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PHYLOGENETIC ANALYSES OF SPINY POCKET MICE (HETEROMYIDAE: HETEROMYINAE) BASED ON ALLOZYMIC AND MORPHOLOGICAL DATA

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The subfamily Heteromyinae (spiny pocket mice) represents a well-defined monophyletic group within the rodent family Heteromyidae. Although 2 genera of spiny pocket mice, *Heteromys* and *Liomys*, are recognized in the subfamily, no phylogenetic analysis has demonstrated their reciprocal monophyly. A recent study using DNA-sequence data from the mitochondrial gene cytochrome *b* suggested that *Liomys* is paraphyletic but included few species of *Heteromys*. Here, we conduct phylogenetic analyses of the subfamily with dense taxonomic sampling using allozymic data from a previous study and external and cranial morphological data; our aim is to assess generic monophyly and elucidate phylogenetic structure within the genera, to the degree possible with these data. We also reidentify selected voucher specimens from the allozymic study. Parsimony-based analyses indicate 3 clades in the subfamily: (A) *Liomys irroratus*, *L. pictus*, and *L. spectabilis*; (B) *L. adspersus* and *L. salvini*; and (C) all examined species of *Heteromys*. However, the relationships among these clades are unresolved. The genus *Heteromys* is characterized by strong support and several unreversed morphological synapomorphies. In contrast, our analyses fail to indicate any synapomorphies for *Liomys*, but can neither demonstrate nor reject its monophyly. The 3 clades identified here match those recovered from a recent mitochondrial DNA–sequencing study, which found a resolved (B (A + C)) topology. Within *Heteromys*, we recover 5 lineages, but the relationships among them remain unresolved. The examined South American species of *Heteromys* formed a clade, but 2 species recently described from Ecuador and Venezuela were not included here. Samples referred to as *H. desmarestianus crassirostris* and *H. d. planifrons* were quite distinct from other samples of *H. desmarestianus*, emphasizing the need for alpha-level taxonomic revision of this species complex. Given the current results, future studies can now examine relationships among species of *Heteromys* using samples of *Liomys* as outgroups, but studies of *Liomys* must take into account its likely paraphyletic nature.

Key words: allozymes, Heteromyinae, *Heteromys*, *Liomys*, morphology, phylogeny, spiny pocket mice, step matrix

The rodent family Heteromyidae is comprised of 3 subfamilies: Heteromyinae (spiny pocket mice), Perognathinae (silky pocket mice), and Dipodomyinae (kangaroo rats and kangaroo mice—Patton 2005). The relationships among the subfamilies remain unclear, and some questions exist regarding the monophyly of the Perognathinae (Alexander and Riddle 2005). However, the Heteromyinae represents a well-defined monophyletic group distinct from either of the 2 other living subfamilies (Hafner 1981; Hafner and Hafner 1983; Wahlert 1991; but see Ryan 1989:94–98).

Two genera of spiny pocket mice, *Heteromys* and *Liomys*, are recognized in the Heteromyinae (Patton 2005; Williams et al. 1993). They can be distinguished from each other by a few morphological characters (Anderson 2003:11; Williams

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TABLE 1.—Currently recognized species of spiny pocket mice (genera *Heteromys* and *Liomys*), following Williams et al. (1993) and Patton (2005), with additions and modifications from Anderson (1999), Anderson and Jarrín-V. (2002), Anderson (2003), and Anderson and Timm (2006). Except for *H. oresterus* (see Rogers 1989), karyological data (2n = diploid number; FN = fundamental number) are summarized from Patton and Rogers (1993); see also Anderson and Timm (2006).

Species	Distribution	Standard karyotype
H. anomalus	Colombia, Venezuela, Trinidad and Tobago	2n = 60, FN = 68
H. australis	Panama, Colombia, Ecuador, Venezuela	Unknown
H. desmarestianus	Mexico to Colombia	2n = 60, FN = 67–90
H. gaumeri	Mexico, Guatemala, Belize	2n = 56, FN = 76
H. nelsoni	Mexico, Guatemala	2n = 42, FN = 72
H. nubicolens	Costa Rica	2n = 60, FN = 86
H. oasicus	Venezuela	Unknown
H. oresterus	Costa Rica	2n = 60, FN = 78
H. teleus	Ecuador	Unknown
L. adspersus	Panama	2n = 56, FN = 84
L. irroratus	United States (Texas), Mexico	2n = 58–60, FN = 60–62
L. pictus	Mexico, Guatemala	2n = 48, FN = 62–66
L. salvini	Mexico to Costa Rica	2n = 56, FN = 86
L. spectabilis	Mexico	2n = 48, FN = 64

et al. 1993), but no phylogenetic study has demonstrated their reciprocal monophyly. A distance-based analysis of protein variation at 30 presumptive gene loci failed to recover the 2 genera (Rogers 1990). However, because basal relationships in the subfamily were not well supported (and no character-based phylogenetic analysis was accomplished), the monophyly of each of the genera was neither bolstered nor effectively challenged.

Present taxonomy recognizes 9 species of *Heteromys*, including 3 recently described taxa (Anderson 2003; Anderson and Jarrín-V. 2002; Anderson and Timm 2006; Patton 2005; Table 1). Species richness in the genus is probably much higher, however, because several studies have indicated that the widespread *H. desmarestianus* represents a complex of several externally similar species. Across the range of this species complex, considerable variation exists in karyotypes, allozymes, and cranial morphology (Anderson 1999; Anderson and Timm 2006; Mascarello and Rogers 1988; Rogers 1986, 1989, 1990; see also Burton et al. 1987; Engstrom et al. 1987; Genoways 1973:298). In addition to the nominotypical subgenus *Heteromys* (with type species *H. anomalus*), the subgenus *Xylomys* was proposed for *H. nelsoni* by Merriam (1902; see also Goldman 1911). Subsequently, Hall and Kelson (1959) and Hall (1981) also considered *H. oresterus* a member of the subgenus *Xylomys*, but the characters used to unite it with *H. nelsoni* did not hold up to later scrutiny (Anderson and Timm 2006; Rogers 1986; Rogers and Rogers 1992). Rather, examination of morphological, karyological, and genetic data suggests that *H. oresterus* may be more closely related to members of the *H. desmarestianus* species complex than to *H. nelsoni* (Mascarello and Rogers 1988; Rogers 1986:186–191, 1989, 1990). Species of *Heteromys* generally inhabit mesic (typically evergreen) forests and range from southern Mexico to western Ecuador (Table 1). One notable exception is *H. gaumeri*, which is found in deciduous forests of the Yucatán Peninsula in Mexico, Belize, and Guatemala.

Currently, 5 species are recognized in the genus *Liomys* (Patton 2005; Williams et al. 1993; Table 1). However, several studies have shown that *L. pictus* represents a complex of similar species and that *L. salvini* may be composite as well (Morales and Engstrom 1989; Rogers 1990; Rogers and Engstrom 1992; Rogers and Vance 2006). No subgenera have been proposed in *Liomys*, but previous distance-based analyses indicated 2 groupings: *L. adspersus* + *L. salvini* in one group, and *L. irroratus* + *L. pictus* + *L. spectabilis* in another; the association of *L. spectabilis* with the *L. pictus* species complex has been especially clear (Genoways 1973:316–328; Rogers 1990). These groupings were upheld by a recent phylogenetic study based on cytochrome-*b* sequence data (Rogers and Vance 2006). The type species of *Liomys* is the form *alleni*, currently considered a synonym of *L. irroratus*. In contrast to *Heteromys*, species of *Liomys* inhabit deciduous forests and other semiarid tropical and subtropical habitats; they are distributed from northern Mexico and the southern United States (Texas) to Panama (Table 1).

Karyological studies have indicated strong cytogenetic differences among species of spiny pocket mice (Table 1). Except for *Heteromys gaumeri* (diploid number [2n] = 56) and *H. nelsoni* (2n = 42), all species of *Heteromys* with known karyotypes have a diploid number of 2n = 60 (Engstrom et al. 1987; Rogers 1989). However, the species with a diploid number of 2n = 60 vary widely in fundamental number (FN). At least 9 karyotypic forms exist within the *H. desmarestianus* species complex (including *H. goldmani*—Mascarello and Rogers 1988; Rogers 1989; see also Burton et al. 1987; Engstrom et al. 1987; Genoways 1973:298). Some species of *Heteromys* also differ strongly in karyological banding patterns (Mascarello and Rogers 1988; Rogers 1989). Species of *Liomys* vary widely in diploid number (2n = 48–60) as well as in fundamental number (FN = 60–86).

Evolutionary relationships within the Heteromyinae.—A recent phylogenetic study addressed relationships among species of *Liomys* using DNA sequences from the mitochondrial gene cytochrome *b* for all recognized species of *Liomys* and a few species of *Heteromys* (Rogers and Vance 2006; see also Anderson and Jansa, in press, for additional cytochrome-*b* data for *Heteromys*). Although the taxonomic sampling of *Heteromys* in Rogers and Vance (2006) was too sparse to address its monophyly, the analyses indicated the paraphyly of *Liomys*, recovering 2 well-supported clades in the subfamily: one composed of *L. adspersus* and *L. salvini*, and another including all other taxa examined. The latter clade was made up of 2 well-supported subclades: one containing *L. irroratus*, *L. pictus*, and *L. spectabilis*; and another including the examined species of *Heteromys* (*H. anomalus*, *H. desmarestianus*, and *H. gaumeri*).

Here, we conduct phylogenetic analyses of the subfamily with dense taxonomic sampling using allozymic (Rogers 1990) and

morphological data. Rogers (1990) performed distance-based analyses because phylogenetic analysis considering more than 1 character-state (e.g., more than 1 allele per locus) for a single taxon was not possible at the time. Given the presence of multiple alleles at many loci for several samples, reducing the data set to 1 character-state per locus for each taxon would have resulted in a substantial loss of information. Subsequently, Mabee and Humphries (1993) suggested a method for examining polymorphic data that has been widely used with allozymic data sets. For the transition between fixed loci, each polymorphic combination is considered as a new character-state intermediate to the fixed loci. A Sankov step matrix of costs is constructed to accommodate the number of steps necessary for all possible transitions. Hence, a change from allele A to allele B would cost 2 steps (the loss of A and the acquisition of B), whereas the change from A to AB would cost only 1 step (the gain of allele B—Mardulyn and Pasteels 1994; for examples, see Arellano et al. 2003; Rogers et al. 2005; Simmons 1996).

In addition to the allozymic data, we also include some morphological data from a previous study (Wahlert 1991) as well as other morphological characters that we code ourselves. We also take advantage of recent taxonomic work on *Heteromys* to reexamine many voucher specimens of that genus from Rogers (1990), providing some re-identifications. Although the current data sources are unlikely to resolve fully the relationships among species of the subfamily, they may show signal at deeper levels of phylogeny, sufficient for addressing generic monophyly and elucidating major groups within genera. Hence, we conduct the current study with multiple character sets to provide a phylogenetic framework for subsequent studies (i.e., in anticipation of future DNA-sequence analyses).

Materials and Methods

Data sources.—We examined voucher specimens and used allozymic data corresponding to specimens housed in the following museum collections (abbreviations follow Hafner et al. [1997]; Appendices I and II): AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; KU, University of Kansas Natural History Museum, Lawrence; LSUMZ, Louisiana State University Museum of Natural Science, Baton Rouge; MSB, Museum of Southwestern Biology, University of New Mexico, Albuquerque; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; TCWC, Texas Cooperative Wildlife Collection, Texas A&M University, College Station; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, United States National Museum of Natural History, Washington, D.C. Where relevant, we also provide the numbers by which the tissue samples of Rogers (1990) were tracked in the laboratory, namely the following museum karyotype–tissue number series, collector field catalog numbers, or both (Appendix I): AK, TCWC karyotype–tissue numbering series; DJH, David J. Hafner field catalog series; DSR, Duke S. Rogers field catalog series; MDE, Mark D. Engstrom field catalog series; MSH, Mark S. Hafner field catalog series; NK, MSB karyotype–tissue numbering series; TK, Texas Tech University karyotype–tissue numbering series.

Allozymes.—We used the allozymic data from Rogers (1990; Table 2), who examined protein variation at 30 presumptive gene loci among 36 populations of spiny pocket mice (Heteromyinae) representing all species of the subfamily accepted at the time (Fig. 1). Four taxa from the 2 other living subfamilies of heteromyids (Dipodomyinae and Perognathinae) were used as outgroups. We examined voucher specimens for many samples of *Heteromys* used in Rogers (1990; Appendix I) and updated the identifications of some specimens. To begin denoting taxonomic structure within the confusing *H. desmarestianus* species complex, we use Latin trinomials for some samples. In such cases, we use an available name that we consider conspecific with that sample as a subspecific epithet. If the entities we recognize here are later considered to be valid species, some of the subspecific epithets we use may represent the valid names for those species (see ''Discussion'' for specific nomenclatural issues). Re-identifications for *Heteromys* follow. We consider localities 1–5 to be *H. d. temporalis*. Following Rogers (1990) and Williams et al. (1993), locality 10 is considered *H. d. goldmani*. Locality 12 represents *H. nubicolens*, and localities 16 and 17 are considered *H. d. planifrons* (see Anderson and Timm 2006). Locality 26 (originally identified as *H. australis*) represents *H. d. crassirostris*, and locality 27 (originally *H. anomalus*) constitutes *H. australis* (see Anderson 1999).

We also follow recent taxonomic work for *Liomys*. As with the *H. desmarestianus* species complex, we use trinomials to refer to groups within the *L. pictus* species complex. Locality 30 represents *L. salvini*, and locality 29 is *L. adspersus* (as in the appendix and column headers of table 1 from Rogers [1990]; the locality numbers were reversed in table 1 of that publication). Locality 33 represents *L. p. hispidus*, locality 34 is *L. p. plantinarensis*, and locality 36 corresponds to *L. p. pictus* (following Rogers and Engstrom 1992; Rogers and Vance 2006).

Morphology.—We used 8 morphological characters that we scored ourselves and 13 from Wahlert (1991; see also Wahlert 1985; Table 3; Appendix III). Cranial nomenclature follows Wahlert (1985) and Anderson (2003). We name the characters that we scored ourselves as A1–A8 and denote the characters taken from Wahlert (1991) using his original number preceded by a ''W.'' We scored 8 characters of the cranial and external anatomy using preserved cranial material and study skins of specimens that we deem conspecific with the respective samples from Rogers (1990); we used holotypes and paratypes whenever possible (Appendix II). We generally scored characters based on adult specimens (reported here), but we also evaluated characters in ontogenetic series when possible (see Rogers and Schmidly [1982] and Genoways [1973] for discussions of age-related variation in heteromyines). Although *H. oasicus* and *H. teleus* were not included in the present analysis (because they lack allozymic data), we also scored these characters for those species and present the data here for use by future workers. The 8 characters that we scored document morphological variability within the subfamily Heteromyinae. As noted in Appendix III, characters A1, A2, A6, and A8 are modified from the generic diagnoses of *Heteromys* and *Liomys* in Williams et al. (1993:100, 111), and character A4 is modified from character 13 of Wahlert (1991). Other differences between *Heteromys* and *Liomys* listed by Williams et al. (1993:100, 111) in their diagnoses of the genera are probably real tendencies (at least for many species of the respective genera), but we were not able to code them, especially given extensive ontogenetic variation and toothwear in this group (i.e., skull elongate in *Heteromys*; anterior cingulum in lower molars and posterior cingulum in upper molars nearly as high as remainder of crown, giving them 3 lophs [~ ''accessory enamel island''] before wear in *Heteromys*, in contrast to accessory enamel island present on molars only for brief time (in unworn dentition) in *Liomys*; and cheek teeth high crowned in *Heteromys*, whereas medium–high crowned in *Liomys*).

TABLE 2.—Step matrix for allozymic data (see Rogers [1990] for the alleles present at each locus for each sample). States a–p are individual alleles observed in the terminal taxa; states q–B are new character-states derived from the polymorphic data (1st column) observed in the terminal taxa; and states C–L are intermediate character-states created following the rules proposed by Mardulyn and Pasteels (1994).

		a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	w	x	y	z	0	1	2	3	4	5	6	7	8	9	A	B	C	D	E	F	G	H	I	J	K	L
	a	.	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	4	2	2	4	4	4	4	4	4	4	4
	b	2	.	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	3	1	1	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	2	2	4	4	4	4	4	4
	c	2	2	.	2	2	2	2	2	2	2	2	2	2	2	2	2	3	1	1	3	3	1	1	1	3	3	3	3	3	3	3	3	3	3	3	3	2	2	4	4	2	4	2	2	2	4	4	4
	d	2	2	2	.	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	1	3	1	3	3	1	1	3	3	3	3	3	3	3	3	3	3	4	2	2	4	4	2	2	2	4	2	4	4
	e	2	2	2	2	.	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	1	3	1	3	1	3	1	3	3	3	3	3	3	3	3	3	4	4	4	2	2	2	2	4	2	4	4	4
	f	2	2	2	2	2	.	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	1	3	1	1	1	1	3	3	3	3	3	3	3	4	4	4	4	4	4	4	2	2	2	4	4
	g	2	2	2	2	2	2	.	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	1	3	1	1	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	2	4
	h	2	2	2	2	2	2	2	.	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	1	3	1	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	2	4
	i	2	2	2	2	2	2	2	2	.	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	1	3	1	1	1	3	3	3	4	4	4	4	4	4	4	4	4	2	2	2
	j	2	2	2	2	2	2	2	2	2	.	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	3	3	4	4	4	4	4	4	4	4	4	4	4	2
	k	2	2	2	2	2	2	2	2	2	2	.	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4
	l	2	2	2	2	2	2	2	2	2	2	2	.	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	1	1	3	4	4	4	4	4	4	4	4	4	4	4	4	2
	m	2	2	2	2	2	2	2	2	2	2	2	2	.	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4
	n	2	2	2	2	2	2	2	2	2	2	2	2	2	.	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	1	4	4	4	4	4	4	4	4	4	4	4	4
	o	2	2	2	2	2	2	2	2	2	2	2	2	2	2	.	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	4	4	4	4	4	4	4	4	4	4	4	4
	p	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	.	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4
[ab]	q	1	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	.	2	2	2	2	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	1	3	1	1	3	3	5	5	5	5	5	5
[ac]	r	1	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3	2	.	2	4	4	2	2	2	4	4	4	4	4	4	4	4	4	4	4	4	1	3	3	3	3	5	3	3	3	5	5	5
[bc]	s	3	1	1	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	.	2	2	2	2	2	4	4	4	4	4	4	4	4	4	4	4	4	1	1	3	3	1	3	3	3	3	5	5	5
[bd]	t	3	1	3	1	3	3	3	3	3	3	3	3	3	3	3	3	2	4	2	.	2	2	4	4	2	2	4	4	4	4	4	4	4	4	4	4	3	1	1	3	3	1	3	3	5	3	5	5
[be]	u	3	1	3	3	1	3	3	3	3	3	3	3	3	3	3	3	2	4	2	2	.	4	2	4	2	4	2	4	4	4	4	4	4	4	4	4	3	3	3	1	1	1	3	5	3	5	5	5
[cd]	v	3	3	1	1	3	3	3	3	3	3	3	3	3	3	3	3	4	2	2	2	4	.	2	2	2	2	4	4	4	4	4	4	4	4	4	4	3	1	3	5	3	3	1	1	3	3	5	5
[ce]	w	3	3	1	3	1	3	3	3	3	3	3	3	3	3	3	3	4	2	2	4	2	2	.	2	2	4	2	4	4	4	4	4	4	4	4	4	3	3	5	3	1	3	1	3	1	5	5	5
[cf]	x	3	3	1	3	3	1	3	3	3	3	3	3	3	3	3	3	4	2	2	4	4	2	2	.	4	2	2	2	2	4	4	4	4	4	4	4	3	3	5	5	3	5	3	1	1	3	5	5
[de]	y	3	3	3	1	1	3	3	3	3	3	3	3	3	3	3	3	4	4	4	2	2	2	2	4	.	2	2	4	4	4	4	4	4	4	4	4	5	3	3	3	3	1	1	3	3	3	5	5
[df]	z	3	3	3	1	3	1	3	3	3	3	3	3	3	3	3	3	4	4	4	2	4	2	4	2	2	.	2	2	2	4	4	4	4	4	4	4	5	3	3	5	5	3	3	1	3	1	5	5
[ef]	0	3	3	3	3	1	1	3	3	3	3	3	3	3	3	3	3	4	4	4	4	2	4	2	2	2	2	.	2	2	4	4	4	4	4	4	4	5	5	5	3	3	3	3	3	1	3	5	5
[fg]	1	3	3	3	3	3	1	1	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	2	4	2	2	.	2	2	2	4	4	4	4	4	5	5	5	5	5	5	5	3	3	3	3	5
[fi]	2	3	3	3	3	3	1	3	3	1	3	3	3	3	3	3	3	4	4	4	4	4	4	4	2	4	2	2	2	.	4	2	2	2	4	4	4	5	5	5	5	5	5	5	3	3	1	3	3
[gh]	3	3	3	3	3	3	3	1	1	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	2	4	.	2	2	4	4	4	4	5	5	5	5	5	5	5	5	5	1	5
[gi]	4	3	3	3	3	3	3	1	3	1	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	2	2	2	.	2	2	4	4	4	5	5	5	5	5	5	5	5	3	1	3
[hi]	5	3	3	3	3	3	3	3	1	1	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	2	2	2	2	.	2	4	4	4	5	5	5	5	5	5	5	5	3	1	3
[il]	6	3	3	3	3	3	3	3	3	1	3	3	1	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	2	4	2	2	.	2	2	4	5	5	5	5	5	5	5	5	3	3	1
[jl]	7	3	3	3	3	3	3	3	3	3	1	3	1	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	2	.	2	4	5	5	5	5	5	5	5	5	5	5	5	1
[ln]	8	3	3	3	3	3	3	3	3	3	3	3	1	3	1	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	2	2	.	2	5	5	5	5	5	5	5	5	5	5	5	3
[no]	9	3	3	3	3	3	3	3	3	3	3	3	3	3	1	1	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	2	.	5	5	5	5	5	5	5	5	5	5	5	5
[abc]	A	2	2	2	4	4	4	4	4	4	4	4	4	4	4	4	4	1	1	1	3	3	3	3	3	5	5	5	5	5	5	5	5	5	5	5	5	.	2	2	2	2	4	4	4	4	6	6	6
[bcd]	B	4	2	2	2	4	4	4	4	4	4	4	4	4	4	4	4	3	3	1	1	3	1	3	3	3	3	5	5	5	5	5	5	5	5	5	5	2	.	2	4	2	2	2	2	4	4	6	6
[abd]	C	2	2	4	2	4	4	4	4	4	4	4	4	4	4	4	4	1	3	3	1	3	3	5	5	3	3	5	5	5	5	5	5	5	5	5	5	2	2	.	2	4	2	4	4	6	4	6	6
[abe]	D	2	2	4	4	2	4	4	4	4	4	4	4	4	4	4	4	1	3	3	3	1	5	3	5	3	5	3	5	5	5	5	5	5	5	5	5	2	4	2	.	2	2	4	6	4	6	6	6
[bce]	E	4	2	2	4	2	4	4	4	4	4	4	4	4	4	4	4	3	3	1	3	1	3	1	3	3	5	3	5	5	5	5	5	5	5	5	5	2	2	4	2	.	2	2	4	2	6	6	6
[bde]	F	4	2	4	2	2	4	4	4	4	4	4	4	4	4	4	4	3	5	3	1	1	3	3	5	1	3	3	5	5	5	5	5	5	5	5	5	4	2	2	2	2	.	2	4	4	4	6	6
[cde]	G	4	4	2	2	2	4	4	4	4	4	4	4	4	4	4	4	5	3	3	3	3	1	1	3	1	3	3	5	5	5	5	5	5	5	5	5	4	2	4	4	2	2	.	2	2	4	6	6
[cdf]	H	4	4	2	2	4	2	4	4	4	4	4	4	4	4	4	4	5	3	3	3	5	1	3	1	3	1	3	3	3	5	5	5	5	5	5	5	4	2	4	6	4	4	2	.	2	2	6	6
[cef]	I	4	4	2	4	2	2	4	4	4	4	4	4	4	4	4	4	5	3	3	5	3	3	1	1	3	3	1	3	3	5	5	5	5	5	5	5	4	4	6	4	2	4	2	2	.	4	6	6
[dfi]	J	4	4	4	2	4	2	4	4	2	4	4	4	4	4	4	4	5	5	5	3	5	3	5	3	3	1	3	3	1	5	3	3	3	5	5	5	6	4	4	6	6	4	4	2	4	.	4	4
[ghi]	K	4	4	4	4	4	4	2	2	2	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	3	3	1	1	1	3	5	5	5	6	6	6	6	6	6	6	6	4	.	4
[ijl]	L	4	4	4	4	4	4	4	4	2	2	4	2	4	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	3	5	3	3	1	1	3	5	6	6	6	6	6	6	6	6	4	4	.

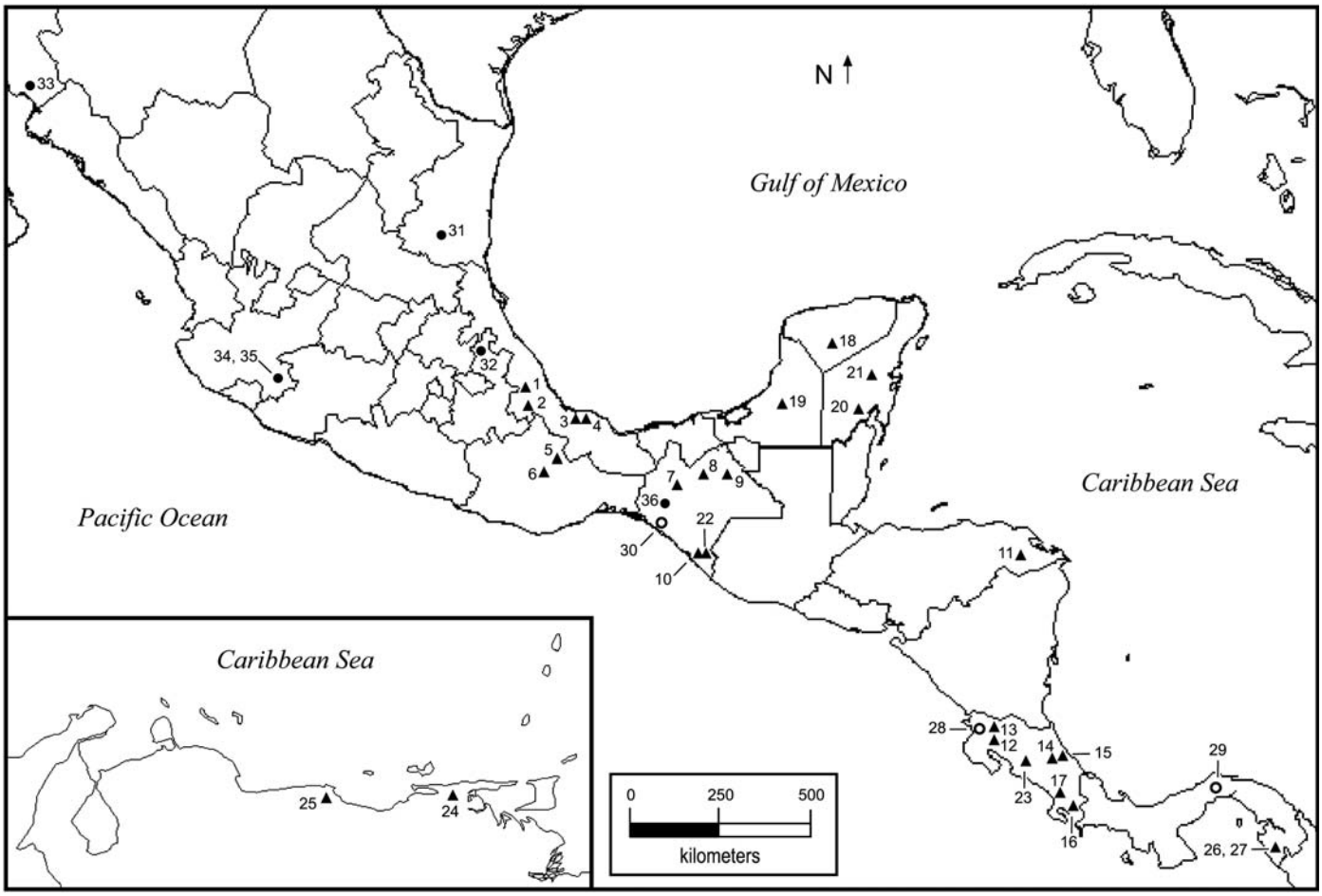


Fig. 1.—Map of Mexico and Central America (with an inset of north-central South America) showing the location of samples of *Heteromys* and *Liomys* for the allozymic data of Rogers (1990). Localities are numbered to correspond to their listing in Appendix I, which provides a list of specimens from each. Different symbols are used to identify members of 3 clades recovered in a recent phylogenetic analysis (Rogers and Vance 2006). Triangles represent species of *Heteromys*, and circles denote species of *Liomys*. Within *Liomys*, closed circles indicate localities of *L. irroratus*, *L. pictus*, and *L. spectabilis*; whereas open circles correspond to localities of *L. adspersus* and *L. salvini*.

In a study of the relationships of heteromyids, geomyids, and many of their extinct relatives, Wahlert (1991) described and scored 50 morphological characters; in the family Heteromyidae, he scored them for the Heteromyinae, Perognathinae, *Microdipodops*, and *Dipodomys*. Of those characters, we include here only the 13 discrete osteological characters of the cranium that were variable among extant genera of heteromyids. We excluded 1 character that was extremely variable within some species of heteromyines (character 22 of Wahlert [1991; J. Wahlert, pers. comm.]) and modified character 13 of Wahlert (1991) and scored it ourselves (character A4; see Appendix III). Two characters coded by Walhert (1991) as variable for the Perognathinae (W20 and W35) were rescored as different states for each perognathine genus based on the specimens examined in Wahlert (1985; see Appendix III). For simplicity, character-states not found in extant heteromyids were deleted (characters W5, W27, W29, and W37). Although the characters from Wahlert (1991) are invariant within the Heteromyinae, they have the potential to provide signal at a deeper level.

Analyses.—We conducted 2 separate phylogenetic analyses, one retaining each sample from Rogers (1990) as a separate terminal taxon, and a 2nd one combining localities that we judged likely to be conspecific. In the 1st analysis, however, we combined 3 localities of *H. gaumeri* that showed identical allozymic alleles (localities 18, 20, and 21). Morphological character-states (see Appendices II and III) were assigned to each of the corresponding samples from Rogers (1990; see Appendix I).

In the 2nd analysis, we combined localities into entities more closely representing our understanding of the species present in the subfamily. For the *H. desmarestianus* species complex, we treated distinct karyomorphs (i.e., each unique FN) as separate terminals but combined samples with identical standard karyotypes, with a single exception: because of their geographic distance, we did not combine samples of FN = 86 from Mexico (localities 3 and 4) with those showing the same standard karyotype from Costa Rica (localities 13 and 15). In addition, we combined nearby samples of *H. d. planifrons* from southwestern Costa Rica (based on examinations of voucher specimens indicating their conspecificity; see ''Discussion''). Based on Rogers and Engstrom (1992), we maintained all samples of the *L. pictus* species complex separate. Using these criteria, the following new terminals were created from combined samples: *H. d. temporalis* (localities 1, 2, and 5; FN = 82), *H. d. temporalis* (localities 3 and 4; FN = 86), *H. desmarestianus* ssp. (localities 7 and 8; FN = 67), *H. desmarestianus* ssp. (localities 13 and 15; FN = 86), *H. d. planifrons* (localities 16 and 17; FN = 90 for locality 16), *H. gaumeri* (localities

TABLE 3.—Morphological data matrix for the subfamily Heteromyidae (*Heteromys* and *Liomys*) and outgroups (*Chaetodipus*, *Perognathus*, *Microdipodops*, and *Dipodomys*). Characters preceeded by a "W" were taken from Wahlert (1991), and characters A1–A8 were scored for each species or sample (see Appendices II and III). Because all samples of *H. desmarestianus* showed the same character-states, we here combine them for presentation.

	Character																				
Taxon	A1	A2	A3	A4	A5	A6	A7	A8	W5	W14	W20	W27	W29	W30	W31	W32	W33	W35	W37	W38	W41
H. anomalus	1	1	1	1	1	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
H. australis	1	1	1	1	1	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
H. desmarestianus	1	1	1	1	1	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
H. gaumeri	1	1	1	1	01	1	1	0	0	2	1	0	0	0	1	0	1	0	0	0	0
H. nelsoni	1	1	1	1	0	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
H. nubicolens	1	1	1	1	1	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
H. oasicus	1	1	1	1	1	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
H. oresterus	1	1	1	1	1	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
H. teleus	1	1	1	1	1	1	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0
L. adspersus	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	0	0
L. irroratus	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	0	0
L. pictus hispidus	0	0	01	0	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	0	0
L. p. pictus	0	0	0	0	0	0	1	0	0	2	1	0	0	0	1	0	1	0	0	0	0
L. p. plantinarensis	0	0	0	0	0	0	1	0	0	2	1	0	0	0	1	0	1	0	0	0	0
L. salvini	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	0	0
L. spectabilis	0	0	0	0	0	0	1	0	0	2	1	0	0	0	1	0	1	0	0	0	0
C. hispidus	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	1	1	0
P. longimembris	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	0
M. megacephalus	—	0	0	0	0	0	0	0	1	1	0	1	2	2	0	1	0	2	1	1	1
D. merriami	—	1	0	0	0	0	0	0	1	0	1	1	2	2	0	1	0	2	1	1	1

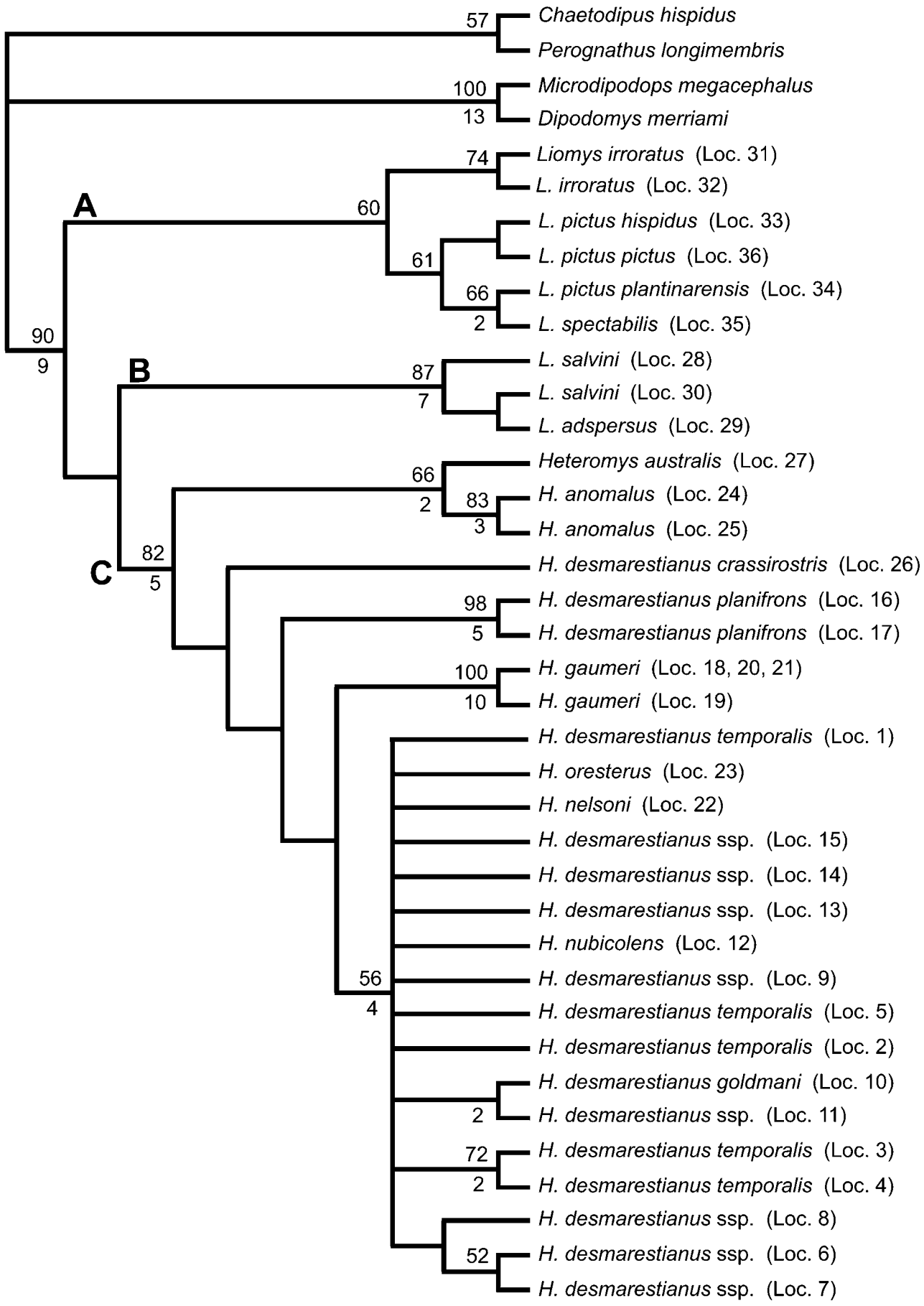
18–21; 2n = 56, FN = 76), *H. anomalus* (localities 24 and 25; FN = 68), *L. salvini* (localities 28 and 30), and *L. irroratus* (localities 31 and 32).

Cladistic parsimony analyses were performed using the data sets explained above. *Chaetodipus hispidus*, *Perognathus longimembris*, *Dipodomys merriami*, and *Microdipodops megacephalus* were used as outgroups (Rogers 1990). All analyses were conducted with unconstrained ingroup and outgroup designations (Nixon and Carpenter 1993), and trees were subsequently rooted on the assumption of heteromyine monophyly. Character polarity was determined after rooting the trees. The heuristic search algorithm implemented by PAUP* 4.0b10 (Swofford 2001) was used in all analyses. Each heuristic search employed 1,000 replicates of random-taxon addition with tree-bisection-reconnection branch swapping. Only clades with at least 1 unambiguous synapomorphy were retained (i.e., synapomorphies present under both ACCTRAN [ACCelerated TRANsformation] and DELTRAN [DELayed TRANsformation] optimization criteria for character reconstructions—Wilkinson 1995; commands PSET COLLAPSE = MIN; FILTER BEST in PAUP*). This option avoids some of the undesirable analytical artifacts of missing data reported by Platnick et al. (1991), and it reduces the number of fundamental trees to a minimal conservative set. Characters were equally weighted in all analyses. A step matrix (Table 2) was constructed for the allozymic data following Mabee and Humphries (1993) and Mardulyn and Pasteels (1994). Other than characters W14, W29, and W35 (Appendix III), morphological characters were treated as unordered. Characters were optimized on fundamental cladograms with both accelerated (ACCTRAN) and delayed (DELTRAN) transformation options. Throughout the text, we report only unambiguous synapomorphies (recovered by both ACCTRAN and DELTRAN optimizations), unless otherwise indicated.

We assessed nodal support using bootstrapping analyses (Felsenstein 1985) and by calculating Bremer decay indices (Bremer 1988, 1994); support values are indicated on the corresponding node of the strict-consensus tree of the respective analysis. Bootstrap values were calculated from 1,000 pseudoreplicated data sets using heuristic searches with 10 random-addition replicates and tree-bisection-reconnection branch swapping; a maximum of 200 trees was retained in each random-addition replicate (for a total of 2,000 trees per pseudoreplicate). To calculate Bremer support values, heuristic searches (with 20 random-addition replicates and tree-bisection-reconnection branch swapping) were performed with a constraint placed on each node found in the consensus tree and using the ENFORCE REVERSE options on the heuristic search command in PAUP*. We also calculated partitioned Bremer support values to assess the additive contributions of each individual data set (allozymes and morphology) for the nodes recovered in the combined analyses (allozymes plus morphology—Baker and DeSalle 1997). Following Lambkin et al. (2002), we present the range of partitioned Bremer values for each node, rather than averaging the values for multiple trees (i.e., the fundamental cladograms from a given analysis). Finally, we calculated the lengths of trees that were constrained to include a monophyletic *Liomys*, in comparison with other possible resolutions of the basal clades of the subfamily Heteromyinae.

RESULTS

Monophyly of the genera.—The 1st analysis with all samples analyzed separately yielded 17 equally most-parsimonious trees of 487 steps each (49 parsimony-informative characters; consistency index [CI] = 0.62, retention index [RI] = 0.76). The strict consensus of these 17 trees recovered several well-supported clades (Fig. 2). Monophyly of the subfamily Heteromyinae was strongly supported (bootstrap = 90%, Bremer = 9). The subfamily is divided into 3 clades: (A) *Liomys irroratus*, *L. pictus*, and *L. spectabilis*; (B) *L. adspersus* and *L. salvini*; and (C) all examined species of *Heteromys*.


57
Chaetodipus hispidus
Perognathus longimembris
100
13
Microdipodops megacephalus
Dipodomys merriami
74
Liomys irroratus (Loc. 31)
L. irroratus (Loc. 32)
A
60
L. pictus hispidus (Loc. 33)
61
L. pictus pictus (Loc. 36)
66
2
L. pictus plantinarensis (Loc. 34)
L. spectabilis (Loc. 35)
90
9
B
87
7
L. salvini (Loc. 28)
L. salvini (Loc. 30)
L. adspersus (Loc. 29)
Heteromys australis (Loc. 27)
66
2
83
3
H. anomalus (Loc. 24)
H. anomalus (Loc. 25)
82
5
C
H. desmarestianus crassirostris (Loc. 26)
98
5
H. desmarestianus planifrons (Loc. 16)
H. desmarestianus planifrons (Loc. 17)
100
10
H. gaumeri (Loc. 18, 20, 21)
H. gaumeri (Loc. 19)
H. desmarestianus temporalis (Loc. 1)
H. oresterus (Loc. 23)
H. nelsoni (Loc. 22)
H. desmarestianus ssp. (Loc. 15)
H. desmarestianus ssp. (Loc. 14)
H. desmarestianus ssp. (Loc. 13)
H. nubicolens (Loc. 12)
56
4
H. desmarestianus ssp. (Loc. 9)
H. desmarestianus temporalis (Loc. 5)
H. desmarestianus temporalis (Loc. 2)
H. desmarestianus goldmani (Loc. 10)
2
H. desmarestianus ssp. (Loc. 11)
72
2
H. desmarestianus temporalis (Loc. 3)
H. desmarestianus temporalis (Loc. 4)
H. desmarestianus ssp. (Loc. 8)
52
H. desmarestianus ssp. (Loc. 6)
H. desmarestianus ssp. (Loc. 7)

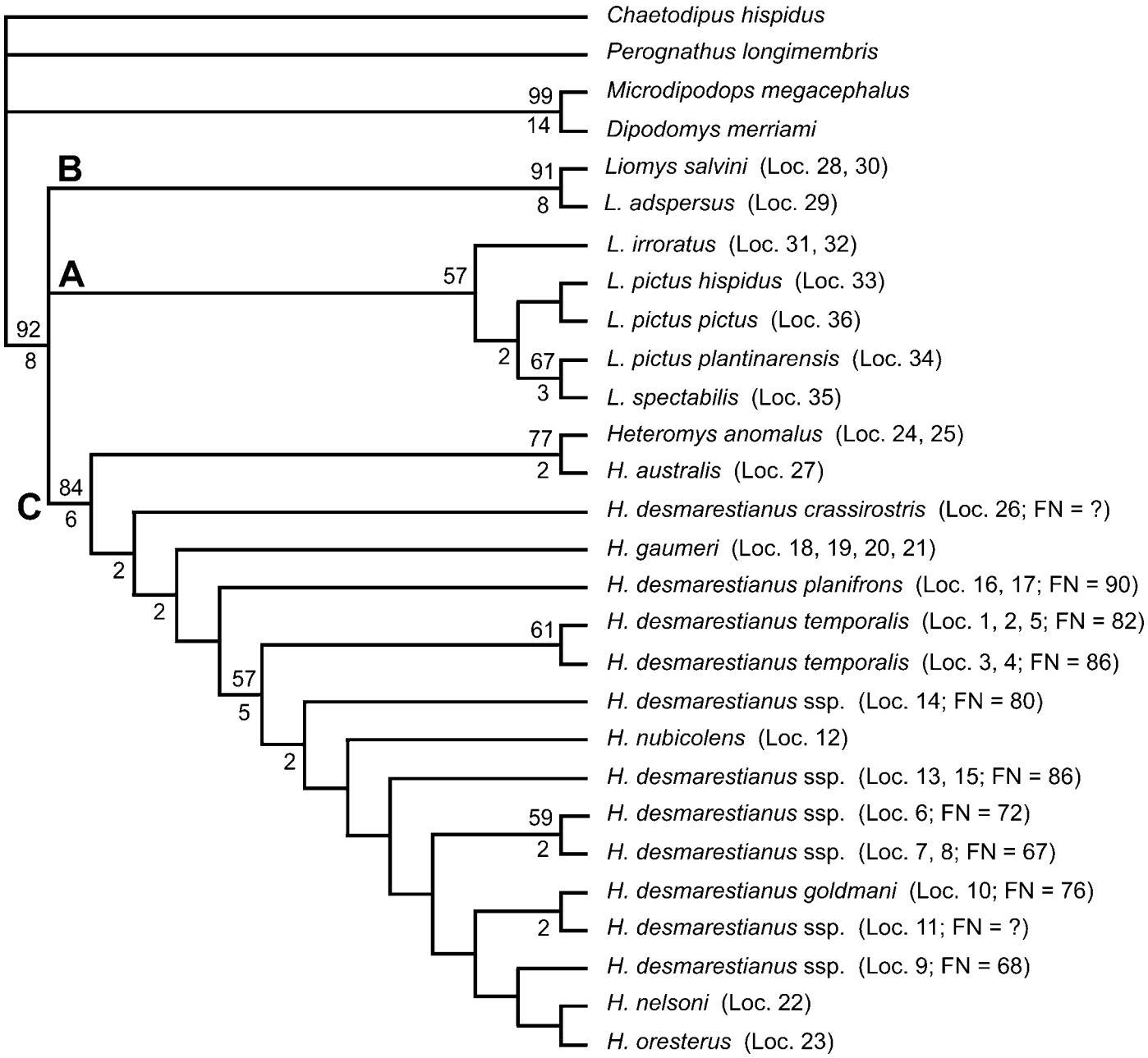


Fig. 3.—Strict consensus of 2 minimum-length trees resulting from a parsimony analysis of allozymic and morphological data for the subfamily Heteromyinae, with other heteromyids used as outgroups; these results are based on the analysis combining samples of Rogers (1990) considered likely to be conspecific (49 parsimony-informative characters; tree length = 462; CI = 0.63, RI = 0.69). Numbers above and below branches refer to the bootstrap resampling percentage (only those > 50%) and Bremer decay index (only those > 1), respectively. Letters A, B, and C indicate clades discussed in the text. Fundamental number (FN) is given for terminal taxa of *Heteromys desmarestianus* to facilitate recognition of combined samples (see text and Appendix I).

←

Fig. 2.—Strict consensus of 17 minimum-length trees resulting from a parsimony analysis of allozymic and morphological data for the subfamily Heteromyinae, with other heteromyids used as outgroups; these results are based on the analysis retaining each sample from Rogers (1990) as a separate terminal taxon (49 parsimony-informative characters; tree length = 487; CI = 0.62, RI = 0.76). Numbers above and below branches refer to the bootstrap resampling percentage (only those > 50%) and Bremer decay index (only those > 1), respectively. Letters A, B, and C show the clades discussed in the text, and numbers after the scientific name for each heteromyine taxon indicate the locality from Rogers (1990); see also Appendix I.

Clade A showed weak bootstrap support (60%) and a low Bremer decay index (1). In contrast, both clade B and clade C showed high values for both measures (bootstrap = 87% and 82%, respectively; Bremer = 7 and 5, respectively). Although the consensus cladogram indicated the relationship (A + (B + C)), that arrangement was tenuous, because the sister-group status of clades B and C had weak bootstrap and Bremer support. A tree with a monophyletic *Liomys* is only 1 step longer than each of the most-parsimonious trees (as is a tree depicting *Heteromys* as the sister group to clade A). In sum, the 1st analysis provided strong support for the monophyly of the subfamily Heteromyinae and the genus *Heteromys* but lacked definitive support for either the monophyly or paraphyly of *Liomys*.

The 2nd analysis with samples combined into species or karyomorphs produced 2 equally most-parsimonious trees of 462 steps each (49 parsimony-informative characters; CI = 0.63, RI = 0.69). In the strict consensus of those 2 trees, the monophyly of the subfamily was again strongly supported (Fig. 3; bootstrap = 92%, Bremer = 8). Within the subfamily, the same 3 clades were present as in the 1st analysis, but in a basal polytomy. Support was weak for clade A (bootstrap = 57%, Bremer = 1), but strong for clades B and C (bootstrap = 91% and 84%, respectively; Bremer = 8 and 6, respectively). One of the 2 most-parsimonious trees indicated a monophyletic *Liomys*; the other indicated *Heteromys* as the sister group to clade A. A tree with *Heteromys* as the sister group to clade B was only 1 step longer than those trees. Hence, similar to the analysis with each sample analyzed separately, this analysis indicated the monophyly of the Heteromyinae and of *Heteromys* but neither demonstrated nor contradicted the monophyly of *Liomys*.

Relationships of species within the genera.—Five lineages were recovered within *Heteromys*, but the relationships among these groups were not well supported (Figs. 2 and 3). In the analysis with each sample representing a terminal taxon (Fig. 2), the examined South American species (*H. anomalus* and *H. australis*) appeared as sister taxa, and within that clade the 2 samples of *H. anomalus* grouped together (with moderate support values; bootstrap = 66% and 83%, respectively; Bremer = 2 and 3, respectively). The 2 samples identified as *H. d. planifrons* formed a clade with very strong support (bootstrap = 98%, Bremer = 5), as did samples of *H. gaumeri* (bootstrap = 100%, Bremer = 10). The lone sample of *H. d. crassirostris* was placed near the base of the genus, but without substantial support for that arrangement. Finally, a large group containing all remaining samples grouped together with weak-to-moderate support (bootstrap = 56%, Bremer = 4). This group included *H. nelsoni*, *H. oresterus*, *H. nubicolens*, and all samples referred to as either *H. desmarestianus* ssp., *H. d. goldmani*, or *H. d. temporalis*. Within this group, the only apparent structure was the affinity of 2 samples of *H. d. temporalis* (bootstrap = 72%, Bremer = 2). Within *Heteromys*, the analysis with combined samples (Fig. 3) gave results similar to those of the 1st analysis (Fig. 2).

Some phylogenetic structure was apparent within one of the *Liomys* clades (Figs. 2 and 3), but support for these relationships was weak to moderate. In the 1st analysis, the 2 samples of *L. irroratus* grouped together within clade A (bootstrap = 74%, Bremer = 1). Also within clade A, the *L. pictus* species complex formed a monophyletic group along with *L. spectabilis* (bootstrap = 61%, Bremer = 1). However, one form of *L. pictus* (*L. p. plantinarensis*) was more closely related to *L. spectabilis* than it was to other samples of *L. pictus* (bootstrap = 66%, Bremer = 2). In contrast, the relationships recovered among samples of clade B showed very weak support (bootstrap < 50%, Bremer = 1). Relationships among the taxa of clade A (and support for those relationships) were similar in the analysis with combined samples (Fig. 3).

Characters supporting particular nodes.—Partitioned Bremer support values (which assess the additive contributions of the individual data sets) indicated that the allozymic data set provided support for most clades (especially the resolution within *Heteromys*), whereas the signal from morphological characters was concentrated on a few basal clades. Partitioned Bremer support for the morphological data set was 0 to −2 for most clades in both analyses, with the exception of the subfamily Dipodomyinae (+5 in both analyses); the subfamily Heteromyinae (from +4 to +10 in the 1st analysis with all samples analyzed separately; +5 in the 2nd analysis with samples combined into species or karyomorphs); and the genus *Heteromys* (+6 in the 1st analysis; +7 in the 2nd). In contrast, the allozymic data set was the principal contributor to Bremer support for the majority of the other clades (i.e., except for the 3 clades mentioned above; from +1 to +9 in the 1st analysis; from +1 to +10 in the 2nd). Partitioned Bremer support for allozymic characters for those 3 clades follows: subfamily Dipodomyinae (+8 in the 1st analysis; +9 in the 2nd); subfamily Heteromyinae (from −1 to +5 in the 1st analysis; +3 in the 2nd); and genus *Heteromys* (−1 in both analyses).

Several morphological synapomorphies exist for the subfamily Heteromyinae and the genus *Heteromys*. Given the current outgroup comparisons, 7 characters represent synapomorphies of the subfamily Heteromyinae (characters W14, W27, W29, W30, W33, W37, and W38; all are unique and unreversed). Results of our analyses also indicated 3 unique, unreversed synapomorphies of the genus *Heteromys* (characters A1, anterior margin of posterior loph of permanent upper premolar [P4] with long fold; A4, optic foramen small, with posterior border generally formed by strong bar of bone; and A6, permanent lower premolar [p4] with 3 or more lophids). Two other characters represented unreversed synapomorphies for *Heteromys* but also were present in some outgroups (character A2, hamular process of pterygoid thin, also present in some Dipodomyinae) or in some *Liomys* (character A3, tubercle at posteroventral border of infraorbital foramen weak or absent, also found in some individuals of *L. pictus hispidus*). Two characters were synapomorphies for *Heteromys* but showed reversals (characters A5, anterior extension of premaxillary convex, with smooth lateral border of rostrum, reversed in *H. nelsoni* and in some *H. gaumeri*; and A8, plantar surface of hind feet naked, reversed in *H. gaumeri*).

Five unique, unreversed synapomorphies were evident in the allozymic data. Two characters (allele b for malate dehydroge-

nase 1 [*MDH1*]; and allele c for peptidase C [*PEPC*]) constituted synapomorphies for the clade containing *Heteromys nelsoni*, *H. nubicolens*, *H. oresterus*, *H. desmarestianus* ssp., *H. d. goldmani*, and *H. d. temporalis*. Similarly, 2 characters (allele a for malate dehydrogenase 2 [*MDH2*]; and allele c for hexose diphosphatase [*HDP*]) represented synapomorphies for *L. salvini* + *L. adspersus* (clade B). Finally, 1 character (allele a for *MDH1*) was a synapomorphy for *L. pictus* + *L. spectabilis*.

Discussion

Monophyly of the subfamily Heteromyinae (spiny pocket mice).—As in previous studies, our analyses demonstrated strong support for the monophyly of the subfamily Heteromyinae (Hafner 1981; Hafner and Hafner 1983; Wahlert 1991). Our purpose was to confirm monophyly of the Heteromyinae and assess relationships among species of spiny pocket mice. Hence, polarization of characters by comparison with members of the 2 other living subfamilies (Dipodomyinae and Perognathinae) was warranted (Watrous and Wheeler 1981). However, study of character evolution among the subfamilies (and synapomorphies for the subfamily Heteromyidae) would be better addressed through analyses comparing with the Geomyidae (pocket gophers) and fossil taxa within the superfamily Geomyoidea (e.g., *Harrymys*—see Wahlert 1991). Therefore, we only discuss character evolution within the Heteromyinae (see below).

Monophyly of the genera.—This study provides the 1st character-based phylogenetic analysis of heteromyines with dense taxonomic sampling across the subfamily. Our results demonstrate monophyly of the genus *Heteromys* and provide morphological synapomorphies for it. Although the monophyly of *Heteromys* had not been seriously questioned in the past (but see Rogers 1990), it had neither been demonstrated nor rigorously tested in a character-based analysis. Furthermore, only a few unpolarized characters were available for its diagnosis (Williams et al. 1993). Of the 7 synapomorphies identified for *Heteromys*, 4 are of special utility for identification of specimens of the subfamily (because they are unique and unreversed within the Heteromyinae). Three of these are unique to the genus (characters A1, posterior loph of permanent upper premolar with long fold; A4, optic foramen small; and A6, permanent lower premolar with 3 or more lophids). The other is not unique, being found also in some Dipodomyinae (character A2, hamular process of pterygoid thin). In addition, although we were not able to score it as a discrete character (because of its continuous nature), we note that the lateral terminations of the lophs of the upper molars and lophids of the lower molars tend to be smooth in species of *Heteromys*, but generally pointed in *Liomys* and the dipodomyine and perognathine outgroups; however, we stress that this feature is subjective. Given the present results, future studies evaluating the evolutionary relationships among species of *Heteromys* can assume monophyly of the genus and use species of *Liomys* as outgroups.

However, our analyses failed to support the monophyly of *Liomys*. Relationships among the 3 major heteromyine lineages (clades A, B, and C; Figs. 2 and 3) were not resolved with strong support. Hence, our analyses demonstrate neither the monophyly nor the paraphyly of *Liomys*. The other possible resolutions among the 3 main clades were maximally 1 step longer than the relationships in the respective fundamental cladograms. Notably, we found no synapomorphy for all species of *Liomys*. Although we were not able to score it as a discrete character, we did observe that in the upper molars of *Liomys*, the anterior loph is often much wider than the posterior loph (whereas the 2 lophs appeared to be subequal in width in *Heteromys*). Comparisons with dipodomyines and perognathines indicate that the condition in *Liomys* would be derived. However, we reiterate that this feature was too subjective to score in a straightforward manner.

In contrast to our equivocal results, the phylogenetic analyses of Rogers and Vance (2006) based on cytochrome-*b* data provide evidence against the monophyly of *Liomys*. Their results indicate that the species in our clade A (*L. irroratus*, *L. pictus*, and *L. spectabilis*; also clade A of Rogers and Vance [2006]) are more closely related to species of *Heteromys* (our clade C; their clade B) than they are to other species of *Liomys* (*L. adspersus* and *L. salvini*; our clade B; their clade I). Because their analyses are based on a maternally inherited mitochondrial gene, firm conclusions regarding the relationships among these 3 clades await future work (e.g., sequence data from unlinked nuclear genes). Nevertheless, the results of Rogers and Vance (2006) seriously question the monophyly of the genus *Liomys*. If future studies corroborate the paraphyly of *Liomys*, nomenclatural changes will be necessary, likely the restriction of *Liomys* (with type species *alleni*, a synonym of *irroratus*) to clade A (*irroratus*, *pictus*, and *spectabilis*) and proposal of a new genus for clade B (*adspersus* and *salvini*). In any case, given the current results, future phylogenetic studies of species of *Liomys* should either examine all species of the genus, as well as selected species of *Heteromys*, with perognathine or dipodomyine outgroups (or both); or be restricted in scope to include only species of either clade A or clade B as the ingroup (with representatives of *Heteromys* and the other clade of *Liomys* as outgroups).

Species within Heteromys.—Our analyses indicate 5 lineages within *Heteromys*, but the relationships among these lineages are unclear. One clade is composed of the South American species examined in this study (*H. anomalus* and *H. australis*; the sample of the latter was identified as *H. anomalus* by Rogers [1990]). Two other South American species (*H. oasicus* and *H. teleus*) were not included here because of the lack of allozymic data. However, they show morphological features that may indicate a close evolutionary relationship to *H. anomalus* and *H. australis* (Anderson 2003:13—although these characters proved too continuous to score unambiguously here). First, the 4 South American species all share a straight, moderately long fold in the anterior margin of the posterior loph of P4; this fold makes approximately a 45° angle with the anterior margin of the loph. In the current study, this condition falls within character-state (1), or ''long'' fold, for character A1, in contrast to character-state (2), the absent or slight fold

characteristic of species of *Liomys*. In Anderson and Jarrín-V. (2002), the condition in *H. australis* and *H. teleus* was considered a ''short'' fold, in implicit comparison with the even longer fold present in species from Mexico and Central America (see below), rather than in comparison with the condition present in *Liomys*. In contrast to the South American species, *Heteromys* from Mexico and Central America generally have an even longer fold, which is bent and shows a lateral termination. Second, the South American species generally show an especially small optic foramen (i.e., generally even smaller than species of *Heteromys* from Mexico and Central America). Again, these differences proved too tenuous to score here, and definitive placement of *H. oasicus* and *H. teleus* awaits future phylogenetic studies (e.g., based on DNA sequences).

Two Central American forms currently considered part of the *H. desmarestianus* species complex also constitute distinct lineages within the genus. *Heteromys d. crassirostris* (type locality, Panama: Darién: Mount Pirri [= Cerro Pirre], near head of Río Limón) inhabits easternmost Panama and extreme northwestern Colombia (Anderson 1999—the sample from locality 26 was considered *H. australis* by Rogers [1990]). The extent of its distribution to the west in other regions of Panama remains unclear, but it may be conspecific with the form *panamensis* named from central Panama (also currently considered a synonym of *H. desmarestianus*). Similarly, the 2 samples referred to as *H. d. planifrons* from southwestern Costa Rica (localities 16 and 17) are strongly divergent from true *H. desmarestianus* (so much so that Rogers [1990] considered them to represent an undescribed species). Comparison of voucher specimens with type material by RPA demonstrates that these samples are conspecific with the form *H. d. planifrons*, which was described from the nearby type locality of Costa Rica: San José: San Gerónimo, Pirris (originally and currently considered a synonym of *H. desmarestianus*). In addition, however, several other named species-level taxa of *Heteromys* are from type localities in Costa Rica and western Panama, and some (but probably not all) of them may be conspecific with the form *planifrons* as well (*chiriquensis*, *repens*, *subaffinis*, *underwoodi*, and *zonalis*). Hence, although both of these taxa (*H. d. crassirostris* and *H. d. planifrons*) clearly are not conspecific with *H. desmarestianus*, their elevation to specific status awaits detailed morphological studies characterizing their morphological distinctiveness and determining the valid name for each (see also Anderson and Timm 2006).

Heteromys gaumeri represents the 4th unresolved lineage within the genus. It possesses a distinctive karyotype for the genus (2n = 56; unique within *Heteromys* but present in some *Liomys*; Table 1), and its distinctive morphology has been recognized previously (Engstrom et al. 1987). Interestingly, it retains 2 character-states plesiomorphic to the Heteromyinae that are also present in *Liomys*. First, it constitutes the only species of *Heteromys* with the plantar surface of the hind feet well-furred (character A8). Second, although the anterior extension of the premaxillary is convex in most *Heteromys*, it is concave in *H. nelsoni* and in some *H. gaumeri* (like *Liomys*; character A5). Finally, we note that *H. gaumeri* is notable within the genus by consistent possession of an orange lateral stripe (character A7). In our study, this character-state also was found in some samples of the *L. pictus–L. spectabilis* complex. Notably, *H. gaumeri* inhabits drier habitats than any other species of the genus (*H. anomalus* is the only other species of *Heteromys* to inhabit large expanses of deciduous tropical forest, but it also is found in many evergreen forests). Engstrom et al. (1987) recommended removal of *H. gaumeri* from the *H. desmarestianus* species-group (then considered to include *H. desmarestianus*, *H. gamueri*, and *H. goldmani*), a change consistent with our analyses.

The last lineage in the genus recovered in our analyses is composed of *H. nelsoni*, *H. nubicolens*, *H. oresterus*, and the remaining samples from the *H. desmarestianus* species complex (*H. desmarestianus* ssp., *H. d. goldmani*, and *H. d. temporalis*). Although showing only weak bootstrap support (56–57%), this clade had values of 4–5 for the Bremer decay index and is supported by 2 unique, unreversed synapomorphies (allele b for *MDH1* and allele c for *PEPC*). *H. nelsoni* inhabits highland areas in southeastern Mexico and southwestern Guatemala and constitutes the type species for the subgenus *Xylomys*. Interestingly, in contrast to most *Heteromys*, the anterior extension of the premaxillary is concave in *H. nelsoni* and in some *H. gaumeri* (like *Liomys*; character A5). *H. nelsoni* also has a highly divergent karyotype (2n = 42). *H. nubicolens* and *H. oresterus* are endemic to small montane regions of Costa Rica (see also Anderson and Jansa, in press). Although these 3 species and 14 samples of the *H. desmarestianus* species complex are recovered as a clade (albeit with weak support), relationships among the entities of this group remain obscure. Some of these taxa (e.g., samples referred to as *H. d. temporalis*) may represent valid species that should be removed from *H. desmarestianus* (in addition to removal of the species referred to here as *H. d. crassirostris* and *H. d. planifrons*, see above), but such action awaits detailed future studies.

All told, our results indicate 5 clades in the genus *Heteromys* but fail to reconstruct the basal relationships among them. Future work should address the monophyly of the 5th group (see above), which is composed of many geographically disparate samples and was recovered with only weak support. Hence, recognition of subgenera within *Heteromys* is not wise at present. The results of the current study also reiterate the need for alpha-level taxonomic research determining species boundaries within the *H. desmarestianus* species complex (especially regarding the entities we denote as *H. d. crassirostris*, *H. d. planifrons*, and *H. d. temporalis*).

Species within Liomys.—Two distinct lineages comprise the genus *Liomys*, at least as it is currently recognized. One group (clade B) is made up of *L. adspersus* (found only in Panama) and *L. salvini* (widely distributed from Mexico to Costa Rica). Two unique, unreversed synapomorphies support this clade (allele a for *MDH2* and allele c for *HDP*), but no morphological synapomorphies for it are known. The fact that the 2 samples of *L. salvini* did not appear as sister taxa in the 1st analysis supports the conclusion by Rogers and Vance (2006—based on

much denser geographic sampling of *L. salvini*) that more than 1 species may be present within *L. salvini*.

Our analyses indicate some structure within the 2nd lineage of *Liomys* (clade A). As in previous studies, *L. irroratus* falls as the sister group to the *L. pictus–L. spectabilis* complex (which is supported by a unique, unreversed synapomorphy; allele a for *MDH1*). However, no synapomorphies (molecular or morphological) appear in our analysis for the overall clade A. Also echoing the findings of other authors (Morales and Engstrom 1989; Rogers and Engstrom 1992; Rogers and Vance 2006), *L. pictus* appears to represent a complex of similar species, because 1 sample ascribed to *L. p. plantinarensis* is more closely related to *L. spectabilis* than to other samples of *L. pictus*.

Closing remarks.—Given the current lack of resolution of phylogenetic relationships within the subfamily, comparative studies and firm biogeographic interpretations remain premature. However, the current data sets demonstrate the monophyly of the genus *Heteromys* and support previous work that identified 2 clades within the genus *Liomys*. Future research is necessary to resolve the relationships among these 3 clades. Our analyses also indicate several lineages within *Heteromys* and corroborate the need for alpha-level systematic research to elucidate the species present in the *H. desmarestianus* and *L. pictus* species complexes.

Resumen

La subfamilia Heteromyinae (ratones de abazones espinosos) constituye un clado monofilético bien definido dentro de la familia de roedores Heteromyidae. Aunque se reconocen 2 géneros en la subfamilia (*Heteromys* y *Liomys*), ningún análisis filogenético ha demostrado su recíproca monofilia. Un reciente estudio basado en datos de secuencias de ADN del gen mitocondrial citocromo *b* sugirió que *Liomys* es parafilético, pero tal estudio incluyó pocas especies de *Heteromys*. Aquí realizamos análisis filogenéticos de la subfamilia con un muestreo taxonómico denso, utilizando datos de aloenzimas de un estudio previo así como datos morfológicos externos y craneanos; nuestro objetivo es probar la monofilia de los géneros y esclarecer las relaciones filogenéticas dentro de ellos, en la medida posible con los datos disponibles. Además, reidentificamos algunos ejemplares de museo que corresponden a muestras del estudio genético previo. Los análisis de parsimonia indican 3 clados dentro de la subfamila: (A) *Liomys irroratus*, *L. pictus* y *L. spectabilis*; (B) *L. adspersus* y *L. salvini*; y (C) las especies examinadas de *Heteromys*. Sin embargo, las relaciones entre los 3 clados quedan sin resolver. El género *Heteromys* recibe fuerte apoyo y posee varias sinapomorfias morfológicas sin reversiones. En contraste, los análisis no indican ninguna sinapomorfia para *Liomys*, pero ni apoyan ni rechazan su monofilia. Los 3 clados identificados en los presentes análisis concuerdan con los encontrados en un reciente estudio de secuenciación de ADN mitocondrial, en el cual se halló una topología resuelta (B (A + C)). Dentro de *Heteromys* se reconstruyen 5 linajes, pero las relaciones entre éstos quedan sin resolver. Las especies examinadas de *Heteromys* de Suramérica forman un clado, pero no se incluyeron acá a 2 especies recientemente descritas de Ecuador y Venezuela. Las muestras aquí referidas a *H. desmarestianus crassirostris* y *H. d. planifrons* fueron muy distintas en comparación a las demás muestras de *H. desmarestianus*, destacando la necesidad de realizar revisiones taxonómicas a nivel alfa en este complejo de especies. Dados los presentes resultados, futuros estudios podrán examinar las relaciones entre especies de *Heteromys* usando muestras de *Liomys* como grupo externo, pero estudios de *Liomys* deben tomar en cuenta su probable parafilia.

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APPENDIX I

Collection localities and voucher specimens for the allozymic data from Rogers (1990). For heteromyine vouchers, we provide museum catalog number, as well as field collector number, tissue number, or both. Voucher specimens for *Heteromys* reexamined by RPA are here denoted with an asterisk. For voucher specimens not examined by RPA, we obtained museum catalog numbers and field numbers via consultation of museum databases and collector field notes. Localities are roughly ordered according to the numbering system of Rogers (1990) but are rearranged slightly to present samples of the same taxa together. Standard karyotypes reported in previous works are provided for samples of *Heteromys* where available (for details regarding numbers of individuals examined for karyological studies, see original cited sources). *H.* = *Heteromys*; *L.* = *Liomys*. (Abbreviations for specimen numbers are given in ''Materials and Methods.'')

Locality 1, H. desmarestianus temporalis.—Mexico: Veracruz: Ojo de Agua, 1,400 feet (AMNH 254692* = DSR 920 = AK 3097, AMNH 254693* = DSR 921 = AK 3098, AMNH 254694* = MDE 1010); Ojo de Agua, circa 500 m (MVZ 159463* = DSR 1663, MVZ 161232* = DSR 1679, MVZ 161233* = DSR 1680, MVZ 161234* = DSR 1681, MVZ 161235* = DSR 1682, MVZ 161236* = DSR 1683, MVZ 161237* = DSR 1684). 2n = 60, FN = 82 (Rogers 1989).

Locality 2, H. desmarestianus temporalis.—Mexico: Veracruz: 1 mile NW Motzorongo, 700 feet (CM 79532 = DSR 922 = AK 3099, CM 79533 = DSR 923 = AK 3100). 2n = 60, FN = 82 (Rogers 1989).

Locality 3, H. desmarestianus temporalis.—Mexico: Veracruz: Playa Escondida, 8.2 miles ENE (by road) Sontecomapán (MVZ 159465* = DSR 1556, MVZ 159466* = DSR 1557, MVZ 159467* = DSR 1558, MVZ 159468* = DSR 1559, MVZ 159469* = DSR 1560, MVZ 159470* = DSR 1561, MVZ 159471* = DSR 1562); 8.5 km ENE (by road) Sontecomapán, 25 m (MVZ 159481* = DSR 1544, MVZ 159482* = DSR 1545, MVZ 159483* = DSR 1546). 2n = 60, FN = 86 (Rogers 1989).

Locality 4, H. desmarestianus temporalis.—Mexico: Veracruz: 9.5 miles SE (by road) Catemaco, 50 m (MVZ 159462* = DSR 1568, MVZ 161231* = DSR 1678). 2n = 60, FN = 86 (Rogers 1989).

Locality 5, H. desmarestianus temporalis.—Mexico: Oaxaca: 23 miles SSW (by road) Tuxtepec, 250 feet (AMNH 254697* = DSR 936 = AK 3110). 2n = 60, FN = 82 (Rogers 1989).

Locality 6, H. desmarestianus ssp.—Mexico: Oaxaca: Vista Hermosa, 1,000 m (CM 79530 = DSR 934 = AK 3108, CM 79531 = DSR 935 = AK 3109); Vista Hermosa, Distrito Ixtlán, 1,000 m (MVZ 161229* = DSR 1685, MVZ 161230* = DSR 1686). 2n = 60, FN = 72 (Rogers 1989).

Locality 7, H. desmarestianus ssp.—Mexico: Chiapas: Pozo de Petróleo, 7 miles N (by road) Berriozábal, 950 m (MVZ 159457* = DSR 1494, MVZ 159458* = DSR 1495, MVZ 161226* = DSR 1671, MVZ 161227* = DSR 1672); 12 km N Berriozábal (TCWC 37064 = MDE 2450 = AK 4217). 2n = 60, FN = 67 (Rogers 1989).

Locality 8, H. desmarestianus ssp.—Mexico: Chiapas: 3.5 miles SE (by road) Rayón, circa 1,000 m (MVZ 159459* = DSR 1496, MVZ 159460* = DSR 1497, MVZ 159461* = DSR 1662, MVZ 161228* = DSR 1673). 2n = 60, FN = 67 (Rogers 1989).

Locality 9, H. desmarestianus ssp.—Mexico: Chiapas: 9.4 km S (by road) Palenque (TCWC 37063 = MDE 2173 = AK 4032). 2n = 60, FN = 68 (Rogers 1989; see also Engstrom et al. 1987).

Locality 11, H. desmarestianus ssp.—Honduras: Gracias a Dios: Río Mairin Tingni, 0.5 km up from Río Plátano (MSB 45811 = NK 4007, MSB 45812 = NK 4015, MSB 45813 = NK 4037). Standard karyotype unknown.

Locality 13, H. desmarestianus ssp.—Costa Rica: Guanacaste, 4.1 km NE (by road) Tilarán, 650 m (MVZ 164828* = DSR 2123, MVZ 164829* = DSR 2124, MVZ 164830* = DSR 2125, MVZ 164831* = DSR 2134, MVZ 164832* = DSR 2138, MVZ 164834* = DSR 2142, MVZ 164838* = DSR 2120); 5.0 km NE (by road) Tilarán, 650–675 m (MVZ 164839* = DSR 2121, MVZ 164840* = DSR 2122, MVZ 164841* = DSR 2140, MVZ 164842* = DSR 2145, MVZ 164843* = DSR 2235). 2n = 60, FN = 86 (Rogers 1989).

Locality 14, H. desmarestianus ssp.—Costa Rica: Cartago: Río Reventazón, 5.6 km SE (by road) Turrialba, 450 m (MVZ 164823* = DSR 2153, MVZ 164824* = DSR 2154, MVZ 164825* = DSR 2166, MVZ 164826* = DSR 2167, MVZ 164827* = DSR 2246). 2n = 60, FN = 80 (Rogers 1989).

Locality 15, H. desmarestianus ssp.—Costa Rica: Limón: 4.6 km W (by road) Limón (MVZ 164844* = DSR 2150, MVZ 164845* = DSR 2151, MVZ 164846* = DSR 2155, MVZ 164847* = DSR 2163, MVZ 164848* = DSR 2164, MVZ 164849* = DSR 2165, MVZ 164851* = DSR 2245). 2n = 60, FN = 86 (Rogers 1989).

Locality 10, H. desmarestianus goldmani.—Mexico: Chiapas: 15.5 miles SE (by road) Mapastepec, 150 feet (AMNH 254695* = DSR 1029, AMNH 254696* = DSR 1030, CM 79527 = DSR 999 = AK 3148, CM 79528 = DSR 1000 = AK 3149, CM 79529 = MDE 1224 = AK 3150). 2n = 60, FN = 76 (Rogers 1989).

Locality 12, H. nubicolens.—Costa Rica: Puntarenas: Monteverde, Campbell's Woods (MVZ 161224* = DSR 1744, MVZ 161225* = DSR 1745). 2n = 60, FN = 86 (Rogers 1989).

Locality 16, H. desmarestianus planifrons.—Costa Rica: Puntarenas: 1.1 km SE (by road) Ciudad Nielly, 25 m (MVZ 164852* = DSR 2193, MVZ 164853* = DSR 2194, MVZ 164854* = DSR 2195, MVZ 164855* = DSR 2230, MVZ 164856* = DSR 2242, MVZ 164865* = DSR 2222). 2n = 60, FN = 90 (Rogers 1989).

Locality 17, H. desmarestianus planifrons.—Costa Rica: San José: 16.3 km SE (by road) San Isidro, 525 m (MVZ 164858* = DSR 2178, MVZ 164859* = DSR 2179). Standard karyotype unknown.

Locality 18, H. gaumeri.—Mexico: Yucatán, Cenote Seco, 2 km E Chichen Itzá (TCWC 37163 = MDE 2404 = AK 4185, TCWC 37164 = MDE 2408 = AK 4189, TCWC 37165 = MDE 2410 = AK 4191, TCWC 41482 = MDE 2405 = AK 4186, TCWC 41483 = MDE 2409 = AK 4190). 2n = 56, FN = 76 (Engstrom et al. 1987).

Locality 19, H. gaumeri.—Mexico: Campeche: 7.5 km W Escarcega (TCWC 37066 = MDE 2259 = AK 4108, TCWC 37067 = MDE 2260 = AK 4109, TCWC 41443 = MDE 2249 = AK 4098, TCWC 41444 = MDE 2250 = AK 4099, TCWC 41446 = MDE 2252 = AK 4101, TCWC 41447 = MDE 2253 = AK 4102, TCWC 41449 = MDE 2255 = AK 4104, TCWC 41450 = MDE 2256 = AK 4105, TCWC 41451 = MDE 2257 = AK 4106, TCWC 41452 = MDE 2258 = AK 4107). 2n = 56, FN = 76 (Engstrom et al. 1987).

Locality 20, H. gaumeri.—Mexico: Quintana Roo: 2 km N, 8 km W Bacalar (TCWC 37146 = MDE 2350 = AK 4157, TCWC 37147 = MDE 2351 = AK 4158, TCWC 37148 = MDE 2352 = AK 4159, TCWC 37149 = MDE 2353 = AK 4160, TCWC 37150 = MDE 2354 = AK 4161). 2n = 56, FN = 76 (Engstrom et al. 1987).

Locality 21, H. gaumeri.—Mexico: Quintana Roo: 8 miles NNE Felipe Carillo Puerto (TCWC 37158 = MDE 2384 = AK 4177, TCWC 37159 = MDE 2385 = AK 4178, TCWC 37160 = MDE 2386 = AK 4179, TCWC 37161 = MDE 2394 = AK 4181); 2.5 miles NNE Felipe Carillo Puerto (TCWC 37162 = MDE 2387 = AK 4180). 2n = 56, FN = 76 (Engstrom et al. 1987).

Locality 22, H. nelsoni.—Mexico: Chiapas: 13.5 miles NW (by road) Motozintla de Mendoza, Cerro Mozotól, 2,800 m (MVZ 159488* = DSR 1399, MVZ 159489* = DSR 1400, MVZ 159490* = DSR 1404, MVZ 159491* = DSR 1411, MVZ 159492* = DSR 1480, MVZ 161244* = DSR 1670). 2n = 42, FN = 72 (Rogers 1989).

Locality 23, H. oresterus.—Costa Rica: San José: 2.2 km E (by road) La Trinidad de Dota, 2,600 m (MVZ 164860* = DSR 2091, MVZ 164861* = DSR 2092, MVZ 164862* = DSR 2102, MVZ 164863* = DSR 2107, MVZ 164864* = DSR 2221, MVZ 165786* = DSR 2244). 2n = 60, FN = 78 (Rogers 1989; not Patton and Rogers 1993).

Locality 24, H. anomalus.—Venezuela: Sucre: 40 km NW Caripito (CM 78166* = MDE 1999 = AK 3411, CM 78167* = MDE 2033 = AK 3436, CM 78168* = MDE 2034 = AK 3437, CM 78169* = MDE 2062 = AK 3449, TCWC 39715* = MDE 2032 = AK 3435). 2n = 60, FN = 68 (Engstrom et al. 1987).

Locality 25, H. anomalus.—Venezuela: Miranda: 25 km N Altagracia de Orituco (CM 78170* = MDE 2087 = AK 3468, CM 78172* = MDE 2130 = AK 3483, TCWC 39719* = MDE 2086 = AK 3467, TCWC 37494 = MDE 2091 = AK 3472); 40 km N Altagracia (TCWC 39720* = MDE 2129 = AK 3482). 2n = 60, FN = 68 (for individuals from 25 km N Altagracia de Orituco—Engstrom et al. 1987).

Locality 26, H. desmarestianus crassirostris.—Panama: Darién: circa 6 km NW Cana, E slope Cerro Pirre, 1,400 m (LSUMZ 25450* = DJH 2426, LSUMZ 25451* = DJH 2427). Standard karyotype unknown.

Locality 27, H. australis.—Panama: Darién: circa 6 km NW Cana, E slope Cerro Pirre, 1,200 m (LSUMZ 25452* = MSH 1187 = TK 22565). Standard karyotype unknown.

Locality 28, L. salvini.—Costa Rica: Guanacaste: 3.9 km SE (by road) Playas del Coco, 100 m (MVZ 164808 = DSR 2127, MVZ 164809 = DSR 2128, MVZ 164810 = DSR 2129, MVZ 164811 = DSR 2130, MVZ 164812 = DSR 2131).

Locality 30, L. salvini.—Mexico: Chiapas: 1.1 miles SE Cabeza de Toro (CM 79512 = MDE 1104 = AK 3136, CM 79513 = MDE 1105 = AK 3137, CM 79514 = MDE 1107 = AK 3139, CM 79515 = MDE 1108 = AK 3140, CM 79516 = MDE 1109 = AK 3141).

Locality 29, L. adspersus.—Panama: Panamá: 1.8 km N (by road) Fort Clayton, 5 m (MVZ 165784 = DSR 2302).

Locality 31, L. irroratus.—Mexico: Tamaulipas: 2.2 miles N Soto la Marina (TCWC 42044 = MDE 3280 = AK 4335, TCWC 42045 = MDE 3281 = AK 4336, TCWC 42046 = MDE 3282 = AK 4337, TCWC 42047 = MDE 3283 = AK 4338, TCWC 42048 = MDE 3284 = AK 4339).

Locality 32, L. irroratus.—Mexico: Puebla: 4 miles SW Xicotepec de Juarez (CM 79450 = MDE 986 = AK 3083, CM 79451 = MDE 987 = AK 3084, TCWC 41724 = MDE 984 = AK 3082).

Locality 33, L. pictus hispidus.—Mexico: Sonora: 7.6 miles (by road) SE Alamos, Río Cuchajaqui (MSB 55519 = NK 6584, MSB 55521 = NK 6583, MSB 55522 = NK 6593, MSB 55523 = NK 6592, NK 6605 [no voucher specimen available]).

Locality 34, L. pictus plantinarensis.—Mexico: Jalisco: 3 miles NE Contla, 3,600 feet (TCWC 42401 = MDE 3019 = AK 5890, TCWC 42402 = MDE 3020 = AK 5891, TCWC 42403 = MDE 3021 = AK 5892, TCWC 42405 = MDE 3023 = AK 5894).

Locality 36, L. pictus pictus.—Mexico: Chiapas: 7.5 miles SW (by road) Ixtapa (TCWC 37057 = MDE 2418 = AK 4198, TCWC 37059 = MDE 2420 = AK 4200, AK 4196 [no voucher specimen available], AK 4197 [no voucher specimen available]).

Locality 35, L. spectabilis.—Mexico: Jalisco: 3 miles NE Contla, 3,600 feet (TCWC 42412 = MDE 3013 = AK 5884, TCWC 42413 = MDE 3014 = AK 5885, TCWC 42414 = MDE 3030 = AK 5901).

Chaetodipus hispidus.—United States: Texas: Frio County, 3 miles S, 3.5 miles W Pearsall (5 individuals, TCWC).

Dipodomys merriami.—Mexico: Baja California del Norte: Rancho Sangre de Cristo, 31.1 miles E Ensenada (1 individual, MVZ).

Microdipodops megacephalus.—United States: Nevada: Lincoln County (1 individual, MVZ).

Perognathus longimembris.—United States: California: San Bernardino County, 2 miles N Searles Station, 9 miles NNE Johannesburg (1 individual, MVZ).

Appendix II

Specimens examined for morphological characters A1–A8. Taxa are ordered to correspond to the numbering of localities in Rogers (1990). (Museum abbreviations for specimen numbers are given in ''Materials and Methods.'')

Heteromys desmarestianus temporalis (data concatenated to allozymic data for localities 1–5).—Mexico: Veracruz: Motzorongo (holotype and paratypes of *H. temporalis*), USNM 63718, 63719 (holotype), 63720.

Heteromys desmarestianus desmarestianus (data concatenated to allozymic data for localities 6–9, 11, 13–15).—Guatemala: Quetzaltenango: Finca Helvetia, USNM 275235–275238.

Heteromys desmarestianus goldmani (data concatenated to allozymic data for locality 10).—Mexico: Chiapas: Chicharras (holotype and paratypes of *H. goldmani*), USNM 77576 (holotype), 77577, 77579, 77580, 77582.

Heteromys nubicolens (data concatenated to allozymic data for Locality 12).—Costa Rica: Puntarenas: Monteverde, Monteverde Cloud Forest Reserve, Investigator's Trail (holotype and paratypes of *H. nubicolens*), KU 159022–159024, 159025 (holotype), 159026, 159027.

Heteromys desmarestianus planifrons (data concatenated to allozymic data for localities 16, 17).—Costa Rica: San José: San Gerónimo Pirris (holotype and paratypes of *H. desmarestianus planifrons*), USNM 250348 (holotype), 250349, 256445.

Heteromys gaumeri (data concatenated to allozymic data for localities 18–21).—Mexico: Yucatán: Chichenitza [= Chichén Itzá] (holotype and paratypes of *H. gaumeri*), AMNH 12028/10461 (holotype), 12029/10462, 12030/10463, 12031/10464.

Heteromys nelsoni (data concatenated to allozymic data for locality 22).—Mexico: Chiapas: Pinabete (holotype and paratype of *H. nelsoni*), USNM 77578, 77920 (holotype).

Heteromys oresterus (data concatenated to allozymic data for locality 23).—Costa Rica: San José: El Copey de Dota (paratypes of *H. oresterus*), UMMZ 64026, 64030–64032.

Heteromys anomalus (data concatenated to allozymic data for localities 24, 25).—Trinidad and Tobago: Trinidad: Caura, AMNH 7567/5960, 7568/5961, 7569/5962, 7572/5964.

Heteromys desmarestianus crassirostris (data concatenated to allozymic data for locality 26).—Panama: Darién: Mt. Pirri [= Cerro Pirre], near head of Río Limón (holotype and paratypes of *H. crassirostris*), USNM 178998–179000, 179002, 179016 (holotype).

Heteromys australis (data concatenated to allozymic data for locality 27).—Ecuador: Esmeraldas: San Javier (paratypes of *H. australis*), USNM 113304–113307.

Heteromys oasicus (data not analyzed).—Venezuela: Falcón: 49 km N, 32 km W of Coro, Cerro Santa Ana (holotype and paratype of *H. oasicus*), USNM 456325 (holotype), 456327.

Heteromys teleus (data not analyzed).—Ecuador: Guayas: Cerro Manglar Alto, western slope (holotype and paratypes of *H. teleus*), AMNH 64684, 64685, 64692, 64694 (holotype).

Liomys salvini (data concatenated to allozymic data for localities 28, 30).—Guatemala: Escuintla: Masagua, USNM 275264–275268.

Liomys adspersus (data concatenated to allozymic data for locality 29).—Panama: Panamá: Fort Kobbe, USNM 296299–296302.

Liomys irroratus (data concatenated to allozymic data for localities 31, 32).—Mexico: Oaxaca: Oaxaca (topotypes of *L. irroratus*, by designation—Genoways 1973: 111), USNM 68363–68366.

Liomys pictus hispidus (data concatenated to allozymic data for locality 33).—Mexico: Nayarit: Terro Tepic, Compostela, Rancho El Colomo (holotype and paratype of *H. hispidus*), AMNH 8333/6667 (holotype), 8334/6668.

Liomys pictus plantinarensis (data concatenated to allozymic data for locality 34).—Mexico: Jalisco: Plantinar (holotype of *L. plantinarensis*), USNM 33595/45630 (holotype); Mexico: Michoacán: Los Reyes (other specimens of *L. pictus plantinarensis*), USNM 125661–125663.

Liomys spectabilis (data concatenated to allozymic data for locality 35).—Mexico: Jalisco: 2.2 miles NE Contla (holotype and paratypes of *L. spectabilis*), KU 96049, 96050, 96051 (holotype), 96052–96054, 96064.

Liomys pictus pictus (data concatenated to allozymic data for locality 36).—Mexico: Jalisco: San Sebastián (topotypes of *L. pictus*), USNM 88175, 88177–88179.

Chaetodipus hispidus.—United States: Texas: Maverick County: 1 mile S Eagle Pass, KU 52268, 52273 (used to score characters A1–A8); United States: Texas: Cameron County: Brownsville, AMNH 4160/3192 (used to score characters W20 and W35).

Perognathus longimembris.—United States: Nevada: Elko County: 3 mile W Halleck, KU 46540, 46545 (used to score characters A1–A8); United States: California: Tulare County: Chimney Meadow, AMNH 138595 (used to score characters W20 and W35).

Microdipodops megacephalus.—United States: Nevada: Washoe County: 8 miles SSW of Sutcliffe, Pyramid Lake, AMNH 135606, 135610.

Dipodomys merriami.—Mexico: Baja California: San Felipe, KU 58924, 58927.

Appendix III

Descriptions of all morphological characters used in this study. Characters preceded by an ''A'' were scored here, and those preceded by a ''W'' were taken from Wahlert (1991). See Appendix II for specimens examined for characters A1–A8.

A1.—Anterior margin of posterior loph of permanent upper premolar (P4) without indentation or fold or with slight indentation or fold (0); or with long fold (1). State (0) is similar to the characterization ''entostyle closely united to hypocone so that Y-shape of median valley of upper premolar is poorly formed'' in Williams et al. (1993:111).

A2.—Hamular process of pterygoid robust (0); or thin (1). States (0) and (1) are highly but not perfectly correlated with the characterization of the interpterygoid fossa as ''U-shaped anteriorly'' or ''V-shaped anteriorly,'' respectively, in Williams et al. (1993:100, 111).

A3.—Distinct tubercle or swelling present at posteroventral border of infraorbital foramen (0); or tubercle weak or absent (1).

A4.—Optic foramen very large, with posterior border formed by thin spine of bone (0); or small, with posterior border generally formed by strong bar of bone (1). See also character 13 of Wahlert (1991).

A5.—Anterior extension of premaxillary deeply concave (collapsed), typically creating distinct step in lateral border of rostrum (0); or convex, with smooth lateral border of rostrum (1).

A6.—Permanent lower premolar (p4) with only 2 lophids (in worn dentition, no more than 1 tiny fossette present in anterior lophid) (0); or with 3 or more lophids (in worn dentition, 2 or more fossettes present in anterior lophid) (1). This character is modified from Williams et al. (1993:100, 111).

A7.—Orange lateral stripe absent (0); or present (1).

A8.—Plantar surface of hind feet well furred (to approximately level of most-proximal plantar pad) (0); or naked (1). This character is modified from Williams et al. (1993:100, 111).

W5.—Maxillary–premaxillary suture intersects incisive foramina at back (0); or near middle (1).

W14.—Anterior alar fissure rises far posterior to M3 (0); or just posterior to M3 (1); or above or anterior to M3 (2). Character-states treated as ordered.

W20.—Masticatory and buccinator foramina separate (0); or united in 1 opening (1).

W27.—Auditory bulla with no ventral inflation (0); or with some ventral inflation (1).

W29.—Mastoid without dorsal inflation (0); or with great inflation (1); or with very great inflation, joining bulla anterior to meatus (2). Character-states treated as ordered. See also character 28 of Wahlert (1991).

W30.—Anteromedial bullar processes not present (0); or present (1); or present and meeting in midline (2).

W31.—Bullar texture not frothy (0); or frothy (1).

W32.—Bulla thick (0); or thin (1).

W33.—Stapedial artery present (0); or absent (1).

W35.—Interparietal without bullar consticition (0); or with some constriction (1); or with great constriction (2). Character-states treated as ordered.

W37.—Parietal somewhat retreated from occiput (0); or parietal does not come near occiput (1).

W38.—Squamosal entire posteriorly (0); or emarginate posteriorly (1).

W41.—Anterior squamosal foramen absent (0); or present (1).