PHYLOGENETIC RELATIONSHIPS AND HISTORICAL BIOGEOGRAPHY OF THE GENUS *AKODON* (RODENTIA: CRICETIDAE)

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PHYLOGENETIC RELATIONSHIPS AND

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AKODON (RODENTIA: CRICETIDAE)

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CHAPTER I

INTRODUCTION TO A STUDY OF *AKODON* PHYLOGENETICS AND BIOGEOGRAPHY

Despite comprising only 12% of the Earth's landmass, South America supports nearly one quarter of all extant species of mammals (Wilson and Reeder 2005). The rich biological history of South America can be traced back to its beginnings as part of the supercontinent Pangaea, through a period as part of Gondwana, followed by an isolation period as an island continent that lasted for more than 100 million years. Following the formation of the Panamanian Land Bridge about 2.5 million years ago, South America reconnected with North America to form the continent as it is known today (Lawver and Gahagan 2003; Marshall et al. 1979; Stehli and Webb 1995; Webb 1991). Formation of the Panamanian Land Bridge facilitated the reciprocal migration of North and South American mammalian fauna with groups such as armadillos (Family Dasypodidae), porcupines (Family Erethizontidae), and opossums (Family Didelphidae) moving north while bears (Family Ursidae) and camels (Family Camelidae) among others, moved south.

The most successful colonizers of South America are members of the subfamily Sigmodontinae (Musser and Carleton 2005; Smith and Patton 1999). These early

immigrants from North America diversified into approximately 70 extant genera and more than 350 extant species present in South America today. Taxa included within the subfamily are organized into seven or eight tribes and a number of unique lineages. Taxa that make up these unique lineages are considered *incertae sedis*, or of uncertain tribal affinity (Musser and Carleton 2005; Reig 1980; Smith and Patton 1999, 2007). Sigmodontinae exhibits high diversity at multiple levels (morphological, genetic, and ecological) and has colonized the entire South American continent with Sigmodontine rodents present at all elevations and in all ranges of climates and habitats (D'Elía 2003; D'Elía et al 2003; Musser and Carleton 2005; Pardiñas et al. 2002).

The timing and location of the subfamily's apparent rapid diversification is at the key of a continuing debate. An "early-arrival" hypothesis supports the overwater dispersal of the ancestral sigmodontine during the Miocene, possibly from the Old World (Hershkovitz 1966, 1972; Reig 1980, 1984). A "late-arrival" hypothesis suggests that most, if not all, of the genera differentiated in North and Central America prior to arrival in South America during the late Pliocene and early Pleistocene (Baskin 1978; Patterson and Pascual 1972). An alternative "late-arrival" hypothesis proposes the rapid radiation of forms after the sigmodontine ancestor crossed the Panamanian Land Bridge (Simpson 1950, 1969). Fossil evidence collected from the Monte Hermosa formation in the coastal region of central Argentina shows the earliest sigmodontine fossils (i.e. *Auliscomys formosus*) present in their derived forms some 4–5 million years before present (mybp), which seems to be more consistent with a "late-arrival" hypothesis (Pardiñas and Tonni 1998; Reig 1978). Molecular sequence data supports the monophyly of Sigmodontinae (Smith and Patton 1999) and the monophyly of an endemic New World clade

(Sigmodontinae, Neotomyinae, and Tylomyinae; Steppan et al. 2004) providing weak support for a late-arrival hypothesis and ruling out direct descent from the Old World but giving no insight into the location of the radiation of sigmodontines (Pardiñas et al. 2002). Unfortunately fossil sigmodontines are relatively uncommon in the fossil record from South America (Pardiñas et al. 2002). The disparity between the diversity of extant sigmodontines and fossil forms is suspected to be an artifact of this fragmented fossil record, and a more accurate knowledge of the diversity of fossil sigmodontines will provide the information necessary to better evaluate the location of radiations within the group (Pardiñas et al. 2002).

Even since the immigration of sigmodontine rodents into South America, the continent has undergone dramatic geologic and climatic changes (Ortiz-Jaurequizar and Cladera 2006). With events such as the uplift of the Andes, fragmentation of habitats, and the creation of refugia by the expansion and receding of tropical rainforests and Antarctic glaciers, rapid speciation has continued resulting in the diversity of extant forms (Ortiz-Jaureguizar and Cladera 2006; Veblen et al. 2007; Vuilleumier 1971).

To better understand evolutionary and biogeographic questions that have been raised regarding the colonization and radiation of sigmodontine rodents in South America, phylogenetic relationships among and within each of the recognized tribes must be resolved. Of these tribes, Akodontini is the second largest, most widely distributed, and most taxonomically frustrating. The concept of an akodontine tribe is traced to Thomas (1916, 1918) who recognized morphological resemblances between *Akodon* and its allies (*Abrothrix*, *Chroeomys*, *Deltamys*, *Hypsimys*, *Necromys*, *Thalpomys*, and *Thaptomys*). First use of the term Akodontini to refer to the akodont group was by

Vorontzov (1959 cited in Reig 1987). As many as 22 genera have been included within the tribe Akodontini (D'Elía et al. 2003; McKenna and Bell 1997; Reig 1986; Smith and Patton 1999). Recently, a number of molecular studies beginning in the early 1990s (D'Elia 2003; D'Elia et al. 2003; Patton and Smith 1992a, 1992b, Smith and Patton 1991, 1993, 1999, 2007), along with morphologic (e.g. Hershkovitz 1990a, 1990b, 1998; Myers 1989; Myers and Patton 1989a, 1989b; Myers et al. 1990), cytogenetic (e.g. Barquez et al. 1980; Blaustein et al. 1992; Fagundes et al. 1998; Geise et al. 1998, 2001; Liascovich 1991; Sbalquiero and Nascimento 1996; Silva and Yonenaga-Yassuda 1998; Spotorno 1987) and allozymic data (e.g. Apfelbaum and Reig 1989; Barrantes et al. 1993; Patton et al. 1989; Rieger et al. 1995; Spotorno 1987), have greatly advanced our understanding of the Tribe Akodontini. These studies helped resolve higher-level taxonomic relationships, excluded taxa historically placed within Akodontini, established species limits, defined sister-taxa at multiple taxonomic levels, and in nearly all of the studies, the taxonomic limits of the tribe were reconsidered or redefined.

Several studies found the traditionally defined akodontine tribe to be polyphyletic (Smith and Patton 1993, 1999). Six genera (*Abrothrix*, *Chelemys*, *Chroeomys*, *Geoxus*, *Notiomys*, and *Pearsonomys*) formed a well supported Andean clade that was not sister to the rest of Akodontini. This clade, the tribe Abrothrochini, is linked by mitochondrial DNA and protein electrophoretic data, and members also share a common karyotype, male bacular morphology, and ectoparasites (D'Elía et al. 2007; Smith and Patton 1993, 1999).

The redefined Akodontini tribe includes at least 14 genera and more than 70 species making it the second most diverse sigmodontine tribe behind Oryzomyini

(Musser and Carleton 2005; Smith and Patton 1993, 1999). Within the Tribe Akodontini, perhaps the most taxonomically challenging and most crucial to understanding the phylogeny of Akodontini is the genus *Akodon*. Taxonomic changes to the tribe have elevated the *Akodon* subgenera *Deltamys*, *Thalpomys*, and *Thaptomys* to generic status. Even with such revisionary changes, *Akodon* retains more than one half of all recognized akodontine species and has been described as standing "at the nexus of a host of specific- and generic-level taxonomic problems" (Musser and Carleton 2005).

The genus *Akodon*, collectively known as South American grass mice, occurs from northern Venezuela to southern Argentina extending east of the Andes to the Atlantic Ocean and south of the Amazon lowlands to just north of Tierra del Fuego and extends northward in a band along the northern Andes and is absent from the Amazon lowlands and west of the Andes (Fig. 1.1). It is among the most speciose groups of South American rodents, second only to the genus *Ctenomys* (Family Ctenomyidae). Species of *Akodon* are known to inhabit a variety of habitats from subtropical and tropical moist forest to the altiplano and deserts (Braun et al. 2008; Jayat et al. 2010; Musser and Carleton 2005; Myers 1989; Myers and Patton 1989b; Myers et al. 1990; Smith and Patton 1992a).

Akodon (Meyen 1833) contains approximately 65 named forms organized into 46 extant species. Historically, species limits have been unstable and ambiguous with a number of systematic revisions increasing or decreasing the number of recognized species, subspecies, and supraspecific groups (see Cabrera 1961; Ellerman 1941; Honacki et al. 1982; Musser and Carleton 2005; Reig 1986; Smith and Patton 1993, 1999; Tate, 1932). The 46 extant species are currently organized into four species groups: an *aerosus*

group, a *boliviensis* group, a *cursor* group, and a *varius* group (Table 1.1). The *boliviensis* group also includes a fifth previously recognized species group, the *fumeus* group (Myers and Patton 1989a; Smith and Patton 2007). Additionally, a number of ambiguous lineages remain unassigned to any of the currently recognized species groups and are referred to as *incertae sedis* lineages. The number of currently recognized species remains dynamic with the continuation of new species descriptions as taxonomists and systematists attempt to tease apart the relationships within the genus (Braun et al. 2000, 2008, 2010; Christoff et al. 2000; Diaz et al. 1999; González et al. 1998; Jayat et al. 2010; Pardiñas et al. 2005).

Although previous studies have attempted to resolve the relationships within the genus, relatively unresolved phylogenies were obtained, especially above the species level. As most of these studies were focused on higher taxonomic level relationships, they were limited in the number of *Akodon* species included. Additionally previous studies of *Akodon* have used only a single molecular marker.

The objective of this study was to obtain a well-resolved phylogeny for the genus *Akodon* based upon dense taxonomic sampling using multiple genetic markers. By obtaining a well-resolved phylogeny, the validity and monophyly of currently and previously recognized species, subspecies, and species groupings can be assessed and the biogeographic relationships of the genus can be evaluated.

LITERATURE CITED

Apfelbaum, L. I., and O. A. Reig. 1989. Allozyme genetic distances and evolutionary relationships in species of akodontine rodents (Cricetidae: Sigmodontinae). Biological Journal of the Linnean Society 38:257–280.

Barquez, R. M., D. F. Williams, M. A. Mares, and H. H. Genoways. 1980. Karyology and morphometrics of three species of *Akodon* (Mammalia, Muridae) from northwestern Argentina. Annals of Carnegie Museum 49:379–403.

Barrantes, G. E., M. O. Ortells, and O. A. Reig. 1993. New studies on allozyme genetic distance and variability in akodontine rodents (Cricetidae) and their systematic implications. Biological Journal of the Linnean Society 48:283–298.

Baskin, J. A. 1978. *Bensonomys*, *Calomys*, and the origin of the phyllotine group of Neotropical cricetines (Rodentia, Cricetidae). Journal of Mammalogy 59:125–135.

Blaustein, S. A., R. C. Liascovich, L. I. Apfelbaum, L. Daleffe, R. M. Barquez, and O. A. Reig. 1992. Correlates of systematic differentiation between two closely related allopatric populations of the *Akodon boliviensis* group from NW Argentina (Rodentia: Cricetidae). Zeithschrift für Säugetierkunde 57:1–13.

Braun, J. K., M. A. Mares, and R. A. Ojeda. 2000. A new species of grass mouse, genus *Akodon* (Muridae: Sigmodontinae), from Mendoza Province, Argentina. Zeitschrift für Säugetierkunde 65:216–225.

Braun, J. K., B. S. Coyner, M. A. Mares, and R. A. Van Den Bussche. 2008. Phylogenetic relationships of South American grass mice of the *Akodon varius*

group (Rodentia, Cricetidae, Sigmodontinae) in South America. Journal of Mammalogy 89:768–777.

Braun, J. K., M. A. Mares, B. S. Coyner, and R. A. Van Den Bussche. 2010. New species of *Akodon* (Rodentia, Cricetidae, Sigmodontinae) from central Argentina. Journal of Mammalogy 91:387–400.

Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. II. (Sirenia-Perissodactyla-Artiodactyla-Lagomorpha-Rodentia-Cetacea). Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Naturales 4:308–732.

Christoff, A. U., V. Gafundes, I. J. Sbalqueiro, M. S. Mattevi, and Y. Yonenaga-Yassuda. 2000. Description of a new species of *Akodon* (Rodentia: Sigmodontinae) from southern Brazil. Journal of Mammalogy 81:838–851.

D'Elía, G. 2003. Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307–323.

D'Elía, G., E. M. González, and U. F. J. Pardiñas. 2003. Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus *Deltamys*. Mammalian Biology 68:351–364.

D'Elía, G., U. F. J. Pardiñas, P. Teta, and J. L. Patton. 2007. Definition and diagnosis of a new tribe of Sigmodontine rodents (Cricetidae: Sigmodontinae), and a revised classification of the subfamily. Gayana 71:187–194.

Diaz, M. M., R. M. Barquez, J. K. Braun, and M. A. Mares. 1999. A new species of *Akodon* (Murinae, Sigmodontinae) from northwestern Argentina. Journal of Mammalogy 80:786–798.

Ellerman, J. R. 1941. The families and genera of living rodents. Vol. II. Family Muridae. British Museum (Natural History), London, 690 pp.

Fagundes, V., A. U. Christoff, and Y. Yonenaga-Yassuda. 1998. Extraordinary chromosomal polymorphism with 28 different karyotypes in the Neotropical species *Akodon cursor* (Muridae: Sigmodontinae), one of the smallest diploid number in rodents (2n=16, 15 and 14). Hereditas 129:263–274.

Geise, L., F. C. Canavez, and H. N. Seuánez. 1998. Comparative karyology in *Akodon* (Rodentia, Sigmodontinae) from southeastern Brazil. Journal of Heredity 89:158–163.

Geise, L., M. F. Smith, and J. L. Patton. 2001. Diversification in the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern South America: mitochondrial DNA sequence analysis. Journal of Mammalogy 82:92–101.

González, E. M., A. Langguth, and L. F. de Oliveira. 1998. A new species of *Akodon* from Uruguay and southern Brazil (Mammalia: Rodentia: Sigmodontinae). Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo 191:108.

Hershkovitz, P. 1990a. Mice of the *Akodon boliviensis* size class (Sigmodontinae, Cricetidae), with the description of two new species from Brazil. Fieldiana: Zoology 57:1–35.

Hershkovitz, P. 1990b. The Brazilian rodent genus *Thalpomys* (Sigmodontinae, Cricetidae) with a description of a new species. Journal of Natural History 24:777–783.

Hershkovitz, P. 1998. Report on some sigmodontine rodents collected in southeastern Brazil with descriptions of a new genus and six new species. Bonner Zoologische Beiträge 47:193–256.

Honacki, J. H., K. E. Kinman, and J. W. Koeppl (eds.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Jayat, J. P., P. E. Ortiz, J. Salazar-Bravo, U. F. J. Pardiñas, and G. D'Elía. 2010. The *Akodon boliviensis* species group (Rodentia: Cricetidae: Sigmodontinae) in Argentina: species limits and distribution, with the description of a new entity. Zootaxa 2409:1–61.

Lawver, L. A., and L. M. Gahagan. 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeography, Palaeoclimatology, Palaeoecology 198:11–37.

Liascovich, R. C. 1991. Cariosistemática y evolución cromosómica en cricétidos akodontinos (Rodentia, Muriodea). Ph. D. dissertation, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, 185 pp.

Marshall, L. G., R. F. Butler, R. E. Drake, G. G. Curtis, and R. H. Tedford. 1979. Calibration of the Great American Interchange. Science 204:272–279.

McKenna, M. C., and S. K. Bell. 1997. Classification of mammals above the species Level. Columbia University Press, New York.

Meyen, F. J. F. 1833. Beiträge zur Zoologie gesammelt auf einer Reise um die Erde Säugethiere. Nova Acta Academiae Caesareae Leopoldino-Carolinae 16(2):599.

Musser, G. G., and M. D. Carleton. 2005. Superfamily Muroidea. Pp. 894–1531, in Mammal species of the world: a taxonomic and geographic reference, Third Edition (D. E. Wilson and D. M. Reeder, eds.). The Johns Hopkins University Press, Baltimore, Maryland.

Myers, P. 1989. A preliminary revision of the *varius* group of *Akodon* (*A. dayi*, *dolores*, *molinae*, *neocenus*, *simulator*, *toba*, and *varius*), Pp. 5–54, in Advances in Neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). The Sandhill Crane Press, Inc., Gainesville, Florida, 614 pp.

Myers, P., and J. L. Patton. 1989a. *Akodon* of Peru and Bolivia: revision of the *fumeus* group (Rodentia: Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 721:1–35.

Myers, P., and J. L. Patton. 1989b. A new species of *Akodon* from the cloud forests of eastern Cochabamba Department, Bolivia (Rodentia: Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 720:1–28.

Myers, P., J. L. Patton, and M. F. Smith. 1990. A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae) with emphasis on Perú and Bolivia. Miscellaneous Publications of the Museum of Zoology. University of Michigan 177:1–104.

Ortiz-Jaureguizar, E. and G. A. Cladera. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. Journal of Arid Environments 66:498–532.

Pardiñas, U. F. J., and E. P. Tonni. 1998. Procedencia estratigráfica y edad de los más antiguos muroideos (Mammalia, Rodentia) de América del Sur. Ameghiniana 35:473–475.

Pardiñas, U. F. J., G. D'Elía, S. Cirignoli, and P. Suarez. 2005. A new species of *Akodon* (Rodentia, Cricetidae) from the northern campos grasslands of Argentina. Journal of Mammalogy 86:462–474.

Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. Pp. 247–309 in Evolution, mammals, and southern continents (A. F. Keast, F. C. Erk, B. Glass, eds.). New York State University, Albany, New York.

Patton, J. L., and M. F. Smith. 1992a. Evolution and systematics of akodontine rodents (Muridae: Sigmodontinae) of Peru, with emphasis on the genus *Akodon*. Memorias del Museo de Historia Natural, U.N.M.S.M. (Lima) 21:83–103.

Patton, J. L., and M. F. Smith. 1992b. mtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. Evolution 46:174–183.

Patton, J. L., P. Myers, and M. F. Smith. 1989. Electromorphic variation in selected South American akodontine rodents (Muridae: Sigmodontinae), with comments on the systematic implications. Zeithschrift für Säugetierkunde 54:347–359.

Prevosti, F. J., and U. F. J. Pardiñas. 2009. Comment on "The Oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): Late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange" by D. H. Verzi and C. I. Montalvo [Palaeogeography, Palaeoclimatology, Palaeoecology 267 (2008) 284-291]. Palaeogeography, Palaeclimatology, Palaeoecology 280:543-547.Reig, O. A. 1978. Roedores cricétidos del Plioceno Superior de la Provincia

de Buenos Aires. Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" 2:164–190.

Reig, O. A. 1980. A new fossil genus of South American cricetid rodents allied to *Wiedomys*, with an assessment of the Sigmodontinae. Journal of Zoology, London 192:257–281.

Reig, O. A. 1984. Distribução geográfica e historia evolutiva dos roedores muroideos sulamericanos (Cricetidae: Sigmodontinae). Revista Brasileira de Genética 7:333–365.

Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404–440, in High altitude tropical biogeography (F. Vuilleumier and M. Monasterio, eds.). Oxford University Press, New York, 649 pp.

Reig, O. A. 1987. An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Sigmodontinae). Pp. 347–401, in Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana, Zoology 39:1–506.

Rieger, T. T., A. Langguth, and T. A. Waimer. 1995. Allozymic characterization and evolutionary relationships in the Brazilian *Akodon cursor* species group (Rodentia – Cricetidae). Biochemical Genetics 33:283–295.

Sbalquiero, I. F., and A. P. Nascimento. 1996. Occurrence of *Akodon cursor* (Rodentia, Cricetidae) with 14, 15, 16 chromosome cytotypes in the same geographic area in southern Brazil. Revista Brasileira de Genética 19:565–569.

Silva, M. J. de J, and Y. Yonenaga-Yassuda. 1998. Karyotype and chromosomal polymorphism of an undescribed *Akodon* from central Brazil, a species with the lowest diploid chromosome number in rodents. Cytogenetics and Cell Genetics 81:46–50.

Simpson, G. G. 1950. History of the fauna of Latin America. American Scientist 38:361–389.

Simpson, G. G. 1969. South American mammals. Pp. 879–909, in Biogeography and ecology of South America (E. J. Fittkau et al., eds.). The Hague, W. Junk.

Smith, M. F., and J. L. Patton. 1991. Variation in mitochondrial cytochrome b sequence in natural populations of South American akodontine rodents (Muridae: Sigmodontinae). Molecular Biology and Evolution 8:85–103.

Smith, M. F., and J. L. Patton. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149–177.

Smith, M. F., and J. L. Patton. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome b. Journal of Mammalian Evolution 6:89–128.

Smith, M. F., and J. L. Patton. 2007. Molecular phylogenetics and diversification of South American grass mice, genus *Akodon*. Pp. 827-858 in The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson (D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1-981.

Spotorno, A. 1987. Systematics and evolutionary relationships of Andean phyllotine and akodontine rodents. Ph. D. dissertation, University of California, Berkeley.

Stehli, F. G., and S. D. Webb, eds. 1985. The Great American Biotic Interchange. Plenum, New York City, New York.

Tate, G. H. H. 1932. The taxonomic history of the South and Central American akodont genera: *Thalpomys*, *Deltamys*, *Thaptomys*, *Hypsimys*, *Bolomys*, *Chroeomys*, *Abrothrix*, *Scotinomys*, *Akodon*, (*Chalcomys* and *Akodon*), *Microxus*, *Podosymys*, *Lenoxus*, *Oxymycterus*, *Notiomys*, and *Blarinomys*. American Museum Novitates 582:1–32.

Thomas, O. 1916. The grouping of the South American Muridae commonly referred to *Akodon*. Annals and Magazine of Natural History ser. 8, 17:336–340.

Thomas, O. 1918. On small mammals from Salta and Jujuy collected by Mr. E. Budin. Annals and Magazine of Natural History ser. 9, 1s:186–193.

Veblen, T. T., K. R. Young, and A. R. Orme. 2007. The Physical Geography of South America. Oxford University Press, Oxford, England.

Vorontzov, N. N. 1959. Sistema khomiakov (Cricetinae) morovoi fauny I ikh filogeneticheskie sviazi. Biuletin Moskovskogo Obshtschestva Ispitately Prirody, Otdel Biologia 44:134–137.

Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173:771–780.

Webb, S. D. 1991. Ecogeography of the Great American interchange. Paleobiology 17:266–280.

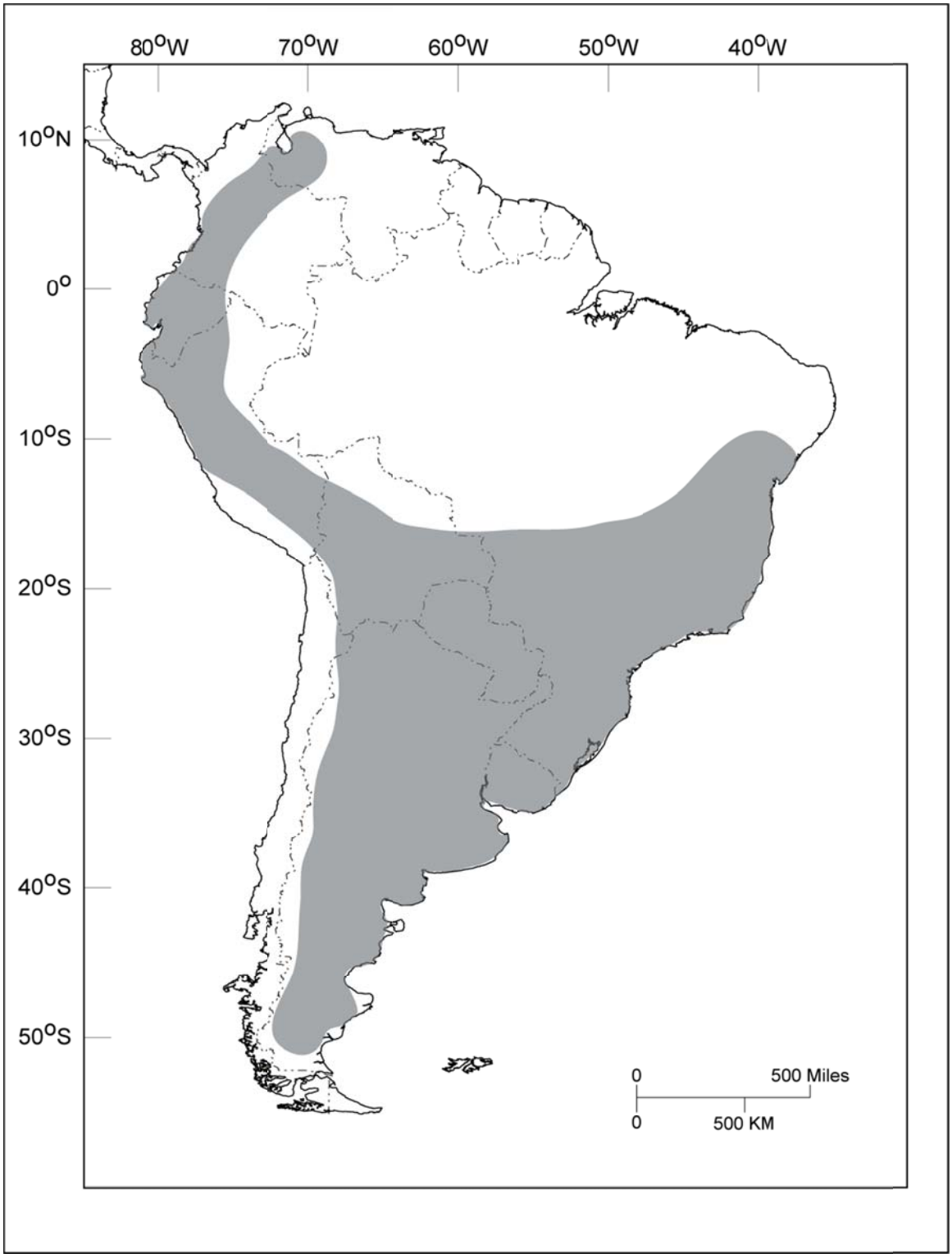
Wilson, D. E., and D. M. Reeder. 2005. Mammal species of the world: a taxonomic and geographic reference (3rd ed). John Hopkins University Press, Baltimore, Maryland.

TABLE 1.1.—Species of *Akodon* divided into the four species groups (Braun et al. 2008; Musser and Carleton 2005; Myers 1989; Myers et al. 1989; Rieger et al. 1995; Smith and Patton 1992a, 2007) and taxa considered *incertae sedis*. Taxa marked with astericks were unavailable for inclusion in this study.

A. aerosus group	*A. boliviensis* group	*A. cursor* group	*A. varius* group	*Incertae sedis*
A. aerosus	*A. aliquantulus**	*A. cursor*	*A. dayi*	*A. azarae*
A. affinis	*A. boliviensis*	*A. montensis*	*A. dolores*	*A. bogotensis**
A. albiventer	*A. fumeus*	*A. mystax*	*A. glaucinus*	*A. latebricola**
A. budini	*A. juninensis*	*A. paranaensis*	*A. iniscatus*	*A. lindberghi*
A. mollis	*A. kofordi*	*A. reigi*	*A. molinae**	*A. mimus*
A. orophilus	*A. leucolimnaeus**	*A. sanctipaulensis**	*A. neocenus**	*A. philipmyersi*
A. siberiae	*A. lutescens*		*A. oenos**	*A. serrensis*
*A. surdus**	*A. pervalens**		*A. simulator*	
A. torques	*A. polopi**		*A. tartareus*	
	A. spegazzinii		*A. toba*	
	A. subfuscus		*A. varius*	
	A. sylvanus			
	A. viridescens			

FIGURE LEGENDS

FIG. 1.1.— Distribution (approximate; from Braun et al. 2008; Jayat et al. 2010; Musser and Carleton 2005; Myers 1989; Myers and Patton 1989b; Myers et al. 1990; Smith and Patton 1992a, 1993) of the genus *Akodon*.


80°W
70°W
60°W
50°W
40°W
10°N
0°
10°S
20°S
30°S
40°S
50°S
0
500 Miles
0
500 KM

CHAPTER II

PHYLOGENETIC RELATIONSHIPS OF SOUTH AMERICAN GRASS MICE OF THE GENUS *AKODON* (RODENTIA, CRICETIDAE) BASED UPON THE CYTOCHROME B GENE

ABSTRACT – The genus *Akodon* consists of 46 extant named species that are often divided into four species groups. Taxa corresponding to 34 species were obtained for inclusion in this study. The entire cytochrome b gene for 189 individuals was sequenced and analyzed under maximum parsimony, maximum likelihood, and Bayesian phylogenetics. Results revealed a monophyletic *Akodon* clade with *A. serrensis* being most basal and diverged from the remaining *Akodon* taxa. Although four of the included species were paraphyletic and none of the recognized species groups were recovered as monophyletic, tests of monophyly rejected only the monophyly of *A. orophilus* and *A. mollis*. Sequence divergence values among some of the currently recognized subspecies are higher than divergence values between sister species indicating the possibility that these subspecies may represent distinct species.

INTRODUCTION

The genus *Akodon* consists of South American grass mice of the Tribe Akodontini. It is among the most speciose groups of rodents in South America where it occurs from northern Venezuela to southern Argentina. The genus is present east of the Andes to the Atlantic Ocean and south of the Amazon lowlands to just north of Tierra del Fuego. Its distribution continues in a band along the northern Andes to the northern side of the Amazon lowlands. These grassland specialists are absent from the Amazon lowlands and west of the Andes (Fig. 2.1).

Since first described in 1833 (Meyen), the genus has proven taxonomically problematic. Tate (1932) and Ellerman (1941) reviewed the taxonomic history of the genus recognizing 90 species and 62 species, respectively. These authors included a number of taxa that today are no longer assigned to the genus *Akodon* (i.e. *Abrothrix*, *Brucepattersonius*, *Chelemys*, *Deltamys*, *Lenoxus*, *Necromys*, *Phyllotis*, *Podoxymys*, *Thalpomys*, and *Thaptomys*). Cabrera (1961) recognized only 38 specific level taxa, and this number was further reduced to 33 species (Honacki et al. 1982). Of the 46 currently recognized species, 13 have been described or reelevated to species status since 1989 (Braun et al. 2000, 2008, 2010; Christoff et al. 2000; Diáz et al. 1999; González et al. 1998; Hershkovitz 1990a, 1998; Jayat et al. 2010; Myers and Patton 1989a, 1989b; Myers et al. 1990; Pardiñas et al. 2005; Reeder et al. 2007).

The 46 *Akodon* species are partitioned into four species groups: an *aerosus* group, a *boliviensis* group, a *cursor* group, and a *varius* group (Table 2.1). The affinity for members of the *aerosus* group was originally realized in a molecular analysis of the akodonts of Peru, where five species of the *Akodon* (*A. aerosus*, *A. affinis*, *A. mollis*, *A.*

orophilus, and *A. torques*) that occupy elfin and upper tropical forests along the slopes of the Andes were found to ally together (Smith and Patton 1992a). Additional members were added based upon their molecular affinities (Smith and Patton 2007). The *boliviensis* group contains small bodied *Akodon* known from Peru and high elevations of Bolivia and mid to high elevations in Argentina (Myers et al. 1990). The *boliviensis* group also includes a fifth previously recognized species group, the *fumeus* group (Myers and Patton 1989a) which included only *A. fumeus* and *A. kofordi* based upon their overall morphological similarity but that fall within the *boliviensis* group in molecular analyses (Smith and Patton 2007). A *cursor* species complex was originally used by Liascovich and Reig (1989) to refer to three morphologically similar species (*A. cursor*, *A. montensis*, and *A. paranaensis* [as *A. serrensis*]) from the coastal forests of Brazil, Paraguay, Uruguay, and Argentina. The close relationship between *A. cursor* and *A. montensis*, and a chromosomal variant referred to as *A.* aff. *cursor*, was confirmed by electrophoretic data (Rieger et al 1995), and additional taxa were added to the *cursor* group based upon molecular affinities (*A. mystax* — Hershkovitz 1998, *A. reigi* — González et al. 1998, and *A. sanctipaulensis* — Hershkovitz 1990a). The *varius* group contains the largest members of the genus that occupy low to mid elevations of the eastern slopes of the Andes and lowland regions of Argentina, Bolivia, and Paraguay (Myers 1989). Additionally a number of species fail to ally with any of the currently recognized species groups and are referred to as *incertae sedis* lineages. The number of recognized species remains dynamic as new species are described and researchers reevaluate the taxonomy of the genus.

In addition to the four species groups, three taxa (*Chalcomys*, *Hypsimys*, and *Microxus*) have been treated as subgenera of *Akodon*. Although *Chalcomys* was described as a subgenus of *Akodon* (Thomas 1916), its type species and only member *A.* (*Chalcomys*) *aerosus* is nested within the subgenus *Akodon* and *Chalcomys* is currently recognized as a synonym of *Akodon* (Musser and Carleton 2005; Smith and Patton 1992a, 2007). The other two taxa, *Hypsimys* and *Microxus*, were described as distinct genera (Thomas 1909, 1918) but were relegated and are maintained as subgenera of *Akodon* (Musser and Carleton 2005). The subgenus *Hypsimys* contains two species, *A. budini* and *A. siberiae*. *Microxus* contains *A. mimus* and *A. latebricola*, but the inclusion of a third taxon, *A. bogotensis*, within *Microxus* and the recognition of *Microxus* as a subgenus is debatable (Musser and Carleton 2005; Patton and Smith 1992 a; Patton et al. 1989; Smith and Patton 1991, 1993).

In the last 30 years, work within the genus increased rapidly with a number of investigators evaluating the morphology (e.g. Hershkovitz 1990a, 1990b, 1998; Myers 1989; Myers and Patton 1989a, 1989b; Myers et al. 1990) and karyology (e.g. Barquez et al. 1980; Blaustein et al. 1992; Fagundes et al. 1998; Geise et al. 1998, 2001; Liascovich 1991; Sbalquiero and Nascimento 1996; Silva and Yonenaga-Yassuda 1998; Spotorno 1987) of the group, as well as amassed allozymic (e.g. Apfelbaum and Reig 1989; Barrantes et al. 1993; Patton et al. 1989; Rieger et al. 1995; Spotorno 1987) and molecular genetic data (D'Elía 2003; D'Elía et al. 2003; Patton and Smith 1992a, 1992b, Smith and Patton 1991, 1993, 1999, 2007). Results of these studies removed taxa previously included within the genus such as *Abrothrix* and *Chroeomys*, have refined relationships within the genus and at higher taxonomic levels, and have provided

information on relationships within the genus. As most of these studies were focused on higher taxonomic level relationships, they were limited by taxonomic and geographic sampling of the genus *Akodon* and were therefore limited in the phylogenetic and biogeographic conclusions they could make about the genus.

Therefore the objective of this study was to obtain a well-resolved phylogeny for the genus *Akodon* based upon a dense taxonomic and geographic sampling of the genus and using the cytochrome b gene. By obtaining a well-resolved phylogeny, we can then evaluate the validity and monophyly of currently and previously recognized species, subspecies, and species groupings.

MATERIALS AND METHODS

Taxon Sampling.—For this study, individuals corresponding to 35 of the 46 currently recognized *Akodon* species were obtained. Individuals from each of the species groups were included: 8 of 9 from the *A. aerosus* group, 9 of 13 from the *A. boliviensis* group, 5 of 6 from the *A. cursor* group, 8 of 11 from the *A. varius* group, and 5 of 7 of the *incertae sedis* taxa.

Six additional taxa were also included. Two samples of *Necromys lactens* and one sample of *Thaptomys nigrita* were included as non-*Akodon* representatives of the Tribe Akodontini. One sample of *Abrothrix longipilis* and one sample of *Chroeomys jelskii* representing the Tribe Abrothrochini were included for comparison. Two additional species (*Andinomys edax* and *Oligoryzomys destructor*) were included as representatives of the Tribes Phyllotini and Oryzomyini, respectively.

Extraction, Amplification, and Sequencing.—Whole genomic DNA was isolated from heart, kidney, liver, or skeletal muscle tissues following standard protocol (Longmire et al. 1997) or using the DNEasy Tissue Kit (Quiagen, Valencia, California). Amplifications were performed in 25 µl reactions containing 200-500 ng of DNA, 1 unit of Taq polymerase, 0.2 µM of each external primer, 1.2 mg/ml bovine serum albumin (BSA), 3 mM of MgCl2, 6 µl of 5X buffer, 0.17 mM of each dinucleotide triphosphate, and water to volume.

The entire cytochrome b (cytb) gene was amplified and sequenced using external primers MVZ05 and MVZ14 or H15915 (Irwin et al. 1991; Smith and Patton 1993) and a series of internal primers (Braun et al. 2008; Smith and Patton 1993). Six additional internal primers were developed and used for sequencing in this project. Developed light-strand primers were Ak2CytB740R (TCTCCGAGGATGTCTGG), Cytb-R1 (GGRATTTTGTCRGAGTCTGA), and Cytb-R2 (GYTTGATDATATTRTTCTCG), and developed heavy-strand primers were Ak2CytB740F (CCAGACATCCTCGGAGA), Cytb-F1 (TACGRAARAAYCACCCRCTA), and Cytb-F2 (AAAGCYACCCTMACCCGCTT). The PCR thermal profile included an initial denaturation at 95°C for 3 min, followed by 35 cycles at 95°C for 30 s, 52°C for 50 s, and 72°C for 1 min. A final elongation at 72° for 10 min was performed to ensure completeness of reactions.

Double stranded PCR products were purified using the Wizard PCR Prep DNA Purification System (Promega, Madison, Wisconsin), and products were sequenced on a 3130 Genetic Analyzer using BigDye Terminator v1.1 Sequencing Kits and POP-7 polymer (Applied Biosystems, Carlsbad, California). Upon completion of sequencing,

overlapping fragments were assembled and aligned using the ClustalW2 option in Geneious Pro 4.6.1 (Drummond et al. 2008; Larkin et al. 2007). For phylogenetic analysis, nucleotides were coded as unordered discrete characters, and character state changes were polarized by designating representatives of *A. edax* and *O. destructor* as outgroups.

Data Analyses.—Phylogenetic relationships within and between species of *Akodon* were estimated under the criteria of maximum parsimony and maximum likelihood using PAUP (Swofford 2000) and Bayesian phylogenetics using MRBAYES (Huelsenbeck and Ronquist 2001). Clades were considered strongly supported if bootstrap values of ≥70% and Bayesian posterior probabilities of ≥0.95 were obtained in at least two of the three analyses.

For maximum parsimony, stability of clades was evaluated by performing 1000 bootstrap pseudoreplicates with 25 random additions of input taxa and tree-bisection-reconnection (TBR) branch-swapping. Prior to maximum-likelihood analysis, jModeltest was used to determine the model of DNA sequence evolution that best fit the data (Guindon and Gascuel 2003; Posada 2008). The TVM+G model of evolution was chosen, along with the following parameters: base frequencies = 0.3272, 0.3047, 0.0949, 0.2732; nst = 6; rmat = 0.4881, 7.2488, 0.5353, 0.3140, 7.2488; rates = gamma with shape parameter (α) = 0.395. Stability of clades on the resulting tree was evaluated using a bootstrap analysis with 100 replications and Nearest-Neighbor Interchange (NNI) branch-swapping. Bayesian analysis was performed using the GTR+Γ model of DNA sequence evolution, along with site-specific rate variation calculated for each of the three positions of the codon via the "ssgamma" option in MRBAYES. Four simultaneous Markov chains

were run for 5,000,000 generations, with random, unconstrained, starting trees. Trees were sampled every 100 generations, with a "temperature" set at 0.02. Three independent runs of MRBAYES were performed using a different outgroup taxon for each run.

A priori hypotheses regarding the monophyly of species groups and other supraspecific taxa were tested by conducting Shimodaira-Hasegawa tests (SH; Shimodaira and Hasegawa 1999) under likelihood criterion in PAUP. Percent sequence divergence within and among species clades was computed based upon Kimura 2-parameter corrected distances to allow for comparison of sequence divergence and evaluation of cryptic species (Baker and Bradley 2006; Bradley and Baker 2001).

RESULTS

Complete cytb sequences were obtained by direct sequencing or from Genbank for 189 individuals. Of the 1140 sequenced bases, 580 were constant and 560 were variable with 132 at the 1st position, 58 at the 2nd position, and 370 at the 3rd position. Maximum likelihood analysis produced a single optimal tree (score = –17706.94630) and bootstrap analysis revealed 99 clades supported in ≥70% of the iterations. Unweighted parsimony analysis resulted in 100 equally parsimonius trees of 3549 steps (consistency index, excluding uninformative characters = 0.2236; retention index = 0.8310). Bootstrap analysis revealed 112 clades supported in ≥70% of the iterations. Bayesian analysis reached stationarity with *A. edax* at 300,000 generations, with *O. destructor* (OMNH 34497) at 200,000 generations, and *O. destructor* (OMNH 34399) at 175,000 generations. All resulting topologies from Bayesian analysis were identical and revealed 113 clades supported with a posterior probability of ≥0.95.

In the composite tree (Fig. 2.2), 25 of the included species are recovered as monophyletic clades, while 4 of the included species (*A. aerosus*, *A. mimus*, *A. mollis*, and *A. orophilus*) are recovered as paraphyletic clades. Five species (*A. budini*, *A. juninensis*, *A. lindberghi*, *A. reigi*, and *A. sylvanus*) are represented by a single specimen, and therefore their monophyly cannot be assessed. The genus *Akodon* is recovered as a strongly supported monophyletic clade, and the species *A. serrensis*, considered *incertae sedis*, is basal to a monophyletic clade containing all other species included here (Fig. 2.2). The four species groups were not recovered as strongly supported monophyletic clades but their monophyly could not be rejected (see SH Tests in Table 2.3). A clade containing the *boliviensis* and *cursor* groups, as well as the species *A. azarae*, was strongly supported. The *aerosus* and *varius* groups fall outside of this clade. Two well supported monophyletic clades are recovered from samples of *A. mimus,* considered *incertae sedis*, but their sister relationship is not supported and divergence within the species is high (8.519%). A monophyletic clade, containing a strongly supported sister relationship between *A. budini* and *A. siberiae* (Fig. 2.6), corresponds to the subgenus *Hypsimys* (Thomas 1918).

Kimura 2-parameter corrected distances were used to evaluate percent sequence divergence within and among clades. Within clades, divergence values (Table 2.2) ranged from 0.088% in *A. siberiae* and *A. philipmyersi* to 8.519% in *A. mimus*. Divergence values within clades were also high within *A. aerosus* (5.936%) and *A. orophilus* (5.023%). All other within clade divergence values were less than 4% and most were less than 2%. Among clades, percent sequence divergence (Table 2.2) was lowest between *A. fumeus* and *A. kofordi* (2.294%), *A. tartareus* and *A. glaucinus* (2.307%), and *A. toba* and

A. dolores (2.549%). Divergence values were highest between *A. budini* and *A. philipmyersi* (17.306%), *A. siberiae* and *A. philipmyersi* (17.596%), *A. serrensis* and *A. dolores* (17.623%), and *A. serrensis* and *A. budini* (17.769%). *Akodon serrensis* is highly divergent from all other *Akodon* species (15.567%).

The monophyly of the *A. aerosus* group, the *A. boliviensis* group, the *A. cursor* group, the *A. varius* group, and five *Akodon* species were tested by constraining each group and independently comparing likelihood scores to the score of the ML tree (Table 2.3). Constraining the monophyly of the four species groups did not result in significantly different likelihood scores. Likewise, constraining the monophyly of three species, *A. aerosus*, *A. lutescens*, and *A. mimus*, did not result in significantly different likelihood scores. However, constraining the monophyly of *A. mollis* (–ln = 17811.64131; $p < 0.001$) and *A. orophilus* (–ln = 17766.89277; $p = 0.011$) resulted in significantly different likelihood scores.

DISCUSSION

Previous molecular systematic studies of the genus *Akodon* had success in better defining the genus. Taxa historically included within the genus (i.e. *Abrothrix*) were excluded, and although information was provided regarding the relationships for some taxa, most studies had limited success in resolving relationship among species in the genus. In my analyses, nearly twice as many samples of *Akodon* were included compared to previous studies but additional sampling did little to bring resolve relationships among *Akodon*. Below I discuss the phylogenetic relationships recovered in my results and compare my results to those obtained in previous studies of the genus.

In my analyses of the cytb gene, a strongly supported monophyletic *Akodon* clade was recovered. The monophyly of *Akodon* (*sensu stricto*) has been supported by previous studies of cytb and the nuclear interphotoreceptor protein binding protein (IRBP) gene (D'Elía 2003; D'Elía et al. 2003) and cytb and two other nuclear markers (dentin matrix protein gene and thyrotropin; Coyner 2010: Chapter 3) . Previous studies of cytb recovered *Akodon* as paraphyletic with respect to the genus *Deltamys* (Jayat et al. 2010; Smith and Patton 2007). Without samples of Deltamys included in my analyses, I cannot address their relationship and possible congeneric relationship.

Akodon serrensis is the most basal lineage of *Akodon*, being recovered in my analyses outside of a strongly supported clade containing all other members of the genus, and divergence values between *A. serrensis* and other *Akodon* taxa are high (15.567%). Previous studies have also found *A. serrensis* to fall outside of *Akodon* (D'Elía 2003; D'Elía et al. 2003; Smith and Patton 2007). The taxon was recovered as sister to *Thaptomys nigrita* in analyses of cytb and IRBP sequences, and both are distributed in the Atlantic rainforest (D'Elía 2003).

In my analyses, clades corresponding to each of the four species groups are recovered but they are not supported; although monophyly tests could not be rejected for each (Table 2.3). Each is discussed below.

Akodon cursor group.—Rieger et al. (1995) is credited with first recognizing the *cursor* group, although previous authors (Liascovich and Reig 1989) recognized a close relationship between *A. cursor*, *A. montensis*, and *A. paranaensis* (as *A. serrensis*), which they referred to as the *cursor* species complex. Three additional species (*A. mystax*, *A. reigi*, and *A. sanctipaulensis*) were added to the group following molecular analyses

(Geise et al. 2001; Smith and Patton 2007). The status of *A. sanctipaulensis* has not been evaluated using molecular or chromosomal data, and is considered a member of the group based upon geography, habitat affinity, and morphology (Christoff et al. 2000). All members of the *cursor* group occupy coastal forest and tropical savanna habitats in Brazil and Uruguay and adjacent regions of Argentina and Paraguay (Musser and Carleton 2005; Smith and Patton 2007) and the *cursor* group is karyotypically diverse exhibiting diploid numbers of: 2N=14-15 in *A. cursor*, 2N=24-25 in *A. montensis*, and 2N=44, in *A. mystax*, *A. paranaensis*, and *A. reigi* (Geise et al. 2001; Smith and Patton 2007). The karyotype of *A. sanctipaulensis* is unknown (Christoff et al. 2000).

A monophyletic *cursor* group (Fig. 2.3) was not supported in my analyses, but tests of monophyly could not be rejected (Table 2.3). The *cursor* group was also recovered by Jayat et al. (2010) and Smith and Patton (2007), but it was unsupported in their analyses of cytb as well. A strongly supported *cursor* group clade was recovered in Geise et al (2001) containing *A. cursor*, *A. montensis*, *A. lindberghi*, and *A. mystax*, but as they were not evaluating the monophyly of the group, sampling outside the group was not sufficient to test the monophyly of the group. A strongly supported monophyletic containing all 6 species of the *cursor* group, along with an unidentified taxon, was recovered in analyses of cytb data by Pardiñas et al (2005).

Within the *cursor* group as included in my analyses, a number of relationships were recovered. *Akodon montensis*, *A. reigi*, and *A. paranaensis* were recovered as an unresolved polytomy, identical to a clade recovered by Jayat et al. (2010) using cytb data but contrasting with the close relationship between *A. mystax*, *A. reigi*, and *A. paranaensis* another analysis of cytb (Smith and Patton 2007). In my analyses, *A. mystax*

and *A. lindberghi* are sister species. Because of its occurrence in southeastern Brazil, *A. lindberghi* has often been included in studies of the *cursor* group (Geise et al. 1998, 2001) and Goncalvez et al. (2007) recovered *A. lindberghi* as sister to *A. mystax*, but Smith and Patton (2007) were unable to fully resolve the placement of *A. lindberghi*. *Akodon philipmyersi*, an *incertae sedis* taxon restricted to the Campos grasslands of Argentina, appears closely related to the *cursor* group, although its inclusion in the *cursor* group was not sufficiently supported by my data. Another study also indicated that *A. philipmyersi* is closely related to the cursor group as it is the most likely candidate to be sister to the *mystax*+*lindberghi* clade (Goncalvez et al. 2007), but a third recovered *A. philipmyersi* and *A. lindberghi* to be sister species that occurred outside the *cursor* group (Pardiñas et al. 2005).

Akodon boliviensis group.—The *A. boliviensis* species group (*sensu* Myers et al. 1990) contains 13 species of small bodied Akodon that occupy the central Andes from Peru and Bolivia across the Altiplano, or high plateau, into northern Chile and northwestern Argentina (Myers et al. 1990; Smith and Patton 2007). The *boliviensis* group is supported by electrophoretic data (Myers et al. 1990), share a karyotype of 2N=40, FN=42-44 (Barquez et al. 1980; Myers and Patton 1989b; Myers et al. 1990), and species included in the group essentially replace each other from north to south (Myers et al. 1990; Smith and Patton 2007). A second treatment of the *boliviensis* group was broader including *A. azarae*, *A. iniscatus*, *A. lindberghi*, *A. sanctipaulensis* (Hershkovitz 1990), but subsequent analyses have not supported their inclusion in the *boliviensis* group (Braun et al. 2008, 2010; D'Elía 2003; D'Elía et al. 2003; Geise et al. 2001; Goncalvez et al. 2007; Jayat et al. 2010; Smith and Patton 2007).

Nine of the 13 *boliviensis* species are included here (Fig. 2.4). The monophyletic clade they form is not supported but also not rejected by tests of monophyly (Table 2.3). Similar results were found in analyses of cytb data (Jayat et al. 2010). An analysis of the mitochondrial control region recovered a *boliviensis* group that contained *A. azarae* as sister to the species *A. boliviensis* (Hoekstra and Edwards 2000). Smith and Patton (2007) also had difficulties with the placement of *A. azarae*, but they recovered a strongly supported *boliviensis* group containing 7 of the 13 species in their Bayesian analysis as did Braun et al (2010) in their cytb analyses and Coyner 2010 (Chapter 3) in combined analyses of cytb and two nuclear genes.

Akodon kofordi and *A. fumeus* are well supported sister species, a relationship supported by their morphological similarity (Myers and Patton 1989a) and their molecular similarity (Braun et al. 2010; Coyner 2010: Chapter 3; Hoekstra and Edwards 2000; Jayat et al. 2010; Smith and Patton 2007). *Akodon kofordi* and *A. fumeus* were previously included under a distinct species group, the *fumeus* group which was used by Myers and Patton (1989a) to describe the overall similarity of the two taxa. The authors stated phylogenetic relationships between the two species were untestable at the time, so the fumeus group was not meant to represent phylogenetic affinities (Myers and Patton 1989a). Phylogenetic analyses of cytb sequence data (Coyner 2010: Chapter 3: Jayat et al. 2010; Smith and Patton 2007) and the mitochondrial control region (Hoekstra and Edwards 2000) support their sister relationship and place both species in the *boliviensis* group. *Akodon juninensis* has been found in studies of cytb to form a strongly supported relationship with the sister species *A. kofordi* and *A. fumeus* (Jayat et al. 2010; Smith and Patton 2007), but the relationship was not strongly supported by my analyses of cytb data

or by combined analyses of cytb sequences and nuclear markers (Coyner 2010: Chapter 3).

In my analyses, the relationship between *A. subfuscus* and the three subspecies of *A. lutescens* is unclear. *Akodon subfuscus* and *A. lutescens* are closely related (Hoekstra and Edwards 2000; Jayat et al. 2010; Myers et al. 1990; Smith and Patton 2007; my data). *A. lutescens* does not form a monophyletic clade based upon my data, but its monophyly could not be rejected (Table 2.3). Sampling within *A. lutescens* was sufficient to obtain representatives of the three recognized subspecies (*A. l. lutescens*, *A. l. caenosus*, and *A. l. puer*), but the three subspecies and *A. subfuscus* are recovered as an unresolved polytomy (Fig. 2.4). Most previous studies have included only a single sample of *A. lutescens* (Braun et al. 2010; Hoekstra and Edwards 2000; Smith and Patton 2007), but one study (Jayat et al. 2010) included *A. l. lutescens* and *A. l. puer* in addition to *A. subfuscus*. Jayat et al. (2010) also recovered the polytomy in their Bayesian analysis, but they concluded the recovered sister relationship in their parsimony analysis (Jackknife = 53) between *A. l. caenosus* and *A. subfuscus* warranted recognition of *A. caenosus* as a distinct species. In my analyses, the two northern subspecies form a strongly supported monophyletic clade with the single specimen of *A. l. lutescens* sister to the monophyletic clade containing samples of *A. l. puer*. One sample (MSB 63579) of *A. l. caenosus* falls outside the clade that contains all other *A. l. caenosus* specimens. Sequence divergence values between the four lineages of *A. lutescens* (2.077% to 4.278%; Table 2.4A) overlap those of other distinct *Akodon* species (i.e. *A. kofordi* and *A. fumeus*, 2.342%; Table 2.4).

Akodon caenosus (Thomas 1918) was originally described as a subspecies of *A. puer* (Thomas 1902) but shortly after was elevated to species status (Thomas 1920). *A.*

lutescens first described in 1901 (Allen) was relegated to a subspecies of *A. puer* by Myers et al. (1990), but Anderson (1997) noted priority for specific epithet should be given to *A. lutescens* and suggested the three currently recognized subspecies (Musser and Carleton 2005; Myers et al. 1990). Other authors, however, have treated the three taxa as separate species (Hershkovitz 1990a, Mares et al. 1997).

With their low sequence divergence (2.077%; Table 2.4A), identical karyotypes (Myers et al. 1989), and similar morphology (Myers et al. 1990), *A. l. lutescens* and *A. l. puer*, as presented here, are conspecific and represent sister subspecies. But higher sequence divergence is exhibited between *A. l. caenosus* and the two subspecies of *A. lutescens* (3.785%–4.038%: Table 2.4A), and *A. l. caenosus* has a karyotype (2N=34, FN=40) and uniformly darker pelage coloration (Myers et al. 1990) that distinguishes it from the karyotype (2N=40; FN=40) and the lighter pelage coloration shared by other members of *A. lutescens* (Myers et al. 1990) giving sufficient support to recognize *A. caenosus* as a species distinct of *A. lutescens*. With the lack of resolution among *A. lutescens*, *A. caenosus*, and *A. subfuscus*, additional study is required to determine their relationships and to determine the status of the outlier sample of *A. caenosus*.

The type species of *Akodon*, *A. boliviensis*, is the sister species of *A. spegazzinii* (Braun et al. 2010; Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007, my data). Individuals identified as *A. alterus* Thomas (a synonym of *A. spegazzinii*; 1919) and *A. s. tucumanensis* Allen (1901) were included in my analyses, but like a previous study of cytb sequences (Jayat et al. 2010), I found no differentiation between these three taxa in my analyses. *Akodon spegazzinii*, including its current subspecies and synonyms, occupies a wide variety of habitats from moist forest to desert and exhibits considerable

intraspecific morphological variation, particularly pelage coloration which correlates with habitat (Jayat et al. 2010). Despite their variation in pelage color and ecological associations, evaluations of allozyme data and morphological variation also found low levels of divergence between the three taxa (Blaustein et al. 1992).

Akodon viridescens, recently described by Braun et al. (2010), is basal to the sister relationship between *A. boliviensis* and *A. spegazzinii* in my analyses, identical to the relationship recovered in the molecular analyses of cytb sequences by Braun et al. (2010). A single individual of *A. viridescens* (identified as *A. spegazzinii*) was used in sequencing prior to the species formal description (D'Elía 2003; D'Elía et al. 2003; Pardiñas et al. 2005; Smith and Patton 2007). The individual of *A. viridescens* was found to be sister to *A. boliviensis*, but no other samples of *A. spegazzinii* were included in those analyses (Pardiñas et al. 2005; Smith and Patton 2007).

Akodon varius group.—Seven species (*A. dayi*, *A. dolores*, *A. molinae*, *A. neocenus*, three subspecies of *A. simulator, A. toba*, and *A. varius*) of large bodied *Akodon* were allied together within the *varius* group by Myers (1989). The species occupy low and mid elevation habitats on the eastern slopes of the central and southern Andes and lowlands in Argentina, Bolivia, and Paraguay (Braun et al. 2008). Molecular analyses place *A. iniscatus* in the varius group (Smith and Patton 2007), and recently the three subspecies of *A. simulator* were elevated to specific status based upon analyses of cytb sequences (Braun et al. 2008).

In my analyses (Fig. 2.5), the *varius* group is recovered as two monophyletic clades. While the sister relationship between these two clades is not strongly supported, tests of monophyly could not reject the monophyly of the group (Table 2.4). Similar

results were recovered in the parsimony analysis by Jayat et al. (2010), but other analyses have revealed the *varius* group to be invalid (Coyner 2010: Chapter 3; Jayat et al. 2010) with four species allying with the *aerosus* group.

Akodon glaucinus, *A. simulator*, *A. tartareus*, and *A. varius* form a monophyletic clade in my analyses, but the relationships between these four taxa are unresolved (Fig. 2.5). Although not shown, these four lineages have very short branch lengths and likely represent a recent and rapid divergence also indicated by their low divergence values (2.307–4.210%). This clade corresponds to the Yungas clade of Braun et al. (2008) in their analyses of cytb sequences. This clade is recovered nested within the *aerosus* clade in analyses of a combined dataset containing cytb and two nuclear genes (Coyner 2010: Chapter 3) and in the Bayesian analysis of cytb sequences by Jayat et al. (2010).

The remaining individuals of the *varius* group, included here, are recovered as a monophyletic clade, the lowland clade of Braun et al. (2008). The relationships among these four taxa (*Akodon dayi*, *A. dolores*, *A. iniscatus*, and *A. toba*) are well resolved and all strongly supported (Fig. 2.5). Other studies (Braun et al. 2008; Coyner 2010: Chapter 3; Jayat et al. 2010; Smith and Patton 2007) have recovered identical topologies based upon cytb and/or nuclear sequences. Like other studies (Braun et al. 2008, Smith and Patton 2007), no difference between *A. dolores* and individuals previously identified as *A. molinae* was found. Without sequences from samples from near the type locality, the relegation of *A. molinae* to a synonym of *A. dolores* cannot be done with complete confidence, but data from studies based upon morphology, behavior, and cytogenetics have suggested to two to be conspecific (Apfelbaum and Blanco 1984; Bianchi et al. 1979; Braun et al. 2008; Merani et al. 1978; Wittouck et al. 1995).

Despite being unable to reject the varius group with data presented here, Coyner (2010: Chapter 3) and Jayat et al. (2010) present data that makes a strong case against a *varius* group, and I agree with their conclusions on reassigning the four members of Braun et alia's (2008) Yungas clade to the aerosus group and referring to the clade that contains the lowland species as the *A. dolores* species group.

Akodon aerosus group.— The affinity for members of the *aerosus* group was first discussed in a molecular analysis containing five Peruvian *Akodon* species (*A. aerosus*, *A. affinis*, *A. mollis*, *A. orophilus*, and *A. torques*; Smith and Patton 1992a). Additional members (*A. albiventer*, *A. budini*, and *A. siberiae*) were added based upon their molecular affinities (D'Elía 2003; D'Elía et al. 2003; Smith and Patton 2007). With the exception of *A. albiventer*, all species of the *aerosus* group occupy elfin and upper tropical forests along the slopes of the central and northern Andes (Smith and Patton 1992a; 2007). *Akodon albiventer* occurs on the Altiplano, a high elevation grassland plateau, and represents the only species of the *aerosus* group known to occur above the tree line (Smith and Patton 2007).

As discussed above in the *A. varius* group, the *aerosus* group as traditionally defined (Smith and Patton 2007) is paraphyletic with respect to four species historically included in the *varius* group. But my analyses of cytb sequence data here did not reveal the paraphyly (Fig. 2.6). While no strongly supported *A. aerosus* group was recovered, its monophyly were not rejected (Table 2.4).

Three of the aerosus group species, *A. aerosus*, *A. mollis*, and *A. orophilus*, are not monophyletic, as included here (Fig. 2.6). Previous studies also recovered *A. aerosus* and *A. orophilus* as paraphyletic (Patton and Smith 1992a; Smith and Patton 2007), but

their study and other previous studies (Hoekstra and Edwards 2000; Patton and Smith 1992a; Smith and Patton 1991, 1993, 1999) have included only a single sample of *A. mollis* so no testing of this taxon was previously possible.

Constraining *A. mollis* and *A. orophilus* results in significantly lower likelihood scores compared to the best tree obtained in my analyses (Table 2.4). In my analyses a single sample of *A. orophilus* (MVZ 173057) is sister to a sample of *A. mollis* (FMNH 129212). *Akodon orophilus orientalis* is represented by a single individual, and *A. orophilus orophilus* forms a monophyletic clade of 3 individuals, but the relationship between the two subspecies is unresolved (Fig. 2.6). Likewise *A. mollis* is also represented by both of its subspecies, *A. mollis mollis* and *A. mollis altorum*.

Tests of monophyly were not rejected for *A. aerosus* (Table 2.4), but as presented here, A. *aerosus* is paraphyletic with respect to *A. affinis*. *Akodon aerosus* occurs in disjunct populations in montane forests of the eastern slopes of the Andes in Peru. The species is restricted to 1200-2000 m elevations (Patton and Smith 1992a), and there is considerable variation in diploid number (2N=22-40) among populations of *A. aerosus* (Gardner and Patton 1976; Patton et al. 1990). The sequence divergence values between the three *aerosus* lineages, recovered in my analyses, range from 6.742-8.877% (Table 2.4B).

Explanations for the relationships recovered have been proposed by Smith and Patton (2007). These include incomplete lineage sorting in which the species and gene trees do not match, the presence of multiple distinct species included in the currently recognized species, or morphologic similarity being caused not by evolutionary relationships but rather due to convergence or parallel evolution (Smith and Patton 2007).

A more thorough analysis, using both molecular and morphological characters, needs to be conducted of the three paraphyletic species (*A. aerosus*, *A. mollis*, and *A. orophilus*) to resolve the paraphyly.

Also included in my analyses, *Akodon siberiae* and a single sample of *A. budini* form a monophyletic clade. These two species are members of the subgenus *Hypsimys* (Thomas 1918), but they have previously been considered members of the *aerosus* group based primarily upon the alliance between *A. siberiae* and members of the *aerosus* group (D'Elía 2003; D'Elía et al. 2003; Smith and Patton 2007). The relationship, as obtained by my data, is less clear. No strongly supported relationship between the two *Hypsimys* taxa and any other members of *Akodon* is recovered (Fig. 2.6). Constraining the *aerosus* clade containing *A. siberiae* and *A. budini* did not result in a significantly worse topology, but alternative topologies approached significance (P=0.097, Table 2.4). Jayat et al. (2010) recovered *A. siberiae* and *A. budini* as sister to *A. mimus* in both of their analyses, but neither analysis was supported; in their maximum parsimony analysis, *A. siberiae*, *A. budini*, and *A.mimus* are all contained within a supported clade containing the *aerosus* group, but in their Bayesian analysis the clade containing the three species formed no alliance with any other species. With the lack of stability in the placement of *A. budini* and *A. siberiae*, the taxa may actually represent *incertae sedis* species, rather than members of the *aerosus* group. The taxonomic status of *Hypsimys* cannot be determined until the placement of *A. budini* and *A. siberiae* is resolved.

Incertae sedis lineages.—Besides *A. serrensis*, two additional *incertae sedis* taxa were included here (Fig. 2.2). *Akodon mimus* was recovered in my analyses as two lineages whose sister relationship was unsupported; tests of monophyly were not rejected

(Table 2.4). Additionally *A. mimus* did not ally with any other species of *Akodon* in my analyses, being recovered at the basal node within *Akodon* (excluding A. serrensis) as a polytomy with the *A. varius* group and the *A. aerosus* group. The unsupported sister relationship and lack of alliance between *A. mimus* and other species was also recovered in combined analyses of cytb and nuclear sequence data (Coyner 2010: Chapter 3). Analyses of the mitochondrial control region recovered *A. mimus* as the most basal taxon of *Akodon* species included in their study (Hoekstra and Edwards 2000), but other analyses of cytb found the placement of *A. mimus* to be variable (Jayat et al. 2010; Smith and Patton 2007). Smith and Patton (2007) recovered it as sister to *Deltamys kempii* and included in an unsupported clade containing the aerosus group. Jayat et al (2010) also recovered a close relationship between *A. mimus* and *Deltamys kempii* and the *aerosus* group in their parsimony analysis, but support values were low. *Deltamys* has been supported as a distinct genus (D'Elía 2003; D'Elía et al. 2003).

In my analyses, sequence divergence within the taxon is 8.519%, and sequence divergence values indicate three distinct lineages within the species (Table 2.4D). But without understanding the relationship within *A. mimus*, it is difficult to determine the status of the lineages contained within it. Two additional species, *A. bogotensis* and *A. latebricola*, have historically been included in *Microxus*, but *A. bogotensis* exhibits traits that are not shared by other *Akodon* including *A. mimus* and *A. latebricola* (Musser and Carleton 2005; Voss and Linzey 1981). Additional study of *A. mimus*, *A. latebricola*, and *A. bogotensis* is needed to understand the relationships within and among these three taxa and other species of *Akodon*.

Akodon azarae was also included in my analyses but its placement cannot be fully resolved. Like other studies (D'Elía 2003; D'Elía et al. 2003; Jayat et al. 2010: Smith and Patton 2007), we find *A. azarae* to ally with the *cursor* and *boliviensis* groups, but the relationship among the three groups remains unresolved. In analyses of the mitochondrial control region, *A. azarae* was recovered nested within the boliviensis group (Hoekstra and Edwards 2000). Recent analyses of cytb and nuclear sequence data recovered *A. azarae* basal to a well supported sister relationship between the *boliviensis* and *cursor* groups (Coyner 2010: Chapter 3). But in my analyses of cytb, *A. azarae* does not fall within either the *boliviensis* or *cursor* group and is not recovered as basal to them, so its *incertae sedis* status remains.

CONCLUDING REMARKS

Previous molecular systematic studies of the genus *Akodon* included relatively few samples as compared to the diversity present within the genus. These studies better defined the genus by excluding taxa historically included in the genus but had limited success in determining relationship between species in the genus. Doubling the number of included samples, making efforts to encompass geographic and morphologic variation, did little to bring additional resolution to the phylogenetic trees.

A number of taxa (i.e. *A. aerosus*, *A. mollis*, *A. orophilus*, and *A. mimus*) warrant deeper examination to determine the true number of species included within each taxon. Also *A. serrensis* deserves additional attention to determine if it deserves recognition as a separate genus. Taxa that have not yet been available for sequencing (e.g. *A. latebricola*, *A. oenos*, and many others) need to be obtained to determine their placement in the molecular tree.

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LITERATURE CITED

Apfelbaum, L. I., and A. Blanco. 1984. Genetic similarity between species of *Akodon* (Rodentia, Cricetidae). Journal of Experimental Zoology 229:1–5.

Apfelbaum, L. I., and O. A. Reig. 1989. Allozyme genetic distances and evolutionary relationships in species of akodontine rodents (Cricetidae: Sigmodontinae). Biological Journal of the Linnean Society 38:257–280.

Baker, R. J., and R. D. Bradley. 2006. Speciation in mammals and the Genetic Species Concept. Journal of Mammalogy 97:643-662.

Barquez, R. M., D. F. Williams, M. A. Mares, and H. H. Genoways. 1980. Karyology and morphometrics of three species of *Akodon* (Mammalia, Muridae) from northwestern Argentina. Annals of Carnegie Museum 49:379–403.

Barrantes, G. E., M. O. Ortells, and O. A. Reig. 1993. New studies on allozyme genetic distance and variability in akodontine rodents (Cricetidae) and their systematic implications. Biological Journal of the Linnean Society 48:283–298.

Bianchi, N. O., O. A. Reig, O. J. Molina, and F. N. Dulout. 1971. Cytogenetics of the South American akodont rodents (Cricetidae). I. A progress report of Argentinian and Venezuelan forms. Evolution 25:724–736.

Bianchi, N. O., S. Merani, and M. Lizarralde. 1979. Cytogenetics of the South American akodont rodents (Cricetidae). VI. Polymorphism in *Akodon dolores* (Thomas). Genetica 50:99–104

Blaustein, S. A., R. C. Liascovich, L. I. Apfelbaum, L. Daleffe, R. M. Barquez, and O. A. Reig. 1992. Correlates of systematic differentiation between two closely related

allopatric populations of the *Akodon boliviensis* group from NW Argentina (Rodentia: Cricetidae). Zeithschrift für Säugetierkunde 57:1–13.

Bradley, R. D., and R. J. Baker. 2001. A test of the genetic species concept: cytochrome-b sequences and mammals. Journal of Mammalogy 82:960–973.

Braun, J. K., M. A. Mares, and R. A. Ojeda. 2000. A new species of grass mouse, genus *Akodon* (Muridae: Sigmodontinae), from Mendoza Province, Argentina. Zeitschrift für Säugetierkunde 65:216–225.

Braun, J. K., B. S. Coyner, M. A. Mares, and R. A. Van Den Bussche. 2008. Phylogenetic relationships of South American grass mice of the *Akodon varius* group (Rodentia, Cricetidae, Sigmodontinae) in South America. Journal of Mammalogy 89:768–777.

Braun, J. K., M. A. Mares, B. S. Coyner, and R. A. Van Den Bussche. 2010. New species of *Akodon* (Rodentia, Cricetidae, Sigmodontinae) from central Argentina. Journal of Mammalogy 91:387–400.

Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. II. (Sirenia-Perissodactyla-Artiodactyla-Lagomorpha-Rodentia-Cetacea). Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Naturales 4:308–732.

Christoff, A. U., V. Gafundes, I. J. Sbalqueiro, M. S. Mattevi, and Y. Yonenaga-Yassuda. 2000. Description of a new species of *Akodon* (Rodentia: Sigmodontinae) from southern Brazil. Journal of Mammalogy 81:838–851.

D'Elía, G. 2003. Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307–323.

D'Elía, G., E. M. González, and U. F. J. Pardiñas. 2003. Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus *Deltamys*. Mammalian Biology 68:351–364.

Diáz, M. M., R. M. Barquez, J. K. Braun, and M. A. Mares. 1999. A new species of *Akodon* (Murinae, Sigmodontinae) from northwestern Argentina. Journal of Mammalogy 80:786–798.

Drummond, A. J., et al. 2008. Geneious version 4.6.1, available from http://www.geneious.com.

Ellerman, J. R. 1941. The families and genera of living rodents. Vol. II. Family Muridae. British Museum (Natural History), London, 690 pp.

Fagundes, V., A. U. Christoff, and Y. Yonenaga-Yassuda. 1998. Extraordinary chromosomal polymorphism with 28 different karyotypes in the Neotropical species *Akodon cursor* (Muridae: Sigmodontinae), one of the smallest diploid number in rodents (2n=16, 15 and 14). Hereditas 129:263–274.

Geise, L., F. C. Canavez, and H. N. Seuánez. 1998. Comparative karyology in *Akodon* (Rodentia, Sigmodontinae) from southeastern Brazil. Journal of Heredity 89:158–163.

Geise, L., M. F. Smith, and J. L. Patton. 2001. Diversification in the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern South America: mitochondrial DNA sequence analysis. Journal of Mammalogy 82:92–101.

Goncalvez, P. R., P. Myers, J. F. Vilela, and J. A. de Oliveira. 2007. Systematics of species of the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern Brazil and implications for the biogeography of the *Campos de Altitude*. Miscellaneous Publications Museum of Zoology, University of Michigan 197:1–24.

González, E. M., A. Langguth, and L. F. de Oliveira. 1998. A new species of *Akodon* from Uruguay and southern Brazil (Mammalia: Rodentia: Sigmodontinae). Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo 191:108.

Guindon S., and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52:696–704.

Hershkovitz, P. 1990a. Mice of the *Akodon boliviensis* size class (Sigmodontinae, Cricetidae), with the description of two new species from Brazil. Fieldiana: Zoology 57:1–35.

Hershkovitz, P. 1990b. The Brazilian rodent genus *Thalpomys* (Sigmodontinae, Cricetidae) with a description of a new species. Journal of Natural History 24:777–783.

Hershkovitz, P. 1998. Report on some sigmodontine rodents collected in southeastern Brazil with descriptions of a new genus and six new species. Bonner Zoologische Beiträge 47:193–256.

Hoekstra, H. E., and S. V. Edwards. 2000. Multiple origins of XY female mice (genus *Akodon*): phylogenetic and chromosomal evidence. Proceedings of the Royal Society B: Biological Sciences 267:1825–1831.

Honacki, J. H., K. E. Kinman, and J. W. Koeppl. 1982. Mammal Species of the world: a taxonomic and geographic reference. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Huelsenbeck, J. P., and F. R. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754–755.

Irwin D. M., T. D. Kocher, and A. C. Wilson. 1991. The evolution of the cytochrome b gene in mammals. Journal of Molecular Evolution 32(2):128–144.

Jayat, J. P., P. E. Ortiz, J. Salazar-Bravo, U. F. J. Pardiñas, and G. D'Elía. 2010. The *Akodon boliviensis* species group (Rodentia: Cricetidae: Sigmodontinae) in Argentina: species limits and distribution, with the description of a new entity. Zootaxa 2409:1–61.

Larkin, M. A., et al. 2007. Clustal W and Clustal X version 2.0. Bioinformatics 23:2947-2948.

Liascovich, R. C. 1991. Cariosistemática y evolución cromosómica en cricétidos akodontinos (Rodentia, Muriodea). Ph. D. dissertation, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, 185 pp.

Longmire, J. L., M. Maltbie, and R. J. Baker. 1997. Use of "lysis buffer" in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1–2.

Merani, S., M. Lizarralde, D. Oliveira, and N. O. Bianchi. 1978. Cytogenetics of the South American akodont rodents (Cricetidae). IV. Interspecific crosses between *Akodon dolores* × *Akodon molinae*. Journal of Experimental Zoology 206:343–346.

Meyen, F. J. F. 1833. Beiträge zur Zoologie gesammelt auf einer Reise um die Erde Säugethiere. Nova Acta Academiae Caesareae Leopoldino-Carolinae 16(2):599.

Musser, G. G., and M. D. Carleton. 2005. Superfamily Muroidea. Pp. 894–1531, in Mammal species of the world: a taxonomic and geographic reference, Third Edition (D. E. Wilson and D. M. Reeder, eds.). The Johns Hopkins University Press, Baltimore, Maryland.

Myers, P. 1989. A preliminary revision of the *varius* group of *Akodon* (*A. dayi*, *dolores*, *molinae*, *neocenus*, *simulator*, *toba*, and *varius*), Pp. 5–54, in Advances in Neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). The Sandhill Crane Press, Inc., Gainesville, Florida, 614 pp.

Myers, P., and J. L. Patton. 1989a. *Akodon* of Peru and Bolivia: revision of the *fumeus* group (Rodentia: Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 721:1–35.

Myers, P., and J. L. Patton. 1989b. A new species of *Akodon* from the cloud forests of eastern Cochabamba Department, Bolivia (Rodentina: Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 720:1–28.

Myers, P., J. L. Patton, and M. F. Smith. 1990. A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae) with emphasis on Perú and Bolivia. Miscellaneous Publications of the Museum of Zoology. University of Michigan 177:1–104.

Ortiz-Jaureguizar, E., and G. A. Cladera. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. Journal of Arid Environments 66:498–532.

Pardiñas, U. F. J., G. D'Elía, S. Cirignoli, and P. Suarez. 2005. A new species of *Akodon* (Rodentia, Cricetidae) from the northern campos grasslands of Argentina. Journal of Mammalogy 86:462–474.

Patton, J. L., and M. F. Smith. 1992a. Evolution and systematics of akodontine rodents (Muridae: Sigmodontinae) of Peru, with emphasis on the genus Akodon. Memorias del Museo de Historia Natural, U.N.M.S.M. (Lima) 21:83–103.

Patton, J. L., and M. F. Smith. 1992b. mtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. Evolution 46:174–183.

Patton, J. L., P. Myers, and M. F. Smith. 1989. Electromorphic variation in selected South American akodontine rodents (Muridae: Sigmodontinae), with comments on the systematic implications. Zeithschrift für Säugetierkunde 54:347–359.

Posada, D. 2008. jModelTest: Phylogenetic Model Averaging. Molecular Biology and Evolution 25:1253–1256.

Reeder, D. M., K. M. Helgen, and D. E. Wilson. 2007. Global trends and biases in new mammal species discoveries. Occasional Papers of the Museum of Texas Tech University 269:1–36.

Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404–440, in High altitude tropical biogeography (F. Vuilleumier and M. Monasterio, eds.). Oxford University Press, New York, 649 pp.

Reig, O. A. 1987. An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Sigmodontinae). Pp. 347–401, in Studies in Neotropical mammalogy: essays in honor of Philip

Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana, Zoology 39:1–506.

Rieger, T. T., A. Langguth, and T. A. Waimer. 1995. Allozymic characterization and evolutionary relationships in the Brazilian *Akodon cursor* species group (Rodentia – Cricetidae). Biochemical Genetics 33:283–295.

Sbalquiero, I. F., and A. P. Nascimento. 1996. Occurrence of *Akodon cursor* (Rodentia, Cricetidae) with 14, 15, 16 chromosome cytotypes in the same geographic area in southern Brazil. Revista Brasileira de Genética 19:565–569.

Shimodaira, H., and M. Hasegawa. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 16:1114-1116.

Silva, M. J. de J, and Y. Yonenaga-Yassuda. 1998. Karyotype and chromosomal polymorphism of an undescribed *Akodon* from central Brazil, a species with the lowest diploid chromosome number in rodents. Cytogenetics and Cell Genetics 81:46–50.

Smith, M. F., and J. L. Patton. 1991. Variation in mitochondrial cytochrome b sequence in natural populations of South American akodontine rodents (Muridae: Sigmodontinae). Molecular Biology and Evolution 8:85–103.

Smith, M. F., and J. L. Patton. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149–177.

Smith, M. F., and J. L. Patton. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome b. Journal of Mammalian Evolution 6:89–128.

Smith, M. F., and J. L. Patton. 2007. Molecular phylogenetics and diversification of South American grass mice, genus *Akodon*. Pp. 827-858 in The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson (D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1-981.

Spotorno, A. 1987. Systematics and evolutionary relationships of Andean phyllotine and akodontine rodents. Ph. D. dissertation, University of California, Berkeley.

Swofford, D. L. 2000. PAUP* Phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Tate, G. H. H. 1932. The taxonomic history of the South and Central American akodont genera: *Thalpomys*, *Deltamys*, *Thaptomys*, *Hypsimys*, *Bolomys*, *Chroeomys*, *Abrothrix*, *Scotinomys*, *Akodon*, (*Chalcomys* and *Akodon*), *Microxus*, *Podoxymys*, *Lenoxus*, *Oxymycterus*, *Notiomys*, and *Blarinomys*. American Museum Novitates 582:1–32.

Thomas, O. 1909. Notes on some South-American Mammals, with Descriptions of new Species. Annals and Magazine of Natural History ser. 8, 4:230–242.

Thomas, O. 1916. The grouping of the South American Muridae commonly referred to *Akodon*. Annals and Magazine of Natural History ser. 8, 17:336–340.

Thomas, O. 1918. On small mammals from Salta and Jujuy collected by Mr. E. Budin. Annals and Magazine of Natural History ser. 9, 1s:186–193.

Wittouck, P., E. Pinna Senn, C. A. Soñez, M. C. Provensal, J. J. Polop, and J. A. Lisanti. 1995. Chromosomal and synaptonemal complex analysis of Robertsonian polymorphisms in *Akodon dolores* and *Akodon molinae* (Rodentia: Cricetidae) and their hybrids. Cytologia 60:93–102.

TABLE 2.1.—Species of *Akodon* divided into the four species groups (Braun et al. 2008; Musser and Carleton 2005; Myers 1989; Myers et al. 1989; Rieger et al. 1995; Smith and Patton 1992a, 2007) and taxa considered *incertae sedis*. Taxa marked with astericks were unavailable for inclusion in this study.

A. aerosus group	*A. boliviensis* group	*A. cursor* group	*A. varius* group	*Incertae sedis*
A. aerosus	*A. aliquantulus**	*A. cursor*	*A. dayi*	*A. azarae*
A. affinis	*A. boliviensis*	*A. montensis*	*A. dolores*	*A. bogotensis**
A. albiventer	*A. fumeus*	*A. mystax*	*A. glaucinus*	*A. latebricola**
A. budini	*A. juninensis*	*A. paranaensis*	*A. iniscatus*	*A. lindberghi*
A. mollis	*A. kofordi*	*A. reigi*	*A. molinae**	*A. mimus*
A. orophilus	*A. leucolimnaeus**	*A. sanctipaulensis**	*A. neocenus**	*A. philipmyersi*
A. siberiae	*A. lutescens*		*A. oenos**	*A. serrensis*
*A. surdus**	*A. pervalens**		*A. simulator*	
A. torques	*A. polopi**		*A. tartareus*	
	A. spegazzinii		*A. toba*	
	A. subfuscus		*A. varius*	
	A. sylvanus			
	A. viridescens			

TABLE 2.2.—Percentage sequence divergence of cytochrome b corrected by Kimura 2-parameter model (Kimura 1980) for comparisons within and between clades of *Akodon* recovered in phylogenetic analyses (Figs. 2.2–2.6). The number of pairwise comparisons is given in parentheses.

		Between clades					
Taxon	Within clade	1	2	3	4	5	6
1 *A. serrensis*	3.722 (6)						
2 *A. mimus*	8.519 (10)	15.106 (20)					
3 *A. budini*	-	17.769 (4)	12.129 (5)				
4 *A. siberiae*	0.088 (1)	16.092 (8)	11.435 (10)	3.588 (2)			
5 *A. albiventer*	1.044 (28)	15.579 (32)	12.846 (40)	12.988 (8)	13.318 (16)		
6 *A. varius*	0.176 (1)	15.585 (8)	11.986 (10)	12.275 (2)	12.209 (4)	11.018 (16)	
7 *A. tartareus*	0.117 (3)	14.773 (12)	11.707 (15)	11.759 (3)	11.045 (6)	10.936 (24)	3.532 (6)
8 *A. glaucinus*	0.247 (3)	14.915 (12)	12.664 (15)	11.825 (3)	11.279 (6)	11.145 (24)	3.504 (6)
9 *A. simulator*	1.422 (15)	16.393 (24)	12.431 (30)	12.911 (6)	11.935 (12)	11.584 (48)	4.210 (12)
10 *A. iniscatus*	0.766 (3)	16.764 (12)	13.382 (15)	14.771 (3)	14.164 (6)	13.449 (24)	13.863 (6)
11 *A. dayi*	2.697 (1)	16.676 (8)	14.639 (10)	16.709 (2)	16.394 (4)	15.568 (16)	15.071 (4)
12 *A. toba*	0.589 (3)	16.649 (12)	13.779 (15)	15.420 (3)	15.115 (6)	13.141 (24)	14.064 (6)
13 *A. dolores*	0.607 (28)	17.623 (32)	14.090 (40)	16.157 (8)	15.771 (16)	15.037 (64)	14.676 (16)
14 *A. aerosus*	5.936 (21)	16.031 (28)	11.677 (35)	12.370 (7)	11.859 (14)	11.137 (56)	10.697 (14)
15 *A. affinis*	-	16.473 (4)	11.204 (5)	11.555 (1)	11.383 (2)	10.552 (8)	10.185 (2)
16 *A. orophilus*	5.023 (10)	15.528 (20)	11.385 (25)	11.002 (5)	10.319 (10)	11.415 (40)	10.533 (10)
17 *A. mollis*	3.849 (15)	14.340 (24)	11.346 (30)	11.455 (6)	11.642 (12)	10.669 (48)	9.318 (12)

TABLE 2.2.—Continued.

Taxon	Within clade	Between clades 1	2	3	4	5	6
18 *A. torques*	1.179 (10)	14.675 (20)	10.852 (25)	11.299 (5)	10.686 (10)	11.218 (40)	9.848 (10)
19 *A. azarae*	3.841 (21)	16.341 (28)	14.018 (35)	16.124 (7)	16.518 (14)	14.307 (56)	13.086 (14)
20 *A. philipmyersi*	0.088 (1)	16.797 (8)	15.840 (10)	17.306 (2)	17.596 (4)	15.448 (16)	14.614 (4)
21 *A. cursor*	2.929 (10)	15.916 (20)	13.715 (25)	15.489 (5)	15.358 (10)	14.963 (40)	14.351 (10)
22 *A. lindberghi*	-	16.582 (4)	13.222 (5)	14.663 (1)	14.708 (2)	13.988 (8)	12.657 (2)
23 *A. mystax*	0.197 (15)	15.602 (24)	12.853 (30)	14.851 (6)	14.996 (12)	13.596 (48)	12.698 (12)
24 *A. montensis*	1.300 (66)	16.420 (48)	15.074 (60)	15.234 (12)	15.222 (24)	15.296 (96)	13.458 (24)
25 *A. reigi*	-	14.154 (4)	12.773 (5)	13.808 (1)	14.086 (2)	13.895 (8)	11.509 (2)
26 *A. paranaensis*	1.833 (105)	15.778 (60)	13.233 (75)	14.474 (15)	14.720 (30)	14.705 (120)	13.560 (30)
27 *A. juninensis*	-	15.367 (4)	13.310 (5)	14.478 (1)	14.522 (2)	13.914 (8)	13.480 (2)
28 *A. kofordi*	1.421 (1)	14.814 (8)	13.208 (10)	14.406 (2)	14.107 (4)	14.495 (16)	13.146 (4)
29 *A. fumeus*	1.252 (45)	14.884 (40)	13.444 (50)	15.053 (10)	14.298 (20)	14.586 (80)	13.531 (20)
30 *A. subfuscus*	0.705 (1)	15.687 (8)	15.104 (10)	15.818 (2)	15.864 (4)	14.757 (16)	13.978 (4)
31 *A. lutescens*	2.610 (105)	14.217 (60)	12.802 (75)	14.058 (15)	14.773 (30)	12.856 (120)	12.895 (30)
32 *A. sylvanus*	-	15.302 (4)	12.641 (5)	14.529 (1)	14.243 (2)	13.820 (8)	13.028 (2)
33 *A. viridescens*	0.201 (21)	15.016 (28)	13.264 (35)	14.725 (7)	15.552 (14)	14.297 (56)	13.029 (14)
34 *A. boliviensis*	0.532 (3)	14.538 (12)	13.829 (15)	14.473 (3)	14.672 (6)	13.497 (24)	13.744 (6)
35 *A. spegazzinii*	1.288 (120)	15.155 (64)	13.527 (80)	14.345 (16)	14.803 (32)	13.502 (128)	13.519 (32)

TABLE 2.2.—Continued.

Taxon	Between clades						
	7	8	9	10	11	12	13
8 *A. glaucinus*	2.307 (9)						
9 *A. simulator*	3.576 (18)	2.775 (18)					
10 *A. iniscatus*	11.990 (9)	12.807 (9)	12.833 (18)				
11 *A. dayi*	14.872 (6)	15.209 (6)	15.706 (12)	10.648 (6)			
12 *A. toba*	12.825 (9)	13.979 (9)	13.884 (18)	9.891 (9)	6.594 (6)		
13 *A. dolores*	13.809 (24)	14.870 (24)	14.747 (48)	10.053 (24)	6.336 (16)	2.549 (24)	
14 *A. aerosus*	10.677 (21)	10.791 (21)	11.236 (42)	13.592 (21)	14.831 (21)	14.240 (21)	14.937 (56)
15 *A. affinis*	9.886 (3)	10.845 (3)	10.814 (6)	13.335 (3)	14.672 (2)	13.931 (3)	15.224 (8)
16 *A. orophilus*	9.111 (15)	9.639 (15)	10.183 (30)	12.354 (15)	13.927 (10)	12.786 (15)	13.707 (40)
17 *A. mollis*	8.421 (18)	8.700 (18)	9.405 (36)	12.267 (18)	13.719 (12)	13.318 (18)	13.784 (48)
18 *A. torques*	9.086 (15)	9.625 (15)	9.818 (30)	12.123 (15)	13.108 (10)	12.668 (15)	13.394 (40)
19 *A. azarae*	12.423 (21)	13.676 (21)	13.550 (42)	13.376 (21)	13.917 (14)	12.770 (21)	13.620 (56)
20 *A. philipmyersi*	14.075 (6)	14.609 (6)	14.909 (12)	14.342 (6)	14.287 (4)	14.681 (6)	15.394 (16)
21 *A. cursor*	13.580 (15)	14.148 (15)	14.555 (30)	14.084 (15)	13.865 (10)	14.402 (15)	14.483 (40)
22 *A. lindberghi*	10.736 (3)	12.059 (3)	12.287 (6)	13.024 (3)	14.003 (2)	13.281 (3)	13.843 (8)
23 *A. mystax*	11.222 (18)	12.577 (18)	12.782 (36)	13.177 (18)	13.851 (12)	13.864 (18)	14.135 (48)
24 *A. montensis*	12.894 (36)	13.690 (36)	14.007 (72)	14.162 (36)	14.427 (24)	15.133 (36)	14.772 (96)
25 *A. reigi*	10.755 (3)	12.024 (3)	12.556 (6)	13.055 (3)	12.220 (2)	13.070 (3)	12.901 (8)

TABLE 2.2.—Continued.

Taxon	Between clades						
	7	8	9	10	11	12	13
26 *A. paranaensis*	12.453 (45)	13.197 (45)	13.290 (90)	14.034 (45)	14.231 (30)	14.786 (45)	14.606 (120)
27 *A. juninensis*	12.617 (3)	13.689 (3)	14.312 (6)	13.137 (3)	13.762 (2)	14.570 (3)	14.287 (8)
28 *A. kofordi*	12.240 (6)	13.158 (6)	13.550 (12)	14.341 (6)	13.275 (4)	14.422 (6)	13.702 (16)
29 *A. fumeus*	12.526 (30)	13.528 (30)	14.110 (60)	13.984 (30)	13.623 (20)	14.482 (30)	13.886 (80)
30 *A. subfuscus*	14.013 (6)	14.504 (6)	15.080 (12)	14.546 (6)	13.266 (4)	14.107 (6)	14.336 (16)
31 *A. lutescens*	11.716 (45)	12.957 (45)	13.429 (90)	12.386 (45)	12.855 (30)	12.944 (45)	13.229 (120)
32 *A. sylvanus*	12.370 (3)	14.029 (3)	14.199 (6)	13.454 (3)	14.233 (2)	13.958 (3)	13.683 (8)
33 *A. viridescens*	13.272 (21)	13.698 (21)	13.731 (42)	13.495 (21)	13.380 (14)	13.026 (21)	13.458 (56)
34 *A. boliviensis*	13.516 (9)	14.237 (9)	14.399 (18)	15.135 (9)	14.221 (6)	13.939 (9)	14.427 (24)
35 *A. spegazzinii*	12.830 (48)	13.630 (48)	14.177 (96)	14.725 (48)	14.068 (32)	14.235 (48)	14.461 (128)

TABLE 2.2.—Continued.

Taxon	Between clades						
	14	15	16	17	18	19	20
15 *A. affinis*	6.319 (7)						
16 *A. orophilus*	8.327 (35)	7.970 (5)					
17 *A. mollis*	8.195 (42)	7.782 (6)	7.342 (30)				
18 *A. torques*	8.124 (35)	7.758 (5)	6.756 (25)	6.498 (30)			
19 *A. azarae*	14.451 (49)	14.110 (7)	14.545 (35)	13.827 (42)	13.153 (35)		
20 *A. philipmyersi*	15.923 (14)	15.860 (2)	15.575 (10)	14.833 (12)	14.090 (10)	13.316 (14)	
21 *A. cursor*	14.339 (35)	14.388 (5)	13.667 (25)	13.181 (30)	13.036 (25)	12.665 (35)	12.385 (10)
22 *A. lindberghi*	12.648 (7)	12.063 (1)	12.343 (5)	10.839 (6)	11.501 (5)	12.260 (7)	11.198 (2)
23 *A. mystax*	12.756 (42)	12.071 (6)	12.438 (30)	10.973 (36)	11.540 (30)	12.633 (42)	11.393 (12)
24 *A. montensis*	15.787 (84)	16.280 (12)	14.539 (60)	13.370 (72)	13.832 (60)	11.952 (84)	12.826 (24)
25 *A. reigi*	12.234 (7)	11.914 (1)	11.872 (5)	11.405 (6)	11.681 (5)	10.385 (7)	12.133 (2)
26 *A. paranaensis*	13.412 (105)	13.530 (15)	12.619 (75)	12.345 (90)	12.650 (75)	11.971 (105)	12.663 (30)
27 *A. juninensis*	13.661 (7)	13.889 (1)	13.664 (5)	12.086 (6)	12.883 (5)	12.369 (7)	12.779 (2)
28 *A. kofordi*	14.438 (14)	14.775 (2)	13.394 (10)	12.923 (12)	12.442 (10)	11.486 (14)	11.697 (4)
29 *A. fumeus*	14.439 (70)	14.809 (10)	14.102 (50)	13.348 (60)	12.596 (50)	11.739 (70)	12.195 (20)
30 *A. subfuscus*	14.346 (14)	14.462 (2)	14.574 (10)	14.036 (12)	13.012 (10)	12.917 (14)	12.962 (4)
31 *A. lutescens*	13.106 (105)	13.086 (15)	13.122 (75)	11.785 (90)	12.051 (75)	10.867 (105)	11.006 (30)
32 *A. sylvanus*	13.565 (7)	14.047 (1)	13.868 (5)	12.747 (6)	12.722 (5)	10.617 (7)	10.674 (2)

TABLE 2.2.—Continued.

Taxon	Between clades						
	14	15	16	17	18	19	20
33 *A. viridescens*	13.588 (49)	13.811 (7)	14.248 (35)	12.771 (42)	12.850 (35)	11.289 (49)	11.718 (14)
34 *A. boliviensis*	14.386 (21)	14.841 (3)	14.610 (15)	13.259 (18)	13.276 (15)	11.601 (21)	11.949 (6)
35 *A. spegazzinii*	14.477 (112)	14.965 (16)	14.636 (80)	13.446 (96)	13.802 (80)	11.650 (112)	12.039 (32)

TABLE 2.2.—Continued.

Taxon	Between clades						
	21	22	23	24	25	26	27
22 *A. lindberghi*	11.181 (5)						
23 *A. mystax*	10.664 (30)	1.725 (6)					
24 *A. montensis*	10.141 (60)	10.634 (12)	10.380 (72)				
25 *A. reigi*	9.448 (5)	9.098 (1)	8.819 (6)	8.161 (12)			
26 *A. paranaensis*	9.693 (75)	10.191 (15)	10.033 (90)	8.062 (180)	5.942 (15)		
27 *A. juninensis*	10.633 (5)	10.351 (1)	10.169 (6)	9.878 (12)	8.899 (1)	10.053 (15)	
28 *A. kofordi*	10.900 (10)	10.549 (2)	10.372 (12)	10.124 (24)	8.897 (2)	10.291 (30)	7.668 (2)
29 *A. fumeus*	11.036 (50)	11.024 (10)	11.116 (60)	10.378 (120)	9.350 (10)	10.747 (150)	7.832 (10)
30 *A. subfuscus*	12.295 (10)	11.839 (2)	12.366 (12)	11.931 (24)	9.674 (2)	11.696 (30)	10.034 (2)
31 *A. lutescens*	10.316 (75)	9.391 (15)	9.168 (90)	10.527 (180)	7.981 (15)	10.154 (225)	7.689 (15)
32 *A. sylvanus*	10.345 (5)	10.760 (1)	10.998 (6)	10.905 (12)	9.594 (1)	10.314 (15)	8.905 (1)
33 *A. viridescens*	10.974 (35)	11.433 (7)	11.513 (42)	11.271 (84)	9.458 (7)	10.978 (105)	8.932 (7)
34 *A. boliviensis*	10.245 (15)	10.967 (3)	10.875 (18)	10.838 (36)	10.031 (3)	11.280 (45)	9.111 (3)
35 *A. spegazzinii*	10.566 (80)	10.966 (16)	10.884 (96)	11.228 (192)	10.577 (16)	10.853 (240)	9.306 (16)

TABLE 2.2.—Continued.

Taxon	Between clades						
	28	29	30	31	32	33	34
29 *A. fumeus*	2.342 (20)						
30 *A. subfuscus*	9.164 (4)	9.354 (20)					
31 *A. lutescens*	7.511 (30)	7.513 (150)	5.563 (30)				
32 *A. sylvanus*	8.333 (2)	8.541 (10)	9.802 (2)	7.985 (15)			
33 *A. viridescens*	8.728 (14)	8.904 (70)	9.367 (14)	7.202 (105)	5.372 (7)		
34 *A. boliviensis*	7.858 (6)	8.417 (30)	9.598 (6)	7.701 (45)	5.517 (3)	4.844 (21)	
35 *A. spegazzinii*	8.251 (32)	8.546 (160)	9.829 (32)	8.190 (240)	5.748 (16)	5.323 (112)	3.020 (48)

TABLE 2.3.—Likelihood scores and p-values used to evaluate the monophyly of constrained clades as given under Shimodaira-Hasegawa (SH) criterion in PAUP. Significant p-values are indicated by asterisks.

Taxon	–Ln	p
Species group		
A. aerosus group	–17722.81330	0.097
excluding subgenus *Hypsimys*	–17710.08117	0.457
A. boliviensis group	–17708.99963	0.922
A. cursor group	–17711.69636	0.831
A. varius group	–17731.22569	0.270
Species		
A. aerosus	–17730.20498	0.269
A. lutescens	–17710.47834	0.408
A. mimis	–17711.46106	0.761
A. mollis	–17811.64131	<0.001*
A. orophilus	–17766.89277	0.011*

TABLE 2.4.—Percentage sequence divergence of cytochrome b corrected by Kimura 2-parameter model (Kimura 1980) for comparisons within and between subspecies of *Akodon* recovered in phylogenetic analyses (Figs. 2.2–2.6). The number of pairwise comparisons is given in parentheses. A) *A. lutescens*, B) *A. aerosus*, C) *A. mollis* and *A. orophilus*, and D) *A. mimus*.

A.

		Between clades			
Taxon	Within clade	1	2	3	4
1 *A. lutescens lutescens*	-				
2 *A. lutescens puer*	0.494 (10)	2.077 (5)			
3 *A. lutescens caenosus* – All	1.193 (36)	3.785 (9)	4.038 (45)		
4 *A. lutescens caenosus* – A	-	4.061 (1)	4.278 (5)	-	
5 *A. lutescens caenosus* – B	0.065 (28)	3.750 (8)	4.009 (40)	-	3.083 (8)

B.

		Between clades			
Taxon	Within clade	1	2	3	4
1 *A. aerosus aerosus*	2.366 (3)				
2 *A. aerosus baliolus*	1.623 (3)	6.742 (9)			
3 *A. aerosus* – MVZ 171679	-	8.470 (3)	8.877 (3)		

TABLE 2.4.—Continued.

C.

Taxon	Within clade	Between clades 1	2	3	4	5
1 *A. orophilus orophilus*	0.235 (3)					
2 *A. orophilus orientalis*	-	6.519 (3)				
3 *A. orophilus* – MVZ 173057	-	7.206 (3)	8.349 (1)			
4 *A. mollis altorum*	1.561 (6)					
5 *A. mollis mollis*	-				2.828 (4)	
6 *A. mollis* – FMNH 129212	-			2.692 (1)	7.383 (4)	7.5521 (1)

D.

Taxon	Within clade	Between clades 1	2	3	4
1 *A. mimus* – MCXMTCYTBB	-				
2 *A. mimus* – NK30599	-	10.274 (1)			
3 *A. mimus*	0.240 (3)	12.094 (3)	12.637 (3)		

FIGURE LEGENDS

FIG. 2.1.—Distribution (approximate; from Braun et al. 2008; Jayat et al. 2010; Musser and Carleton 2005; Myers 1989; Myers and Patton 1989b; Myers et al. 1990; Smith and Patton 1992a, 1993) of the genus *Akodon*.

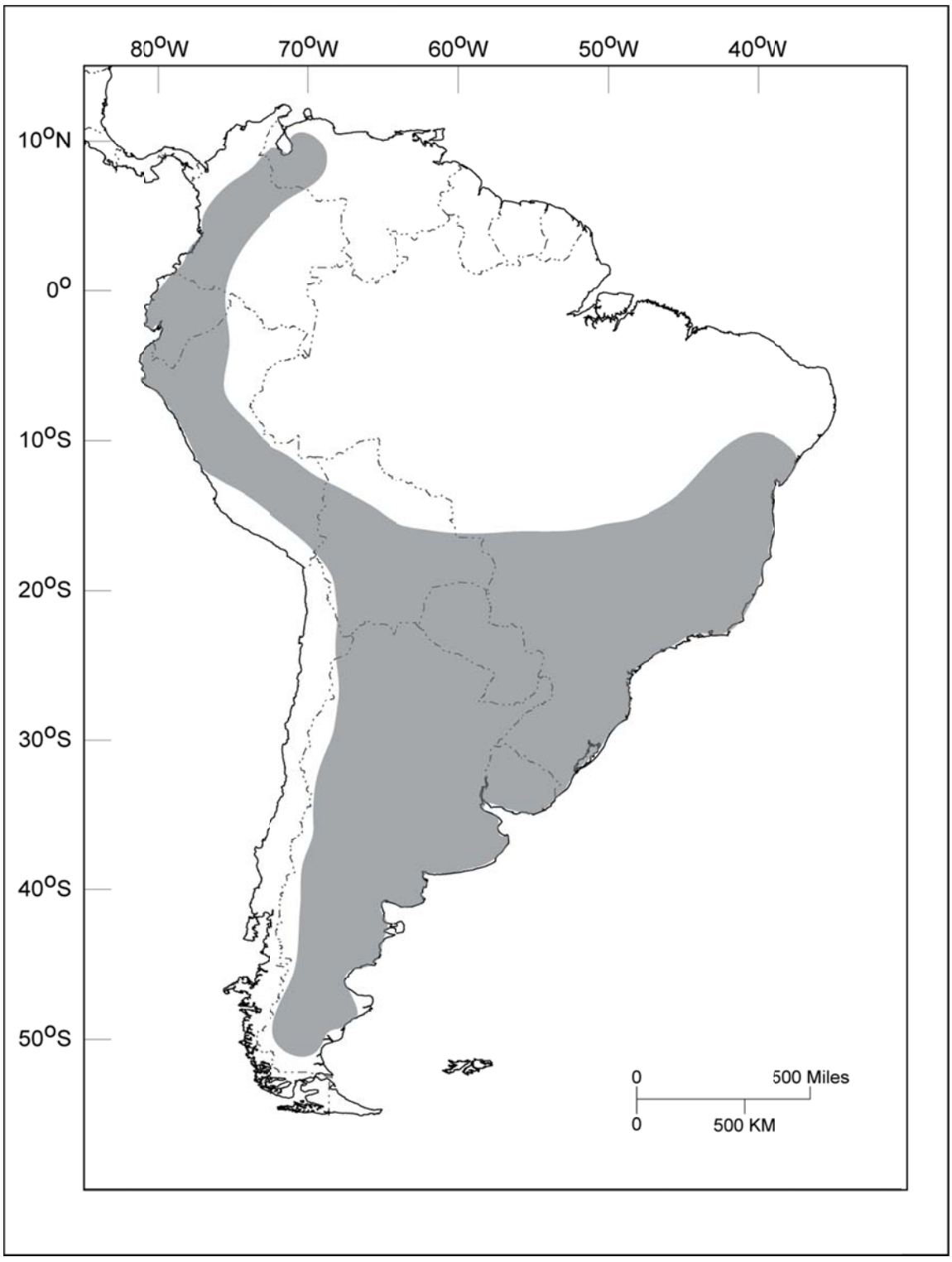
FIG. 2.2.—Cladogram depicting relationships of *Akodon* based upon analysis of the cytochrome b gene under maximum parsimony, maximum likelihood, and Bayesian phylogenetic criterion. Values given at each node correspond to bootstrap percentages for maximum parsimony followed by maximum likelihood given above the branch and Bayesian posterior probabilities given below the branch. Nodes are not labeled within each group (see Figs. 2.3-2.6 for these values). Triangles are proportional to the number of individuals included within each species clade.

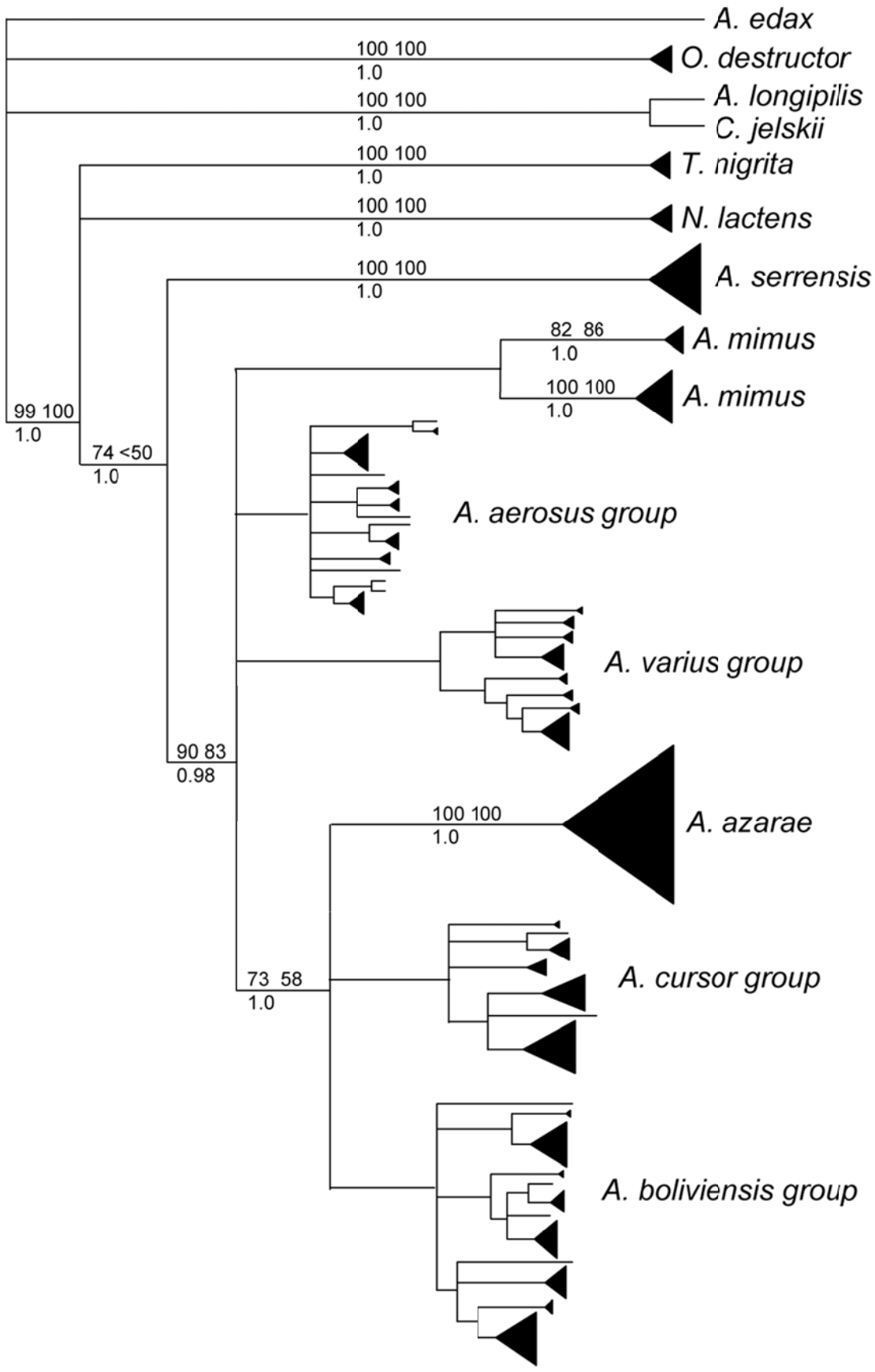
FIG. 2.3.—Cladogram depicting relationships within the *A. cursor* group. Values given at each node correspond to bootstrap percentages for maximum parsimony followed by maximum likelihood given above the branch and Bayesian posterior probabilities given below the branch. Triangles are proportional to the number of individuals included within each species clade.

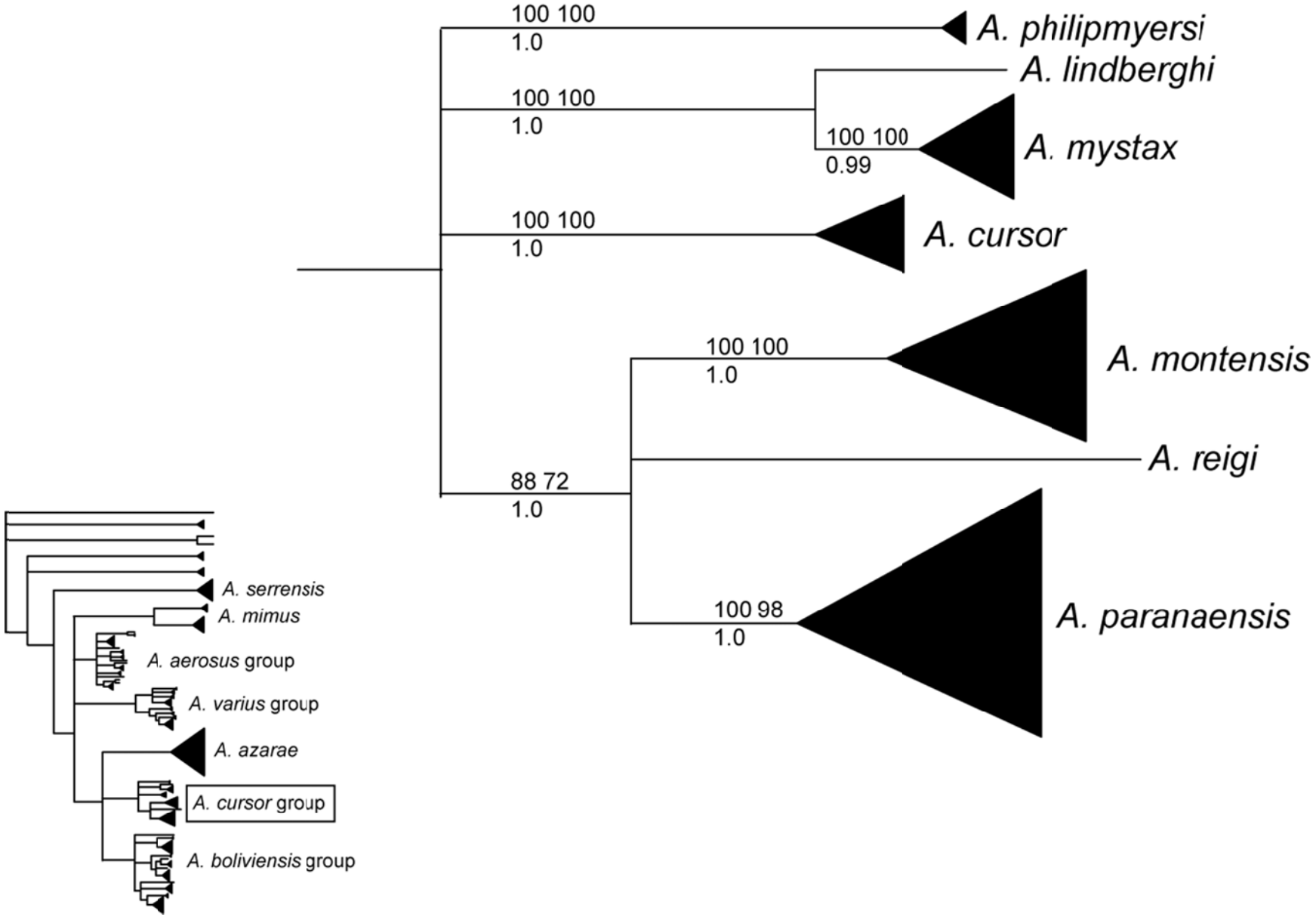
FIG. 2.4.—Cladogram depicting relationships within the *A. boliviensis* group. Values given at each node correspond to bootstrap percentages for maximum parsimony followed by maximum likelihood given above the branch and Bayesian posterior probabilities given below the branch. Triangles are proportional to the number of individuals included within each species clade.

FIG. 2.5.—Cladogram depicting relationships within the *A. varius* group. Values given at each node correspond to bootstrap percentages for maximum parsimony followed by maximum likelihood given above the branch and Bayesian posterior probabilities given below the branch. Triangles are proportional to the number of individuals included within each species clade.

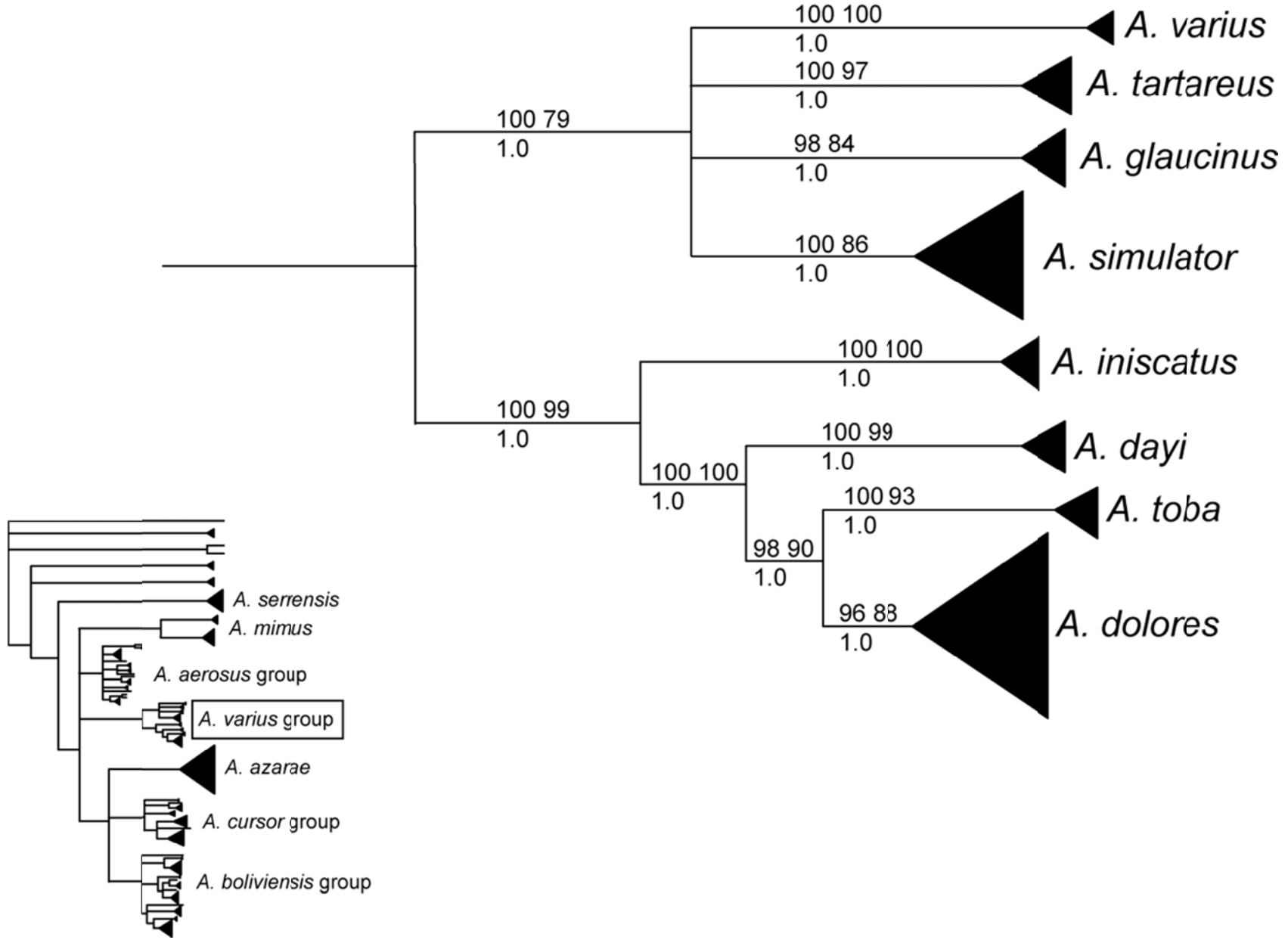
FIG. 2.6.—Cladogram depicting relationships within the *A. aerosus* group. Values given at each node correspond to bootstrap percentages for maximum parsimony followed by maximum likelihood given above the branch and Bayesian posterior probabilities given below the branch. Triangles are proportional to the number of individuals included within each species clade.


80°W
70°W
60°W
50°W
40°W
10°N
0°
10°S
20°S
30°S
40°S
50°S
0
500 Miles
0
500 KM


A. edax
100 100
1.0
O. destructor
100 100
1.0
A. longipilis
C. jelskii
100 100
1.0
T. nigrita
100 100
1.0
N. lactens
100 100
1.0
A. serrensis
82 86
1.0
A. mimus
100 100
1.0
A. mimus
99 100
1.0
74 <50
1.0
A. aerosus group
A. varius group
90 83
0.98
100 100
1.0
A. azarae
73 58
1.0
A. cursor group
A. boliviensis group


100 100
1.0
A. philipmyersi
A. lindberghi
100 100
1.0
100 100
0.99
A. mystax
100 100
1.0
A. cursor
100 100
1.0
A. montensis
A. reigi
88 72
1.0
100 98
1.0
A. paranaensis
A. serrensis
A. mimus
A. aerosus group
A. varius group
A. azarae
A. cursor group
A. boliviensis group

A. juninensis
70 71
0.99
A. kofordi
100 100
1.0
80 83
0.99
A. fumeus
100 100
1.0
A. subfuscus
A. lutescens lutescens
98 100
1.0
98 95
1.0
100 100
1.0
A. lutescens puer
A. lutescens caenosus
97 79
1.0
A. lutescens caenosus
A. sylvanus
100 100
1.0
A. viridescens
100 81
1.0
100 99
1.0
A. boliviensis
99 <50
1.0
99 <50
1.0
A. spegazzinii
A. serrensis
A. mimus
A. aerosus group
A. varius group
A. azarae
A. cursor group
A. boliviensis group


100 100
1.0
A. varius
100 97
1.0
A. tartareus
100 79
1.0
98 84
1.0
A. glaucinus
100 86
1.0
A. simulator
100 100
1.0
A. iniscatus
100 99
1.0
100 99
1.0
A. dayi
100 100
1.0
100 93
1.0
A. toba
98 90
1.0
96 83
1.0
A. dolores
A. serrensis
A. mimus
A. aerosus group
A. varius group
A. azarae
A. cursor group
A. boliviensis group

A. serrensis
A. mimus
A. aerosus group
A. varius group
A. azarae
A. cursor group
A. boliviensis group

100 100
1.0
A. budini
100 100
1.0
A. siberiae
100 100
1.0
A. albiventer
A. aerosus - MVZ171679
100 96
1.0
A. aerosus baliolus
94 96
1.0
100 100
1.0
A. aerosus aerosus
A. affinis
A. mollis mollis
100 98
1.0
83 85
0.74
A. mollis altorum
100 100
1.0
A. orophilus orophilus
A. orophilus orientalis
100 100
1.0
A. mollis - FMNH129212
A. orophilus - MVZ173057
94 80
1.0
98 95
1.0
A. torques

CHAPTER III

PHYLOGENETIC RELATIONSHIPS AND HISTORICAL BIOGEOGRAPHY OF THE GENUS *AKODON* (RODENTIA, CRICETIDAE) USING A MULTI-GENE APPROACH

ABSTRACT – Phylogenetic relationships among 81 individuals of *Akodon* from throughout South America were examined using a concatenated dataset consisting of one mitochondrial gene (cytochrome b), one nuclear gene (dentin matrix protein), and one nuclear intron (thyrotropin). The combined dataset included 2,841 base pairs and was analyzed phylogenetically under maximum parsimony, maximum likelihood, and Bayesian criteria. A monophyletic *Akodon* clade is recovered, and relationships within the genus are well resolved. Monophyly of the *boliviensis* and the *cursor* groups are supported, and the two form a strongly supported sister relationship. *Akodon azarae* is basal to and forms a monophyletic group with the *boliviensis*+*cursor* group, resolving the placement of *A. azarae*. The *aerosus* group and the *varius* group are paraphyletic as four members of the *varius* group (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) fall within the *aerosus* group. Based upon BEAST analysis, the initial divergence within *Akodon* began during the Pliocene and ancestors of the four extant species groups emerge

around the Pleistocene-Pliocene boundary. Most of the divergence within *Akodon* occurred between 0.5-1.5 million years before present (mybp), but some taxa diverged as recently as 300,000 years ago. The concatenation of genes resulted in a well-resolved tree, the best molecular phylogeny in terms of resolution and nodal support of *Akodon* obtained to date, and future studies should include not only rare and geographically limited species of *Akodon* but also should utilize a multi-gene approach.

INTRODUCTION

With approximately 70 genera and more than 350 species, North American immigrants of the subfamily Sigmodontinae (Rodentia, Muridae) are the most successful colonizers, in terms of diversity, of South America (Musser and Carleton 2005; Smith and Patton 1999). The diversity of forms of Sigmodontinae surpasses that of any other clade of northern immigrants. Within the subfamily, taxa are separated into seven or eight tribes and a number of "unique lineages" with taxa considered *incertae sedis*, or of uncertain tribal affinity (D'Elía et al. 2007; Musser and Carleton 2005; Reig 1980; Smith and Patton, 1999). Sigmodontine rodents have colonized the entire South American continent with individuals present at both low (sea level) and high elevations (4500 m) and in all ranges of climates and habitats (Musser and Carleton 2005).

To better understand evolutionary and biogeographic radiation of sigmodontine rodents in South America, phylogenetic relationships among and within the seven or eight tribal lineages must be clarified. Among these tribes, Akodontini is the second largest, most widely distributed, and arguably, the most taxonomically challenging. The concept of an akodontine group or tribe is traced to Thomas (1916, 1918) who recognized morphological resemblances between *Akodon* and its allies (*Abrothrix*, *Chroeomys*,

Deltamys, *Hypsimys*, *Bolomys*, *Thalpomys*, and *Thaptomys*). Formal use of the term Akodontini referring to this akodont group was first coined by Vorontzov (1959 cited in Reig 1987). Genera included in the tribe have remained relatively dynamic with 22 genera being included at one time or another (D'Elía et al. 2003; McKenna and Bell 1997; Reig 1986; Smith and Patton 1999). Until recently, systematic relationships and genus and species limits remained unresolved and problematic. A number of molecular studies beginning in the early 1990s (D'Elía 2003; D'Elía et al. 2003; Patton and Smith 1992a, 1992b, Smith and Patton 1991, 1993, 1999, 2007), along with morphologic (e.g. Hershkovitz 1990a, 1990b, 1998; Myers 1989; Myers and Patton 1989a, 1989b; Myers et al. 1990), cytogenetic (e.g. Barquez et al. 1980; Blaustein et al. 1992; Fagundes et al. 1998; Geise et al. 1998, 2001; Liascovich 1991; Sbalquiero and Nascimento 1996; Silva and Yonenaga-Yassuda 1998; Spotorno 1987) and allozymic (e.g. Apfelbaum and Reig 1989; Barrantes et al. 1993; Patton et al. 1989; Rieger et al. 1995; Spotorno 1987) data, have greatly advanced our understanding of the taxonomy and systematics of Akodontini. These studies helped to resolve higher-level taxonomic relationships, exclude taxa historically placed within Akodontini, establish species limits, define sister-taxa at multiple levels, and reconsider and redefine taxonomic limits of the tribe.

Recent studies found the tribe, as it was traditionally defined, to be polyphyletic (Smith and Patton 1993, 1999). Six genera (*Abrothrix*, *Chelemys*, *Chroeomys*, *Geoxus*, *Notiomys*, and *Pearsonomys*) formed a well supported Andean clade that was not sister to the remaining genera of Akodontini. This Andean clade, to become known as the Tribe Abrothrochini, is not only linked by mitochondrial DNA and protein electrophoretic loci but also shares a common karyotype, male bacular morphology, and ectoparasites, and

the clade is present in the Andes from central Peru to Tierra del Fuego, thus offering support that it is distinct from the traditionally-defined akodontine tribe (D'Elía et al. 2007; Smith and Patton 1993, 1999).

Without the abrothricines, the redefined Akodontini includes at least 14 genera (including *Bibimys*, *Kunsia*, and *Scapteromys* of the previously recognized tribe Scapteromyini) and more than 70 species making it the second most diverse sigmodontine tribe behind Oryzomyini (Musser and Carleton 2005; Smith and Patton 1993, 1999). Of the genera remaining in Akodontini, perhaps the most taxonomically challenging and most crucial to understanding the phylogeny of Akodontini is the genus *Akodon*. Despite revisionary changes that reelevated the *Akodon* subgenera *Deltamys*, *Thalpomys*, and *Thaptomys*, all originally described as distinct genera, to generic status, *Akodon* retains more than one half of all recognized akodontine species and has been described as standing "at the nexus of a host of specific- and generic-level taxonomic problems" (Musser and Carleton 2005).

The genus *Akodon*, collectively known as South American grass mice, occurs from northern Venezuela to southern Argentina extending east of the Andes to the Atlantic Ocean and south of the Amazon lowlands to just north of Tierra del Fuego (Fig. 3.1). The genus extends northward in a band along the northern Andes and is absent from the Amazon lowlands and west of the Andes. Species of *Akodon* are known to inhabit a variety of habitats from subtropical and tropical moist forest to the altiplano and deserts (Braun et al. 2008; Jayat et al. 2010; Musser and Carleton 2005; Myers 1989; Myers and Patton 1989b; Myers et al. 1990; Smith and Patton 1992a).

Akodon, first described in 1833 (Meyen), contains approximately 65 named forms organized into 46 species. Species of *Akodon* are partitioned into four species groups (Table 2.1): an *aerosus* group containing species that occupy the elfin and upper tropical forests along the slopes of the Andes from Colombia to northern Argentina (Smith and Patton 1992a, 2007), a *boliviensis* group containing small bodied *Akodon* known from Peru and high elevations of Bolivia and mid to high elevations in Argentina (Myers et al. 1990), a *cursor* group containing species that occupy the coastal forests of Brazil, Paraguay, Uruguay, and northeastern Argentina (Geise et al. 2001; Smith and Patton 2007), and a *varius* group containing the largest species of *Akodon* that occupy low to mid elevations of the eastern slopes of the Andes and lowland regions of Argentina, Bolivia, and Paraguay (Myers 1989). Additionally a number of species remain unassigned to any of the species groups and are referred to as *incertae sedis* taxa.

Previous studies on *Akodon* often were constrained by feasibility and access to samples or focused on higher-level systematic and taxonomic relationships. Therefore to date, all previous studies have included only a subset of *Akodon* species. Despite the taxonomic diversity of the genus, only 30 taxa have been used in molecular studies represented by 43 individuals for the complete mitochondrial cytochrome b gene and 12 individuals for the nuclear interphotoreceptor binding protein gene (IRBP). Based on those limited samples and recognizing the limitations of their results, previous studies have detected the following patterns and clades (see D'Elía 2003; D'Elía *et al*. 2003; Smith and Patton 1993, 1999, 2007). Species of *Akodon* (*sensu stricto*) form a strongly supported monophyletic clade with four commonly recovered groups of species and several ambiguous lineages (Table 3.1). The four species groups can be separated based

on geographic distributions, but levels of support and phylogenetic resolution vary greatly (Table 3.2).

The lack of resolution in current *Akodon* phylogenies makes it difficult to evaluate the biogeographic relationships of the genus. A few recent studies have attempted, with limited success, to evaluate the group's biogeography (see Geise et al. 2001; Patton and Smith 1992a, 1992b; Patton et al. 1990; Smith and Patton 1999, 2007). Based on those studies, preliminary conclusions included sister taxa speciations being allopatric, broadly overlapping species not correlating to sister taxa, and the possibility that diversification took place across ecological gradients. It was clear to those authors that a more resolved phylogeny is necessary before a more critical and detailed biogeographical assessment of the genus can occur.

Therefore, the purpose of this study was to examine the relationships among species of the genus *Akodon* (*sensu stricto*), investigate the validity of the informal species groupings, evaluate the status of supraspecific taxa, and clarify any remaining taxonomic uncertainties. By resolving interspecific relationships of *Akodon*, major steps can be made in understanding the evolution of Akodontini, which in turn can help in answering many questions regarding the sigmodontine radiation.

MATERIALS AND METHODS

TAXON SAMPLING.—For this study, individuals corresponding to 24 of the 46 currently recognized *Akodon* species were obtained. Individual from each of the species groups were included: 5 of 9 from the *A. aerosus* group, 7 of 13 from the *A. boliviensis*

group, 2 of 6 from the *A. cursor* group, 8 of 11 from the *A. varius* group, and 2 of 7 of the *incertae sedis* taxa.

Five additional taxa were also included. One sample of *Necromys lactens* was included as a non-*Akodon* representative of the Tribe Akodontini. One sample of *Abrothrix olivaceus* was included as a representative of the Tribe Abrothrochini. One sample of *Andinomys edax* and two samples of *Oligoryzomys destructor* were included as representatives of the Tribes Phyllotini and Oryzomyini, respectively.

EXTRACTION, AMPLIFICATION, AND SEQUENCING.—Whole genomic DNA was isolated from heart, kidney, liver, or skeletal muscle tissues following standard protocol (Longmire et al. 1997) or using the DNEasy Tissue Kit (Quiagen, Valencia, California). The mitochondrial cytochrome b gene and two nuclear genes (dentin matrix protein and thyrotropin) were selected for amplification and sequencing based upon their observed and expected utility in resolving relationships at the taxonomic level of interest in this study (Jansa et al. 2006; Matthee et al. 2004; Smith and Patton 1991, 1993, 1999, 2007; Van Den Bussche et al. 2003). Amplifications for all primer pairs were performed in 25 µl reactions containing 200-500 ng of DNA, 1 unit of Taq polymerase, 0.2 µM of each external primer, 1.2 mg/ml bovine serum albumin (BSA), 3 mM of $MgCl_2$, 6 µl of 5X buffer, 0.17 mM of each dinucleotide triphosphate, and water to volume.

The entire cytochrome b (cytb) gene was amplified and sequenced using external primers MVZ05 and MVZ14 or H15915 (Irwin et al. 1991; Smith and Patton 1993) and a series of internal primers (Braun et al. 2008; Smith and Patton 1993). Additional internal primers developed for this project are listed in Table 3.3. The thermal profile used when amplifying cytb included an initial denaturation at 95°C for 3 min, followed by 35 cycles

at 95°C for 30 s, 52°C for 50 s, and 72°C for 1 min. A final elongation at 72° for 10 min was performed to ensure completeness of reactions.

Exon 6 of the dentin matrix protein 1 (DMP1) gene was amplified and sequenced using external primers Den2 and Den12 and a series of previously developed internal primers (Jansa et al. 2006; Van Den Bussche et al. 2003). Additional internal primers were developed and are listed in Table 3.3. The thermal profile used to amplify DMP1 included an initial denaturation at 95°C for 3 min, followed by 35 cycles at 95°C for 30 s, 48-52°C for 50 s, and 72°C for 1 min. A final elongation at 72° for 10 min was also performed.

An intron, thyrotropin (THY), was amplified and sequenced using the previously published primer pair RabbitTHYa and RabbitTHYb (Matthee et al. 2004). A number of individuals could not be amplified using RabbitTHYa and RabbitTHYb, so a second primer pair (THYF and THYR; Table 3.3) was developed for this project. The primer pair annealed approximately 10-30 base pairs internal to ends of the gene, and therefore sequences from the individuals using this pair of primers have missing data at each end. The thermal profile used to amplify THY included an initial denaturation at 95°C for 3 min, followed by 35 cycles at 95°C for 30 s, 48-55°C for 50 s, and 72°C for 1 min, followed by a final elongation at 72° for 10 min.

All double stranded PCR products were purified using the Wizard PCR Prep DNA Purification System (Promega, Madison, Wisconsin), and products were sequenced on a 3130 Genetic Analyzer using BigDye Terminator v1.1 Sequencing Kits and POP-7 polymer (Applied Biosystems, Carlsbad, California). Upon completion of sequencing, overlapping fragments for each gene for each taxon were assembled in Geneious Pro

4.6.1 (Drummond et al. 2008). Each data set was then aligned using the ClustalW2 option and visually inspected in Geneious Pro 4.6.1 (Drummond et al. 2008; Larkin et al. 2007). For phylogenetic analysis, nucleotides were coded as unordered discrete characters.

Five taxa were included to serve as outgroups. One sample of *Necromys lactens* was included as a non-*Akodon* representative of the Tribe Akodontini. One sample of *Abrothrix longipilis* representing the Tribe Abrothrochini was included for comparison, and three individuals from two species (*Andinomys edax* and *Oligoryzomys destructor*) were included as representatives of the Tribe Phyllotini and the Tribe Oryzomyini, respectively. During analysis, the samples of *Oligoryzomys* and *Andinomys* were explicitly defined as outgroups, as they represent the most distantly related taxa included here.

DATA ANALYSES.—Phylogenetic relationships within *Akodon* and between genera of the Tribe Akodontini were estimated for each gene separately under the criteria of maximum parsimony and maximum likelihood using PAUP (Swofford 2000) and Bayesian phylogenetics using MRBAYES (Huelsenbeck and Ronquist 2001). Because each approach has its own strengths and weaknesses, a "pluralistic" approach was employed. Despite recent discussion that has concluded such "pluralism" is widely used but not well justified (Giribet et al. 2002), a clade was considered strongly supported if bootstrap values were ≥70% and the Bayesian posterior probability was ≥0.95 in at least two of the three analyses.

For maximum parsimony, stability of clades was evaluated by performing 1000 bootstrap pseudoreplicates with 25 random additions of input taxa and tree-bisection-reconnection (TBR) branch-swapping. Prior to maximum-likelihood analysis,

jMODELTEST was used to determine the model of DNA sequence evolution that best fits the data (see Table 3.4 for model parameters by dataset; Guindon and Gascuel 2003; Posada 2008). Stability of clades on the resulting tree was evaluated using a bootstrap analysis with 100 replications and Nearest-Neighbor Interchange (NNI) branch-swapping. Bayesian analysis was performed using the GTR+Γ model of DNA sequence evolution, along with site-specific rate variation calculated for each of the 3 positions of the codon via the "ssgamma" option in MRBAYES. Four simultaneous Markov chains were run for 5,000,000 generations, with random, unconstrained, starting trees. Trees were sampled every 100 generations, with a "temperature" set at 0.02. Three independent runs of MRBAYES were performed using a different outgroup taxon (*A. edax* – MSB 57099, *Oligoryzomys destructor* – OMNH 34497, *O. destructor* – OMNH 34399).

Gaps were present in the datasets of both DMP1 and THY. Because these gaps appeared phylogenetically informative, a binary matrix, for the presence or absence of gaps, was constructed using the program SeqState (Müller 2005). The binary matrix was appended to the character matrix in the maximum parsimony and Bayesian analyses of the each dataset to consider any information contained in the gaps (Simmons and Ochoterena 2000). Maximum likelihood analyses does not account for gaps, which can only be coded as missing data. Gaps are unknown in cytb, and therefore gap coding will not affect its analyses.

A combined data analysis was performed by concatenating the data from the three genes, including appended gap binary matrices, into a single file. Maximum parsimony, maximum likelihood, and Bayesian analyses was carried out as in the separate analyses. Clades in the combined analyses were considered strongly supported if bootstrap values

of ≥70% and Bayesian posterior probabilities of ≥0.95 are recovered in two of the three analyses. A molecular clock test was performed under the likelihood criterion in PAUP, and the differences between the maximum tree score and the tree score obtained when enforcing a molecular clock were compared with a chi-square distribution.

A priori hypotheses regarding the monophyly of species groups and other supraspecific taxa were tested by conducting Shimodaira-Hasegawa tests (SH; Shimodaira and Hasegawa 1999) under likelihood criterion in PAUP. The SH tests allow for comparison of a priori hypotheses (monophyly of supraspecific taxa) with a posteriori hypotheses (trees generated here). Percent sequence divergence within and among strongly supported clades was computed for the cytb gene based upon Kimura 2-parameter corrected distances to allow for comparison of sequence divergence and evaluation of cryptic species (Baker and Bradley 2006; Bradley and Baker 2001).

Times of divergence were estimated using BEAST v1.5.4 (Drummond and Rambaut 2007). The BEAST dataset included information from all three genes that was pruned to 28 samples, including one individual of *Necromys* and a single representative of each of the recognized *Akodon* species and subspecies included in the study. An uncorrelated relaxed clock, a lognormal distribution for rate variation among branches, and an assumption of independent rates among branches were employed during the BEAST analysis. Additionally, the GTR + I + Γ model of sequence evolution and a Yule species prior on rates of evolution were used. Divergence dates obtained from the fossil record were available for two nodes, the *Necromys-Akodon* split at 3.5 million years before present (mybp) and the initial divergence within *Akodon* at 2.5 mybp (Cione and Tonni 2001; Pardiñas and Tonni 1998; Pardiñas et al. 2002; Smith and Patton 1999,

2007). Five independent runs were completed on the BEAST dataset, with each run consisting of 20,000,000 generations and 10 percent burn-in. Each analysis was inspected to make sure each converged and log files from the 5 independent runs were combined in TRACER v. 1.4 (Rambaut and Drummond 2007). Trees were summarized using TreeAnnotator in BEAST and visualized using FigTree v. 1.3.1 (Rambaut 2006)

RESULTS

For this study, 81 individuals corresponding to 24 currently recognized *Akodon* species were included. An additional eight species were obtained but sequencing of all three genes was unsuccessful. A number of *Akodon* species are rare or geographically restricted and remain uncommon in scientific collections or unavailable for destructive sampling.

Complete sequences for cytb were obtained for 74 individuals. Problems arose with sequencing the ends of the cytochrome b gene for some individuals, therefore partial sequences that have missing data at each end (4-68 base pairs) were obtained for an additional 12 individuals. Of the 1140 sequenced bases, 641 were constant and 499 were variable with 106 at the 1st position, 38 at the 2nd position, and 355 at the 3rd position. Maximum likelihood analysis produced a single optimal tree (tree score = –12207.99914) and bootstrap analysis revealed 50 clades supported in ≥70% of the iterations (Fig. 3.2). Unweighted parsimony analysis resulted in 100 equally parsimonius trees of 2081 steps (consistency index, excluding uninformative characters = 0.3134; retention index = 0.7954). Bootstrap analysis revealed 51 clades supported in ≥70% of the iterations (Fig. 3.2). Bayesian analysis reached stationarity with *A. edax* at 300,000 generations, with *O.*

destructor (OMNH 34497) at 300,000 generations, and *O. destructor* (OMNH 34399) at 200,000 generations. All resulting topologies from Bayesian analysis were identical and revealed 55 clades supported with a posterior probability of ≥0.95 (Fig. 3.2).

Sequence data were generated for 86 individuals for the dentin matrix protein gene with sequence lengths ranging from 1102-1126 base pairs. Similar to cytochrome b, some individuals produced partial sequences (1 – 57 base pairs missing) for the 3' end of this portion of DMP1. Of the 27 individuals with partial sequences, 13 produced sequences missing only the last base pair. Of the 1126 positions within the DMP1 alignment, 932 were constant and 194 were variable with 40 at the 1st position, 47 at the 2nd position, and 107 at the 3rd position. Maximum likelihood analysis produced a single optimal tree (tree score = –3769.85022) and bootstrap analysis revealed 14 clades supported in ≥70% of the iterations. Unweighted parsimony analysis resulted in 100 equally parsimonius trees of 331 steps (consistency index, excluding uninformative characters = 0.5542; retention index = 0.8601). Bootstrap analysis revealed 15 clades supported in ≥70% of the iterations. Bayesian analysis reached stationarity with *A. edax* at 500,000 generations, with *O. destructor* (OMNH 34497) at 550,000 generations, and *O. destructor* (OMNH 34399) at 450,000 generations. All resulting topologies from the three independent Bayesian runs were identical with the exception of the support values for 3 clades. A clade uniting 2 samples of *A. cursor* (MSB 67433 and MSB 67439) with one sample of *A. montensis* (FMNH 141622) was highly supported (posterior probability = 0.99) in one of the Bayesian runs but was only marginally supported in the other two runs (posterior probabilities = 0.90 and 0.87). Two other clades, one revealing a sister relationship between 2 samples of *A. spegazzinii* (OMNH 35926 and OMNH 37398) and

the other revealing a sister relationship between one sample of *A. spegazzinii* (CML XXXX – Arg 4994) and one sample of *A. toba* (MSB 80493), are strongly supported in two of the Bayesian runs (posterior probability of 0.95-0.99) and marginally supported in the 3rd run (0.91-0.92). Like the maximum likelihood and maximum parsimony analyses, the Bayesian analyses of the DMP1 gene were relatively unresolved and revealed only 17-18 clades supported with a posterior probability of ≥0.95, depending upon the run.

The sequence alignment for THY consisted of 86 individuals, with individual *Akodon* sequence lengths ranging from 573-575 base pairs. The same difficulties in sequencing end regions resulted in 10 individuals missing data at the 5' end, 17 individuals missing data at the 3' end, and 7 individuals producing sequences missing data at both ends. Missing data ranged in length from 2-27 base pairs at the 5' end and 1-11 base pairs at the 3' end. Of the 575 base positions in the THY dataset, 483 were constant and 92 were variable. Like the DMP1 dataset, a binary matrix containing gap information for 11 gaps was appended to the THY dataset. Maximum likelihood analysis produced a single optimal tree (tree score = –1558.30835) and bootstrap analysis revealed 3 clades supported in ≥70% of the iterations. Unweighted parsimony analysis resulted in 100 equally parsimonius trees of 137 steps (consistency index, excluding uninformative characters = 0.6842; retention index = 0.8855). Bootstrap analysis revealed 5 clades supported in ≥70% of the iterations. Bayesian analysis reached stationarity with *A. edax* at 450,000 generations, with *O. destructor* (OMNH 34497) at 400,000 generations, and *O. destructor* (OMNH 34399) at 400,000 generations. All resulting topologies from Bayesian analysis were identical and 9 strongly supported clades were revealed. Two additional nodes have slightly lower posterior probability (posterior probability ≥0.90).

Worth noting is that one of these nodes reveals the monophyletic clade of *Akodon* (*sensu stricto*) with a Bayesian posterior probability of 0.91.

The concatenated dataset for all 86 individuals included 2,841 base pairs of sequence data. The two appended gap matrices were included adding 22 characters for analysis. Maximum likelihood analysis produced a single optimal tree (tree score = –17293.80225) with 59 clades supported in ≥70% of the bootstrap iterations. Unweighted parsimony analysis resulted in 12 equally parsimonius trees of 2,695 steps (consistency index, excluding uninformative characters = 0.3323; retention index = 0.7861). Bootstrap analysis revealed 59 clades supported in ≥70% of the iterations. Bayesian analyses reached stationarity with all three outgroup taxa at 200,000 generations. All resulting topologies from Bayesian analysis were identical and 58 strongly supported clades were revealed.

In the composite tree (Fig. 3.3) containing information from all analyses for the combined dataset, strongly supported monophyletic clades corresponding to 15 of the species included are identifiable. Seven additional species are represented by a single specimen each and, therefore, their monophyly cannot be assessed. The monophyly of two species, *A. mimus* and *A. simulator*, are not supported. Clades corresponding to the *boliviensis* group and *cursor* groups are monophyletic and sister to each other. Basal to these two clades, *A. azarae* emerges with strong levels of support for a sister relationship between *A. azarae* and the larger clade containing the *boliviensis* and *cursor* groups. The *aerosus* group also emerges in all analyses (Fig. 3.3), but levels of support for its monophyly are low. Irrespective of the monophyly of the *aerosus* group, part of the *varius* group (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) is contained within

a clade containing all members of the *aerosus* group and *A. albiventer* but not including the remaining members of the *varius* group. A clade containing the remaining taxa of the *varius* group is monophyletic, but the relationship between this clade and the other clades within *Akodon* is unresolved. The monophyly of *A. mimus* is recovered but with low support values, and divergence within *A. mimus* is high at 8.515%.

Kimura 2-parameter corrected distances of the cytb gene were used to evaluate percent sequence divergence within and among clades. Within clades, divergence values (Table 3.3) ranged from 0.053% in *A. viridescens* to 5.124% in *A. aerosus*. Percent sequence divergence among clades (Table 3.5) were lowest between *A. fumeus* and *A. kofordi* (2.294%), *A. tartareus* and *A. glaucinus* (2.331%), and *A. toba* and *A. dolores* (2.454%). Divergence values were highest between *A. dayi* and *A. simulator* (15.815%), *A. albiventer* and *A. dayi* (15.885%), and *A. montensis* and *A. aerosus* (15.949%).

The null hypothesis that the data were evolving under a strict molecular clock was rejected (-ln = 17368.35338; $2\Delta L = 149.10226$; $p < 0.001$). The monophyly of the *A. varius* group was tested by constraining each group and independently comparing likelihood scores to the score of the ML tree. Constraining the monophyly of the *A. varius* group resulted in a significantly different likelihood score (likelihood of constrained tree = –17322.65840; $p = 0.030$).

BEAST analysis recovered a topology (Fig. 3.4) nearly identical to the composite tree with one exception. *Akodon mimus* does not form a monophyletic clade with one sample (MSB 70488) allying with *A. azarae* and the *boliviensis* and *cursor* groups and the other sample (AMNH 261211) allying with the *aerosus* and *varius* groups. While *A. mimus* was recovered as monophyletic in the ML and Bayes trees, the support values

were low so the differing topologies are to be expected. Two nodes recovered in the BEAST tree are unsupported and the ages of these two nodes are unreliable. The node ages obtained in the BEAST analyses (Table 3.6) suggest an initial divergence within the genus at 3.1 mybp during the Pliocene with the oldest lineages diverging during the Pliocene but with most divergences of extant species occurring since the beginning of the Pleistocene.

DISCUSSION

Previous studies of *Akodon* have excluded taxa historically included within the genus and have provided information on relationships within the genus, but conclusions were limited by the support and resolution obtained. An increased genetic sampling, specifically the addition of more conservatively evolving genes, provided greater resolution of the relationships within and among species of *Akodon*. Below I discuss the phylogenetic relationships within Akodon, comparing my results to those obtained in previous studies of the genus, and the biogeography of the Akodon as it relates to timing of diversification and changes in geology, climate, and vegetation.

My results recovered a monophyletic *Akodon* clade which is consistent with previous studies using cytb (Coyner 2010: Chapter 2). *Akodon* has been previously recovered as paraphyletic with respect to the genus *Deltamys* has been recovered in some studies (Jayat et al. 2010; Smith and Patton 2007), but the two taxa form reciprocally monophyletic genera in an analysis of cytb and the nuclear interphotoreceptor binding protein gene (IRBP) combined into a single dataset (D'Elía 2003; D'Elía et al. 2003). As no *Deltamys* was included here, the relationship between it and *Akodon* cannot be

evaluated using the other two nuclear genes. Within the *Akodon* clade, four monophyletic species group clades were recovered. My data place the *Akodon* radiation at 2.54–3.89 million years before present (mybp). This date is slightly older than those presented by other authors (2–2.65 mybp; Smith and Patton 2007). With the date of the *Akodon-Necromys* split dated at 3.58–5.74 mybp, it is most likely that the first *Akodon* appeared during the Pliocene. Until 2.11–3.48 mybp, only two lineages of *Akodon* were present.

South American habitats were affected differently by glacial and interglacial cycles, compared to their North American equivalents (Vuilleumier 1971). In the central and northern Andes, glacial events lowered the snowlines and tree lines and caused a lowering of habitats along the slopes of the Andes, resulting in a downward and outward expansion of grassland habitats (i.e. the Puna and Páramo high elevation grasslands that currently occur above 3000 m; Ortiz-Jaureguizar and Cladera 2006; Vuilleumier 1971). During the cooler, drier glacials, the lowland rainforests of the Amazon were reduced and subtropical and montane forests and savannahs expanded, favoring the expansion of organisms (including species of *Akodon*) adapted to these habitats (Ortiz-Jaureguizar and Cladera 2006; Vuilleumier 1971). During interglacials, the lowland tropical forests reexpanded, the snowlines and tree lines moved to higher elevations, and montane grasslands and forests retreated upward along the Andean slopes potentially isolating previously widespread populations (Ortiz-Jaureguizar and Cladera 2006; Veblen et al. 2007; Vuilleumier 1971). During the late Pliocene, the habitats of the southern plains developed and the final uplift of the Andes created the rain shadow effect that led to the current habitats of southern South America seen today (Ortiz-Jaureguizar and Cladera

2006). It was during this time that *Akodon* began diversifying into the early representatives of the species groups.

AKODON CURSOR GROUP.—Only 2 (*A. cursor* and *A. montensis*) of the 6 species comprising the *cursor* group species were included in this study. A *cursor* species complex is traced to Liascovich and Reig (1989) referring to three morphologically similar species (*A. cursor*, *A. montensis*, and *A. paranaensis* [as *A. serrensis*]) from the coastal forests of Brazil, Paraguay, Uruguay, and Argentina. The close relationship between *A. cursor* and *A. montensis*, and a chromosomal variant referred to as *A.* aff. *cursor*, was confirmed by electrophoretic data (Rieger et al 1995). Additional taxa were added to the *cursor* group as they were described (*A. mystax* — Hershkovitz 1998, *A. reigi* — González et al. 1998, and *A. sanctipaulensis* — Hershkovitz 1990a). The *cursor* group is karyotypically diverse exhibiting diploid numbers from 2N=14-15, in *A. cursor*, to 2N=44, in *A. mystax*, *A. paranaensis*, and *A. reigi* (Geise et al. 2001; Smith and Patton 2007).

A strongly supported sister relationship between *A. cursor* and *A. montensis* was recovered. The sister relationship between these two taxa is likely an artifact of the limited sampling of the group, as another study that included only *A. montensis* and *A. mystax* recovered a sister relationship between them (D'Elía 2003) and other previous studies with broader based upon cytb did not recover a sister relationship between the two (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007). Smith and Patton (2007) instead found *A. cursor* to be basal to a clade containing *A. montensis*, *A. paranaensis*, *A. reigi*, and *A. mystax*. Coyner (2010: Chapter 2) and Jayat et al. (2010) recovered the *cursor* group as three strongly supported monophyletic clades: a clade

containing only the species *A. cursor*, a clade containing *A. mystax* and *A. lindberghi*, and a clade containing *A. montensis*, *A. reigi*, and *A. paranaensis*. Most studies based solely on cytb sequences were unable to obtain sufficient support values for the monophyly of the *cursor* group (Coyner 2010: Chapter 2; Geise et al. 2001; Jayat et al. 2010; Smith and Patton 2007), but tests of monophyly by Coyner (including *A. philipmyersi*; 2010: Chapter 2) could not be rejected. Additionally *A. azarae* was recovered, in some analyses, within the *cursor* group indicating possible paraphyly of the *cursor* group (Smith and Patton 2007).

My analyses supported the *cursor* group as sister to the *boliviensis* group. In previous studies, analyses of cytb sequence data have recovered this relationship but support values were insufficient or the instability of *A. azarae* muddled the relationship between the two groups by causing one of the groups to be recovered as paraphyletic (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007). The two groups began diverging approximately 1.95 mybp (range = 1.48–2.54 mybp). The *cursor* group is isolated to the coastal forests of Brazil, Uruguay, Paraguay, and northeastern Argentina (Smith and Patton 2007), and the *cursor* group ancestor likely spread to the region during a glacial event when montane forests and high elevation (puna) grasslands of the High central Andes spread downward and outward and the lowland tropical forests retreated (Vuilleumier 1971), increasing habitats that favored the spread of grassland specialists like *Akodon* and creating a route between the central Andes and the habitats of southeastern Brazil. Around the time of the *cursor* group and *boliviensis* group split, the final uplift of the central Andes occurred and the associated formation of the Chaco, a hot and semiarid lowland region of Argentina, Bolivia, Paraguay, and Brazil, became a major

barrier to previous dispersal routes between the Andes and the southeastern highlands of Brazil (Ortiz-Jaureguizar and Cladera 2006; Vuilleumier 1971).

The limited taxonomic sampling of the *cursor* group presented here makes it difficult to place a confident estimate on the age and location of divergences within the *cursor* group. *A. cursor* and *A. montensis* are genetically divergent and do not represent sister species (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007), but the two taxa share a common ancestor 1.5 mybp. Therefore, the *cursor* group began diversifying into multiple lineages at least 1.5 mybp following isolation by the Chaco.

AKODON BOLIVIENSIS GROUP.—My analyses recovered a strongly supported monophyletic clade, containing 7 species of small bodied *Akodon* that occupy the central Andes from Peru to northwestern Argentina which correspond to the *boliviensis* group. These results conform to the *boliviensis* group of Myers et al. (1989), as opposed to the broader *boliviensis* group of Hershkovitz (1990) who also included *A. azarae*, *A. iniscatus*, *A. lindberghi*, and *A. sanctipaulensis*. Taxa, included here, that fall within the group include *A. boliviensis*, *A. fumeus*, *A. juninensis*, *A. kofordi*, *A. lutescens*, *A. spegazzinii*, and *A. viridescens*. The *boliviensis* group is supported by electrophoretic data (Myers et al. 1989), all members exhibit a 2N=40, FN=42-44 karyotype, if karyotype is available (Barquez et al. 1980; Myers and Patton 1989b; Myers et al. 1990), and species contained within the group essentially replace each other from north to south with some species overlapping geographically but often segregating by elevation (Myers et al. 1989; Smith and Patton 2007).

My results recovered a strongly supported sister relationship between *A. kofordi* and *A. fumeus*. The close relationship between *A. kofordi* and *A. fumeus* has been

supported by not only their morphological similarity (Myers and Patton 1989a), but also by molecular genetic analyses (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007). These two taxa represent a relatively recent split as indicated by their morphological similarity and low sequence divergence (2.294%), but morphological characters easily distinguish the two species, especially in younger individuals of *A. kofordi* who exhibit a distinctive island in the paraflexus of the first upper molar (Myers and Patton 1989a). The two were previously known as members of the *fumeus* group which was used to recognize the overall similarity of *A. kofordi* and *A. fumeus* and was not meant to represent phylogenetic relationships as they were untestable at the time (Myers and Patton 1989a). Although *A. kofordi* and *A. fumeus* were not originally considered part of the *boliviensis* group, recent analyses of sequence data from cytb (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007) and the mitochondrial control region (Hoekstra and Edwards 2000) support their inclusion in the group.

Akodon juninensis has been found in studies of cytb to form a strongly supported relationship with the sister taxa *A. kofordi* and *A. fumeus* (Jayat et al. 2010; Smith and Patton 2007), but the relationship was not strongly supported by other analyses of cytb data (Coyner 2010: Chapter 2; Jayat et al. 2010) and was not strongly supported here. *Akodon juninensis* was described as a new species in Myers et al. (1989), in the same paper that formalized the *boliviensis* group as the small bodied *Akodon* of the central Andes.

The type species of the genus, *A. boliviensis*, is the sister taxon of *A. spegazzinii*, including individuals identified as *A. alterus* Thomas (a synonym of *A. spegazzinii*; 1919)

and *A. s. tucumanensis* Allen (1901), in the results of my analyses. The sister relationship between *A. boliviensis* and *A. spegazzinii* is also strongly supported by cytb sequence data (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007). *Akodon spegazzinii*, including its current subspecies and synonyms, occupies a variety of habitats from Yungas forest to Monte Desert and exhibits considerable intraspecific morphological variation, particularly pelage coloration. While most authors considered the two taxa to be conspecific with *A. spegazzinii* (Blaustein et al. 1992; Musser and Carleton 2005; Myers et al. 1990), others considered *alterus* and *tucumanensis* as distinct species (Braun and Díaz 1999; Díaz and Barquez 2007; Mares et al. 1997). Despite their variation in pelage color and ecological associations, evaluations of allozyme data and morphological variation found low levels of divergence between the three taxa (Blaustein et al. 1992). Studies using cytb recovered *A. alterus* and *A. tucumanensis* nested within *A. spegazzinii* (Coyner 2010: Chapter 2; Jayat et al. 2010), and a study that included individuals from the type locality of *A. leucolimnaeus* recovered it nested within *A. spegazzinii* as well (Jayat et al. 2010).

The recently described taxon, *A. viridescens* (Braun et al. 2010), is basal to the strongly supported sister relationship between *A. boliviensis* and *A. spegazzinii* in my analyses. A single individual of *A. viridescens* (identified as *A. spegazzinii*) was used in sequencing prior to the species formal description (D'Elía 2003; D'Elía et al. 2003; Pardiñas et al. 2005; Smith and Patton 2007). The individual of *A. viridescens* was found to be sister to *A. boliviensis*, but no other samples of *A. spegazzinii* were included in those analyses (Pardiñas et al. 2005; Smith and Patton 2007).

In my study, sampling within the species *A. lutescens* was sufficient to reveal two well supported clades corresponding to currently recognized subspecies: *A. lutescens puer* and *A. lutescens caenosus*. *Akodon caenosus* (Thomas 1918) was originally described as a subspecies of *A. puer* (Thomas 1902) but shortly after was elevated to species status (Thomas 1920). *A. lutescens* first described in 1901 (Allen) was relegated to a subspecies of *A. puer* by Myers et al. (1990), but Anderson (1997) noted priority for specific epithet should be given to *A. lutescens* and suggested the three currently recognized subspecies (Musser and Carleton 2005; Myers et al. 1990). Other authors, however, have treated the three taxa as separate species (Hershkovitz 1990a, Mares et al. 1997). Analyses of cytb data recovered four lineages of *A. lutescens* with high divergence between each lineage, but support values varied and relationships among the lineages and their sister species, *A. subfuscus*, were unclear (Coyner 2010: Chapter 2). A recent study of cytb recommended recognizing *A. caenosus* as a species distinct of *A. lutescens* based upon their recovery of a sister relationship between *A. caenosus* and *A. subfuscus*, with *A. lutescens* occurring outside of that sister relationship (Jayat et al. 2010), but these relationships were unsupported and a polytomy similar to Coyner (2010: Chapter 2) was actually recovered between the three taxa. Sequence divergence of the two subspecies considered here is 4.046% (Table 3.5), which is well above the divergence values of other currently recognized *Akodon* species such as between *A. kofordi* and *A. fumeus* (2.294%) and between *A. toba* and *A. dolores* (2.454%). However without the inclusion of *A. lutescens lutescens* and with the current relationships between *A. subfuscus* and the subspecies of *A. lutescens* being unclear in analyses of cytb, it is difficult to conclude whether the currently recognized subspecies deserve species or subspecies status.

Upon diverging from the ancestor of the *cursor* group 1.95 mybp, the ancestor of the *boliviensis* group split into two lineages 1.43 mybp. The northwestern lineage, that occupied the southern edge of the central Andes in Peru and Bolivia, gave rise to *A. juninensis* and then *A. kofordi* and *A. fumeus*. *Akodon kofordi* occupies the elfin forests in southeastern Peru and western Bolivia (Myers and Patton 1989a). *Akodon juninensis* is known from central and southern Peruvian bunchgrass and shrub habitats above 3000 m and from woodland patches down to 2700 m (Myers et al. 1990). This taxon diverged from the ancestor of *A. fumeus* and *A. kofordi* around 1.1 mybp, and the current disjunct distribution of *A. juninensis* compared to *A. fumeus* and *A. kofordi* is indicative of a more widespread ancestor that occupied lower elevations during a glacial period and subsequently isolated at higher elevations during an interglacial period (Vuilleumier 1971). *Akodon fumeus* comes into close contact with *A. kofordi* in western Bolivia and Puno Department, Peru, and extends southward into the Yungas forest of Bolivia and northern Argentina (Myers and Patton 1989a). In the region of close contact, individuals of *A. fumeus* inhabit cloud forests (2800 m) up to high elevation paramó grasslands (3500 m) whereas *A. kofordi* is known from lower elevation (2700–2900 m) river drainages occupying habitats with moist bunch grass and disturbed shrublands (Myers and Patton 1989a). These two taxa represent the most recent divergence among current *Akodon* species with an estimated date of divergence at only 300,000 years ago. Like the split with A. juninensis, the initial divergence between *A. fumeus* and *A. kofordi*, allopatric sister species, was caused by the transition from a glacial period to an interglacial period.

The more eastern lineage of the *boliviensis* group began diversifying 1.21 mybp into the lineages that gave rise to *A. lutescens*, *A. boliviensis*, *A. spegazzinii*, and *A.*

viridescens. Members of *A. lutescens* occur in three non-overlapping populations (Smith and Patton 2007) with *A. l. lutescens* restricted to the high elevation puno grasslands of Peru and western Bolivia, *A. l. puer* restricted to puno grasslands in central Bolivia, and *A. l. caenosus* restricted to highlands of northern Argentina and southern Bolivia. These three lineages are diverging, but whether the three are distinct species or simply subspecies of a single species is unclear (Coyner 2010: Chapter 2; Jayat et al. 2010). Along with the lowering of the snow and tree lines causing a spreading of high elevation habitats downward and outward, parts of the central Andes were covered with glaciers and glacial lakes (Vuilleumier 1971). These glacial lakes and tongues of ice, known from regions of Bolivia east of Lake Titicaca, acted as barriers to gene flow during glacial periods despite widespread occurrence of suitable habitats and effectively isolated populations on the eastern and western slopes of the Altiplano (Vuilleumier 1971). As the ancestors of the three subspecies of *A. lutescens*, the Altiplano Akodont, could not have occupied the Altiplano during glacial cycles, they would have occupied lower elevations and been subject to the barriers present in western Bolivia where they first began diverging (~700,000 years before present between *A. l. caenosus* and *A. l. puer*). The temporary barriers disappeared when the species returned to higher elevations during warmer interglacials and the diverging populations were brought back into closer proximity exhibiting genetic boundaries where no ecological or physical boundary exists (Vuilleumier 1971).

The lineage that contains *A. boliviensis*, *A. viridescens*, and *A. spegazzinii* is young. No other species of *Akodon* is known to be sympatric with *A. viridescens*, where it is restricted to high elevation grasslands of the Sierra Centrales, an isolated mountain

range that rises abruptly from adjacent lower lying habitats (Braun et al. 2010). During one of the many glacial periods that caused highland grasslands to lower in elevation and spread outward, the ancestor of *A. viridescens* and *boliviensis-spegazzinii* occupied low elevations areas around the Sierra Centrales. When the glacial period ended and the grasslands retreated upward along montane slopes, *A. viridescens* became isolated in the Sierra Centrales. The lineage that gave rise to *A. boliviensis* and *A. spegazzinii* followed the retreating grassland habitats into northwestern Argentina, Bolivia, and southeastern Peru. Their recent divergence, at 470,000 years ago, left *A. boliviensis* restricted to the Altiplano of southeastern Peru and Bolivia ranging southward into high elevation grasslands of southern Bolivia and extreme northern Argentina while *A. spegazzinii* occupies a variety of grassland, woodland, and forest habitats including of eastern and northwestern Argentina. The divergence between these taxa seems consistent with that of divergence within *A. lutescens*, where glacial lakes and ice tongues acted as barriers in widespread taxa occurring in Bolivia, Peru, and Argentina (Vuilleumier 1971). During the glaciation, *A. boliviensis* and *A. spegazzinii* were isolated on opposite sides of a glacial lake in southwestern Bolivia and northwestern Argentina (Vuilleumier 1971). During the subsequent interglacial, the two diverging taxa recolonized the area previously occupied by the glacial lake.

AKODON AEROSUS GROUP.—Members of the *aerosus* group, with the exception of *A. albiventer*, occupy elfin and upper tropical forests along the slopes of the Andes. The affinity for members of the *aerosus* group was originally realized in a molecular analysis of the akodonts of five species (*A. aerosus*, *A. affinis*, *A. mollis*, *A. orophilus*, and *A. torques*) of *Akodon* that occupy Peru (Smith and Patton 1992a). Additional members (*A.*

albiventer, *A. budini*, and *A. siberiae*) were added based upon their molecular affinities (D'Elía 2003; D'Elía et al. 2003; Smith and Patton 2007).

In my analyses, the *A. aerosus* group, as traditionally defined (Smith and Patton 1992a, 2007), is paraphyletic. A monophyletic clade containing all included members of the *aerosus* group and four members of the *varius* group was recovered, and the monophyly was strongly supported (Fig. 3.3). A recent study of an incomplete fragment of the cytb gene also recovered the *aerosus* group as paraphyletic in their Bayesian analysis but not in their maximum parsimony analysis (Jayat et al. 2010). In their Bayesian tree, a well supported clade containing the 7 traditional *aerosus* group species, *A. budini* and *A. siberiae*, four *varius* group taxa, *A. mimus*, and *Deltamys kempii*, but within that clade only 4 nodes are supported (Jayat et al. 2010).

The results from my analyses recovered a strongly supported clade containing *A. aerosus*, *A. mollis*, *A. orophilus*, and *A. torques*. These taxa, along with *A. affinis*, form the traditional *aerosus* group, first recovered in analyses of the partial cytb sequences from samples of Peruvian Akodon (Patton and Smith 1992a) and subsequently supported by the mitochondrial control region (Hoekstra and Edwards 2000) and to some extent by other studies using cytb (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 1993, 2007). Three (*A. aerosus*, *A. mollis*, and *A. orophilus*) of the four species included in my analysis have been found to be paraphyletic (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007). In those three studies, the same samples proved problematic and none of those samples were included in my analyses (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007); therefore, as presented here, *A. aerosus*, *A. mollis*, and *A. orophilus* were recovered as reciprocally monophyletic.

Despite recent publications containing the *A. varius* group that recovered or hypothesized the group as monophyletic (Braun *et al*. 2008; Smith and Patton 2007), four species (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) of the *varius* group form a monophyletic clade that is contained within a clade also containing all included members of the *A. aerosus* group. The inclusion of these four species within an *aerosus* group clade was also recovered by Jayat et al. (2010). To maintain the monophyly of the *aerosus* species group clade, the four species (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) need to be moved from the *varius* group to the *aerosus* group.

Geographically, the outlier of the *aerosus* group is *A. albiventer*. All other species occur in elfin and upper tropical forests and essentially replace each other from north to south. *Akodon albiventer* occurs above the tree line in Peru and Bolivia across the altiplano and into northern Chile and Argentina. *Akodon albiventer* is an old lineage, diverging from other members of the aerosus group 1.74 mybp. The divergence of *A. albiventer* seems to require dispersal of the ancestor out of elfin and upper montane forest habitats. During the constant ebb and flow of changing habitats, high extinction rates occur alongside rapid diversification (Ortiz-Jaureguizar and Cladera 2006), so it seems likely that *A. albiventer* is the only remaining species of a lineage whose diversity was equal to other *Akodon* lineages (i.e. the *cursor* group or the Yungas clade of the *varius* group) that age from 1.43-1.88 mybp.

The four southernmost species (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) of the *aerosus* group occupy Yungas forest. These four taxa are likely the result of a recent and rapid divergence (Coyner 2010: Chapter 2) beginning around 680,000 years ago. The Yungas are a relatively moist montane forest bordered on the east and

west by more xeric habitats, puna to the west and the Chaco to the east. During the cooler glacials, high elevation grasslands expanded into the area currently occupied by the Yungas, displacing the Yungas which expanded northward into areas currently occupied by tropical forests (Colinvaux et al. 2000; Premoli et al. 2007). During interglacials, the Yungas forest retreated southward and restricted in range (Premoli et al. 2007). The four southern species of the *aerosus* group likely encountered some kind of barriers, whether tongues of ice or glacial lakes in the central Andes or non-montane grassland habitats that existed farther north, during these northern expansions and the four species began diverging. As we are currently experiencing an interglacial, the species are restricted in range and in close geographic proximity yet are allopatric and are reciprocally monophyletic; the monophyly of *A. simulator* was only marginally supported in this study, but cytb data support the monophyly of the species (Fig 3.2, and see Braun et al. 2008; Coyner 2010: Chapter 2).

A better systematic understanding of *A. aerosus*, *A. mollis*, and *A. orophilus* is needed as these species exhibit paraphyly in analyses of cytb (Coyner 2010: Chapter 2; Jayat et al. 2010; Smith and Patton 2007). *Akodon torques* and *A. aerosus* are elevational variants with *A. aerosus* replacing *A. torques* below 2000 m (Smith and Patton 1992a). *Akodon aerosus* is more broadly ranging in disjunct populations on mountain slopes but remains restricted to forests below 2000 m (Smith and Patton 1992a). *Akodon aerosus*, *A. mollis*, and *A. orophilus* (and *A. affinis*, although not included here) diverged much like other northern and central Andean species. During cycles of glacials and interglacials, high elevation grasslands lowered and extended outward and then retracted and retreated in elevation isolating previously widespread taxa (Vuilleumier 1971). Multiple glacial

interglacial cycles account for the current divergence within these species of the *aerosus* group.

AKODON VARIUS GROUP.— As originally described, the *varius* group contained the largest members of *Akodon* that occupy low to mid elevations of the eastern slopes of the Andes and lowland regions of Argentina, Bolivia, and Paraguay (Myers 1989), but no monophyletic *A. varius* group was recovered in my results. Two previous studies recovered or hypothesized a monophyletic *varius* group clade; both studies used only cytb sequence data and lacked a number of taxa included here (Braun et al. 2008; Smith and Patton 2007). Tests of monophyly confirm that a monophyletic *A. varius* clade is significantly unlikely based upon my data.

Four species (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) need to be moved to the *aerosus* group (see discussion above). The remaining members of the former *varius* group include *A. dayi*, *A. dolores*, *A. iniscatus*, *A. molinae*, *A. neocenus*, *A. oenos*, and *A. toba*. Taxa in my analyses included only *A. dayi*, *A. dolores*, *A. iniscatus*, and *A. toba* and form a well supported and internally well-resolved monophyletic clade. The relationships among these four species have been recovered in numerous studies based upon cytb sequence and nuclear genetic data (Braun et al. 2008; Coyner 2010: Chapter 2; D'Elía 2003; D'Elía et al. 2003; Jayat et al. 2010; Smith and Patton 2007). No samples of *A. molinae* are included here, but the validity of *A. molinae* has recently been discussed in light of results based upon cytb gene data and data from other investigators, and there is little support for the recognition of *A. molinae* as a distinct species (Apfelbaum and Blanco 1984; Bianchi et al. 1979; Braun et al. 2008; Merani et al. 1978; Wittouck et al. 1995).

With the reassignment of *A. varius* to the *aerosus* species group, the *A. varius* group is no longer valid and a new name is needed for the monophyletic clade containing the remaining species of the former *varius* group. Of the four species (*A. dayi*, *A. dolores*, *A. iniscatus*, and *A. toba*) that remain in the former *varius* group, *A. dolores* was described first (Thomas 1916) and is given priority for the species group name. Thus I concur with Jayat et al. (2010) in their proposal of the *A. dolores* species group as the new name of the species group that contains the remaining species of the former *varius* group.

The *dolores* group occurs in Patagonia and corresponds to the southernmost species of the genus *Akodon* (Braun et al. 2008; Smith and Patton 2007). Patagonia was affected differently by glacial and interglacial cycles (Vuilleumier 1971). Unlike montane forests of more northern habitats, the forests of the southern Andes did not expand outward, relocating only slightly eastward of its current range (Vuilleuimier 1971). Parts of southern Patagonia were covered with glaciers, and glacial lakes, interglacial sea transgressions, and a freshwater inland lake acted as barriers isolating populations from each other (Vuilleumier 1971).

Akodon iniscatus occurs in the lowlands of central and southern Argentina (Braun et al. 2008) and represents an old lineage, diverging around 1.88 mybp based upon my data. Although the habitat is much less complex in Patagonia, compared to the Central Andes, as this region underwent less dramatic changes during cycles of glacial and interglacial periods, but it is unlikely that the ancestor of *A. iniscatus*, like the ancestor of *A. albiventer*, gave rise to only a single taxon. Two possible taxa are *A. neocenus* and *A. oenos*, two extant taxa not included in my analyses, who are thought to be members of

the *dolores* group (Braun et al. 2008; Smith and Patton 2007). During glaciations, fingers of ice that acted as barriers are known from 36°-38°S latitude (Vuilleumier 1971), locations just north of the present distribution of *A. inisicatus* (Braun et al. 2008; Smith and Patton 2007), providing a mechanism for the divergence of *A. iniscatus* from its northern relatives.

Akodon dayi is broadly distributed in mesic habitats in Bolivia, the extreme northern reaches of the *dolores* group range. *Akodon toba* and *A. dolores* represent a recent split. *Akodon toba* is a Chacoan species that occurs in Bolivia, Paraguay, and Argentina (Braun et al. 2008). In the southern Chaco, *A. dolores* replaces *A. toba* and also occupies regions of the Espinal, a thorny deciduous forest, and Monte Desert (Braun et al. 2008). The Chaco represents a barrier to many other species of *Akodon* (i.e. the ancestor of the *boliviensis* and *cursor* groups) but *A. dolores* and *A. toba*, who are among the most arid adapted species of *Akodon* unlike their closest relative *A. dayi* that is restricted to mesic habitats, occupy the region. All three of these species were likely isolated following the start of an interglacial when high elevation grasslands and montane forests retreated back toward the Andean slopes.

INCERTAE SEDIS LINEAGES.—Two of the "unique" *Akodon* lineages were included in this study. *Akodon mimus*, a representative of the *Microxus* subgenus of *Akodon*, was recovered as two sister lineages but their sister relationship was only supported in the Bayesian analysis of my data; this lack of support was also found in analyses of cytb sequences (Coyner 2010: Chapter 2). In other analyses of cytb data, *A. mimus* was recovered nested within a clade containing the *aerosus* group, and in some cases the genus *Deltamys*, but bootstrap values and posterior probabilities ranged from supported

to unsupported (D'Elia 2003; D'Elia et al. 2003; Jayat et al. 2010; Patton and Smith 1992; Smith and Patton 1993, 2007). Allozyme data also dispute the subgeneric status of *Microxus*, represented by *A. mimus* (Patton et al. 1989). These previous studies did not include multiple members of *A. mimus*, so the monophyly of the species was not tested (Jayat et al. 2010; Patton and Smith 1992; Smith and Patton 1993, 2007). Two additional species, *A. bogotensis* and *A. latebricola*, have been included in the subgenus, *Microxus*, but *A. bogotensis* exhibits traits that are not shared by other *Akodon* including *A. mimus* and *A. latebricola* (Musser and Carleton 2005; Voss and Linzey 1981).

The status of the two lineages of *A. mimus*, as included here, is difficult to determine. If the two lineages prove to be sister, they likely two divergent yet closely related taxa. But if they are not sister, they represent two distantly related yet morphologically similar species. Additional study of *A. mimus*, *A. latebricola*, and *A. bogotensis* is required to tease apart the relationships within and among these three taxa and the remaining species of *Akodon*.

Akodon azarae is the other incertae sedis taxon included in my analyses. Previous studies have been unable to completely resolve the relationship of *A. azarae* to other species of *Akodon* and could only conclude that it was more closely related to the *boliviensis* and *cursor* group than the *aerosus* and *varius* groups (Coyner 2010: Chapter 2; D'Elía 2003; D'Elía et al. 2003; Jayat et al. 2010; Smith and Patton 2007). In analyses of the mitochondrial control region, *A. azarae* was recovered as sister to *A. boliviensis* and thus nested within the *boliviensis* group (Hoekstra and Edwards 2000). In my analyses, *A. azarae* is basal to a clade containing the *A. boliviensis* and *A. cursor* groups, recovered as strongly supported sister groups. *Akodon azarae* represents the second

oldest species included in this study, dating to 2.21 mybp and appearing before the ancestors of the four species groups.

Akodon azarae is relatively widespread in central and northeastern Argentina, Paraguay, Uruguay, and southern Brazil (Smith and Patton 2007). The species occupies the Pampas, a lowland grassland habitat, and dispersed in a fashion similar to, but earlier than, the ancestor of the *cursor* group. During a glacial period, grasslands spread downward and outward allowing dispersal routes between the Central Andes and coastal regions of southeastern Brazil and eastern Argentina whose coastlines extended outward 100 m farther than today (Vuilleumier 1971). During interglacial, the distribution of *A. azarae* was restricted by the retreating coastline, by the interglacial sea transgressions, and by the formation of barrier habitats like the Chaco (Vuilleumier 1971) and isolated from other populations of *Akodon*.

PREVIOUSLY PROPOSED BIOGEOGRAPHIC HYPOTHESIS OF *AKODON*.—The most commonly cited biogeographic hypothesis involving the genus *Akodon* is Reig's scenario for the sigmodontine colonization of South America (Reig 1984, 1986, 1987). Reig (1986) focused on Akodontini, not *Akodon* directly, and suggested that the area of original differentiation for Akodontini was located in the Andes of northwestern Argentina and bordering areas of Chile and Bolivia. Reig hypothesized the Akodontini ancestor diverged from an oryzomyine ancestor during the Late Miocene or early Pliocene in the protopuna region. The akodontine ancestral stock dispersed and speciated into a northern stock, a southern stock, and a south-central stock and eventually speciated into the diversity of forms seen today. Reig's hypothesis is based upon the uplift of the

Andes, the rapid diversification of sigmodontine rodents, and current species distributions.

It is difficult to evaluate Reig's hypothesis with my data. The taxonomy used by Reig is no longer valid. Reig (1986) included *Abrothrix*, *Chroeomys*, and *Deltamys* in *Akodon* and included Abrothrochini genera within Akodontini. Recently, it was found that Reig's hypotheses need revision regarding locations and timings of differentiations (Pardiñas et al. 2002). Additionally my data are from lower taxonomic levels than Reig's scenario addresses.

The high diversity of *Akodon* in the central Andes indicate this region has served as a center of radiation, but the habitats of this region have experienced dramatic changes during the evolution of *Akodon*. Most species of *Akodon* appear to have diverged due to vicariance, as opposed to dispersal, leaving Reig's dispersal routes inaccurate depictions of the evolution of *Akodon*. Most divergence occurred when populations were isolated following widespread occurrence of a taxon, so no single area of differentiation exists for *Akodon*.

CONCLUDING REMARKS

The addition of two nuclear genes resulted in additional resolution among species of *Akodon* compared to analyses containing cytb alone, allowing for a more detailed biogeographic consideration of the genus. The additional resolution confirmed the monophyly of the *A. boliviensis* group and rejected the monophyly of the *A. varius* group. The *aerosus* group is paraphyletic as traditionally defined, but by reassigning four taxa (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) to the aerosus group, a well supported monophyletic new *aerosus* group is recovered. The monophyly of the *cursor*

group is presented with caution as the majority of the *cursor* taxa and the likely ally *A. lindberghi* are not included here. With the inclusion of only *A. cursor* and *A. montensis*, generation of data from additional genes is needed for other taxa within the *A. cursor* group to better resolve relationships within the group. One of the major hurdles in working on *Akodon* continues to be obtaining all named species and subspecies for inclusion in studies. While including these additional taxa in molecular studies is unlikely to strongly affect resolution, the phylogenetic affinities of unincluded taxa cannot currently be assessed.

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LITERATURE CITED

Allen, J. A. 1901. On a further collection of mammals from southeastern Peru, collected by Mr. H. H. Keays, with descriptions of new species. Bulletin of the American Museum of Natural History 14:41–46.

Apfelbaum, L. I., and A. Blanco. 1984. Genetic similarity between species of *Akodon* (Rodentia, Cricetidae). Journal of Experimental Zoology 229:1–5.

Apfelbaum, L. I., and O. A. Reig. 1989. Allozyme genetic distances and evolutionary relationships in species of akodontine rodents (Cricetidae: Sigmodontinae). Biological Journal of the Linnean Society 38:257–280.

Baker, R. J., and R. D. Bradley. 2006. Speciation in mammals and the Genetic Species Concept. Journal of Mammalogy 97:643-662.

Barquez, R. M., D. F. Williams, M. A. Mares, and H. H. Genoways. 1980. Karyology and morphometrics of three species of *Akodon* (Mammalia, Muridae) from northwestern Argentina. Annals of Carnegie Museum 49:379–403.

Barrantes, G. E., M. O. Ortells, and O. A. Reig. 1993. New studies on allozyme genetic distance and variability in akodontine rodents (Cricetidae) and their systematic implications. Biological Journal of the Linnean Society 48:283–298.

Bianchi, N. O., S. Merani, and M. Lizarralde. 1979. Cytogenetics of the South American akodont rodents (Cricetidae). VI. Polymorphism in *Akodon dolores* (Thomas). Genetica 50:99–104

Blaustein, S. A., R. C. Liascovich, L. I. Apfelbaum, L. Daleffe, R. M. Barquez, and O. A. Reig. 1992. Correlates of systematic differentiation between two closely related allopatric populations of the *Akodon boliviensis* group from NW Argentina (Rodentia: Cricetidae). Zeithschrift für Säugetierkunde 57:1–13.

Bradley, R. D., and R. J. Baker. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960–973.

Braun, J. K., and M. M. Díaz. 1999. Key to the native mammals of Catamarca Province, Argentina. Occassional Papers of the Oklahoma Museum of Natural History 4:1–16.

Braun, J. K., M. A. Mares, and R. A. Ojeda. 2000. A new species of grass mouse, genus *Akodon* (Muridae: Sigmodontinae), from Mendoza Province, Argentina. Zeitschrift für Säugetierkunde 65:216–225.

Braun, J. K., B. S. Coyner, M. A. Mares, and R. A. Van Den Bussche. 2008. Phylogenetic relationships of South American grass mice of the *Akodon varius* group (Rodentia, Cricetidae, Sigmodontinae) in South America. Journal of Mammalogy 89:768–777.

Braun, J. K., M. A. Mares, B. S. Coyner, and R. A. Van Den Bussche. 2010. New species of *Akodon* (Rodentia, Cricetidae, Sigmodontinae) from central Argentina. Journal of Mammalogy 91:387–400.

Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. II. (Sirenia-Perissodactyla-Artiodactyla-Lagomorpha-Rodentia-Cetacea). Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Naturales 4:308–732.

Christoff, A. U., V. Gafundes, I. J. Sbalqueiro, M. S. Mattevi, and Y. Yonenaga-Yassuda. 2000. Description of a new species of *Akodon* (Rodentia: Sigmodontinae) from southern Brazil. Journal of Mammalogy 81:838–851.

Cione, A. L., and E. P. Tonni. 2001. Correlation of Pliocene to Holocene southern South American and European vertebrate-bearing units. Bolletino della Societá Paleontologica Italiana 40:167–173.

Colinvaux, P. A., P. E. De Oliveira, and M. B. Bush. 2000. Amazonian and Neotropical plant communities on glacial time-scales: the failure of aridity and refuge hypotheses. Quaternary Science Reviews 19:141–169.

Coyner, B. S. 2010. Phylogenetic relationships and historical biogeography of the genus *Akodon* (Rodentia: Cricetidae). Ph. D. dissertation, Oklahoma State University, Stillwater, Oklahoma.

D'Elía, G. 2003. Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307–323.

D'Elía, G., E. M. González, and U. F. J. Pardiñas. 2003. Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus *Deltamys*. Mammalian Biology 68:351–364.

D'Elía, G., U. F. J. Pardiñas, P. Teta, and J. L. Patton. 2007. Definition and diagnosis of a new tribe of Sigmodontine rodents (Cricetidae: Sigmodontinae), and a revised classification of the subfamily. Gayana 71:187–194.

Díaz, M. M., and R. M. Barquez. 2007. The wild mammals of Jujuy Province, Argentina: systematics and distribution. Pp. 417-578 in The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson (D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1-981.

Díaz, M. M., R. M. Barquez, J. K. Braun, and M. A. Mares. 1999. A new species of *Akodon* (Murinae, Sigmodontinae) from northwestern Argentina. Journal of Mammalogy 80:786–798.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214.

Drummond, A. J., M. Kearse, J. Heled, R. Moir, T. Thierer, B. Ashton, A. Wilson, and S. Stones-Havas. 2008. Geneious version 4.6.1, available from http://www.geneious.com.

Ellerman, J. R. 1941. The families and genera of living rodents. Vol. II. Family Muridae. British Museum (Natural History), London, 690 pp.

Fagundes, V., A. U. Christoff, and Y. Yonenaga-Yassuda. 1998. Extraordinary chromosomal polymorphism with 28 different karyotypes in the Neotropical

species *Akodon cursor* (Muridae: Sigmodontinae), one of the smallest diploid number in rodents (2n=16, 15 and 14). Hereditas 129:263–274.

Geise, L., F. C. Canavez, and H. N. Seuánez. 1998. Comparative karyology in *Akodon* (Rodentia, Sigmodontinae) from southeastern Brazil. Journal of Heredity 89:158–163.

Geise, L., M. F. Smith, and J. L. Patton. 2001. Diversification in the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern South America: mitochondrial DNA sequence analysis. Journal of Mammalogy 82:92–101.

Giribet, G., R. DeSalle, and W. C. Wheeler. 2002. 'Pluralism' and the aims of phylogenetic research. Pp. 141-146, in Molecular Systematics and Evolution: theory and practice (R. DeSalle, G. Giribet, and W. Wheeler, eds.). Birkhäuser Verlag, Switzerland.

González, E. M., A. Langguth, and L. F. de Oliveira. 1998. A new species of *Akodon* from Uruguay and southern Brazil (Mammalia: Rodentia: Sigmodontinae). Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo 191:108.

Guindon S., and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52:696-704.

Hershkovitz, P. 1990a. Mice of the *Akodon boliviensis* size class (Sigmodontinae, Cricetidae), with the description of two new species from Brazil. Fieldiana: Zoology 57:1–35.

Hershkovitz, P. 1990b. The Brazilian rodent genus *Thalpomys* (Sigmodontinae, Cricetidae) with a description of a new species. Journal of Natural History 24:777–783.

Hershkovitz, P. 1998. Report on some sigmodontine rodents collected in southeastern Brazil with descriptions of a new genus and six new species. Bonner Zoologische Beiträge 47:193–256.

Honacki, J. H., K. E. Kinman, and J. W. Koeppl (eds.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Huelsenbeck, J. P., and F. R. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754–755.

Irwin D. M., T. D. Kocher, and A. C. Wilson. 1991. The evolution of the cytochrome b gene in mammals. Journal of Molecular Evolution 32(2):128–144.

Jansa, S. A. J. F. Forsman, and R. S. Voss. 2006. Different patterns of selection on nuclear genes IRBP and DMP-1 affect the efficiency but not the outcome of phylogeny estimation for didelphid marsupials. Molecular Phylogenetics and Evolution 38:363-380.

Jayat, J. P., P. E. Ortiz, J. Salazar-Bravo, U. F. J. Pardiñas, and G. D'Elía. 2010. The *Akodon boliviensis* species group (Rodentia: Cricetidae: Sigmodontinae) in Argentina: species limits and distribution, with the description of a new entity. Zootaxa 2409:1–61.

Larkin, M. A., G. Blackshields, N. P. Brown, R. Chenna, P. A. McGettigan, H. McWilliam, F. Valentin, I. M. Wallace, A. Wilm, R. Lopez, J. D. Thompson, T. J.

Gibson, and D. G. Higgins. 2007. Clustal W and Clustal X version 2.0. Bioinformatics 23:2947–2948.

Liascovich, R. C. 1991. Cariosistemática y evolución cromosómica en cricétidos akodontinos (Rodentia, Muriodea). Ph. D. dissertation, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, 185 pp.

Longmire, J. L., M. Maltbie, and R. J. Baker. 1997. Use of "lysis buffer" in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1–2.

Mares, M. A., R. A. Ojeda, J. K. Braun, and R. M. Bárquez. 1997. Systematics, distribution, and ecology of the mammals of Catamarca Province, Argentina. Pp. 89-141 in Life Among the Muses: Papers in Honor of James S. Findley (T. L. Yates, W. L. Gannon, and D. E. Wilson, eds.). Special Publication, The Museum of Southwestern Biology, The University of New Mexico, Alburquerque, New Mexico, USA.

Matthee, C. A., B. J. Van Vuuren, D. Bell, and T. J. Robinson. 2004. A molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. Systematic Biology 53:433–447.

McKenna, M. C., and S. K. Bell. 1997. Classification of mammals above the species Level. Columbia University Press, New York.

Merani, S., M. Lizarralde, D. Oliveira, and N. O. Bianchi. 1978. Cytogenetics of the South American akodont rodents (Cricetidae). IV. Interspecific crosses between

Akodon dolores × *Akodon molinae*. Journal of Experimental Zoology 206:343–346.

Meyen, F. J. F. 1833. Beiträge zur Zoologie gesammelt auf einer Reise um die Erde Säugethiere. Nova Acta Academiae Caesareae Leopoldino-Carolinae 16(2):599.

Müller, K. 2005. SeqState – primer design and sequence statistics for phylogenetic DNA data sets. Applied Bioinformatics 65–69.

Musser, G. G., and M. D. Carleton. 2005. Superfamily Muroidea. Pp. 894–1531, in Mammal species of the world: a taxonomic and geographic reference, Third Edition (D. E. Wilson and D. M. Reeder, eds.). The Johns Hopkins University Press, Baltimore, Maryland.

Myers, P. 1989. A preliminary revision of the *varius* group of *Akodon* (*A. dayi*, *dolores*, *molinae*, *neocenus*, *simulator*, *toba*, and *varius*), Pp. 5–54, in Advances in Neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). The Sandhill Crane Press, Inc., Gainesville, Florida, 614 pp.

Myers, P., and J. L. Patton. 1989a. *Akodon* of Peru and Bolivia: revision of the *fumeus* group (Rodentia: Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 721:1–35.

Myers, P., and J. L. Patton. 1989b. A new species of *Akodon* from the cloud forests of eastern Cochabamba Department, Bolivia (Rodentina: Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 720:1–28.

Myers, P., J. L. Patton, and M. F. Smith. 1990. A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae) with emphasis on Perú and Bolivia.

Miscellaneous Publications of the Museum of Zoology. University of Michigan 177:1–104.

Ortiz-Jaureguizar, E., and G. A. Cladera. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. Journal of Arid Environments 66:498–532.

Pardiñas, U. F. J., and E. P. Tonni. 1998. Procedencia estratigráfica y edad de los más antiguos muroideso (Mammalia, Rodentia) de América del Sur. Amehiniana 35:473–475.

Pardiñas, U. F. J., G. D'Elía, and P. E. Ortiz. 2002. Sigmodontinos fósiles (Rodentia, Muroidea, Sigmodontinae) de América del Sur: estado actual de su conocimiento y prospectiva. Mastozoología Neotropical 9:209–252.

Pardiñas, U. F. J., G. D'Elía, S. Cirignoli, and P. Suarez. 2005. A new species of *Akodon* (Rodentia, Cricetidae) from the northern campos grasslands of Argentina. Journal of Mammalogy 86:462–474.

Patton, J. L., and M. F. Smith. 1992a. Evolution and systematics of akodontine rodents (Muridae: Sigmodontinae) of Peru, with emphasis on the genus *Akodon*. Memorias del Museo de Historia Natural, U.N.M.S.M. (Lima) 21:83–103.

Patton, J. L., and M. F. Smith. 1992b. mtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. Evolution 46:174–183.

Patton, J. L., P. Myers, and M. F. Smith. 1989. Electromorphic variation in selected South American akodontine rodents (Muridae: Sigmodontinae), with comments on the systematic implications. Zeithschrift für Säugetierkunde 54:347–359.

Patton, J. L., P. Myers, and M. F. Smith. 1990. Vicariant versus gradient models of diversification; the small mammal fauna of eastern Andean slopes of Peru. Pp.

355–371, in Vertebrates in the tropics (G. Peters and R. Hutterer, eds.). Museum Alexander Koenig, Bonn, Germany.

Posada, D. 2008. jModelTest: Phylogenetic Model Averaging. Molecular Biology and Evolution 25:1253–1256.

Premoli, A. C., R. F. del Castillo, A. C. Newton, S. Bekessy, M. Caldiz, C. Martínez-Araneda, P. Mathiasen, M. C. Nuñez-Ávila, P. Quiroga, C. Souto, and S. Trujillo-Argueta. 2007. Patterns of genetic variation in tree species and their implications for conservation. Pp. 120–157 in Biodiversity loss and conservation in fragmented forest landscapes. The forests of montane Mexico and temperate South America. (A. C. Newton, ed.). CABI, Wallingford, Oxfordshire, UK.

Rambaut, A. 2006. FigTree v. 1.3.1 http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut, A., and A. J. Drummond. 2007. TRACER v. 1.4. http://beast.bio.ed.ac.uk/Tracer.

Reig, O. A. 1980. A new fossil genus of South American cricetid rodents allied to *Wiedomys*, with an assessment of the Sigmodontinae. Journal of Zoology, London 192:257–281.

Reig, O. A. 1984. Distribução geográfica e historia evolutiva dos roedores muoideos sulamericanos (Cricetidae: Sigmodontinae). Revista Brasileira de Genética 7:333–365.

Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404–440, in High altitude tropical biogeography (F. Vuilleumier and M. Monasterio, eds.). Oxford University Press, New York, 649 pp.

Reig, O. A. 1987. An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Sigmodontinae). Pp. 347–401, in Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana, Zoology 39:1–506.

Rieger, T. T., A. Langguth, and T. A. Waimer. 1995. Allozymic characterization and evolutionary relationships in the Brazilian *Akodon cursor* species group (Rodentia – Cricetidae). Biochemical Genetics 33:283–295.

Sbalquiero, I. F., and A. P. Nascimento. 1996. Occurrence of *Akodon cursor* (Rodentia, Cricetidae) with 14, 15, 16 chromosome cytotypes in the same geographic area in southern Brazil. Revista Brasileira de Genética 19:565–569.

Shimodaira, H., and M. Hasegawa. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 16:1114-1116.

Silva, M. J. de J, and Y. Yonenaga-Yassuda. 1998. Karyotype and chromosomal polymorphism of an undescribed *Akodon* from central Brazil, a species with the lowest diploid chromosome number in rodents. Cytogenetics and Cell Genetics 81:46–50.

Simmons, M. P., and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49:369–381.

Smith, M. F., and J. L. Patton. 1991. Variation in mitochondrial cytochrome b sequence in natural populations of South American akodontine rodents (Muridae: Sigmodontinae). Molecular Biology and Evolution 8:85–103.

Smith, M. F., and J. L. Patton. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149–177.

Smith, M. F., and J. L. Patton. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome b. Journal of Mammalian Evolution 6:89–128.

Smith, M. F., and J. L. Patton. 2007. Molecular phylogenetics and diversification of South American grass mice, genus *Akodon*. Pp. 827-858 in The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson (D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1-981.

Spotorno, A. 1987. Systematics and evolutionary relationships of Andean phyllotine and akodontine rodents. Ph. D. dissertation, University of California, Berkeley.

Swofford, D. L. 2000. PAUP* Phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Tate, G. H. H. 1932. The taxonomic history of the South and Central American akodont genera: *Thalpomys*, *Deltamys*, *Thaptomys*, *Hypsimys*, *Bolomys*, *Chroeomys*, *Abrothrix*, *Scotinomys*, *Akodon*, (*Chalcomys* and *Akodon*), *Microxus*, *Podosymys*, *Lenoxus*, *Oxymycterus*, *Notiomys*, and *Blarinomys*. American Museum Novitates 582:1–32.

Thomas, O. 1916. The grouping of the South American Muridae commonly referred to *Akodon*. Annals and Magazine of Natural History ser. 8, 17:336–340.

Thomas, O. 1918. On small mammals from Salta and Jujuy collected by Mr. E. Budin. Annals and Magazine of Natural History ser. 9, 1s:186–193.

Thomas, O. 1920. A further collection of mammals from Jujuy. Annals and Magazine of Natural History ser. 9, 5:188–196.

Van Den Bussche, R. A., S. R. Reeder, E. W. Hansen, and S. R. Hoofer. 2003. Utility of the Dentin Matrix Protein 1 (DMP1) gene for resolving mammalian intraordinal phylogenetic relationships. Molecular Phylogenetics and Evolution 26:89–101.

Vorontzov, N. N. 1959. Sistema khomiakov (Cricetinae) morovoi fauny I ikh filogeneticheskie sviazi. Biuletin Moskovskogo Obshtschestva Ispitately Prirody, Otdel Biologia 44:134–137.

Voss, R. S., and A. V. Linzey. 1981. Comparative gross morphology of male accessory glands among Neotropical Muridae (Mammalian: Rodentia) with comments on systematic implications. Miscellaneous Publications Museum of Zoology, University of Michigan 159: i–iv, 1–41.

Wittouck, P., E. Pinna Senn, C. A. Soñez, M. C. Provensal, J. J. Polop, and J. A. Lisanti. 1995. Chromosomal and synaptonemal complex analysis of Robertsonian polymorphisms in *Akodon dolores* and *Akodon molinae* (Rodentia: Cricetidae) and their hybrids. Cytologia 60:93–102.

TABLE 3.1.—Species of *Akodon* divided into the four species groups (Braun et al. 2008; Musser and Carleton 2005; Myers 1989; Myers et al. 1989; Rieger et al. 1995; Smith and Patton 1992a, 2007) and taxa considered *incertae sedis*.

A. aerosus group	*A. boliviensis* group	*A. cursor* group	*A. varius* group	*Incertae sedis*
A. aerosus	*A. aliquantulus**	*A. cursor*	*A. dayi*	*A. azarae*
*A. affinis**	*A. boliviensis*	*A. montensis*	*A. dolores*	*A. bogotensis**
A. albiventer	*A. fumeus*	*A. mystax**	*A. glaucinus*	*A. latebricola**
*A. budini**	*A. juninensis*	*A. paranaensis**	*A. iniscatus*	*A. lindberghi**
A. mollis	*A. kofordi*	*A. reigi**	*A. molinae**	*A. mimus*
A. orophilus	*A. leucolimnaeus**	*A. sanctipaulensis**	*A. neocenus**	*A. philipmyersi**
*A. siberiae**	*A. lutescens*		*A. oenos**	*A. serrensis**
*A. surdus**	*A. pervalens**		*A. simulator*	
A. torques	*A. polopi**		*A. tartareus*	
	A. spegazzinii		*A. toba*	
	*A. subfuscus**		*A. varius*	
	*A. sylvanus**			
	A. viridescens			

TABLE 3.2.—Species group clades and ambiguous lineages of *Akodon* obtained from previous studies. Descriptions include number of named forms, current geographic distribution, level of support for the lineage, and comments regarding the placement of previously recognized taxa.

Lineages	Species	Geographic Distribution	Support Levels	Additional comments
A. aerosus group	9	Slopes of the northern Andes from Colombia to northwestern Argentina.	Mixed	Includes the subgenera *Hypsimys* and *Chalcomys*.
A. boliviensis group	13	Central Andes from Peru to northwestern Argentina.	Mixed	Includes the *fumeus* group of Myers and Patton (1989a).
A. cursor group	6	Coastal forests of Brazil, Paraguay, Uruguay, and Argentina.	Low	
A. varius group	11	Eastern slopes of the Andes and adjacent lowlands of Bolivia, Argentina, and Paraguay.	High	
Ambiguous lineages	7	Widespread	Mixed	Includes the subgenus/genus *Microxus*.

TABLE 3.3.—Primer sequences developed for *Akodon*. Ambiguous bases follow the International Union of Pure and Applied Chemistry (IUPAC) with: R representing a purine (A or G); Y representing a pyrimidine (C or T); M representing an amino (C or A); and D representing A, G, or T.

Primer	Source or Sequence (5' to 3')
Cytochrome b	
Ak2CytB740F	CCAGACATCCTCGGAGA
Cytb-F1	TACGRAARAAYCACCCRCTA
Cytb-F2	AAAGCYACCCTMACCCGCTT
Ak2CytB740R	TCTCCGAGGATGTCTGG
Cytb-R1	GGRATTTTGTCRGAGTCTGA
Cytb-R2	GYTTGATDATATTRTTCTCG
Dentin Matrix Protein 1	
DMP400F	GACAGCCAGGCTGTGGGATTT
DMP-F1	GATGAGGACAATGGTCCAG
DMP-F2	CTGACAGCATCAGCAGGGAAA
DMP750R	GACTTTCTGAGCTGGA
DMP-R1	TCACTGCTGCTTTCCTGGGAT
DMP-R2	TTGGTCACCGATGGGTTTGT
Thyrotropin	
THYF	TATTGTATGACACGGGTATGT
THYR	AAATAAGGAGYAACATGGTGT

Table 3.4.—Maximum likelihood parameters by gene estimated using jModeltest. Preferred model was the one chosen under the Akaike Information Criterion (AIC) option.

Gene	Model	A-C	A-G	A-T	C-G	C-T	G-T	I	Γ
Cytb	TrN+I+G	1	29.0109	1	1	17.8903	1	0.5280	1.3610
DMP1	TIM1+I+G	1	3.6838	1.4433	1.4433	8.7734	1	0.5040	0.5610
THY	TrN+G	1	8.5630	1	1	5.8316	1	-	0.3190
Combined	GTR+I+G	1.7279	12.6813	2.2899	1.2741	24.0733	1	0.5040	0.3960

TABLE 3.5.—Percentage sequence divergence of cytochrome b corrected by Kimura 2-parameter model (Kimura 1980) for comparisons within and between clades of *Akodon* recovered in phylogenetic analyses (Fig. 3.3). The number of pairwise comparisons is given in parentheses.

		Between clades					
Taxon	Within clade	1	2	3	4	5	6
1 *A. mimus* – MSB 70488	-						
2 *A. mimus*	0.362 (1)	12.592 (2)					
3 *A. albiventer*	0.960 (6)	14.436 (4)	11.763 (8)				
4 *A. aerosus*	5.124 (6)	13.229 (4)	10.800 (8)	10.813 (16)			
5 *A. mollis altorum*	1.561 (6)	12.135 (4)	10.886 (8)	10.547 (16)	8.159 (16)		
6 *A. orophilus orophilus*	0.352 (1)	12.037 (2)	10.345 (4)	11.541 (8)	8.117 (8)	7.283 (8)	
7 *A. torques*	1.179 (10)	11.501 (5)	10.402 (10)	11.083 (20)	8.011 (20)	6.742 (20)	6.945 (10)
8 *A. varius*	-	12.711 (1)	11.656 (2)	10.830 (4)	10.725 (4)	9.754 (4)	10.708 (2)
9 *A. glaucinus*	0.176 (1)	13.518 (2)	12.374 (4)	11.045 (8)	10.855 (8)	8.822 (8)	9.750 (4)
10 *A. tartareus*	0.117 (3)	12.795 (3)	11.197 (6)	10.892 (12)	10.783 (12)	8.356 (12)	9.315 (6)
11 *A. simulator*	1.396 (3)	13.319 (3)	12.167 (6)	11.347 (12)	11.192 (12)	9.646 (12)	10.252 (6)
12 *A. iniscatus*	-	14.729 (1)	12.599 (2)	13.328 (4)	13.819 (4)	12.306 (4)	12.652 (2)
13 *A. dayi*	-	15.101 (1)	13.968 (2)	15.885 (4)	14.956 (4)	14.182 (4)	14.287 (2)
14 *A. toba*	-	15.074 (1)	12.651 (2)	13.217 (4)	14.459 (4)	13.413 (4)	12.728 (2)
15 *A. dolores*	0.529 (3)	14.655 (3)	13.567 (6)	14.816 (12)	15.246 (12)	13.673 (12)	13.634 (6)

16 *A. azarae*	0.796 (1)	14.853 (2)	13.403 (4)	13.325 (8)	13.833 (8)	13.575 (8)	14.447 (4)

TABLE 3.5.—Continued.

		Between clades					
Taxon	Within clade	1	2	3	4	5	6
17 *A. cursor*	-	14.844 (1)	13.687 (2)	14.611 (4)	14.493 (4)	13.463 (4)	14.311 (2)
18 *A. montensis*	0.618 (1)	15.135 (1)	14.908 (4)	14.657 (8)	15.949 (8)	13.084 (8)	14.620 (4)
19 *A. juninensis*	-	13.970 (1)	13.365 (2)	13.845 (4)	13.669 (4)	12.130 (4)	14.238 (2)
20 *A. kofordi*	-	12.741 (1)	13.379 (2)	14.601 (4)	13.961 (4)	12.970 (4)	13.622 (2)
21 *A. fumeus*	1.104 (21)	13.124 (7)	13.908 (14)	14.716 (28)	14.315 (28)	13.385 (28)	14.570 (14)
22 *A. lutescens* – All	2.598 (78)	13.433 (13)	12.876 (26)	12.651 (52)	13.010 (52)	11.723 (52)	13.612 (26)
23 *A. lutescens puer*	0.494 (10)	13.859 (5)	13.762 (10)	12.813 (20)	13.518 (20)	12.600 (20)	14.221 (10)
24 *A. lutescens caenosus*	1.282 (28)	13.167 (8)	12.322 (16)	12.551 (32)	12.921 (32)	11.175 (32)	13.232 (16)
25 *A. viridescens*	0.053 (10)	13.194 (5)	13.229 (10)	14.129 (20)	13.340 (20)	12.589 (20)	14.666 (10)
26 *A. boliviensis*	0.531 (3)	14.337 (3)	14.114 (6)	13.465 (12)	14.342 (12)	12.991 (12)	15.007 (6)
27 *A. spegazzinii*	1.305 (36)	14.380 (9)	13.474 (18)	13.431 (36)	14.478 (36)	13.348 (36)	15.129 (18)

TABLE 3.5.—Continued.

Taxon	Between clades						
	7	8	9	10	11	12	13
8 *A. varius*	9.848 (5)						
9 *A. glaucinus*	9.762 (10)	3.538 (2)					
10 *A. tartareus*	9.086 (15)	3.636 (3)	2.331 (6)				
11 *A. simulator*	9.911 (15)	4.134 (3)	2.787 (6)	3.534 (9)			
12 *A. iniscatus*	12.153 (5)	13.700 (1)	12.472 (2)	11.922 (3)	12.423 (3)		
13 *A. dayi*	13.024 (5)	15.297 (1)	15.414 (2)	15.040 (3)	15.815 (3)	10.275 (1)	
14 *A. toba*	12.867 (5)	14.269 (1)	14.155 (2)	13.006 (3)	14.081 (3)	10.071 (1)	6.324 (1)
15 *A. dolores*	13.445 (15)	14.776 (3)	14.969 (6)	13.875 (9)	14.887 (9)	10.077 (3)	6.031 (3)
16 *A. azarae*	13.139 (10)	12.905 (2)	13.464 (4)	12.151 (6)	13.501 (6)	13.002 (2)	13.644 (2)
17 *A. cursor*	13.506 (5)	14.293 (1)	14.064 (2)	13.400 (3)	14.672 (3)	13.836 (1)	13.260 (1)
18 *A. montensis*	13.956 (10)	13.464 (2)	13.690 (4)	12.922 (6)	14.071 (6)	13.938 (2)	14.475 (2)
19 *A. juninensis*	12.883 (5)	13.424 (1)	13.764 (2)	12.617 (3)	14.403 (3)	13.220 (1)	14.211 (1)
20 *A. kofordi*	12.322 (5)	13.042 (1)	13.042 (2)	12.247 (3)	13.439 (3)	14.427 (1)	13.936 (1)
21 *A. fumeus*	12.764 (35)	13.590 (7)	13.622 (14)	12.570 (21)	14.187 (21)	13.921 (7)	13.985 (7)
22 *A. lutescens* – All	12.113 (65)	12.898 (13)	12.942 (26)	11.747 (39)	13.418 (39)	12.398 (13)	13.432 (13)
23 *A. lutescens puer*	12.441 (25)	13.204 (5)	12.913 (10)	12.068 (15)	13.620 (15)	12.713 (5)	13.780 (5)
24 *A. lutescens caenosus*	11.907 (40)	12.707 (8)	12.959 (16)	11.546 (24)	13.291 (24)	12.201 (8)	13.214 (8)
25 *A. viridescens*	12.835 (25)	12.992 (5)	13.666 (10)	13.307 (15)	13.767 (15)	13.328 (5)	13.724 (5)

TABLE 3.5.—Continued.

Taxon	Between clades						
	7	8	9	10	11	12	13
26 *A. boliviensis*	13.276 (15)	13.725 (3)	14.182 (6)	13.516 (9)	14.570 (9)	15.092 (3)	15.054 (3)
27 *A. spegazzinii*	13.847 (45)	13.532 (9)	13.682 (18)	12.886 (27)	14.297 (27)	14.626 (9)	14.763 (9)

TABLE 3.5.—Continued.

Taxon	Between clades						
	14	15	16	17	18	19	20
15 *A. dolores*	2.454 (3)						
16 *A. azarae*	12.981 (2)	13.625 (6)					
17 *A. cursor*	14.407 (1)	14.340 (3)	12.299 (2)				
18 *A. montensis*	15.064 (2)	14.764 (6)	11.378 (4)	9.483 (2)			
19 *A. juninensis*	14.683 (1)	14.350 (3)	12.061 (2)	10.313 (1)	9.684 (2)		
20 *A. kofordi*	14.633 (1)	13.885 (3)	11.763 (2)	10.583 (1)	9.952 (2)	7.730 (1)	
21 *A. fumeus*	14.420 (7)	13.740 (21)	11.566 (14)	10.420 (7)	10.215 (14)	7.882 (7)	2.294 (7)
22 *A. lutescens* – All	12.940 (13)	13.127 (39)	10.729 (26)	9.897 (13)	10.414 (26)	7.694 (13)	7.522 (13)
23 *A. lutescens puer*	13.882 (5)	13.950 (15)	10.328 (10)	9.146 (5)	10.079 (10)	8.081 (5)	7.698 (5)
24 *A. lutescens caenosus*	12.351 (8)	12.612 (24)	10.980 (16)	10.366 (8)	10.622 (16)	7.452 (8)	7.412 (8)
25 *A. viridescens*	13.173 (5)	13.524 (15)	11.313 (10)	10.750 (5)	11.169 (10)	8.885 (5)	8.887 (5)
26 *A. boliviensis*	14.031 (3)	14.428 (9)	11.771 (6)	9.860 (3)	10.686 (6)	9.111 (3)	7.835 (3)
27 *A. spegazzinii*	14.380 (9)	14.461 (27)	11.485 (18)	10.100 (9)	11.020 (18)	9.356 (9)	8.319 (9)

TABLE 3.5.—Continued.

Taxon	Between clades					
	21	22	23	24	25	26
22 *A. lutescens* – All	7.440 (91)					
23 *A. lutescens puer*	7.035 (35)	-				
24 *A. lutescens caenosus*	7.693 (56)	-	4.046 (40)			
25 *A. viridescens*	8.953 (35)	7.191 (65)	7.232 (25)	7.165 (40)		
26 *A. boliviensis*	8.474 (21)	7.713 (39)	7.432 (15)	7.888 (24)	4.809 (15)	
27 *A. spegazzinii*	8.625 (63)	8.208 (117)	7.750 (45)	8.494 (72)	5.253 (45)	2.924 (27)

TABLE 3.6.—Node ages and 95% HPD (Height Posterior Density) obtained from the BEAST analyses. Node numbers correspond to those presented in Figure 3.4.

Node #	Node age (mybp)	95% HPD
1	4.49	3.58–5.74
2	3.10	2.54–3.89
3	2.70	2.11–3.48
4	2.28	1.75–2.98
5	2.21	1.64–2.88
6	1.95	1.48–2.54
7	1.91	1.45–2.50
8	1.88	1.36–2.49
9	1.74	1.27–2.28
10	1.50	1.06–2.01
11	1.43	1.07–1.88
12	1.28	0.94–1.70
13	1.21	0.89–1.61
14	1.14	0.82–1.52
15	1.11	0.78–1.51
16	0.92	0.63–1.25
17	0.87	0.58–1.19
18	0.78	0.55–1.06
19	0.68	0.47–0.92
20	0.66	0.42–0.93
21	0.51	0.34–0.72
22	0.47	0.30–0.67
23	0.43	0.26–0.62
24	0.42	0.25–0.61
25	0.30	0.17–0.45

FIGURE LEGENDS

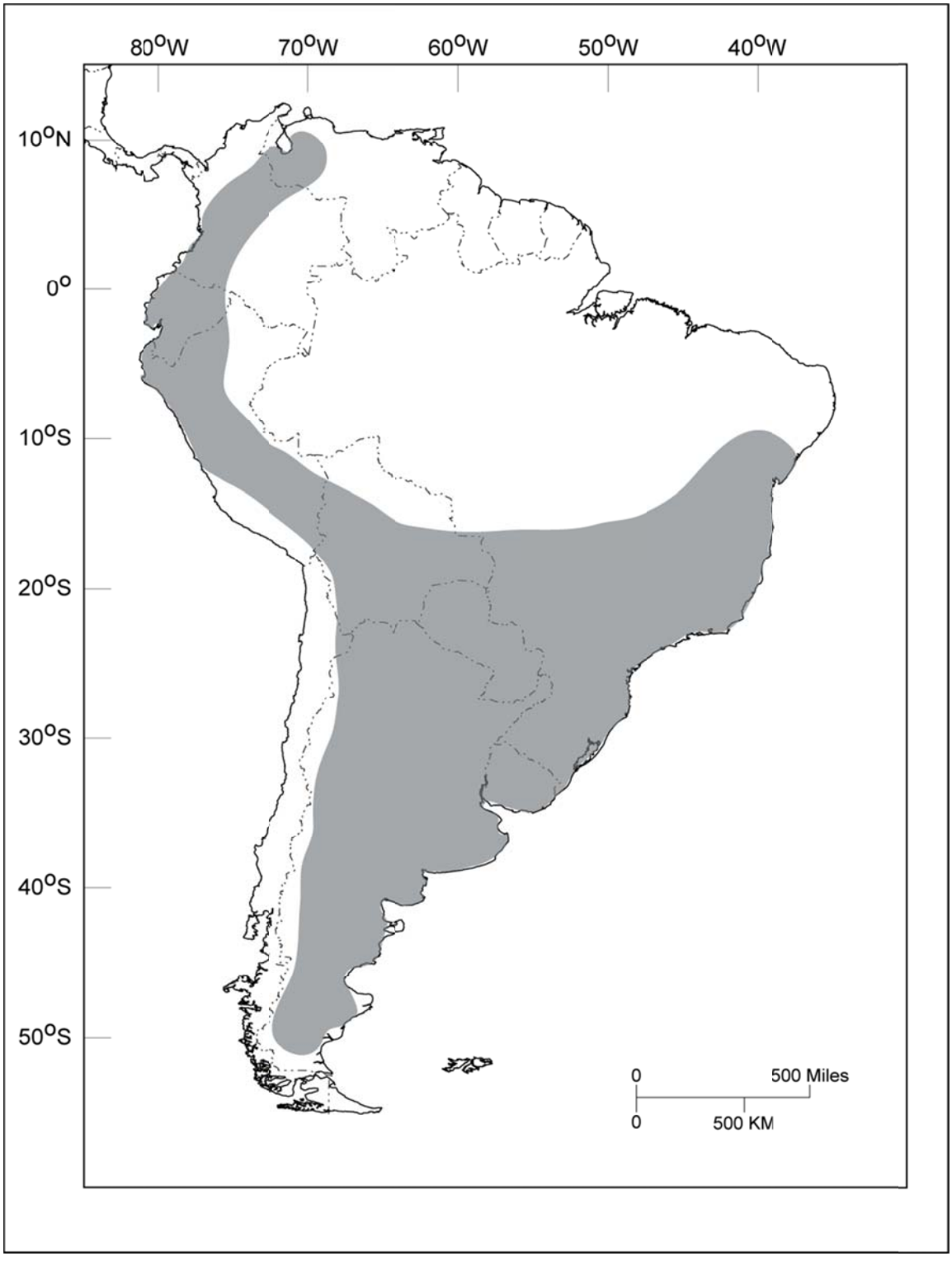
FIG. 3.1.—Distribution (approximate; from Braun et al. 2008; Jayat et al. 2010; Musser and Carleton 2005; Myers 1989; Myers and Patton 1989b; Myers et al. 1990; Smith and Patton 1992a, 1993) of the genus *Akodon*.

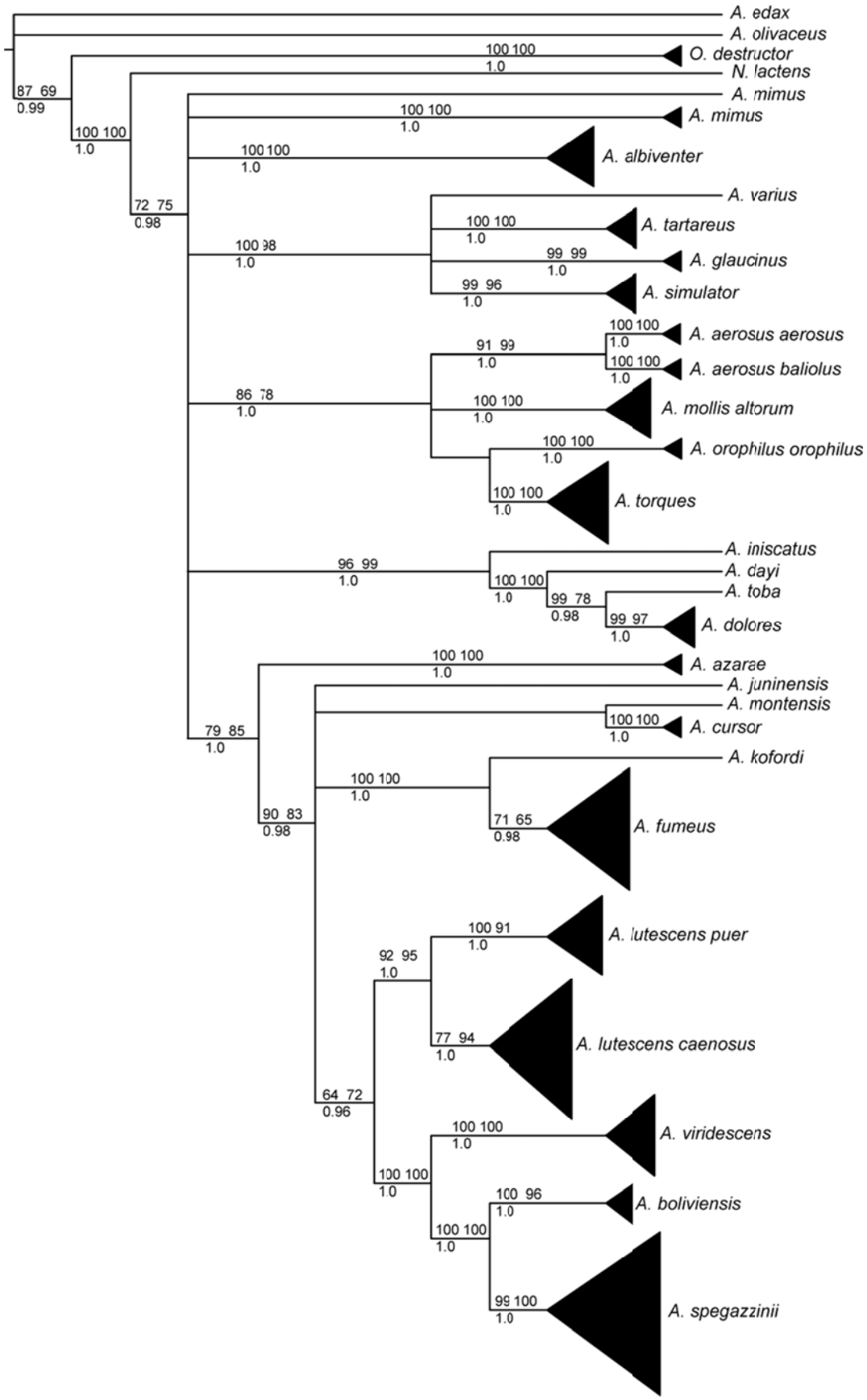
FIG. 3.2.—Cladogram obtained from analysis under maximum likelihood criterion of the cytochrome b gene. Values associated with each node are bootstrap percentages for maximum parsimony followed by bootstrap percentages for maximum likelihood above the branch and Bayesian posterior probabilities below the branch. Branches are collapsed and not shown within each species, and the size of each triangle is proportional to the number of individuals (see Appendix 1 for specimens examined list) included within that species.

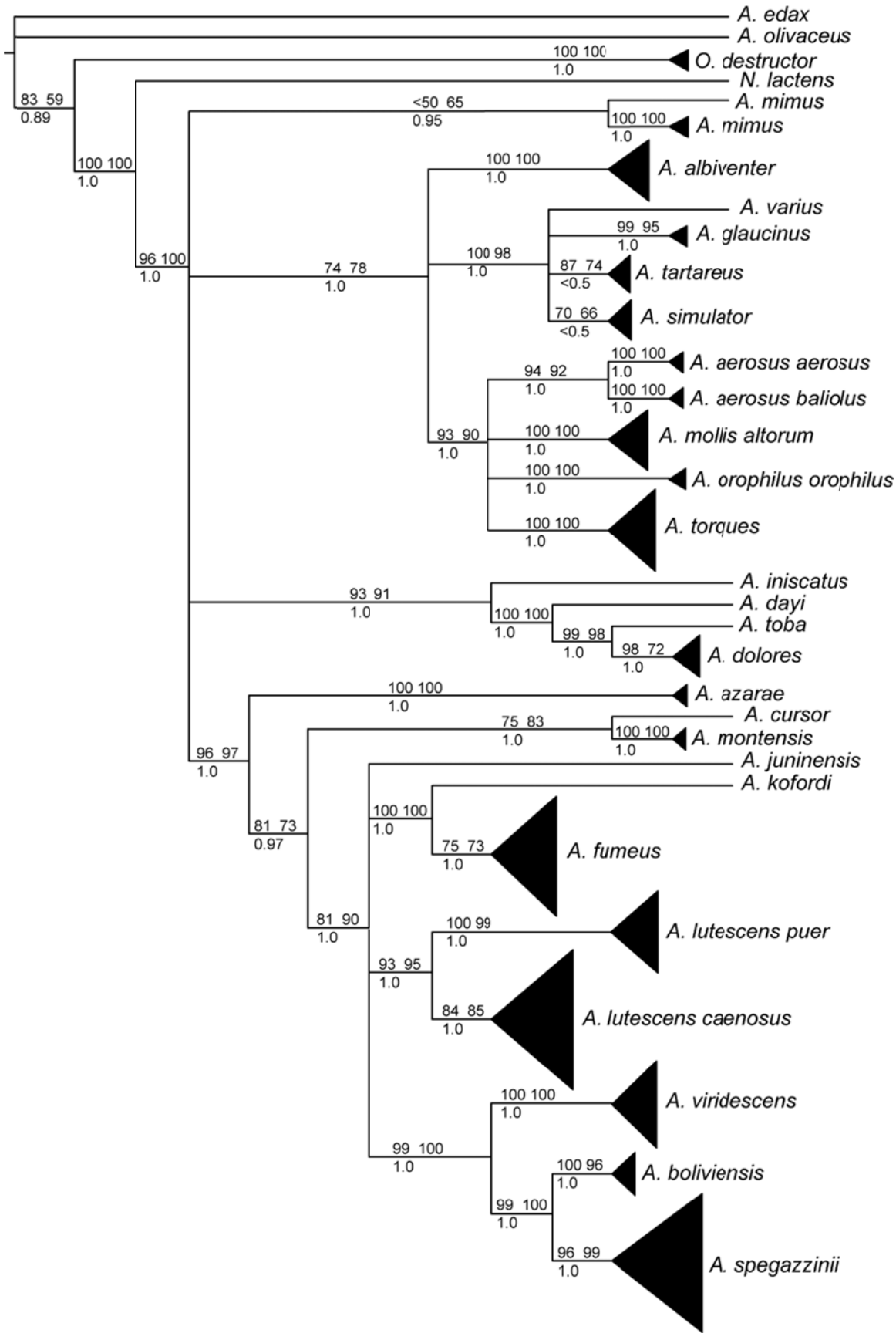
FIG. 3.3.—Cladogram obtained from analysis under maximum likelihood criterion of the concatenated dataset containing the cytochrome b gene, the dentin matrix protein gene, and the thyrotropin intron. Values associated with each node are bootstrap percentages (maximum parsimony followed by maximum likelihood) above the branch and Bayesian posterior probabilities below the branch. Branches within each species are not shown. The triangle representing the collapsed branches is proportional to the number of individuals included within that species clade (see Appendix 1 for the number of individuals in each species).

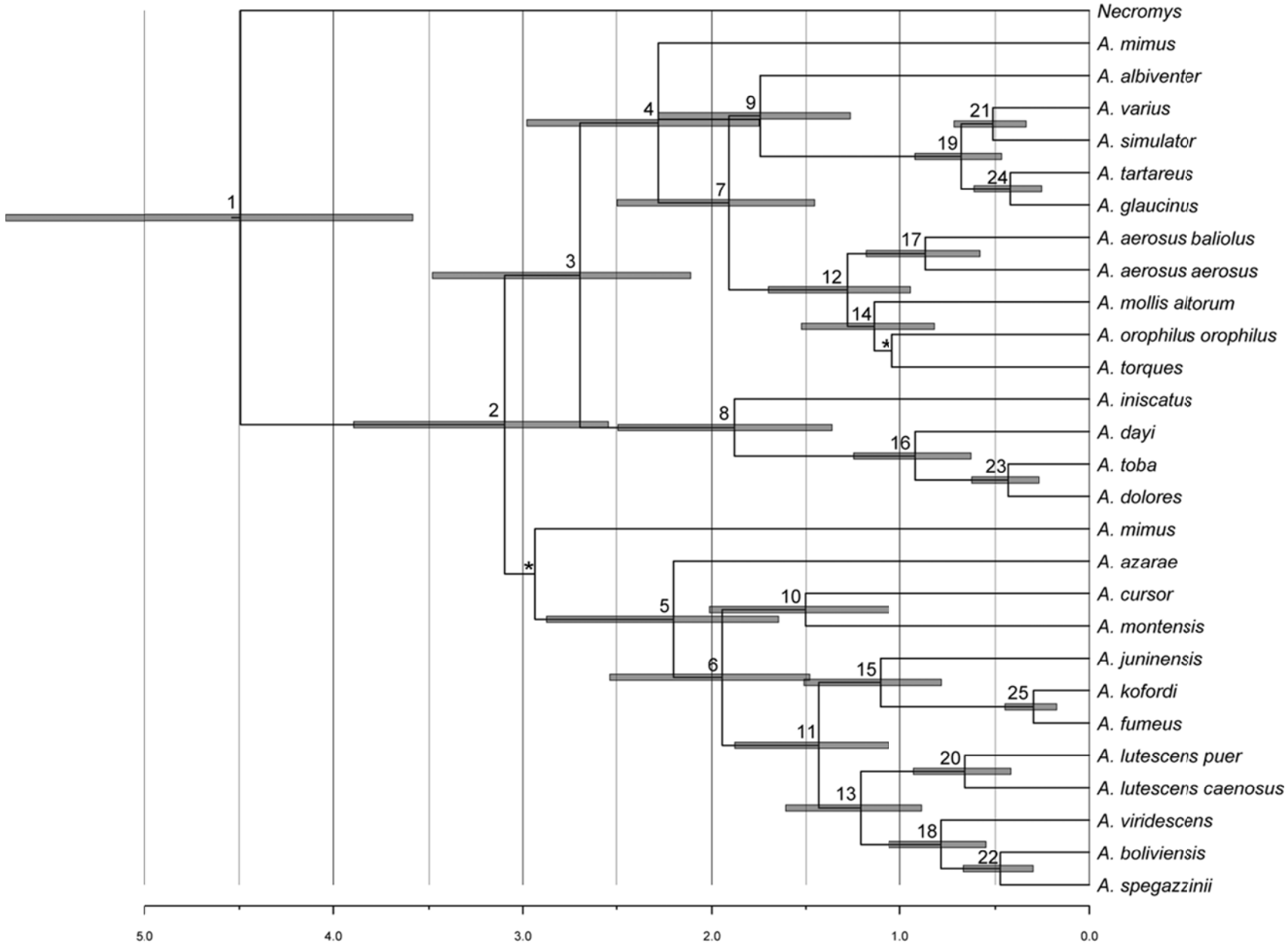
FIG. 3.4.—*Akodon* phylogeny obtained in the BEAST analysis. Numbers at each node correspond to the node numbers in Table 3.6. Grey bars represent the 95% HPD (Height Posterior Density) intervals for the divergence date estimates. Time scale

is given in million years before present (mybp). Nodes marked with asterisks are unsupported; their dates are unreliable.


80°W
70°W
60°W
50°W
40°W
10°N
0°
10°S
20°S
30°S
40°S
50°S
0
500 Miles
0
500 KM


A. edax
A. olivaceus
100 100
1.0
O. destructor
N. lactens
87 69
0.99
A. mimus
100 100
1.0
A. mimus
100 100
1.0
A. albiventer
A. varius
72 75
0.98
100 100
1.0
A. tartareus
100 98
1.0
99 99
1.0
A. glaucinus
99 96
1.0
A. simulator
100 100
1.0
A. aerosus aerosus
91 99
1.0
100 100
1.0
A. aerosus baliolus
86 78
1.0
100 100
1.0
A. mollis altorum
100 100
1.0
A. orophilus orophilus
100 100
1.0
A. torques
A. iniscatus
96 99
1.0
A. dayi
100 100
1.0
A. toba
99 78
0.98
99 97
1.0
A. dolores
100 100
1.0
A. azarae
A. juninensis
A. montensis
79 85
1.0
100 100
1.0
A. cursor
A. kofordi
100 100
1.0
90 83
0.98
71 65
0.98
A. fumeus
100 91
1.0
A. lutescens puer
92 95
1.0
77 94
1.0
A. lutescens caenosus
64 72
0.96
100 100
1.0
A. viridescens
100 100
1.0
100 96
1.0
A. boliviensis
100 100
1.0
99 100
1.0
A. spegazzinii


A. edax
A. olivaceus
100 100
1.0
O. destructor
N. lactens
83 59
0.89
<50 65
0.95
A. mimus
100 100
1.0
A. mimus
100 100
1.0
A. albiventer
A. varius
99 95
1.0
A. glaucinus
96 100
1.0
74 78
1.0
100 98
1.0
87 74
<0.5
A. tartareus
70 66
<0.5
A. simulator
100 100
1.0
A. aerosus aerosus
94 92
1.0
100 100
1.0
A. aerosus baliolus
93 90
1.0
100 100
1.0
A. mollis altorum
100 100
1.0
A. orophilus orophilus
100 100
1.0
A. torques
A. iniscatus
93 91
1.0
A. dayi
100 100
1.0
A. toba
99 98
1.0
98 72
1.0
A. dolores
100 100
1.0
A. azarae
A. cursor
75 83
1.0
100 100
1.0
A. montensis
96 97
1.0
A. juninensis
A. kofordi
100 100
1.0
81 73
0.97
75 73
1.0
A. fumeus
81 90
1.0
100 99
1.0
A. lutescens puer
93 95
1.0
84 85
1.0
A. lutescens caenosus
100 100
1.0
A. viridescens
99 100
1.0
100 96
1.0
A. boliviensis
99 100
1.0
96 99
1.0
A. spegazzinii


Necromys
A. mimus
A. albiventer
A. varius
A. simulator
A. tartareus
A. glaucinus
A. aerosus baliolus
A. aerosus aerosus
A. mollis altorum
A. orophilus orophilus
A. torques
A. iniscatus
A. dayi
A. toba
A. dolores
A. mimus
A. azarae
A. cursor
A. montensis
A. juninensis
A. kofordi
A. fumeus
A. lutescens puer
A. lutescens caenosus
A. viridescens
A. boliviensis
A. spegazzinii
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CHAPTER IV

CONCLUSIONS ON A PHYLOGENETIC AND BIOGEOGRAPHY STUDY OF *AKODON*

The goal of this research was to obtain a well-resolved phylogeny for the genus *Akodon* using the commonly used mitochondrial marker, cytochrome b, along with two nuclear markers, dentin matrix protein 1 and thyrotropin. As compared to previous studies using cytochrome b, significantly more resolution was obtained in the multi-gene phylogeny. Additionally a dataset of cytochrome b data alone was also analyzed in this study. The phylogeny obtained from cytb data alone, while containing more than twice the samples of the analysis containing data from all three genes, resulted in a tree with low support values and little resolution, similar to trees based upon cytb data in previous studies.

Considering the results of both analyses presented in this dissertation (cytochrome b alone and all three genes concatenated), a number of taxonomic recommendations can be made. A reorganization of the genus is needed if these new molecular results are to be incorporated into the species groupings, originally based upon morphology but supported by limited molecular and cytogenetic data. The genus can still be divided into four groups

with some taxa retaining *incertae sedis* status (Table 4.1). Taxa not included in this study are retained as is pending further study.

The *aerosus* group retains the 9 species-level taxa that were previously included within it. Four species (*A. glaucinus*, *A. simulator*, *A. tartareus*, and *A. varius*) from the previously recognized *varius* group should be reassigned to the *aerosus* group. Two sets of subspecies (*A. aerosus aerosus–A. aerosus baliolus* and *A. orophilus orophilus–A. orophilus orientalis*) should each be recognized as separate species based upon their higher degree of divergence as sister subspecies compared to other currently recognized sister species. Finally as three species are paraphyletic (*A. aerosus*, *A. mollis*, and *A. orophilus*) and contain clades without names, samples assigned to these taxa likely represent two, possibly three, new unnamed species.

With the reassignment of *A. varius* to the *aerosus* group, the *varius* group is no longer recognized. Giving precedence to the taxon that was described first, the redefined group, containing 6 species, should be referred to as the *dolores* group. As the species groups were originally described based upon morphological similarities, a reevaluation of the morphology of the *aerosus* group and the new *dolores* group should be done. *Akodon lindberghi*, previously an *incertae sedis* taxon, is officially assigned to the *cursor* group, joining the other 6 *cursor* species. In the *boliviensis* group, two subspecies of *A. lutescens* are retained (*A. lutescens lutescens* and *A. lutescens puer*) while the subspecies *A. lutescens caenosus* as included here represents two distinct species level taxa, one yet to be named.

The results of this study also provide insight into the evolution of the genus. With added resolution, dates of divergence can be assigned to not only sister taxa but

divergences at nodes deeper within the tree. Hypotheses can be formulated for the geographic ranges of ancestral taxa, dispersal routes, and other events that give rise to the current distribution patterns found today.

FUTURE RESEARCH

Efforts should be made in future molecular studies to include not only additional *Akodon* taxa but also to include multiple molecular markers, from both the mitochondrial and nuclear genomes. Eleven of the 46 extant species, just over one quarter, have not been included in a molecular analysis to date. Without their inclusion, morphological and geographical affinities cannot be evaluated to determine if they are supported by molecular data.

A morphological reassessment of the species groups needs to be conducted to determine the characters that unite the redefined species groupings. Thorough analyses of *A. serrensis* and *A. mimus* need to be conducted to assess the inclusion of these species within *Akodon* (*sensu stricto*) and, in the case of *A. mimus*, to determine the number of species contained within it. Other taxa, principally *A. aerosus*, *A. mollis*, and *A. orophilus*, need to be evaluated to address their current paraphyly. Finally studies of *Akodon* in all areas (i.e. ecology, behavior, etc.) need to be conducted to better understand the genus and its species.

TABLE 4.1.—Revision of the genus *Akodon* based upon the results of this study. Asterisks indicate taxa not included in this study.

A. aerosus group	*A. boliviensis* group	*A. cursor* group	*A. dolores* group	*Incertae sedis*
A. aerosus	*A. aliquantulus**	*A. cursor*	*A. dayi*	*A. azarae*
A. affinis	*A. boliviensis*	*A. lindberghi*	*A. dolores*	*A. bogotensis**
A. albiventer	*A. caenosus*	*A. montensis*	*A. iniscatus*	*A. latebricola**
A. baliolus	*A. fumeus*	*A. mystax*	*A. neocenus**	*A. mimus*
A. budini	*A. juninensis*	*A. paranaensis*	*A. oenos**	*A. philipmyersi*
A. glaucinus	*A. kofordi*	*A. reigi*	*A. toba*	*A. serrensis*
A. mollis	*A. leucolimnaeus**	*A. sanctipaulensis**		
A. orientalis	*A. lutescens*			
A. orophilus	*A. pervalens**			
A. siberiae	*A. polopi**			
A. simulator	*A. spegazzinii*			
*A. surdus**	*A. subfuscus*			
A. tartareus	*A. sylvanus*			
A. torques	*A. viridescens*			
A. varius	*A.* n. sp. 3			
A. n. sp. 1				
A. n. sp. 2				

APPPENDIX 1

Specimens examined.—Acronyms for institutions are as follows: Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (OMNH); Oklahoma Collection of Genomic Resources, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (OCGR); Collecíon de Mamíferos Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina (CML); The Field Museum, Chicago, Illinois (FMNH); University of New Mexico, Museum of Southwestern Biology, Albuquerque, New Mexico (MSB NK); Museum of Vertebrate Zoology, University of California, Berkeley, Berkeley, California (MVZ); Museum of Texas Tech University, Texas Tech University, Lubbock, Texas (TTU TK); Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Museu de Zoologia de Universidade de São Paulo (MZUSP); and Museu Nacional, Rio de Janeiro (MN). Locality information, location of voucher skin, skull and/or skeleton and catalog number, location of tissue and catalog number, and specimen field number (from Argentina project, Arg) are given below for all specimens sequenced in this study. Sequences obtained from Genbank are presented by their Genbank accession number.

Abrothrix longipilis (1).—ARGENTINA: RIO NEGRO: Bariloche: La Veranada, 38 km SSW Bariloche, 41.45°S, 71.48°W (MVZ154494/Genbank U03530).

Abrothrix olivaceus (1).—CHILE: AISEN: Coyhaique Alto, 4.5 km E, Fundo El Largo, 45.483°S, 71.6°W, 750 m (FMNNH132951).

Akodon aerosus (1).—PERU: CUZCO: 72 km NE (by road) Paucartambo, km 152, 13.00675°S, 70.15438°W, 1460 m (MVZ 171679/Genbank M35703).

Akodon aerosus aerosus (3).— ECUADOR: PASTAZA: 5 km E Puyo, Safari Hosteria Park (TTU 84936/TTU TK 104164). PERU: CUSCO: Paucartambo: Consuelo, 15.9 km SW Pilcopata, 13°01.417'S, 71°29.511'W (FMNH174951). JUNIN: 10 km WSW (by road) San Ramon, 11.06583°S, 75.36513°W, 1275 m (MVZ 172870/Genbank M35707).

Akodon aerosus baliolus (3).—BOLIVIA: COCHABAMBA: 4.4 km N Tablas Monte, 17°3'51"S, 65°28'33"W, 400 m (MSB 70449/MSB NK 30143). LA PAZ: Serrania Bella Vista, 15°41'S, 67°30'W, 1525 m (MSB 68549/MSB NK 25650). PERU: PUNO: 4 km NNE Ollachea, 13.78326°S, 70.46918°W, 2380 m (MVZ 172818/Genbank M35704).

Akodon affinis (1).—COLOMBIA: RISARALDE: Municipio Pereira, Corregimiento La Florida, vereda La Pastora, camino a Las Cascadas, PRN Ucamarí (Insituto de Ciencias Naturales in Bogotá 16547/JLP 16684/Genbank AY196164).

Akodon albiventer (8).—ARGENTINA: JUJUY: Yavi: 6.8 km al SE de Suripujio, sobre Ruta Provincial No. 5, 3991 m (OMNH 30017/OCGR 3663/Arg 4732). BOLIVIA: ORURO: Escuela Seccional Villa Ventilla, desvio, km 181 S Oruro, 17.983°S, 67.15°W, 4150 m (FMNH162731). POTOSI: 11.5 km by rd N of

Yocalla, 19.37583°S, 65.974917°W, 3860 m (FMNH162741). TARIJA: 4.5 km E Iscayachi, 21°29'S, 64°55'W, 3750 m (MSB 67115/MSB NK 23631). CHILE: TARAPACA: Colchane: Suricayo (12 km N Enquelga) (MSB 209890/MSB NK 96060/Genbank AY341042); Colchane: Enquelga (sitio 1) (MSB 210396/MSB NK 96068/Genbank AY341040); Putre: Socoroma (MSB 209852/MSB NK 96000/Genbank AY341037); ca 72 km E of Arica, 10 km S of Chapiquina, 22 km S of Putre, 18.417°S, 69.55°W, 3650 m (FMNH 129978/Genbank AY494838).

Akodon azarae (7).—ARGENTINA: BUENOS AIRES: Pergamino, FARM INT, GRID L (MSB 204744/MSB NK 114394). CORDOBA: 2 km S Espinillo (TTU 66508/TTU TK 49099). SANTA FE: Arteaga, FARM SKI, GRID L (MSB 200115/MSB NK 109753). PARAGUAY: NEEMBUCU: 5.8 km by road NE Pilar (UMMZ 134443/Genbank U03529). PARAGUARI: Coast of the Tebicuary River, 26°24'S, 57°02'W (GD 264/Genbank DQ444328). URUGUAY: San José: Kiyu (GD 327/Genbank AY702964). No locality information available (Genbank EF622507).

Akodon boliviensis (3).—BOLIVIA: TARIJA: 4.5 km E of Iscayachi, 21°29'S, 64°55'W, 3750 m (MSB 67141/MSB NK 23619; MSB 68571/MSB NK23620). PERU: PUNO: 12 km S Santa Rosa (de Ayaviri) (MVZ 171607/Genbank M35691).

Akodon budini (1).—BOLIVIA: CHUQUISACA: Rinconada del Bufete, 20°49.81'S, 64°22.47'W, 2000 m (LHE 1260/Genbank AY605060).

Akodon cursor (5). —BRAZIL: BAHIA: Estação Experimental Djalma Bahia—CEPLAC—Una, 15°18'S, 39°06'W, 28 m (EDH 30/Genbank AF184053). PARAÍBA: João Pessoa, 7°06'S, 34°51'W (Genbank EF206814). SÃO PAULO:

Estação Biológica de Boracéia, Salesópolis, 22°11'S, 48°46'W, 850 m (MZUSP 29257/Genbank AF184051); Ilha do Cardoso, 25.13°S, 47.97°W, 109 m (FMNH 141724; FMNH 141622).

Akodon dayi (2).—BOLIVIA: PANDO: Remanso, 10.56°S, 66.18°W, 160 m (AMNH 262745/MSB NK 14376/Genbank EU260477). SANTA CRUZ: El Refugio, Parque Nacional Noël Kempff Mercado (LHE 1268/Genbank AY605059).

Akodon dolores (8).—ARGENTINA: CATAMARCA: Capayán: Chumbicha, 0.5 km E of Hwy 38 along Hwy 60, 1500 feet (OMNH 23527/OCGR 1516/Arg 1619/Genbank EU260473). MENDOZA: San Rafael: 2 km S Puesto Punta del Agua, 2700 feet (OMNH 36037/OCGR XXXX/Arg 3113); Santa Rosa: Ñacuñán MaB Reserve (GenBank AY494839 as *A. molinae*; sample from a mouse colony whose original stock was captured from the locality given—Smith and Patton 2007). SAN LUIS: Capital: 15 km E Salinas del Bebedero, 1350 feet (OMNH 35926/OCGR 467/Arg 529/Genbank EU260472); Chacabuco: Papagallos (UP PY 16/Genbank AY273904; locality clarified by Smith and Patton 2007). SANTIAGO DEL ESTERO: Atamisqui: 1 km northeast of junction Río Saladillo and highway 9, 700 feet (OMNH 35928/OCGR 1964/Arg 2353/Genbank EU260474 – AK15353); Guasayán: Virgen del Valle picnic area on highway 64 between Santa Catalina and La Puerta Chiquita, 2300 feet (OMNH 35929/OCGR 1917/Arg 2294/Genbank EU260476 – AK15373); Quebrachos: Buena Vista, 15 km NE Va. Ojo de Agua off of hwy 13, 1300 feet (OMNH 35927/OCGR 1964/Arg 2353/Genbank EU260475 – AK 15294).

Akodon fumeus (10).—ARGENTINA: JUJUY: Gral. Manuel Belgrano: 24.9 km N San Salvador, 1583 m (OMNH 38609/OCGR 7259/Arg 6662). TUCUMÁN: Tafi: 12 km W of La Quebradita, Tafi del Valle, km 81 on Hwy 307, 9500 feet (OMNH 38608/OCGR 4012/Arg 4247). BOLIVIA: CHUQUISACA: Rinconada del Bufete, 20°49.81'S, 64°22.47'W, 2000 m (LHE 1262/Genbank AY605061). COCHABAMBA: Corani, 17°12'43"S, 65°52'4"W, 2630 m (MSB 70476/MSB NK 29793); 21 KM (by road) W of Comarapa, 17.51°S, 64.27°W, 2900 m (AMNH 260580/MSB NK 12088); 28 km W (by road) Comarapa, 17°51'S, 64°40'W, 2800 m (MSB 55226/MSB NK 12020); 4.4 km by rd N Tablas Monte, 17°04'S, 66°00'W, 1833 m (MSB 70703/MSB NK 30300); Tinkusiri, 17 km E of Totora, 17°45'S, 65°02'W (MSB 87113/MSB NK 22858). TARIJA: 5 km NNW Entre Rios, 21°29'S, 64°12'W, 1600 m (MSB 67139/MSB NK 23937); Pirulas, rd to Chiquiaca, 21.6532°S, 64.1025°W, 1550 m (FMNH 162755).

Akodon glaucinus (3).—ARGENTINA: CATAMARCA: Andalgalá: Ambato: El Rodeo, 1.5 km NE of Hwy 4, 4500 ft (OMNH 23699/OCGR 1441/Arg 1544/Genbank EU260483); Choya, 13 km NNW of Andalgalá, 4000 ft (OMNH 23671/OCGR 1697/Arg 2038/Genbank EU260484); Paclin: 3.4 km al S de la union entre las rutas 18 y 9 (provincials), sobre Ruta Provincial No. 18, 1529 m (OMNH 30013/OCGR 4052/Arg 4802).

Akodon iniscatus (3).—ARGENTINA: NEUQUEN: Estáncia La Porteña, Sierra de Cuchillo Curá, Las Lajas (UP 442/Genbank AY605062). RIO NEGRO: Pilcaniyeu: 10 km S Comallo, 41.09°S, 70.21°W, 2900 m (MVZ

182655/Genbank AY273917). CHILE: AISEN: 1 km E Coyhaique Alto, 45.4833°S, 71.6°W, 730 m (FMNH 129845).

Akodon juninensis (1).—PERU: JUNÍN: 22 km N (by road) La Oroya (MVZ 173038/Genbank M35698).

Akodon kofordi (2).—BOLIVIA: LA PAZ: Rio Aceromarca, 16°19'S, 67°53'W, 2990 m (MSB 68528/MSB NK 25816). PERU: PUNO: Agualani, 9 km N Limbani (MVZ 171665/Genbank M35697).

Akodon lindberghi (1). —BRAZIL: MINAS GERAIS (MN 48026/Genbank AF184057).

Akodon lutescens caenosus (9).—ARGENTINA: CATAMARCA: Ambato: El Rodeo, 1.5 km NE of Hwy 4, 4500 ft. (CML 3306/OCGR 1442/Arg 1545); 6 km SW of Hwy 9 on Hwy 18, 5000 ft. (OMNH 34355/OCGR 1330/Arg 1533). JUJUY: El Carmen: On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft. (OMNH 38619/OCGR 2136/Arg 2624); San Antonio: Rio Blanco, 9 km SW San Antonio, 1495 m (OMNH 36486/OCGR 3500/Arg 4267). SALTA: Chicoana: 5 km WSW Pulares, 1482 m (OMNH 38640/OCGR 3707/Arg 4968). BOLIVIA: CHUQUISACA: 2 km SW Monteagudo, 19.833°S, 64.983°W (MSB 63579/MSB NK 21380). TARIJA: Abra Condor, ca 2 km W Junacas, 21.45°S, 64.4583°W, 2650 m (FMNH162756); Erquis, 21°28'S, 64°48'W, 2100 m (MSB 67134/MSB NK 23478); 1 km E Tucumilla, 21°27'S, 64°49'W, 2500 m (MSB 67144/MSB NK 23670).

Akodon lutescens lutescens (1).—PERU: PUNO: 12 km S Santa Rosa (de Ayaviri) (MVZ 171612/Genbank M35693).

Akodon lutescens puer (5).—BOLIVIA: COCHABAMBA: 12.5 km N Corani, Laguna de Corani, 17°14’S, 65°53’W (MSB 70519/MSB NK 30508). SANTA CRUZ: 1 km N and 8 km W of Comarapa, 17°55’S, 64°34’W, 2450 m (AMNH 260494/MSB NK 12094); 21 km (by road) Comarapa, 17°51’S, 64°37’W, 2900 m (MSB 55225/MSB NK 12071; AMNH 260456/MSB NK 12072); 3 km N Torrecillas (by road), 17°51’S, 64°38’W (MSB 67133/MSB NK 229060).

Akodon mimus (5).—BOLIVIA: COCHABAMBA: Corani, 17°12’43”S, 65°52’4”W, 2630 m (MSB 70488/MSB NK 30599); 28 km W (by road) Comarapa, 17°51’S, 64°40’W, 2800 m (MSB 55206/MSB NK 12049); 31 km by road W of Comarapa, 17°51’S, 64°42’W, 2800 m (AMNH 261211/MSB NK 12090). SANTA CRUZ: Serrania Siberia, 11 km NW Torrecillas (by road), 17°49’S, 64°41’W (MSB 67126/MSB NK 22914). PERU: PUNO: 14 km W Yanahuaya, 14.26667°S, 69.32974°W, 2210 m (MVZ 171752/Genbank M35710).

Akodon mollis (1). —PERU: ANCASH: Huari: Rio Mosna, between Chavin and San Marcos, 9.55°S, 77.17°W, 2926 m (FMNH129212).

Akodon mollis altorum (4).—ECUADOR: AZUAY: “Cajas,” 2°47’S, 79°13’W, 3870 m (MSB 196736/MSB NK 30901; MSB 92704/MSB NK 30979). BOLIVAR: Rio Tatahuazo, 2.5 km E of Cruz de Lizo, 1°43’S, 78°59’W, 2800 m (MSB 70722/MSB NK 27694). CHIMBORAZO: Quebrada Guapo Chico, 1°58’S, 78°58’W, 2000 m (MSB 70738/MSB NK 27725).

Akodon mollis mollis (1).—PERU: PIURA: “Machete” on Zapalache Carmen Trail (LSUMZ 27007/Genbank U03546).

Akodon montensis (12).—BRAZIL: PARANÁ: Piraquara, Mananciais da Serra (LMT 425/Genbank EF101873; LMT 428/Genbank EF101874). RIO GRANDE DO SUL: Tainhas, 29°16'S, 50°18'W (Genbank EF206813). SÃO PAULO: Estação Biológica de Boracéia, Salesópolis (FMNH 141602/Genbank AF184055). PARAGUAY: AMAMBAY: Cerro Cora National Park: 33 km SE Pedro Juan Caba (MSB 67439/MSB NK 22525). CANINDEYÚ: Estancia Felicidad (UMMZ 174969/Genbank AY273905). PARAGUARI: IBYCUI National Park, 32 km E (by road) from Ibic, 26.0833°S, 56.8°W (MSB 67433/MSB NK 22501); Sapucái (UMMZ 174969/Genbank AY195864). Locality information unknown (MN 48066/Genbank AY273906; MN 69917/Genbank EU251020; MN 69920/Genbank EU251018; MN 69925/Genbank EU251022)

Akodon mystax (6).—BRAZIL: RIO DE JANERIO: Arrozal (MN 65565/Genbank EF101875; MN 69566/Genbank EF101876; MN 69567/Genbank EF101877; MN 69627/Genbank EF101878; MN 69629/Genbank EF101879; MN 69660/Genbank EF101880).

Akodon orophilus (1).—PERU: JUNIN: 16 km NNE Palca (MVZ 173057/Genbank M35699).

Akodon orophilus orientalis (1).—PERU: HUÁNUCO: Unchog, pass between Churrubamba and Had. Paty, NNW Acomayo, 9.683°S, 76.117°W, 11319 m (LSUMZ 27957/Genbank U03547).

Akodon orophilus orophilus (3).—PERU: AMAZONAS: Chachapoyas: ca 20 km by rd W Leimebamba, 6.75°S, 77.8°W, 2804 m (FMNH 129234/Genbank U03524; FMNH 129235; FMNH 129237).

Akodon paranaensis (15).—BRAZIL: MINAS GERAIS: Brejo da Lapa, Itatiaia, Itamonte (MN 48041/Genbank AF184054). RIO DE JANEIRO: Campos do Itatiaia, Abrigo Rebouças, Pq. Nac. Itatiaia (MN 69686/Genbank EF101886; MN 69700/Genbank EF101887; MN 69726/Genbank EF101888). RÍO GRANDE DO SUL: Parq. Nac. Aparados da Serra (LMT 270/Genbank EF101881; LMT 294/Genbank EF101882). Venancio Aires (CIT 1131/Genbank AY195866). SANTA CATARINA: Urubici (LMT 301/Genbank EF101883; LMT 304/Genbank EF101884). PARAGUAY: (no exact locality; TTU TK 66311/Genbank EU579471). Locality information unknown (LMT 270/Genbank EF101881; LMT 294/Genbank EF101882; LMT 405/Genbank EF101885; MN 48070/Genbank AY273907; MN 69930/Genbank EU251017; MN 69931/Genbank EU251019; Genbank EF622506).

Akodon philipmyersi (2). —ARGENTINA: MISIONES: Posadas: Estancia Santa Inés, Ruta No. 105 km 10, 27°31'32"S, 55°52'19"W, 95 m (CNP 739/Genbank AY702965; CNP 742/Genbank AY702966).

Akodon reigi (1). —URUGUAY: LAVALLEJA: Paso Averías (MNHN 3682/Genbank AY195865)

Akodon serrensis (4).—BRAZIL: RIO DE JANEIRO: (no exact locality; MN 35927/Genbank AF184058); Vale das Antas, Parque Nacional da Serra dos Órgãos (VA 1/Genbank AY273908). SANTA CATARINA: Urubici (LMT 436/Genbank EF101889). Locality information unknown (Genbank EF622508)

Akodon siberiae (2).—BOLIVIA: COCHABAMBA: 28 km by road W Comarapa, 17°51'S, 64°W (MSB 55209/MSB NK 12003/Genbank U03548); 31 km by road

W of Comarapa, 17°51'S, 64°42'W, 2800 m (AMNH 260578/MSB NK 12081/Genbank AY273909).

Akodon simulator (6).—ARGENTINA: JUJUY: San Antonio: Río Blanco, 9 km SW San Antonio, 1495 m (OMNH 33094/OCGR 3510/Arg 4288); Santa Barbara: 5 km E El Palmar, 794 m (OMNH 38617/OCGR 7462/Arg6906). SALTA: Chicoana: 5 km WSW Pulares, 1482 m (OMNH 30014/OCGR 3708/Arg 4969; OMNH 38647/OCGR 3710/Arg 4971); Rosario de la Frontera: Finca Barba Yaco, 8.5 km SE Ojo de Agua, 1347 m (OMNH 29994/OCGR 3643/Arg 4678). TUCUMÁN: Monteros: Reserva La Florida, 7 km W Ibatín, Río Pueblo Viejo, 515 m (OMNH 30004/OCGR 3449/Arg 4074).

Akodon spegazzinii (16).—ARGENTINA: CATAMARCA: Andalgala: Choya, 13 km NNW of Andalgala, 4000 ft (OMNH 23458/OCGR 1678/Arg 2011). Santa Maria: 21 km SW El Desmonte, 2172 m (OMNH 37288/OCGR XXXX/Arg 4502). MENDOZA: Lujan de Cuyo: approx. 3 km SSE Vallecitos (by road) 2193 m (OMNH 37496/OCGR XXXX/Arg 4011; OMNH 37498/OCGR XXXX/Arg 4021). SALTA: Cachi: approx.. 3 km N Cachi Adentro, 2724 m (OMNH 36501/OCGR 4104/Arg 4992; CML XXXX/OCGR 4105/Arg 4994); Chicoana: app. 15 km al W de Escoipe, sobre Ruta Prov. No. 33, 2680 m (OMNH 33006/OCGR 4059/Arg 4818). SAN JUAN: Iglesia: Tudcum, "Nacedero", 6660 ft (OMNH 37505/OCGR 349/Arg 401; OMNH 37506/OCGR 350/Arg 402). TUCUMÁN: Burruyacu: Piedra Tendida, 12 km WNW Burruyacu along Rio Cajon, 2500 ft (OMNH 37375/OCGR 952/Arg 1052); Monteros: Reserva La Florida, 7 km W Ibatín, Río Pueblo Viejo, 515 m (CML XXXX/OCGR 3469/Arg

4160); Tafi: El Infiernillo, km 83 along Rt 307, 10000 ft (OMNH 23647/OCGR 1222/Arg 1324); Tafi del Valle: 2 km below La Heradera along Hwy 307, 3500 ft (OMNH 37398/OCGR 1307/Arg 1410); Tafi del Valle: La Quebradita, km 69 along Hwy 307, 7500 ft (OMNH 23654/OCGR 1328/Arg 1431); Trancas: km SW de Hualinchay, 2822 m (OMNH 38584/OCGR 3691/Arg 4880); Yerba Buena: 4 km west of junction hwy 338 and road to Horco Molle, along hwy 338 (road to San Javier), 2750 ft (OMNH 37431/OCGR 1807/Arg 2179).

Akodon subfuscus (2). —PERU: APURIMAC: 36 km S (by road) Chalhuanca, 16.55°S, 73.31°W, 3510 m (MVZ 174239). AREQUIPA: 15 km S Callalli (MVZ 174109/Genbank M35695).

Akodon sylvanus (1).—ARGENTINA: JUJUY: Santa Barbara: 24.8 km E Santa Clara, 1321 m (OMNH 38610/OCGR 7417/Arg 6861).

Akodon tartareus (3).—BOLIVIA: TARIJA: 3 km SE of Cuyambuyo, 22°16'S, 64°33'W, 900 m (AMNH 264333/MSB NK 23741/Genbank EU260486); 5 km W of Estancia Bolivar, 21°38'S, 62°34'W, 400 m (MSB 67183/MSB NK 23980/Genbank EU260487); Tapecua (AMNH 264306/MSB NK 23378/Genbank EU260485).

Akodon toba (3).—PARAGUAY: (no exact locality; TTU TK 66486/Genbank AY273910 as *A. varius*); BOQUERON: Filadelfia Martens, 22°20'40"S, 60°01'54"W, 100 m (MSB 80493/MSB NK 72371). PRESIDENTE HAYES: 8 km NE Juan de Zalazar (UMMZ 133965/Genbank U03527).

Akodon torques (5).—PERU: CUZCO: La Esperanza, 13°10.664'S, 71°36.271'W, 2880 m (FMNH 174966; FMNH 175011; FMNH 175033); 32 km NE Paucartambo

(MVZ 171720/Genbank M35700); Pillahuata, 13.16219°S, 71.59750°W (FMNH 172222).

Akodon varius (2).—BOLIVIA: CHUQUISACA: Rio Limon (MSB 63483/MSB NK 21723/Genbank EU260478); Rio Limon, 1300 m (AMNH 262675/MSB NK 21740/Genbank EU260479).

Akodon viridescens (7).—ARGENTINA: CÓRDOBA: Pampa de Achala, Repetidora La Posta (UP AC008/Genbank AY196165 as *A. spegazzinii*). SAN LUIS: Coronel Pringles: 1 km N Paso del Rey, along Arroyo de la Cañada Honda, 4400 ft. (OMNH 36354/OCGR 515/Arg 577/Genbank GU595282; OMNH 36355/OCGR 516/Arg 578/Genbank GU595283); 9 km N Paso del Rey, 4800 ft. (OMNH 36363/OCGR 751/Arg 824/Genbank GU595284; OMNH 36364/IADIZA-CM 6268/OCGR 752/Arg 825/Genbank GU595285); 15 km N Paso del Rey, 4700 ft. (OMNH 36388/OCGR 767/Arg 847/Genbank GU595286; OMNH 36365/OCGR 768/Arg 848/Genbank GU595287).

Andinomys edax (1).—BOLIVIA: TARIJA: 61 km E Tarija (by road), Rancho Tambo, 21.45°S, 64.31667°W, 2100 m (MSB 57099/MSB NK 14603).

Chroeomys jelskii (1).—PERU: PUNO: 6.5 km SW Ollachea, 3350 m (MVZ 173073/Genbank M35714).

Necromys lactens (2).—ARGENTINA: CATAMARCA: Paclin: 2.4 km al S de la union entre las rutas 18 y 9 proviciales, sobre ruta prov. No. 18, 1529 m (OMNH 35412/OCGR 3682/Arg 4758/Genbank EU260470). SALTA: Chicoana: app. 15 km al W de Escoipe, sobre Ruta Provincial no. 33, 2680 m (OMNH 34515/OCGR 4221/Arg 4770/Genbank EU260471).

Oligoryzomys destructor (2).—ARGENTINA: JUJUY: El Carmen: along Hwy 9 at border with Salta Province, 4600 ft (OMNH 34497/OCGR 2129/Arg 2583). TUCUMÁN: Yerba Buena: 4 km W Jct. 338 and Rd to Horco Molle along 338, 2750 ft (OMNH 34399/OCGR 1840/Arg 2213).

Thaptomys nigrita (2).—BRAZIL: MINAS GERAIS: Monte Verde, 19°53'S, 41°57'W (Genbank EF206815). SÃO PAULO: : Estação Biológica de Boracéia, 3 km E, 28 km SE Biritiba-Mirim, Municipio de Salesopolis, 23.65°S, 45.9°W, 850 m (MVZ 183044/Genbank AF108666).

VITA

Brandi S. Coyner

Candidate for the Degree of

Doctor of Philosophy

Thesis: PHYLOGENETIC RELATIONSHIPS AND HISTORICAL BIOGEOGRAPHY OF THE GENUS *AKODON* (RODENTIA: CRICETIDAE)

Major Field: Zoology

Biographical:

Personal Data: Born in Oklahoma City, Oklahoma on 14 September 1982, to Ronald and Iris Coyner.

Education: Graduate from Chandler High School, Chandler, Oklahoma in May 2001; received Bachelor of Science degree in Zoology from the University of Oklahoma, Norman, Oklahoma, in 2005. Completed the requirements for the Doctor of Philosophy in Zoology at Oklahoma State University, Stillwater, Oklahoma, in December 2010.

Experience: Teaching: Graduate Teaching Associate: Animal Behavior (1 semester), Human Anatomy (1), Human Heredity (1), Mammalogy (2); Research Scientist/Instructor, Summer Explorology Sciences Institute, Sam Noble Oklahoma Museum of Natural History. Research: NSF Graduate Research Fellow (3 years); Shadle Fellow in Mammalogy (1 year); Graduate Research Associate (1 semester, 3 summers).

Professional Memberships: Society of Systematic Biologists, American Society of Mammalogists, Southwestern Association of Naturalists, Central Plains' Society of Mammalogists, Texas Society of Mammalogists, Oklahoma Academy of Science.

Name: Brandi S. Coyner Date of Degree: December 2010

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: PHYLOGENETIC RELATIONSHIPS AND HISTORICAL BIOGEOGRAPHY OF THE GENUS *AKODON* (RODENTIA: CRICETIDAE)

Pages in Study: 157 Candidate for the Degree of Doctor of Philosophy

Major Field: Zoology

Scope and Method of Study: Despite comprising only 12% of the Earth's landmass, South America supports nearly one quarter of all extant species of mammals (Wilson and Reeder 1993). The genus *Akodon* (Rodentia, Cricetidae) is among the most speciose groups of South American rodents, second only to the genus *Oryzomys*, where its 46 extant species occur from northern Venezuela to southern Argentina. The genus is organized into four species groups and numerous subgenera and subspecies are recognized. In previous molecular studies of the genus, few taxa and single gene datasets dominate. In this study, 3 genes (cytb, DMP1, and THY) were sequenced and analyzed under maximum parsimony, maximum likelihood, and Bayesian phylogenetic criterion to 1) obtain a well-resolved evolutionary history of *Akodon*, 2) to evaluate the validity of a number of subspecific taxa and supraspecific groupings, and 3) to evaluate the historical biogeography of the genus.

Findings and Conclusions: Thirty four of the 46 extant species, as well as numerous subspecies, were included here. Of these 46 species, the monophyly of four (*A. aerosus*, *A. mimus*, *A. mollis*, and *A. orophilus*) are questioned. *A. lindberghi* is assigned to the *cursor* group. In the *boliviensis* group, *A. lutescens caenosus* currently consists of two species level taxa, both to be elevated to full species. Four taxa, including *A. varius*, from the *varius* group are moved to the *aerosus* group. Additionally two subspecies within the *aerosus* group (*A. aerosus baliolus* and *A. orophilus orientalis*) warrant species recognition. Two additional species level taxa fall within the *aerosus* group and are unnamed. The redefined *varius* group is recommened to be referred to as the *dolores* group. Dates of divergence and relationship of taxa provide the information needed to generate a hypothesis regarding the evolution of the genus. Future efforts in the study of *Akodon* systematics need to include not only the addition of previously unavailable taxa but also the inclusion of sequence data from multiple genetic markers for all individuals.

ADVISER'S APPROVAL: Ronald A. Van Den Bussche