torresi* had only two. Increased sample sizes reveal that this character is polymorphic in *B. chacoensis*. Of a sample of 14 specimens from Vedia, Chaco (Argentina) nine individuals had three roots while the rest had two. Some characters do appear to vary slightly among populations referred to different forms. For instance, the basioccipital of *B. chacoensis* is more excavated than that of the other forms, a feature also noted by Shamel (1931) in his description of the type specimen. The premaxillary bones of *B. torresi* appear to project more strongly anteriorly than in the other forms. However, these characters show great intrapopulation variability (Figure 4) and, further, this variation seems to be related to age. Analyses of larger sample sizes, especially of *B. torresi* and *B. labiosus*, are needed to clarify the taxonomic utility of these cranial character states.

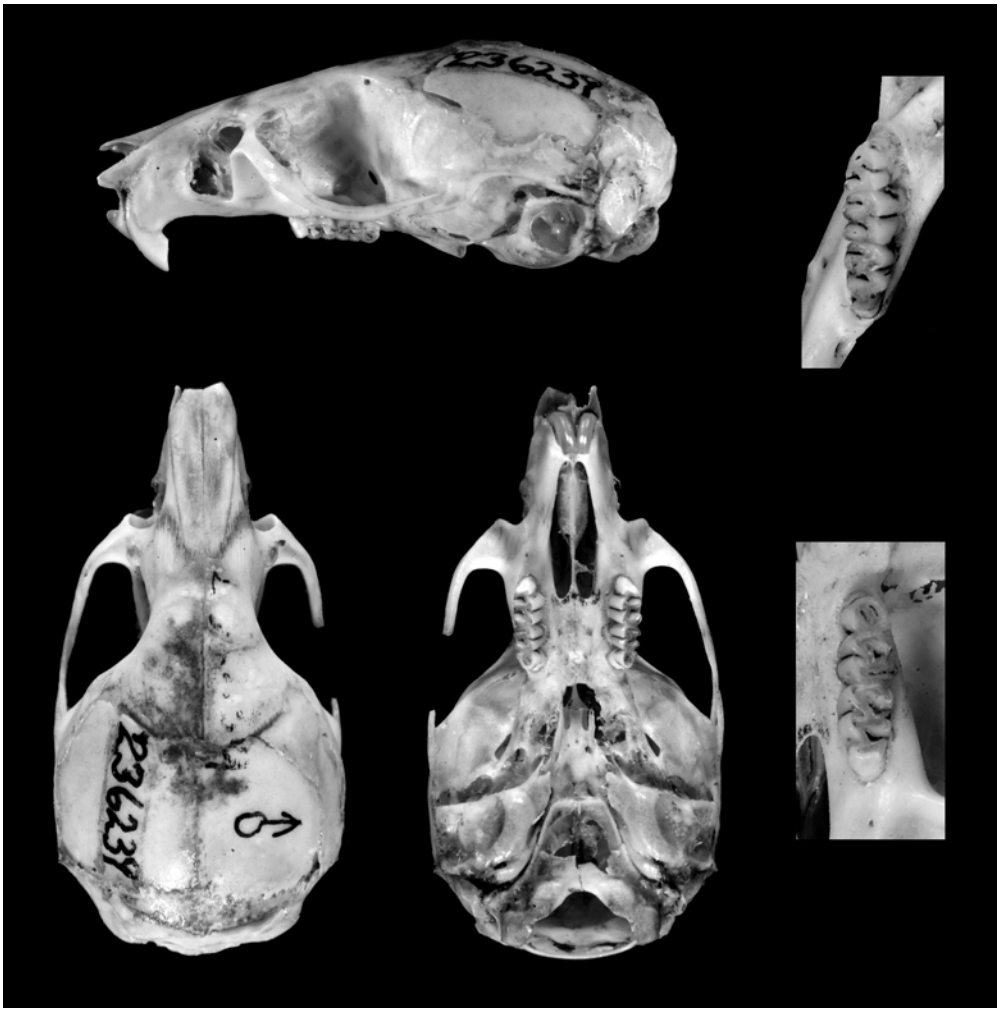

Figure 3. Skull of and molars of *Bibimys chacoensis* (holotype, USNM 236234).

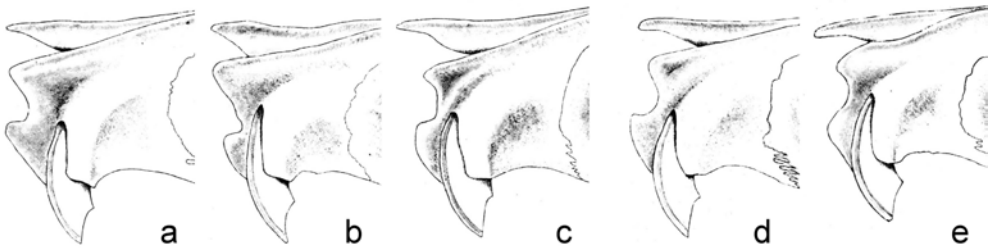

Figure 4. Lateral views of the anterior skull of 5 specimens of *Bibimys*. (a) MMP-Ma 3705, (b) MMP-Ma 3620 (c) MMP-Ma 2502 (d) C-0911, and (e) C-1580. Specimens (a) and (b) are referred to *B. torresi* from Estación Experimental INTA Delta del Parana, Argentina; specimens (c), (d), and (e) are referred to *B. chacoensis* from Paso Mono, Argentina. Note the large intrapopulation variation in the shape of the gnathic process and anterior part of the nasals.

Small sample sizes precluded our testing the statistical significance of differences in measurements among populations of the same versus different forms of *Bibimys*. The skulls of three specimens of *B. torresi* appeared to be slightly larger than specimens of the two other forms (Table 2). For most variables, however, sample sizes are too small to permit any estimate of variation within or among populations. Larger samples, from owl pellets, are available for two variables (upper and lower toothrow length). Analyses of these samples indicate that measurements for the three forms overlap (Figure 5). We note that these measurements were taken by at least five different people; the possibility of systematic error in recording these data cannot be ignored.

In summary, in a critical examination of cranial and dental morphology of both fossil and extant specimens referred to the three species, including the type specimens, we have not discovered any quantitative or qualitative dental or cranial character that unambiguously differentiates *B. chacoensis*, *B. labiosus*, and *B. torresi*. Sample sizes are still much too small, however, for much weight to be given to conclusions based on quantitative traits.

Table 2 -- External and cranial measurements (in mm) of *Bibimys* specimens. For measurement definitions see Myers et al. (1990).

Species	*chacoensis*	*labiosus*[1]	*torresi*
Number	USNM 236239	MZUFV 752	MMP-Ma 3620
	CNP 756	MZUFV 753	MMP-Ma 3705
	MMP-Ma 2502	MN 62061	MACN 20337
	CAF-0911		
	CAF-01580		
Locality	Las Palmas	Viçosa	INTA Delta del Paraná
	Cancha Larga	Viçosa	INTA Delta del Paraná
	Paso Mono	Viçosa	INTA Delta del Paraná
	Paso Mono		
	Paso Mono		
Sex	male	-	female
	male	female	male
	male	male	female
	female		
	male		
Age	adult	-	adult
	subadult	-	old adult
	subadult	-	old adult
	adult		
	adult		
Head and body	94	76	106
length	88	90	127
	107	89	-
	-		
	-		

Table 2. Continued.

Species	*chacoensis*	*labiosus*[1]	*torresi*
Hind foot length (with claw)	22.5 21.5 20.8 - -	21 22 23	21.8 22.9 -
Ear length	- 14 17.7 - -	15 18 14	17.4 17 -
Weight (g)	- 23 32 - -	- - -	35 42 -
Condylobasal length	22.25 22.21 23.26 23.80 23.51	23.80 24.41 24.54	24.41 26.00 26.00
Zygomatic breadth	12.63 12.24 13.34 12.64 13.33	13.20 13.44 13.60	13.97 13.93 13.50
Interorbital constriction	4.39 4.41 4.48 4.33 4.45	4.76 4.96 4.53	4.61 4.76 4.45

Table 2. Continued.

Species	*chacoensis*	*labiosus*[1]	*torresi*
Rostral length	-	-	9.08
	7.65	-	9.70
	8.43	-	8.70
	8.35		
	8.26		
Nasal length	-	9.36	9.35
	8.32	9.06	10.04
	8.77	-	9.49
	9.33		
	9.05		
Rostral width	4.28	4.41	4.70
	4.40	4.25	4.62
	4.17	4.40	4.45
	4.53		
	4.18		
Length frontal	7.88	-	9.37
along midline	8.22	-	9.76
	8.75	-	8.99
	8.5		
	8.56		
Length	2.24	-	2.72
interparietal	2.34	-	2.97
along midline	1.92	-	-
	2.39		
	1.96		
Length of orbit	8.50	-	9.18
	8.23	-	9.78
	9.01	-	-
	8.58		
	8.71		

Table 2. Continued.

Species	*chacoensis*	*labiosus*[1]	*torresi*
Diastema length	5.55	5.31	5.91
	5.46	5.66	6.56
	5.54	5.36	6.05
	5.40		
	5.52		
Maxillary toothrow length	3.79	3.73	4.16
	3.69	3.75	4.22
	3.70	3.80	4.46
	3.75		
	3.83		
Length of incisive foramen	5.63	5.62	5.88
	5.07	5.90	6.77
	5.28	5.45	6.19
	5.73		
	5.30		
Length of palatal bridge	3.58	-	4.17
	3.81	-	3.94
	4.12	-	-
	3.82		
	4.17		
Width of toothrow	5.21	5.48	5.98
	4.86	5.42	5.70
	5.45	5.53	-
	5.33		
	5.38		
Width across occipital condyles	6.79	6.48	6.68
	6.61	6.56	7.04
	6.61	6.80	-
	6.56		
	6.56		

Table 2. Continued.

Species	*chacoensis*	*labiosus*[1]	*torresi*
Breadth across mastoid region	12.24 12.10 12.19 12.12 12.40	- - -	12.73 13.89 12.62
Length of basioccipital at midline	3.67 3.94 4.62 4.77 4.66	3.91 3.75 4.03	4.75 4.94 5.12
Breadth of mesopterygoid fossa	1.27 0.93 1.23 1.28 1.48	- - -	1.34 1.65 1.16
Breadth of zygomatic plate	2.09 2.19 2.58 2.50 2.71	2.51 2.38 2.31	2.58 2.86 2.65
Cranial depth	9.61 9.70 9.50 9.38 9.66	- - -	10.11 9.88 9.90

[1] Data from Gonçalves et al. (this volume).

Gonçalves et al. (this volume) studied the penile and bacular morphology of three individuals of *B. labiosus* and Massoia (1979) provided a description of the baculum of two specimens of *B. torresi*. Minor differences can be seen in these descriptions. The two bacula shown by Massoia (1979: Figure 1), however, differ in a number of aspects; the extent of intrapopulation variability in bacular structure has not been documented for either *B. labiosus* or *B. torresi*.

The karyotype of two of the three *Bibimys* forms is known. Dyzenchauz and Massarini (1999) reported the karyotype of three *B. torresi* specimens from Otamendi, while Gonçalves et al. (this volume) reported the karyotype of three specimens of *B. labiosus* from Viçosa. All six individuals were characterized by $2n = 70$. Two differences, however, are evident among these karyotypes. First, *B. torresi* specimens have 76 arms - four fewer than individuals of *B. labiosus*. In addition, *B. torresi* exhibits C-bands in the X chromosome and in pair 3, while *B. labiosus* has C-bands in the X chromosome only. The biological significance of these differences is unknown. Cytogenetic data, usually differences in diploid number, have been useful for discriminating among morphologically similar sigmodontine species (e.g., Geise et al., 2001). However, analyses of additional individuals from these species, as well as from *B. chacoensis,* are essential given the well-documented chromosomal polytypism and polymorphism reported for other sigmodontine species (e.g., Bianchi et al., 1971; Nachman and Myers, 1989; Sbalqueiro and Nascimento, 1996).

In the phylogenetic analysis described above (Figure 1), all specimens of *Bibimys* constituted a monophyletic group. The level of variation of the cytochrome *b* gene among these putative species was extremely low (Table 3). Only 22 variable sites were found among the four *Bibimys* haplotypes recovered in this study. Of those, two are in first codon positions, and the remaining 20 are in third codon positions. Among those 22 changes, only two are non-synonymous. Of the four haplotypes recovered, the one corresponding to the Viçosa specimens is the most divergent, differing in 16 positions (1.40 %) from the other three haplotypes. The most similar haplotypes are those recovered from individuals from Cancha Larga and the Paraguayan locality (4 substitutions, 0.35 %). These values are much lower than those reported for other akodont species- pairs and are even lower than among-population variation in some akodont species (D'Elía unpublished data; Smith and Patton 1991, 1993). The extremely low levels of genetic variation reported here are remarkable considering the geographic distance among populations (Figure 2).

Despite the lack of critical morphological differences among *Bibimys* taxa and the similarity of their cytochrome *b* sequences, we do not at this time recommend any formal changes in the nomenclature for *Bibimys* species. While the

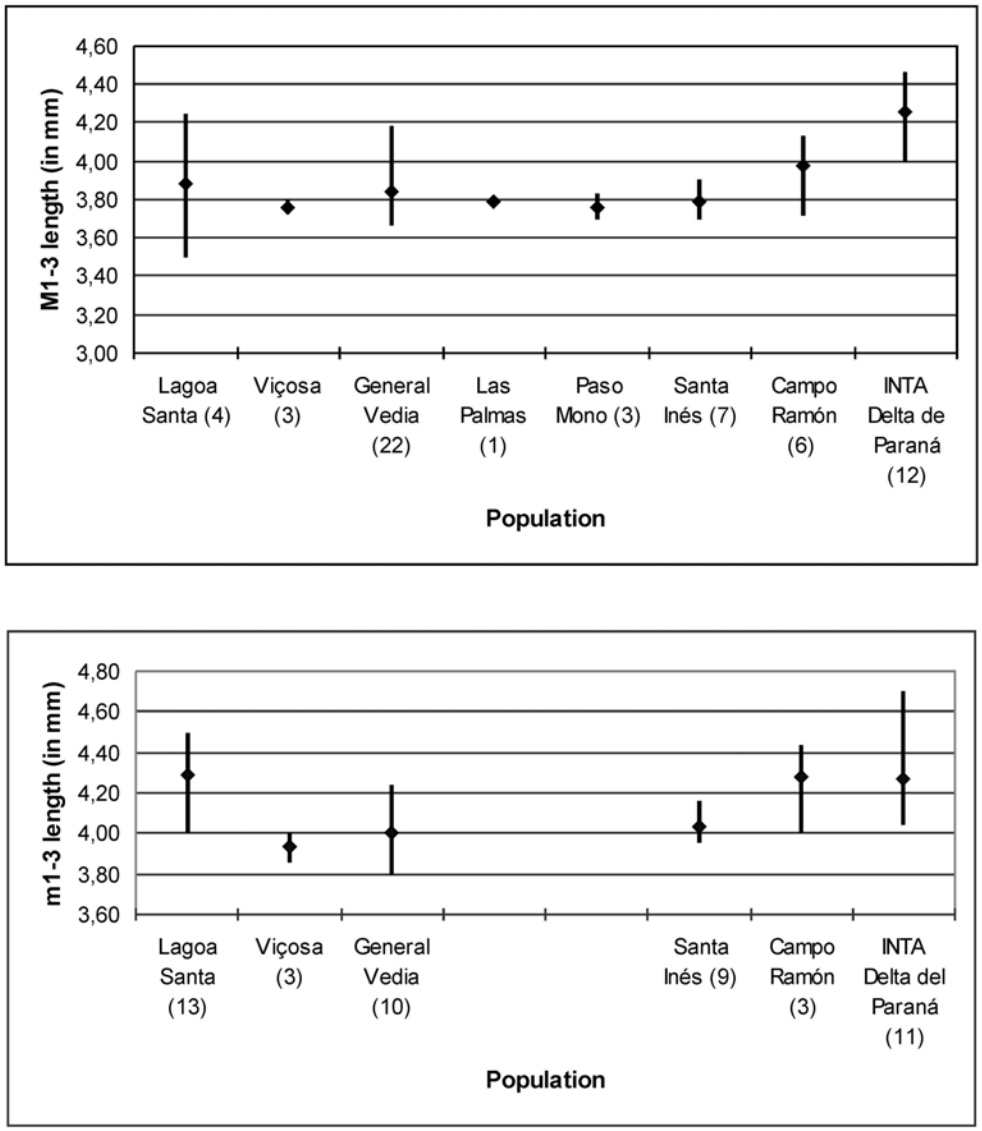

Figure 5. Variation in the length of upper (M1-3) and lower (m1-3) molar series across populations of *Bibimys*. The mean and range of values for each population are indicated by a dot and a bar, respectively. The number next to each population name indicates the sample size. Data from specimens from Lagoa Santa and Viçosa were taken from Gonçalves et al. (this volume). Data from specimens from Campo Ramón were taken from Pardiñas (1996).

available evidence tends to indicate that the genus is composed of a single species, widely distributed in SE Brazil, E Paraguay, and NE Argentina, sample sizes from each of these populations are still very small. If future studies reach the same conclusion, *B. chacoensis* and *B. torresi* would be regarded as junior synonyms of *B. labiosus*.

Table 3. Genetic differences among cytochrome *b* haplotypes recovered from *Bibimys* specimens (see text for details). Values above the diagonal correspond to the observed percentage of divergence. Values below the diagonal are observed number of substitutions.

	MN 62062	CNP 756	GD 153	MMP 3620
MN 62062		1.40	1.40	1.40
CNP 756	16		0.35	0.70
GD 153	16	4		0.70
MMP 3620	16	8	8	

Independent of the validity of the species discussed above, the extremely low levels of geographic variation found are remarkable. The apparent lack of populations located between those represented here is probably not due entirely to lack of sampling. Interestingly, the fossil record indicates that the distribution of *Bibimys* has fluctuated greatly over the last 120,000 years (Pardiñas, 1996, 1999a). Fossil remains of *Bibimys* were recovered from deposits as recent as 300 years before present at Mar del Plata, Argentina, more than 500 km south of the southernmost extant population known (Figure 2). This distributional change is parallel to that of other sigmodontine genera such as *Pseudoryzomys*, *Eligmodontia*, and *Phyllotis*, and has also taken place in other mammals (e.g., *Desmodus*, see Pardiñas and Tonni, 2000). The available evidence suggests that the current fragmentary distribution of *Bibimys* populations may be a recent event. If so, this may explain the low levels of variation found among extant populations. If *Bibimys* populations were interconnected until the recent past, then perhaps not enough time has elapsed for these populations to accumulate significant differences. This hypothesis seems to be supported by the molecular data. Although the number of *Bibimys* specimens sequenced by us (n = 5) is far from adequate to evaluate thoroughly the geographic structure of genetic variation in this genus, it is worth noting that the geographic patter of variation among the four haplotypes detected seems to differ from the expected under a pattern of isolation by distance. This scenario of a recent contraction of the geographic distribution of *Bibimys* can be tested further with

additional studies of new fossil and recent specimens, as well as additional and more variable DNA markers.

CONCLUSIONS

Results of the first phylogenetic analysis that include the sigmodontine genus *Bibimys* indicate that this genus does not form a monophyletic group with *Kunsia* and *Scapteromys*. If this is the case, the Tribe Scapteromyini (*sensu* Massoia, 1979) as currently envisioned (e.g., McKenna and Bell, 1997) is not a natural group. Our results support the conclusion of Smith and Patton (1999) that *Bibimys*, *Kunsia* and *Scapteromys* are part of the akodontine radiation. However, our tree is far from robust. These hypotheses should be tested further using phylogenetic analyses of nuclear DNA sequences and morphological characters.

Results of the first analysis of geographic variation that included individuals assigned to the three currently recognized species of *Bibimys* revealed low levels of morphologic and genetic variation. This homogeneity leads us to question the distinctiveness of the three forms currently recognized at the species level. Fossil evidence shows that *Bibimys* has suffered a recent contraction of its geographic range. This may explain the low levels of variation detected among populations that are several hundred kilometers distant from one another. Analysis of additional specimens is required to test further this scenario.

Note: The material of this paper was presented at Pattonfest in 2001 and formed the basis for subsequent broader phylogenetic analyses published in 2003 (D'Elía, 2003; D'Elía et al., 2003). Regarding *Bibimys*, both studies corroborate the phylogenetic hypothesis advanced here.

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Appendix 1. Specimens included in the phylogenetic analysis of cytochrome *b* gene sequences.

	Taxon	Catalog #[a]	Source[b]
	Ingroup		
1	*Abrothrix andinus*		AF108671
2	*Abrothrix longipilis*		U03530
3	*Abrothrix olivaceus*		AF027305
4	*Abrothrix xanthorhinus*		AF297902
5	*Abrothrix* sp.		AF297894
6	*Akodon aerosus*	MVZ 172870	*
7	*Akodon albiventer*	FMNH 129978	*
8	*Akodon azarae*	GD 264	This study
9	*Akodon boliviensis*		M35691
10	*Akodon cursor*	MAM 24	*
11	*Akodon iniscatus*	MVZ 182655	*
12	*Akodon juninensis*	MVZ 173038	*
13	*Akodon kofordi*	MVZ 171665	*
14	*Akodon lindberghi*	MN 48026	*
15	*Akodon lutescens*	MVZ 171612	*
16	*Akodon mimus*	MVZ 171752	*
17	*Akodon molinae*	AK 222	*
18	*Akodon mollis*	LSU 27007	*
19	*Akodon montensis*	MNHNP 2910	This study
20	*Akodon mystax*	MN 48041	*
21	*Akodon orophilus*	MVZ 173057	*
22	*Akodon serrensis*	MN 35927	*
23	*Akodon siberiae*	MSB 55209	*
24	*Akodon subfuscus*	MVZ 174109	*
25	*Akodon toba*		U03527
26	*Akodon torques*	MVZ 171720	*
27	*Andalgalomys pearsoni*		AF159285
28	*Andalgalomys roigi*		AF159286
29	*Andinomys edax*		AF159284
30	*Bibimys chacoensis*	CNP 756	This study
31	*Bibimys chacoensis*	GD 153	This study
32	*Bibimys labiosus*	MN 62062	This study
33	*Bibimys torresi*	MMP 3620	This study

Appendix 1. Continued.

	Taxon	Catalog #[a]	Source[b]
34	*Blarinomys breviceps*		AF108668
35	*Brucepattersonius iheringi*		AF108667
36	*Brucepattersonius soricinus*		MVZ183036
37	*Brucepattersonius* sp.	LG 108	*
38	*Calomys callosus*		AF159293
39	*Calomys lepidus*		AF159294
40	*Chelemys macronyx*		U03533
41	*Chilomys instans*		AF108679
42	*Chroeomys jelskii*		M35714
43	*Delomys sublineatus*		AF108687
44	*Eligmodontia morgani*		AF108691
45	*Eligmodontia puerulus*		AF159289
46	*Eligmodontia typus*		AF108692
47	*Geoxus valdivianus*		U03531
48	*Graomys domorum*		AF159291
49	*Graomys griseoflavus*		AF159290
50	*Irenomys tarsalis*		U03534
51	*Juscelinomys huanchacae*		AF133667
52	*Kunsia tomentosus*		AF108670
53	*Lenoxus apicalis*		U03541
54	*Loxodontomys micropus*		AF108690
55	*Microryzomys minutus*		AF108698
56	*Necromys amoenus*		M35711
57	*Necromys lasiurus*		U03528
58	*Necromys urichi*		U03549
59	*Oecomys bicolor*		AF108699
60	*Oecomys trinitatus*	LHE 579	*
61	*Oecomys superans*	MVZ 155004	*
62	*Oryzomys megacephalus*		AF108695
63	*Oxymycterus amazonicus*	LHE 603	*
64	*Oxymycterus delator*	UMMZ 133939	*
65	*Oxymycterus hiska*	MVZ 171518	*
66	*Oxymycterus nasutus*	MVZ 182701	*
67	*Oxymycterus paramensis*		U03536
68	*Oxymycterus* sp.	MVZ 183265	*

Appendix 1. Continued.

	Taxon	Catalog #[a]	Source[b]
69	*Phyllotis magister*		U86824
70	*Phyllotis xanthopygus*		AF108693
71	*Reithrodon auritus*		AF108694
72	*Rhipidomys macconnelli*		AF108681
73	*Salinomys delicatus*		AF159292
74	*Scapteromys aquaticus*	UMMZ 174991	This study
75	*Scapteromys tumidus*	MVZ 183269	This study
76	*Scolomys juruaense*		AF108696
77	*Sigmodon alleni*		AF155425
78	*Sigmodon arizonae*		AF155423
79	*Sigmodon hispidus*		AF108702
80	*Sigmodon mascotensis*		AF155424
81	*Sigmodon ochrognathus*		AF155422
82	*Tapecomys primus*		AF159287
83	*Thaptomys nigrita*		AF108666
84	*Thomasomys aureus*		U03540
85	*Thomasomys daphne*		AF108673
86	*Thomasomys gracilis*		AF108674
87	*Thomasomys ischyurus*		AF108675
89	*Thomasomys notatus*		AF108676
90	*Thomasomys oreas*		AF108677
91	*Thomasomys* sp.		AF108678
92	*Juliomys pictipes*		AF108688
93	*Juliomys* sp.		AF108689
	Outgroups		
94	*Alticola macrotis*		AF119273
95	*Arvicola terrestris*		AF159400
96	*Clethrionomys rutilus*		AB031581
97	*Dicrostonyx torquatus*		AF119275
98	*Ellobius fuscocapillus*		AF126430
99	*Eothenomys smithii*		AB037316
100	*Lemmus trimucronatus*		AF119276
101	*Microtus arvalis*		AF159403
102	*Myopus schisticolor*		AF119263

Appendix 1. Continued.

	Taxon	Catalog #[a]	Source[b]
103	*Ondatra zibethicus*		AF119277
104	*Phenacomys intermedius*		AF119260
105	*Synaptomys borealis*		AF119259
106	*Cricetulus griseus*		AB033693
107	*Mesocricetus auratus*		AF119265
108	*Phodopus campbelli*		AF119278
109	*Hodomys alleni*		AF186801
110	*Neotoma floridana*		AF186823
111	*Osgoodomys banderanus*		AF155383
112	*Peromyscus leucopus*		AF131926
113	*Reithrodontomys zacatecae*		AF176252
114	*Scotinomys teguina*		AF108705
115	*Tylomys* sp.	USNM 464887	This study

[a] Catalog numbers are given only for those taxa whose sequences were not retrieved from Genbank.

[b] For those sequences retrieved from Genbank, the corresponding accession numbers are given, otherwise sequence provenance is indicated. Asterisks indicate unpublished complete sequences kindly provided by James L. Patton and M. F. Smith (Museum of Vertebrate Zoology, Berkeley).

Appendix 2. Gazetteer of recording localities of the genus *Bibimys*. The first citation of each locality is given. "This paper" means the locality is first reported in this contribution. Specimens analyzed here are listed after the locality. Asterisks denote those specimens that were sequenced.

RECENT: ARGENTINA, *Province of Buenos Aires*: 1) Arroyo Talaveras, S 34º 04′ W 59º 04′ (Bianchini and Delupi, 1993). 2) Confluence Arroyo Las Piedras y Arroyo Las Cucarachas (Massoia, 1979). 3) Estación Experimental INTA Delta del Paraná, S 34º 09' W 58º 57′ (Massoia, 1979): CEM 5067, skull and skin (holotype of *B. torresi*); CEM 1886, skull and skin (allotype of *B. torresi*); CEM 5015, skull and skin (paratype of *B. torresi*); CEM s/n, 12 incomplete skulls, 12 right mandibles, 10 left mandibles from owl pellets; MACN 20337; skull, MMP-Ma 3620* and MMP-Ma 3705, skull and skin. 4) Ingeniero Rómulo Otamendi, S 34º 13′ W 58º 54′ (Pardiñas 1996). 5) San Fernando, S 34º 26′ W 58º 33′ (González 1997). *Province of Entre Ríos*: 6) Isla Ibicuy, S 33º 44′ W 59º 13′ (Massoia 1980a). *Province of Chaco*: 7) 7 km North of General Vedia, S 26º 53′ W 58º 36′ (this paper): CNP 757, 12 incomplete skulls from owl pellets. 8) Cancha Larga, S 27° 04′ W 58° 43′ (this paper): CNP 756*, skull and skeleton. 9) General Vedia, S 26º 56′ W 58º 40′ (this paper): CNP 758, 39 incomplete skulls, two right maxillas, one left maxilla, 11 right mandibles, 14 left mandibles from owl pellets. 10) Las Palmas, S 27º 04′ S W 58º 41′ (Shamel 1931): USNM 236239, skull and skin (holotype of *B. chacoensis*). 11) Paso Mono, Estancia San Carlos, S ~27º 05' W ~58º 37' (this paper): MMP-Ma 2502, CFA 0911; CFA 1580, skull and skin. *Province of Misiones*: 12) 4 km N Loreto, S 27º 19′ W 55º 32′ (this paper): CNP 759, four incomplete skulls from owl pellets. 13) 11 de Noviembre, S 27º 28′ W 55º 19′ (this paper): CNP 760, one right mandible from owl pellets. 14) Apóstoles, S 27º 55′ W 55º 46′ (Massoia et al. 1989a). 15) Arroyo Yabebyrí, S 27º 17′ W 55º 31′ (Massoia et al. 1989c): CEM without number, 10 incomplete skulls, 11 right mandibles from owl pellets. 16) Bonpland, S 27º 29′ W 55º 29′ (Massoia et al. 1989d). 17) Campo Ramón, S 27º 28′ W 55º 00′, (Massoia 1988). 18) Estación Experimental INTA Cuartel Río Victoria (Massoia 1980b). 19) Los Helechos, S 27º 33′ W 55º 03′ (Massoia et al. 1989b). 20) El Dorado, S 26º 24′ W 54º 35′ (this paper): CNP 761, one incomplete skull from owl pellets. 21) Teyú Cuaré, S 27º 11′ W 55º 39′ (Massoia et al. 1988). 22) Santa Inés, S 27º 34′ W 55º 49′ (this paper): CNP 762, four incomplete skulls, three right maxilla, three left maxilla, six right mandibles, five left mandibles from owl pellets. BRAZIL, *State of Minas Gerais:* 23) Lagoa Santa, S 19º 39′ W 43º 54′ (Winge 1887): MZD (Lund collection without number), incomplete skull and skin (lectotype of *Bibimys labiosus*). 24) Mata do Paraíso (Viçosa), S 20° 45′ W 42° 53′ (Paglia et al. 1995): MN 62062* and MN 62063*. PARAGUAY, 25) See Myers et al. (in prep.): GD 153*, specimen in fluid.

FOSSIL: ARGENTINA, *Province of Buenos Aires*: 26) Balneario Menta, S 38° 00′ W 57° 34', Late Holocene (Pardiñas 1999b): MLP 95-V-1-2, two left maxilla, two right

mandibles, five left mandibles. 27) Centinela del Mar, S 38º 27′ W 58º 14′, Late Holocene (Pardiñas 1995): MLP 91-IV-15-2, four right maxilla, four left maxilla, three right mandibles, three left mandibles; MLP 91-IV-15-2, three right maxilla, one right mandible, three left mandibles. 28) Constitución, S 37º 57′ W 57º 32′, Late Pleistocene (Pardiñas et al. 2004): MLP s/n, isolated m1. 29) La Norma archaeological site, S 34° 55' W 57° 46', Late Holocene (Pardiñas 1999b): MLP s/n, left mandible. 30) Tixi Cave archaeological site, S 37° 57' W 58° 02', Late Holocene (Pardiñas 1995): MLP 84-X-20-10, right mandible; MLP 84-X-20-11, right mandible; MLP 84-X-20-12, left maxilla. BRAZIL, *State of Minas Gerais*: 31) locality not specified, Late Pleistocene-Holocene (this paper): BMNH, Claussen collection without number, right mandible.

MISIDENTIFICATIONS:

1. One unnumbered specimen from an unespecified locality between Capitán Solari and Colonia (S ~26º 50′ W ~59º 37′, Province of Chaco, Argentina) referred to *Bibimys chacoensis* by Contreras (1984), was later identified as *Akodon azarae* (C. Galliari, *com. pers.*);
2. The specimen MLP 24-V-77-1 from Canal 9 (S ~36º 45′ W ~56º 45′, Province of Buenos Aires, Argentina) mentioned by Bianchini and Delupi (1993) as *Bibimys torresi* was later identified as *Akodon azarae* by Pardiñas (1996).