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Molecular Phylogenetics and Evolution 38 (2006) 558–564
MOLECULAR PHYLOGENETICS AND EVOLUTION
www.elsevier.com/locate/ympev

Short communication

On the Sigmodontinae radiation (Rodentia, Cricetidae): An appraisal of the phylogenetic position of *Rhagomys*

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Received 9 May 2005; revised 22 August 2005; accepted 22 August 2005
Available online 4 October 2005

1. Introduction

Cricetid rodents of the subfamily Sigmodontinae (sensu Reig, 1980) are the most diverse and complex group of New World mammals. Currently, living sigmodontines are thought to include 74 genera and 380 species (Musser and Carleton, 2005). Their diversity has challenged researchers studying their phylogenetic relationships and attempting to classify them. Classically, sigmodontine genera have been arranged into different groups, most of which have been formalized as tribes in zoological classifications. In the 1990s, phylogenetic approaches became widely used to delimit these groups (e.g., D'Elía, 2003; D'Elía et al., 2003; Engel et al., 1998; Smith and Patton, 1999; Steppan, 1995; Weksler, 2003), casting new light on the naturalness of groups and also on their limits and contents. These revisions prompted the recognition of a previously unnoted group (the "abrotrichines"), subsumed some major groups within others (e.g., Scapteromyini within Akodontini), and corroborated the distinction of others (e.g., Reithrodontini, Wiedomyini; D'Elía, 2003; Smith and Patton, 1999). However, despite focused analyses, several extant genera could not be assigned with certainty to any monophyletic group beyond Sigmodontinae. In formal classifications, these genera are generally considered as *incertae sedis*.

One of these enigmatic genera is the pentalophodont genus *Rhagomys* (Thomas, 1917). This genus was erected by Thomas, in 1917 to contain *Hesperomys rufescens* (Thomas, 1886) from southeastern Brazil (Pinheiro et al., 2004). In 2003 a second species, *R. longilingua*, was described from montane forests in southeastern Peru (Luna and Patterson, 2003), approximately 3100 km to the west of the known range of *R. rufescens*. *Rhagomys* is one of the most distinctive genera of the Sigmodontinae. Among its remarkable particularities is the presence of a nail on the hallux, a unique character state among New World cricetids. This feature and numerous others from the skull, dentition, and soft anatomy (see Luna and Patterson, 2003) have complicated the placement of *Rhagomys* in any supragenetic group of sigmodontines. Indeed, using cytochrome *b*, Percequillo et al. (2004) found that the phylogenetic position of *Rhagomys* within Sigmodontinae varies with different data analyses, reinforcing the uncertainty of its phylogenetic relationships.

The goal of this study was to assess the phylogenetic position of *Rhagomys* on the basis of a phylogenetic analysis of nucleotide sequences of a nuclear gene. In light of the newly obtained phylogeny, we offer taxonomic judgments on the tribe Thomasomyini and comments on the structure of the sigmodontine radiation.

2. Materials and methods

To assess the phylogenetic position of *Rhagomys* within the sigmodontine radiation, we sought to insure that sigmodontine diversity was represented as thoroughly as possible. As such, the dataset contains representatives of all sigmodontine tribes as well as several sigmodontine genera whose phylogenetic relationships are not clear. Besides *Rhagomys*, our dataset also includes the genus *Aepeomys* for the first time in a phylogenetic analysis based on DNA sequences. This study includes a

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1055-7903/$ - see front matter
doi:10.1016/j.ympev.2005.08.011

total of 39 sigmodontine specimens that represent 39 genera (Table 1).

Although sigmodontine monophyly is well corroborated (Catzeflis et al., 1993; Engel et al., 1998; Jansa and Weksler, 2004; Sarich, 1985; Steppan et al., 2004), its sister group is unidentified. Sigmodontinae forms part of a large cricetid clade containing other major branches of the muroid radiation (Jansa and Weksler, 2004; Steppan et al., 2004; see also

Table 1
List of specimens used in the phylogenetic analysis

	Taxon	Catalog number[a]	IRBP source[b]	Sequence length
Ingroup				
1	*Aepeomys lugens*	MNHN 4350	DQ003722*	1162
2	*Abrothrix olivaceus*	CNP 813	AY277421#	1181
3	*Akodon montensis*	UMMZ 174969	AY277426#	1181
4	*Amphinectomys savamis*	MV 970045	AY163579^	1181
5	*Bibimys chacoensis*	CNP 756	AY277435#	1078
6	*Blarinomys breviceps*	CIT 1391	AY277437#	1181
7	*Calomys callosus*	GD 421	AY277440#	1098
8	*Delomys sublineatus*	MVZ 183075	AF108687^	1143
9	*Eligmodontia typus*	MVZ 182681	AF108692^	1181
10	*Euneomys chinchilloides*	CNP 816	AY277446#	1133
11	*Geoxus valdivianus*	CNP 812	AY277448#	1181
12	*Handleyomys intectus*	ICN 16093	AY163584^	1181
13	*Holochilus chacarius*	GD 071	AY163586^	1181
14	*Irenomys tarsalis*	MVZ 155839	AY277450#	1181
15	*Juliomys pictipes*	MVZ 182079	AY277451#	1172
16	*Lundomys molitor*	MNHN 4292	AY163589^	1181
17	*Melanomys caliginosus*	MHNLS 7698	AY163590^	1154
18	*Microryzomys minutus*	MVZ 16666	AY163592^	1181
19	*Neacomys musseri*	AMNH 272676	AY163596^	1181
20	*Nectomys squamipes*	FMNH 141632	AY163598^	1181
21	*Nesoryzomys swarthi*	ASNH C10003	AY163601^	1181
22	*Notiomys edwardsii*	MVZ 163067	AY163602^	1181
23	*Oecomys bicolor*	AMNH 272674	AY163604^	1181
24	*Oligoryzomys nigripes*	CRB 1422	AY163612^	1181
25	*Oryzomys megacephalus*	GD 463	AY277465#	1181
26	*Oxymycterus nasutus*	MVZ 182701	AY277468#	1181
27	*Pseudoryzomys simplex*	GD 065	AY163633^	1181
28	*Phyllotis xanthopygus*	CNP 817	AY277471#	1181
29	*Reithrodon auritus*	MLP 26.VIII.01.17	AY277473#	1177
30	*Rhagomys longilingua*	FMNH 175218	DQ003723*	1157
31	*Rheomys raptor*	KU 159017	AY163635^	1181
32	*Rhipidomys macconnelli*	MVZ 160082	AY277474#	1166
33	*Scapteromys aquaticus*	UMMZ 174991	AY277477#	1181
34	*Scolomys ucayalensis*	AMNH 272721	AY163638^	1181
35	*Sigmodon hispidus*	NK 27055	AY277479#	1178
36	*Sigmodontomys alfari*	USNM 449895	AY163641^	1181
37	*Thomasomys aureus*	MVZ 170076	AY277483#	1181
38	*Wiedomys pyrrhorhinus*	MVZ 197567	AY277485#	1179
39	*Zygodontomys brevicauda*	AMNH 257321	AY163645^	1181
Outgroup				
40	*Arvicola terrestris*	MVZ 155884	AY277407#	1181
41	*Cricetus cricetus*	MVZ 155880	AY277410#	1181
42	*Neotoma albigula*	MVZ 147667	AY277411#	1181
43	*Peromyscus truei*	MVZ 157329	AY277413#	1171
44	*Scotinomys xerampelinus*	MVZ 192158	AY277416#	1181
45	*Tylomys nudicaudatus*	ROM 103590	AY163643^	1181

Catalog number and the source of IRBP sequences of specimen are indicated.

[a] The vouchers of the specimens sequenced in this study are, or will be, catalogued in the following museum collections: Already catalogued: Argentina: CNP, Centro Nacional Patagónico; MLP, Museo de La Plata, Universidad Nacional de la Plata. United States of America: FMNH, Field Museum of Natural History; NK, Museum of Southwestern Biology, University of New Mexico; MVZ, Museum of Vertebrate Zoology, University of California at Berkeley; UMMZ, The University of Michigan Museum of Zoology. Uruguay: MNHN, Museo Nacional de Historia Natural. To be catalogued: Brazil: CIT (Laboratório de Citogenética de Vertebrados, Instituto de Biociências, Universidade de São Paulo), Museu de Zoologia da Universidade de São Paulo. Uruguay: GD (collected by Guillermo D'Elía), Facultad de Ciencias, Universidad de la República.

[b] Numbers refer to GenBank accession numbers. The source of the IRBP sequences used is the following: *, complete sequences generated in this study. #, partial sequences (ca. 750) taken from D'Elía (2003) and completed in this study. ^, complete sequences taken from Weksler (2003).

D'Elía, 2000). Currently, the relationships among those groups are not clear. Therefore, to root the sigmodontine phylogeny, we have included as outgroups representatives of each of the other primary lineages that comprise the cricetid clade: arvicolines (*Arvicola*), cricetines (*Cricetus*), baiomyines (*Scotinomys*), neotomines (*Neotoma*), peromyscines (*Peromyscus*), and tylomyines (*Tylomys*).

A 1181bp fragment of the first exon of the nuclear gene interphotoreceptor retinoid binding protein (hereafter IRBP) was used as evidence for the phylogenetic analyses. For some specimens a shorter fragment was used. Specimens included in the phylogenetic analysis, and source and length of their sequences are listed in Table 1. IRBP sequences acquired here were amplified in one or two fragments using the primers A1–F1 and E1–D and a "touchdown" protocol reported by Jansa and Voss (2000). Negative controls were included in all experiments. Purified products were sequenced in both directions with the amplification primers and dye-labeled nucleotides (Big Dye, Applied Biosystems). Sequencing reactions were run in an ABI 377 automated sequencer. In all cases, both heavy and light DNA strands were sequenced. Sequences of both strands were reconciled using Sequencer Navigator version 1.0.1 (Applied Biosystems). All sequences were deposited in GenBank (see Table 1).

Sequence alignment was done with Clustal X (Thompson et al., 1997), using the default values for all alignment parameters. A gap of 3 bp was inserted in the IRBP sequence of *Scolomys*. Percentage of observed sequence divergence was estimated with PAUP* (Swofford, 2000), ignoring those sites with missing data. Aligned sequences were subjected to maximum parsimony (MP; Farris, 1982) and maximum-likelihood (ML) analyses (Felsenstein, 1981). In the MP analysis, characters were treated as unordered and equally weighted. Gaps were treated as missing data. PAUP* (Swofford, 2000) was used to perform 500 replicates of heuristic searches with random addition of sequences and tree bisection–reconnection branch swapping. We performed 1000 parsimony jackknife (JK; Farris et al., 1996) replicates with five addition sequence replicates each and the deletion of one-third of the character data. Branches with <50% of support were allowed to collapse. Bremer support values (BS; Bremer, 1994) were computed for each node in PAUP* using command files written in TreeRot version 2 (Sorenson, 1999). A ML analysis was conducted in PAUP* (Swofford, 2000) with 20 replicates of heuristic searches with random addition of sequences, under the transversional model of substitution with equal base frequencies (TVMef+I+G) with the following parameters: percentage of invariable sites = 0.3328; gamma distribution shape parameter = 1.214. This model and its parameters were determined using Modeltest 3.5 (Posada and Crandall, 1998) by evaluating the likelihood of various substitution models optimized on a neighbor-joining tree (Saitou and Nei, 1987) calculated from Jukes and Cantor (1969) corrected distances. Jackknife support for nodes in the maximum-likelihood tree was evaluated for 100 replicates with one addition sequence replicate and the deletion of one-third of the character data.

3. Results

There are 468 variable sites in the IRPB dataset. The observed genetic distance between *Rhagomys* and other genera range from 2.2% (compared to *Thomasomys*) to 5.76% (*Rheomys*), while comparisons between all sigmodontine genera sampled range from 0.76% (*Melanomys–Sigmodontomys* comparison) to 7.28% (*Rheomys–Zygodontomys*).

The dataset has 247 parsimony-informative characters. Analysis of this dataset produced 1382 equally most-parsimonious cladograms. The trees are 945 steps in length, with an ensemble consistency index of 0.620 and a retention index of 0.598. The strict consensus tree, which is presented in Fig. 1, defines 29 nodes belonging to the sigmodontine clade. Support for these nodes is highly variable.

Sigmodontinae (Fig. 1, node K) appears to be well supported (JK 100%; BS = 18). The basal dichotomy within Sigmodontinae is a clade composed by *Sigmodon* and *Rheomys* on one hand and the remaining sigmodontines on the other. Both clades are well supported: JK 100%; BS = 7 and JK 99%; BS = 6, respectively. Relationships within the "sigmodontines excluding *Sigmodon–Rheomys*" clade are partially resolved, with the existence of four polytomies: three within the oryzomyine clade and the other involving seven sigmodontine lineages including the Oryzomyini clade. Except for the thomasomyines, all tribes for which more than one genus was included appear strongly supported (Fig. 1). *Rhagomys* forms part of the thomasomyine clade. It appears sister to *Thomasomys* (JK 76%; BS = 2). *Aepeomys* appears sister to the *Rhagomys–Thomasomys* clade (JK 54%; BS = 1). Finally, *Rhipidomys* is sister to the remaining thomasomyines (JK 65%; BS = 1). Five additional steps are needed to place *Rhagomys* sister to the oryzomyine clade.

In relation to the sigmodontines results of the ML analysis (tree score: $-\ln L = 7002.63357$; Fig. 2) corroborate the MP results. The only relationship recovered in the MP strict-consensus tree that is not corroborated by the ML analysis is that of *Oxymycterus* being sister of the remaining akodontines; the ML tree presents at the base of the akodontine clade a polytomy involving three akodontines lines, one of which is *Oxymycterus*. In spite of this, the ML tree is more resolved than the MP strict consensus tree. In it, the clade "all sigmodontines except *Sigmodon-Rheomys*" includes a polytomy of four lineages, not seven as in the MP strict consensus tree, and only one polytomy in the oryzomyine clade, not three as in the MP strict consensus tree. With regard to *Rhagomys* and Thomasomyini, ML corroborates the MP results; *Rhagomys* again appears sister to *Thomasomys* (JK 70%) in a larger clade that also include *Aepeomys* and *Rhipidomys* (JK 72%). Neither *Delomys* nor *Juliomys* are closely related to this clade.

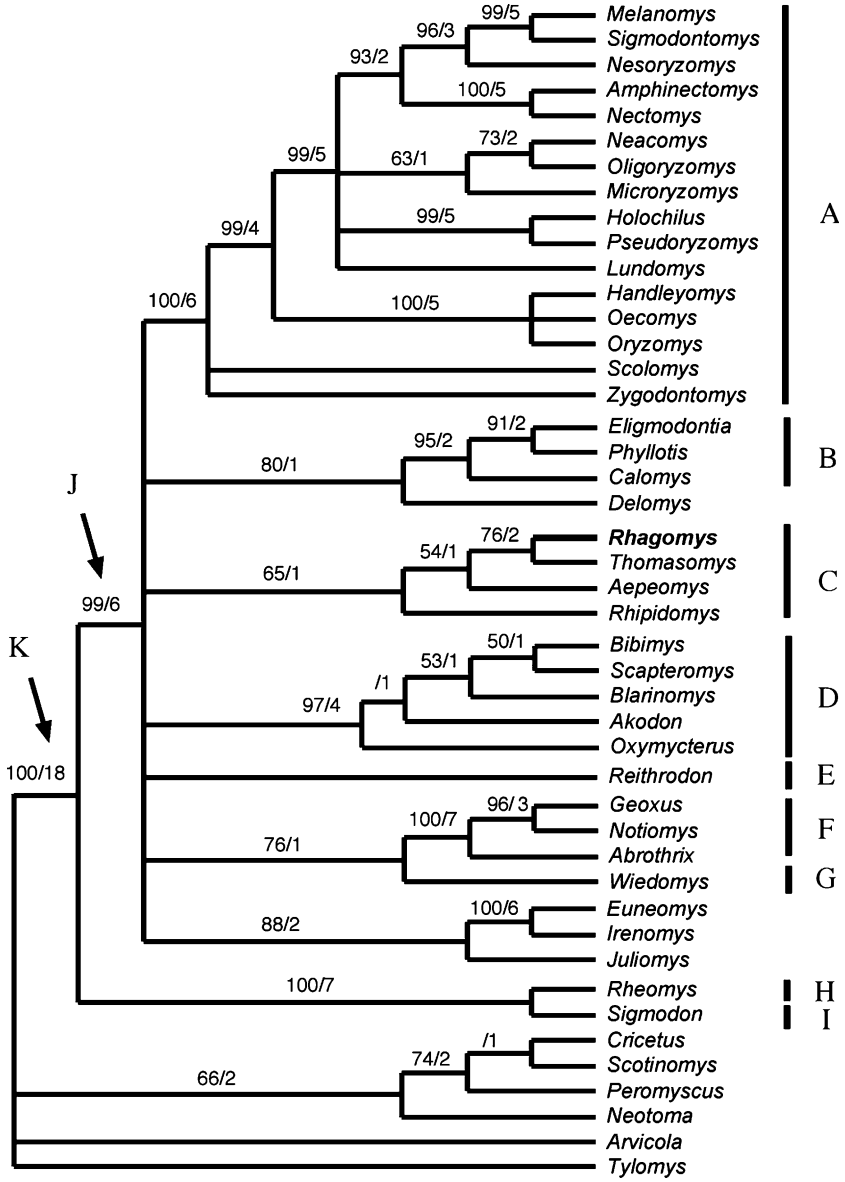

Fig. 1. Strict consensus tree of the 1382 most parsimonious trees (length 945, $CI = 0.620$, $RI = 0.598$) obtained in the maximum parsimony analysis of the IRBP gene sequences. Numbers above branches indicate parsimony jackknife (left of the diagonal) and Bremer support (right) values of the nodes to their right. Only jackknife values >50% are shown. A, Oryzomyini; B, Phyllotini; C, Thomasomyini; D, Akodontini; E, Reithrodontini; F, abrotrichine group; G, Wiedomyini; H, Ichthyomyini; I, Sigmodontini; J, Oryzomyalia; K, Sigmodontinae.

4. Discussion

Currently, *Rhagomys* contains two species, *R. rufescens* and *R. longilingua*, distributed on opposite sides of South America. A phylogenetic analysis based on 104 morphological characters (Luna, 2002) showed that the two *Rhagomys* species form a well supported an easily diagnosable clade. This result is corroborated by preliminary analysis based on cytochrome *b* DNA sequences (Luna and Patterson, unp. data). Further studies, including additional field surveys, are needed to understand *Rhagomys*' distribution and whether the vast geographic gaps in its current distribution are real.

4.1. The phylogenetic position of Rhagomys

Until now, the position of *Rhagomys* within the subfamily Sigmodontinae has remained unclear. Thomas (1917) considered it as part of his "*Oryzomys–Oecomys* series" (the basis of current Oryzomyini), although he noted its similarities with the "*Rhipidomys–Thomasomys* series" (Thomasomyini). Later authors (e.g., Reig, 1984; Smith and Patton, 1999) listed *Rhagomys* as a Sigmodontinae *incertae sedis*; a position followed in most taxonomic catalogues (Musser and Carleton, 2005; McKenna and Bell, 1997). Prior phylogenetic analyses of morphological and mitochondrial DNA characters

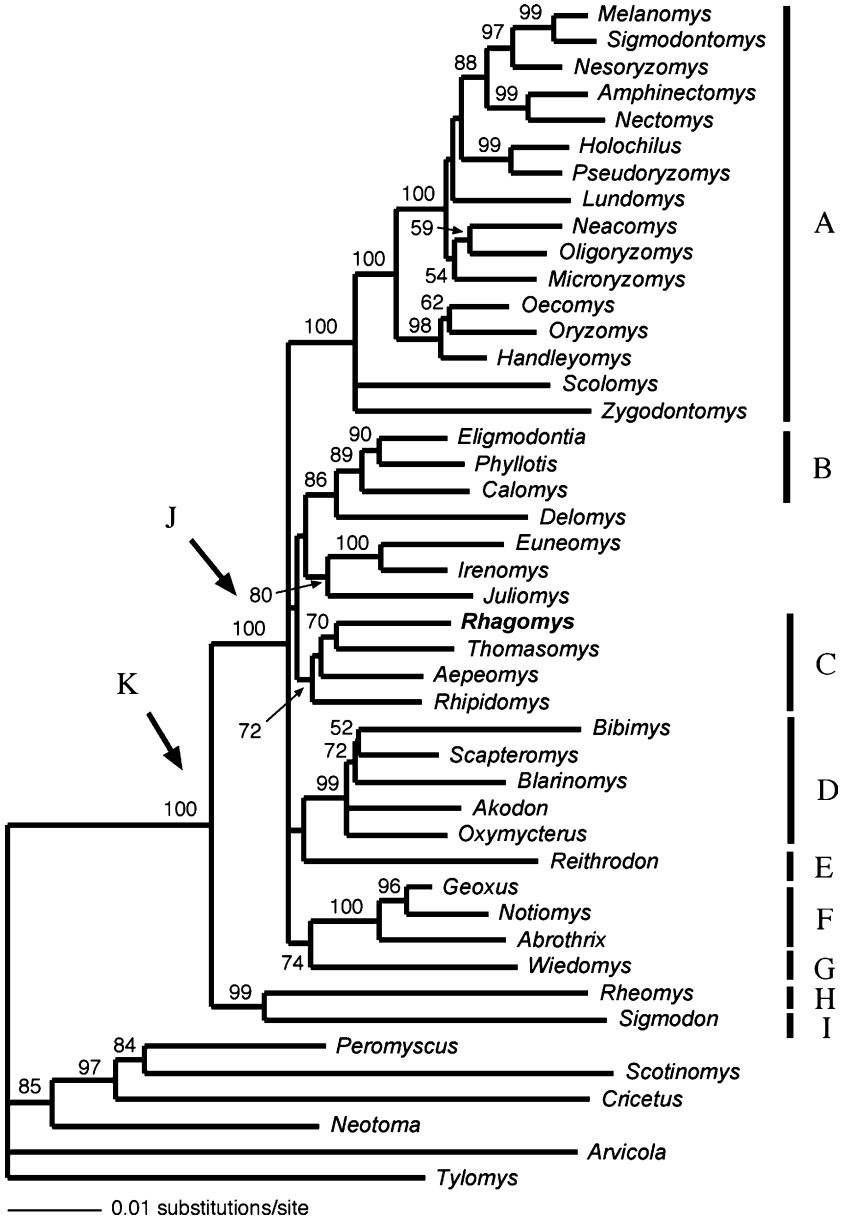

Fig. 2. Tree resulting from the maximum likelihood ($-\ln L = 7002.63357$) analysis of the IRBP gene sequences under the TVMef+I+G substitution model with the following parameters: percentage of invariant sites = 0.3328; gamma distribution shape parameter = 1.214. Numbers above branches indicate jackknife values of the nodes at their right. Only jackknife values >50% are shown. A, Oryzomyini; B, Phyllotini; C, Thomasomyini; D, Akodontini; E, Reithrodontini; F, abrotrichine group; G, Wiedomyini; H, Ichthyomyini; I, Sigmodontini; J, Oryzomyalia; K, Sigmodontinae.

(Luna, 2002 and Percequillo et al., 2004, respectively) failed to clarify the phylogenetic position of *Rhagomys*.

Accordingly, identifying *Rhagomys* as sister to *Thomasomys* (MP: JK 76%, BS = 2; ML: JK 70%) in a larger clade comprising the thomasomyines *Aepeomys* and *Rhipidomys* (MP: JK 65%, BS = 1; ML: 72%) is striking. This clade corresponds to the tribe Thomasomyini (sensu Smith and Patton, 1999), which must now be expanded to include *Rhagomys*. Recently, Pacheco (2003) proposed a morphological diagnosis of Thomasomyini based on eight characters. However, *Rhagomys longilingua* lacks three of these (premaxillae extending anterior to nasals but posterior to the zygomatic notch; palate short; and mesopterygoid fossa posteriorly convergent), two others are indeterminate in that species, and only two are unambiguously present (triangular paragterygoid fossa and M1 with an anteromedial flexus). Clearly, additional character analysis is needed to diagnose the newly identified group.

The taxonomic history of the thomasomyine group is complex, with several episodes of expansions and restrictions in its contents (see account in Pacheco, 2003). Formal phylogenetic analyses provide two main distinctive and alternative schemes on the nature of Thomasomyini. In a taxon-dense phylogenetic analysis based on morphological characters (Pacheco, 2003), all traditional thomasomyine taxa (including *Abrawayaomys*, *Delomys*, *Juliomys*,

Phaenomys, *Rhagomys*, and *Wilfredomys*) plus *Wiedomys* formed a natural group (Wiedomyini regarded as a synonym of Thomasomyini). However, most molecular analyses (e.g., Smith and Patton, 1999) recover a restrictive thomasomyine clade formed by the predominantly Andean genera *Chilomys*, *Rhipidomys*, and *Thomasomys*; whereas the Atlantic Forest endemics *Delomys* and *Juliomys* remain distinct from this clade. (It should be noted that no DNA-based phylogenetic analysis has included representatives of *Abrawayaomys, Phaenomys*, nor *Wilfredomys*, three genera from southeastern South America traditionally considered thomasomyines.)

Our analysis corroborates all but one (see below) of the other molecular-based phylogenetic analyses (D'Elía et al., 2003; Smith and Patton, 1999; Weksler, 2003). We recovered a restrictive thomasomyine group, shown here to include *Rhagomys* and *Aepeomys*, comprised of forms with distributions that include the Andean Cordilleras. We also found that the Atlantic Forest endemics *Delomys* and *Juliomys* were not closely related to that group or to each other. Five additional steps are needed to recover a clade formed by all traditionally recognized "thomasomyine" genera, while in trees three and four steps longer than the most parsimonious trees, *Delomys* and *Juliomys*, respectively, appear sister to the Thomasomyini sensu stricto. To recover a thomasomyine clade that includes all traditional thomasomyine plus *Wiedomys* requires six additional steps. However, *Abrawayaomys*, *Phaneomys*, and *Wilfredomys* have not yet been studied with molecular data. Remarkably, in a combined analysis of mitochondrial and IRBP sequences, which included *Thomasomys* and *Rhipidomys*, D'Elía (2003) failed to recover a monophyletic Thomasomyini. As that study and the present one differ in taxonomic coverage, it is not clear if the mentioned topological dissimilarity is due to the differences in the gene sequences analyzed (i.e., cytochrome *b* plus IRPB vs. IRPB) and/or the taxa included.

4.2. The structure of the sigmodontine radiation

Sigmodontinae appears strongly supported (MP: JK 100%, BS = 18; ML: JK 100%). As in Weksler (2003), this clade includes two groups: a clade composed by *Sigmodon* (tribe Sigmodontini) and *Rheomys* (Ichthyomyini) on one hand (MP: JK 100%, BS = 7; ML: JK 99%) and all other sigmodontines on the other. This latter clade, recently named Oryzomyalia by Steppan et al. (2004, p. 547), is strongly supported (MP: JK 99%, BS = 6; ML: JK 100%). The fact that Sigmodontini and Ichthyomyini constitute the sister group of the remaining sigmodontines has direct implications to understand sigmodontine historical biogeography. Both are distributed in South, Central, and North America. Therefore, a taxon-dense phylogenetic analysis including all species of both tribes is needed to optimize the geographic location of the sigmodontine common ancestor, which is one of the main points of the debate in sigmodontine historical biogeography (reviewed in D'Elía, 2000 and Pardiñas et al., 2002).

Within Oryzomyalia, all sigmodontine tribes (sensu Smith and Patton, 1999) are recovered as monophyletic. All tribes except Thomasomyini as used here are strongly supported. However, relationships among tribes are mostly unresolved. According to the classification of Smith and Patton (1999), in the MP analysis only one clade containing more than one tribe was recovered within Oryzomyalia: Wiedomyini appears sister to the abrotrichine group (MP: JK 76%, BS = 1; ML: JK 74%). Next, all remaining tribes form a large polytomy at the base of Oryzomyalia. In the ML tree (Fig. 2) relationships among tribes appear better resolved, but none of the additional groupings are well supported (<50% jackknife support). Lack of resolution at the base of Oryzomyalia was also found in other phylogenetic analyses (mitochondrial: D'Elía et al., 2003; Smith and Patton, 1999; IRBP: Weksler, 2003; mitochondrial and IRBP: D'Elía, 2003; and growth hormone receptor, breast cancer gene 1, recombination activating gene 1, and the proto-oncogene c-myc: Steppan et al., 2004). A novel and well-supported (MP: JK 88%, BS = 2; ML: JK 80%) clade that reaches this large polytomy merits further scrutiny: Atlantic Forest endemic *Juliomys* and the Andean grooved-incisor genera *Euneomys* and *Irenomys*.

Lack of resolution at the base of Oryzomyalia may reflect this taxon's rapid radiation after its ancestor entered South America around 6 Mya (Steppan et al., 2004). Our results, based on a locus unlinked to those analyzed by Steppan et al. and from the mitochondrial genome, constitute yet another case where the relationships among Oryzomyalia basal lineages cannot be established. A corollary of the hypothesis of Steppan et al. is that the Oryzomyalia inhabiting Central and North America (e.g., selected species of *Oryzomys*, *Oligoryzomys, Melanomys*, and *Sigmodontomys*) represent re-invasions of that continent from South America. Phylogenetic analyses of each genus should show that basal taxa originated in South America. Clearly, integration of fossil evidence with phylogenetic analyses can shed important light on these issues, including minimum dates of divergence for selected nodes.

In the near future, it should be possible to combine, in a single analysis, morphological evidence with that from various unlinked genes. Such a study may at last produce a well-corroborated sigmodontine topology. Now, after extensive and detailed assessments of sigmodontine morphological variation (e.g., Carleton, 1980; Voss, 1988; Steppan, 1995; Luna, 2002; Pacheco, 2003), this goal seems feasible. This is a required foundation for delimiting and diagnosing supraspecific taxa in a cladistic manner (see Steppan, 1995) and for rigorously testing evolutionary hypotheses concerning Sigmodontinae.

Acknowledgment

Laboratory analyses were partially supported by the Barbara E. Brown Mammal Research Fund of Field Museum. The specimens of *Rhagomys longilingua* were collected with support from the National Science Foundation

(DEB 9870191), the Marshall Field Fund of the Field Museum of Natural History, and a gift from George and Catherine Jacobus, with the help of Sergio Solari, and assistance of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos. Two anonymous reviewers made helpful comments on an earlier version of this paper.

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