EVOLUTIONARY RELATIONSHIPS OF WHITE-FOOTED MICE (*PEROMYSCUS*) ON ISLANDS IN THE SEA OF CORTÉZ, MEXICO

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Sixteen populations of *Peromyscus* on islands in the Sea of Cortéz (= Gulf of California), Mexico, were compared with 9 mainland species of *Peromyscus* based on sequence data for a 699-base-pair fragment of the mitochondrial DNA (mtDNA) COIII gene. An unrooted neighbor-joining tree based on corrected pairwise estimates of sequence divergence among variable mtDNA haplotypes indicated a recent (late Pleistocene) origin from a source on the adjacent mainland for 10 island forms representing *P. boylii, P. crinitus, P. eremicus, P. eva, P. fraterculus,* and *P. maniculatus.* Five other populations did not seem to be derived from species currently on the nearest mainland, suggesting overwater dispersal or distributional changes on the mainland after drowning of land-bridge connections. One population, possibly of more ancient origin, on Isla Cerralvo near the Baja California peninsula, probably originated via trans-Gulf rafting from the Sonoran mainland. Based on these results, 4 insular species (*P. stephani, P. interparietalis, P. caniceps,* and *P. dickeyi*) should be considered subspecies of *P. boylii, P. eremicus, P. fraterculus,* and *P. merriami,* respectively. The emergent view of evolutionary relationships within the subgenus *Haplomylomys* in the region reflects pre-Pleistocene phylogeographic events on the mainland surrounding the Gulf and a more recent origin of island populations.

Key words: *Haplomylomys,* island biogeography, mitochondrial DNA, *Peromyscus,* Sea of Cortéz

The generally rocky, desert islands of the Sea of Cortéz (= Gulf of California), Mexico, harbor a subset of arid-adapted rodents from the adjacent coasts of the Baja California peninsula and the Sonoran mainland. Native rodents occur on islands as small as 0.32 km² (Isla Granito) and have been described from 26 of the 41 islands in the Sea of Cortéz that are of at least that size, including the 21 largest islands (Lawlor 1983). The islands are a mix of oceanic islands (originating as volcanic eruptions in the Gulf, or separated by deep-water channels throughout the Pleistocene) and land-bridge islands, which were connected to the adjacent mainland by lowered sea levels during Pleistocene glacial intervals (Gastil et al. 1983). Most are land-bridge islands associated with the Baja California peninsula, and only 7 of the 80 islands are closer to the Sonoran mainland. Of the 26 islands harboring native rodents, 22 are closest to the peninsula.

By far the most ubiquitous rodents on the islands of the Sea of Cortéz are white-footed mice of the genus *Peromyscus,* 25 populations of which are known from 23 of the 26 islands from which native rodents are

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known (*Mus* and *Rattus* have been intro-
duced to several of the islands). Although
derivatives of 18 mainland species of ro-
dents (representing 6 genera and 3 families)
occur on the islands (Hafner and Riddle
1997; Lawlor 1983), 70% of the island pop-
ulations are of 2 genera, including deriva-
tives of 7 mainland species of *Peromyscus*
and of 5 mainland species of pocket mice
(*Chaetodipus*). Further, 18 of the 62 known
insular populations of native rodents are de-
rivatives of mainland species of the *Pero-
myscus* subgenus *Haplomylomys*, and 14 of
those have been considered to be deriva-
tives of *P. eremicus*. The next most com-
mon source species are *C. spinatus*, with 11
insular populations; *Neotoma lepida*, with 9
derivative populations; and *P. maniculatus*,
with 5 insular populations. No other main-
land species has >3 insular derivatives in
the Sea of Cortéz.

It has been reasonable to assume that in-
sular populations are derivatives of a taxon
on the closest adjacent mainland; most is-
lands are land-bridge islands (facilitating
access during glacial maxima), and over-
water dispersal subsequent to submergence
of land bridges is most likely from the near-
est coast. Moreover, the question of source
of insular populations presumed to be de-
rived from *P. eremicus* previously has ap-
peared to be academic, in that *P. eremicus*
was considered to have a circum-Gulf dis-
tribution. However, Lawlor (1971b) argued
that populations of *P. eremicus* on the
southern peninsula represent a distinct spe-
cies, *P. eva*. Riddle et al. (2000a) reported
sequence data from mitochondrial DNA
(mtDNA) that supported specific recogni-
tion of *P. eva* and further demonstrated that
remaining peninsular populations of *P. er-
emicus* instead should be recognized as a
distinct species, *P. fraterculus*. Thus, ≥4
separate species of *Haplomylomys* are dis-
tributed around the Gulf (Fig. 1): *P. eva*, *P.
fraterculus*, *P. eremicus*, and *P. merriami*.
In addition, *P. crinitus* (included within
Haplomylomys by Osgood [1909]) occurs
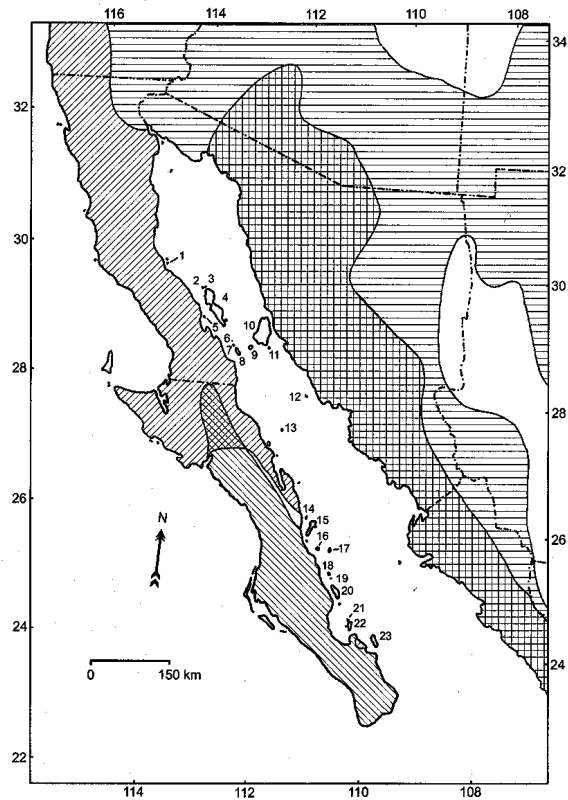at the head of the Gulf and on 1 northern

FIG. 1.—Location of 23 islands in the Sea of
Cortéz, Mexico, harboring native populations of
Peromyscus, and distribution of 4 species of
Peromyscus (subgenus *Haplomylomys*) in the re-
gion: left-oblique = *P. eva*; right-oblique = *P.
fraterculus*; horizontal = *P. eremicus*; vertical =
P. merriami. Islands (samples included in this
study in italics): 1) *San Luís Gonzaga*; 2) Mejía;
3) Granito; 4) Ángel de la Guarda; 5) Coronado
(Smith); 6) *Salsipuedes*; 7) Ánimas (San Lor-
enzo Norte); 8) *San Lorenzo* (*Sur*); 9) *San Es-
teban*; 10) *Tiburón*; 11) *Dátil* (*Turner*); 12) *San
Pedro Nolasco*; 13) *Tortuga*; 14) Coronados; 15)
del Carmen; 16) *Monserrat* (*Monserrate*); 17)
Santa Catalina (*Catalan*); 18) *Santa Cruz*; 19)
San Diego (*San Diegito*); 20) *San José*; 21) *Par-
tida Sur*; 22) Espíritu Santo; 23) *Cerralvo*.

island (San Luís Gonzaga). Identification of
the source of each of the 18 known insular
populations of *Haplomylomys* in the Gulf
has important implications concerning
mechanisms of colonization (whether via
land bridges, overwater dispersal, or both)
and on the distribution of mainland species
during glacial intervals when colonization
via land bridges was possible. As described

by Lawlor (1983:285), "mammals on islands are genetic . . . museums of ancestral founders," and discordant distributions of populations on land-bridge islands and their ancestral species on the immediately adjacent mainland coast likely would indicate substantial geographic shifts in the distribution of mainland species since the last glacial interval.

We recognize that genetic samples thus far available may not represent the full breadth of genetic variation present on the respective island; most islands have been sampled only a few times, and usually at the same or only a few accessible sites. In fact, species inventories of most islands have been based on only a few sampled sites. Until more comprehensive surveys, particularly of the larger islands, are conducted, we must assume that these point-samples represent the entire island population. In addition, the possibility always exists of very recent introduction via fisherman from both the peninsular and Sonoran mainland. For example, fishermen from both sides of the Gulf often use discarded refrigerators for cold storage of fish (J. Sanchez-Avila, pers. comm.); rodents nesting in insulation in the refrigerators could be transported to island fishing camps in this fashion. For the purposes of this study, we assume that populations that occur on land-bridge islands and are closely related to populations on the adjacent mainland originated with submergence of the land bridge. Those populations may have experienced continued, intermittent genetic contact via overwater colonization (whether human-mitigated or not). We further assume that very recent (e.g., human-transported) introductions to oceanic islands or to islands on the opposite side of the Gulf would display very little genetic differentiation from the source population. Genetic information alone cannot distinguish between origin of populations on land-bridge islands before land-bridge submergence or subsequent colonization from the adjacent mainland, or

between human transport or natural rafting, if by a recent colonization event.

An additional objective of this study was to evaluate whether island populations that currently are recognized as endemic species warrant specific status, based on levels of differentiation between island forms and closely related mainland species compared to differentiation among mainland populations. In addition to the 25 populations of *Peromyscus* from the 23 islands in the Sea of Cortéz, 12 populations are known from 10 islands off the Pacific shore of the Baja California peninsula. Of the total of 37 populations, 16 originally were considered subspecies of mainland species and 7 that initially were described as distinct species have been reduced to subspecies of mainland species by Lawlor (1971a), Miller and Kellogg (1955), Nelson and Goldman (1931), or Osgood (1909). Currently, 23 island populations are considered to be subspecies of mainland species, including all of the Pacific populations. Nine endemic species currently are recognized from 14 islands in the Gulf (Musser and Carleton 1993): *P. guardia* (islas Mejía, Granito, and Ángel de la Guarda), *P. interparietalis* (Salsipuedes, Las Ánimas [= San Lorenzo Norte], and San Lorenzo [= San Lorenzo Sur]), *P. stephani* (San Esteban), *P. pembertoni* (San Pedro Nolasco), *P. dickeyi* (Tortuga), *P. pseudocrinitus* (Coronados), *P. caniceps* (Monserrat [= Monserrate]), *P. slevini* (Santa Catalina [= Catalan]), and *P. sejugis* (Santa Cruz and San Diego [= San Diegito]). Banks (1967) and Brand and Ryckman (1969) studied relationships of the midriff-islands species (*P. guardia* and *P. interparietalis*) relative to *P. eremicus* (including *P. fraterculus*) based on morphology, laboratory breeding experiments, and blood-serum protein electrophoresis. Lawlor (1971b) included *P. pseudocrinitus* and *P. pembertoni* in a study of 6 species of *Peromyscus* from the Baja California peninsula and Sonora, using skeletal and phallic characters and karyology. Lawlor (1971a) evaluated the biosystematic relationships among these same

taxa and *P. stephani* based on osteology, pelage, phallic morphology, soft anatomy, serology, and karyology. Avise et al. (1974b) included 6 of the putative insular species (*dickeyi, stephani, sejugis, guardia, interparietalis,* and *caniceps*) in an examination of allozyme variation of island and mainland forms of the subgenus *Haplomylomys.* Hogan et al. (1997) included *P. sejugis* and *P. slevini* in an analysis of systematic relationships within the *P. maniculatus* species group based on sequence data from 3 genes of the mtDNA.

Sequence data from mtDNA have proven to yield reliable identifications of evolutionary and phylogeographic relationships among widespread populations of *Peromyscus* (Hogan et al. 1997; Riddle et al. 2000a). Hogan et al. (1997) evaluated systematic relationships among the *P. maniculatus* species group based on maximum-parsimony and distance-based phylogenetic analyses of sequence data from 3 mtDNA genes (ND3, ND4L, and ND4; 1,439 base pairs [bp]). They included samples from 2 species endemic to the Sea of Cortéz (*P. slevini,* Santa Catalina; *P. sejugis,* Santa Cruz and San Diego), concluding that whereas *P. sejugis* is closely related to *P. m. coolidgei* on the Baja California peninsula, *P. slevini* is not closely related to the *P. maniculatus* species group. Hogan et al. (1997:737) further interpreted the lack of a close relationship between *P. slevini* and *P. m. coolidgei* as challenging the "prevailing view ... that island populations of mammals [in the Sea of Cortéz] ... are derived from the nearest mainland populations." Riddle et al. (2000a) evaluated phylogeographic relationships among 26 populations from throughout the geographic range of the *P. eremicus* species group (*P. eremicus, P. merriami,* and *P. eva*) based on distance, maximum-likelihood, and maximum-parsimony analysis of sequence data for a 699-bp fragment of the mtDNA COIII gene. They included representatives of 5 other species: *P. californicus* and *P. crinitus,* which were included by Osgood (1909)

with the *P. eremicus* species group in the subgenus *Haplomylomys,* and *P. boylii, P. leucopus,* and *P. maniculatus* of the subgenus *Peromyscus.* Analyses of phylogenetic trees generated under 4 separate character-weighting strategies and representing 5 alternative biogeographic hypotheses revealed the existence of a cryptic species (*P. fraterculus,* previously included under *P. eremicus*) on the Baja California peninsula and adjacent southwestern California. Specific recognition of *P. fraterculus* is congruent with previous morphometric (Legg 1978) and allozyme (Avise et al. 1974b) analyses, including comparisons with neighboring *P. eremicus* and *P. eva,* with which *P. fraterculus* is broadly parapatric, is sympatric at several sites (Lawlor 1971b), and shares a sister-taxon relationship (Riddle et al. 2000a).

We examined evolutionary affinities (based on mtDNA sequences) of populations of *Peromyscus* from 16 of the 23 islands in the Sea of Cortéz from which *Peromyscus* is known (Table 1) relative to mainland populations of *P. boylii* (1 sample), *P. californicus* (1), *P. crinitus* (1), *P. eremicus* (4), *P. eva* (2), *P. fraterculus* (4), *P. leucopus* (1), *P. maniculatus* (1), and *P. merriami* (3). Included are samples representing insular populations currently assigned to *P. boylii* (Isla San Pedro Nolasco), *P. crinitus* (San Luís Gonzaga), *P. eremicus* (Cerralvo, Dátil, Tiburón, San José, and Partida Sur), *P. eva* (del Carmen), and 6 of the 9 putative endemic species from islands in the Sea of Cortéz. Three insular species are not included in this study: *P. pseudocrinitus, P. guardia* (considered to be possibly extinct by Mellink [1992] and Alvarez-Castañeda and Cortés-Calva [1999]), and *P. pembertoni* (considered to be extinct by Lawlor 1983).

Materials and Methods

Samples.—Representatives of 16 insular and 18 mainland populations were included in the mtDNA analysis. Tissue samples were assigned unique numbers in the University of Nevada Las

Vegas Tissue Collection (LVT). Each individual was prepared as a standard museum skin and skeleton or skin and skull specimen and is housed in the permanent collections of the Centro de Investigaciones Biológicas del Noroeste (CIB), the New Mexico Museum of Natural History (NMMNH), or the Escuela Nacional de Ciencias Biológicas del Instituto Politécnico Nacional (ENCB). Island samples (current taxon designation, island, GenBank accession numbers, corresponding LVT numbers, and corresponding CIB, NMMNH, or ENCB numbers) are as follows: *P. boylii glasselli,* San Pedro Nolasco, AF343770, AF343771, LVT 1793, 1795, CIB 2307, 2308; *P. caniceps,* Monserrat, AF343761, LVT 2448, CIB 2105; *P. crinitus palidissimus,* San Luís Gonzaga, AF343766, LVT 2440, CIB 2649; *P. dickeyi,* Tortuga, AF343772, AF343773, AF343759, LVT 1791, 1792, 2447, CIB 2150, 2151, 2177; *P. eremicus avius,* Cerralvo, AF343764, AF343763, LVT 1797, 1794, CIB 2265, 2266; *P. eremicus cinereus,* San José, AF343756, LVT 2431, NMMNH 3389; *P. eremicus collatus,* Dátil, AF343768, LVT 2437, CIB 2353; *P. eremicus insulicola,* Partida Sur, AF343765, LVT 2425, NMMNH 3379; *P. eremicus tiburonensis,* Tiburón, AF343760, LVT 2489, CIB 2440; *P. eva carmeni,* del Carmen, AF343754, LVT 2446, CIB 2143; *P. interparietalis interparietalis,* San Lorenzo, AF343758, LVT 2451, CIB 2627; *P. interparietalis ryckmani,* Salsipuedes, AF343757, LVT 2438, CIB 2487; *P. sejugis,* Santa Cruz, AF343769, LVT 2443, ENCB 3899; *P. sejugis,* San Diego, AF343762, LVT 2449, CIB 2068; *P. slevini,* Santa Catalina, AF343774, AF343775, AF343755, LVT 1790, 1796, 2439, CIB 2201, 2202, 2097; *P. stephani,* San Esteban, AF343767, LVT 2444, CIB 2469. Where multiple samples from a population were included, DNA was isolated and polymerase chain reaction amplifications were performed at separate times to ensure that resulting taxon diagnoses were not due to contamination errors.

Eighteen representative reference sequences from 9 species of *Peromyscus* were selected from Riddle et al. (2000a) to include all major haplotypes described in that study, as follows (haplotype designation, GenBank accession, LVT, and NMMNH catalog numbers in parentheses): *P. boylii*—Nevada: Clark County: 1.5 mi S, 1.5 mi E Mountain Springs (B01, AY009175, LVT 1585, NMMNH 4062); *P. cal-*

ifornicus—Mexico: Baja California: 2 mi SW Laguna Hanson, 5,500 ft (A01, AY009176, LVT 3695, NMMNH 2803); *P. crinitus*—California: Riverside County: 9 mi W, 1 mi S Quien Sabe Point (R01, AY009177, LVT 985, NMMNH 2393); *P. eremicus*—Mexico: Chihuahua: 3 mi NE Parral, 5,750 ft (E07, AY009204, LVT 1086, NMMNH 2461); San Luís Potosí: 10 mi S Matehuala, 4,600 ft (E01, AY009217, LVT 1180, NMMNH 2505); Sonora: 2 km N Puerto de la Libertad, 40 m (W17, AY009188, LVT 1224, NMMNH 2713); Arizona: Cochise County: 9.5 mi SE Willcox, 4,400 ft (W13, AY009194, LVT 4729, NMMNH 3441); *P. eva*—Mexico: Baja California Sur: 11 km S Todos Santos, 10 ft (V02, AY009229, LVT 3637, NMMNH 2785; V06, AY009228, LVT 3635, NMMNH 2848); *P. fraterculus*—Mexico: Baja California: 18 mi S Puertecitos, Agua Dulce (F08, AY009221, LVT 2163, NMMNH 2967); 27 km S Punta Prieta, 100 ft (F06, AY009234, LVT 3664, NMMNH 2801); 1 km W Cataviña, 1,800 ft (F02, AY009235, LVT 3713, NMMNH 3063); 8 mi S, 10 mi E Valle de la Trinidad, 3,200 ft (F04, AY009233, LVT 3792, NMMNH 3086); *P. leucopus*—Mexico: Chihuahua: 4 km SW Parrita, 5,200 ft (L01, AY009173, LVT 1045, NMMNH 2440); *P. maniculatus*—Mexico: Baja California Sur: 11 km S Todos Santos, 10 ft (N01, AY009174, LVT 3634, NMMNH 2847); *P. merriami*—Mexico: Sonora: 10 km SSE Alamos, 240 m (M04, AY009179, LVT 1243, NMMNH 2722; M07, AY009178, LVT 1241, NMMNH 2721); Sinaloa: 5 km SW El Fuerte (M02, AY009183, LVT 1282, NMMNH 2741).

Laboratory analysis.—Soft tissues were extracted and placed in liquid nitrogen for transport to the University of Nevada Las Vegas (UNLV); frozen tissue samples are maintained in the collections of CIB and NMMNH. Total genomic DNA was extracted from heart, liver, or kidney tissue using a lysis buffer protocol (Longmire et al. 1991). A fragment of mtDNA including 699 bp of the COIII gene was amplified via polymerase chain reaction using a 1-μL aliquot of DNA and *Taq* polymerase enzyme with the following reaction conditions: 95°C, 1 min; 55°C, 1 min; 72°C, 1 min; 30 cycles. Polymerase chain reaction fragments were extracted from a 1.0% agarose gel and purified using GeneClean (BIO 101, Carlsbad, California) following manufacturers' protocols. Polymerase chain reaction and sequencing primers were

TABLE 1.—Populations of *Peromyscus* known from the islands of the Sea of Cortéz, Mexico, indicating current designation and assignment to species group or subgenus, and taxonomic recommendations based on mitochondrial DNA (mtDNA) diagnoses. Original species-group assignments that specified the peninsular form of *eremicus* have been changed to *fraterculus* following Riddle et al. (2000a).

Current designation of insular taxon	Island	Authority	Assignment	mtDNA diagnosis	Taxonomic recommendation
Subgenus *Peromyscus*					
P. stephani	San Esteban	Townsend (1912)	*Haplomylomys?*	*boylii*	*P. boylii stephani*
		Hooper and Musser (1964)	*boylii*		
		Lawlor (1971a)	*boylii*		
		Avise et al. (1974a, 1979)	*boylii*		
P. boylii glasselli	San Pedro Nolasco	Burt (1932)	*boylii*	*boylii*	*P. boylii glasselli*
		Lawlor (1971a)	*boylii*		
P. maniculatus hueyi	San Luís Gonzaga	Nelson and Goldman (1932)	*maniculatus*		*P. maniculatus hueyi*
P. maniculatus	Coronado (Smith)	Lawlor (1971b)	*maniculatus*		*P. maniculatus*
P. slevini	Santa Catalina	Maillaird (1924)	*Haplomylomys mexicanus?*	*fraterculus*[a]	[b]
		Burt (1934)	*maniculatus*		
		Hooper (1968)	*maniculatus*		
		Lawlor (1983)	*maniculatus*		
		Hogan et al. (1997)	not *maniculatus*		
P. sejugis	San Diego	Burt (1932)	*maniculatus*	*maniculatus*	*P. sejugis*
		Hooper and Musser (1964)	*maniculatus*		
		Avise et al. (1974b, 1979)	*maniculatus*		
		Hogan et al. (1997)	*maniculatus*		
Subgenus *Haplomylomys* (sensu lato)					
P. crinitus pallidissimus	San Luís Gonzaga	Huey (1931)	*crinitus*	*crinitus*	*P. crinitus pallidissimus*
P. eremicus avius	Cerralvo	Osgood (1909)	*eremicus*[c]	*eremicus*[d]	*P. eremicus avius*
		Lawlor (1971b)	*eremicus*[c]		
P. eremicus collatus	Dátil	Lawlor (1971a)	*eremicus*	*eremicus*	*P. eremicus collatus*
P. interparietalis interparietalis	San Lorenzo Sur	Banks (1967)	*fraterculus*	*eremicus*[d]	*P. eremicus interparietalis*
		Brand and Ryckman (1969)	*eremicus*[c]		
		Lawlor (1971a)	*fraterculus*		
P. interparietalis lorenzi	Ánimas	Banks (1967)	*fraterculus*		*P. eremicus lorenzi*
		Brand and Ryckman (1969)	*eremicus*[c]		
		Lawlor (1971a)	*fraterculus*		
P. interparietalis ryckmani	Salsipuedes	Banks (1967)	*fraterculus*	*eremicus*[d]	*P. eremicus ryckmani*
		Brand and Ryckman (1969)	*eremicus*[c]		
		Lawlor (1971a)	*fraterculus*		
		Avise et al. (1974b)	*eremicus*[c]		

TABLE 1.—Continued.

Current designation of insular taxon	Island	Authority	Assignment	mtDNA diagnosis	Taxonomic recommendation
P. eremicus tiburonensis	Tiburón	Osgood (1909)	*eremicus*[c]	*eremicus*	*P. eremicus tiburonensis*
		Lawlor (1971a)	*eremicus*		
P. eva carmeni	del Carmen	Lawlor (1971b)	*eva*	*eva*	*P. eva carmeni*
P. caniceps	Monserrat	Lawlor (1971b)	*eva*	*fraterculus*[d]	*P. fraterculus caniceps*
		Hall (1981)	*crinitus*		
		Avise et al. (1974b, 1979)	*Haplomylomys*		
P. eremicus cinereus	San José	Hall (1931)	*eremicus*[c]	*fraterculus*[d]	*P. fraterculus cinereus*
		Lawlor (197b)	*eremicus*[c]		
		Avise et al. (1974b)	*fraterculus*		
P. eremicus insulicola	Partida Sur	Osgood (1909)	*eremicus*[c]	*fraterculus*[d]	*P. fraterculus insulicola*
P. eremicus insulicola	Espíritu Santo	Osgood (1909)	*eremicus*[c]		*P. fraterculus insulicola*
		Lawlor (1971b)	*eremicus*[c]		
		Avise et al. (1974b)	*fraterculus*		
P. guardia guardia	Ángel de la Guarda	Banks (1967)	*fraterculus*		*P. guardia guardia*
		Brand and Ryckman (1969)	*eremicus*[c]		
		Lawlor (1971a)	*merriami*		
		Avise et al. (1974b)	*eremicus*[c]		
P. guardia harbisoni	Granito	Banks (1967)	*fraterculus*		*P. guardia harbisoni*
		Brand and Ryckman (1969)	*eremicus*[c]		
		Lawlor (1971a)	*merriami*		
P. guardia mejiae	Mejía	Banks (1967)	*fraterculus*		*P. guardia mejiae*
		Brand and Ryckman (1969)	*eremicus*[c]		
		Lawlor (1971a)	*merriami*		
P. dickeyi	Tortuga	Hooper and Musser (1964)	*Haplomylomys*	*merriami*[a]	*P. merriami dickeyi*
		Avise et al. (1974b)	*merriami*		
		Lawlor (1983)	*eremicus*[c]		
P. pembertoni	San Pedro Nolasco	Lawlor (1971b)	*merriami*		*P. pembertoni*
P. pseudocrinitus	Coronados	Hooper (1968)	*crinitus*		*P. pseudocrinitus*
		Lawlor (1971b)	*eremicus*[c]		

[a] Conflicts with current taxonomy.
[b] Awaiting further survey to determine if 2 species occur on Isla Santa Catalina.
[c] Included *eremicus* and *fraterculus*.
[d] Refined designation of mainland source.

published elsewhere (Riddle 1995). Primers H8618 and L9323 were used to sequence both strands of every individual. Polymerase chain reaction templates were sequenced at UNLV using an ABI 310 automated sequencer (Perkin-Elmer Applied Biosystems, Inc., Foster City, California) and Big Dye Terminator Ready Reaction mix (Perkin-Elmer). Sequences were aligned and checked for nucleotide and reading-frame accuracy using The Eyeball Sequence Editor v.3.1 (Cabot and Beckenbach 1989).

COIII gene.—Evolutionary properties of the COIII gene in mammals currently are less well understood than those of the cytochrome-*b* gene (e.g., Irwin et al. 1991), although the COIII gene has been used successfully to elucidate intraspecific phylogeographic structure in a range of small terrestrial mammals (Lee et al. 1996; Riddle 1995; Riddle et al. 2000a, 2000b). A simple comparison of evolutionary rates of COIII and cytochrome *b* in *Peromyscus* was conducted by examining levels of corrected (Tamura–Nei model—Tamura and Nei 1993) sequence divergence between 1 individual each representing the *P. leucopus* and *P. maniculatus* groups (subgenus *Peromyscus*) and *P. eremicus* (subgenus *Haplomylomys*). The alignments for cytochrome *b* included 321 bp (GenBank accession numbers X89790, X89791, X89799) and for COIII included 699 bp.

Tree construction.—Analyses of sequences were conducted using either PAUP* v.4.0b2 (Swofford 1999) or MEGA v.1.01 (Kumar et al. 1993). We used corrected (Tamura and Nei 1993) pairwise estimates of percent sequence divergence among variable mtDNA haplotypes to construct an unrooted neighbor-joining (Saitou and Nei 1987) mtDNA gene tree. Previously (Riddle et al. 2000a), we demonstrated appreciable levels of sequence divergence in the COIII gene between these subgenera and species. It was not our intent in this study to investigate further phylogenetic relationships among species beyond analyses presented previously, and so rooting of the neighbor-joining tree was not relevant to our goals. Nonparametric bootstrapping values (500 replications) summarize relative levels of branch support on the neighbor-joining tree. Maximum parsimony analysis (heuristic search, random addition, 50 replications; unordered and equally weighted characters, tree-bisection-reconnection branch swapping) was used to generate the most-parsimoni-

ous trees, from which a consensus tree was constructed for comparison with the neighbor-joining tree.

RESULTS

COIII versus cytochrome b.—Within the 3 species of *Peromyscus* in which sequence divergence values estimated from COIII and cytochrome *b* were compared, the COIII gene appeared to be evolving slightly more rapidly than the cytochrome-*b* gene. For the following comparisons, percent sequence divergences are listed from cytochrome *b* (321 bp), COIII (all 699 bp), COIII (first 348 bp), and COIII (last 351 bp): between the subgenera *Haplomylomys* and *Peromyscus*, average percent sequence divergence = 15.9, 18.9, 21.3, and 16.7, and between the *P. leucopus* and *P. maniculatus* species groups, average percent sequence divergence = 9.9, 12.4, 12.6, and 12.2. Therefore, we concluded that the COIII gene was at least as informative, and perhaps more so, than the more commonly employed cytochrome-*b* gene for intraspecific phylogeographic studies in small terrestrial mammals. Further, the overall frequency distribution and compositional bias of nucleotides at 1st, 2nd, and 3rd codon positions in COIII of *Peromyscus* (Riddle et al. 2000a) were similar to those of cytochrome *b* across mammalian orders (Irwin et al. 1991).

Neighbor-joining tree.—The neighbor-joining tree based on corrected estimates of sequence divergence in the mtDNA COIII gene (Fig. 2) demonstrated the expected, traditional branching pattern among representative mainland taxa (Riddle et al. 2000a). Two closely related clades of 2 species each (*P. merriami* and *P. eremicus*; *P. eva* and *P. fraterculus*) represented the *P. eremicus* species group, which was then joined by 2 species variously included with that species group in the subgenus *Haplomylomys* (*P. californicus* and *P. crinitus*), and last joined by 3 representatives of the subgenus *Peromyscus* (*P. boylii, P. maniculatus,* and *P. leucopus*). Basic informa-
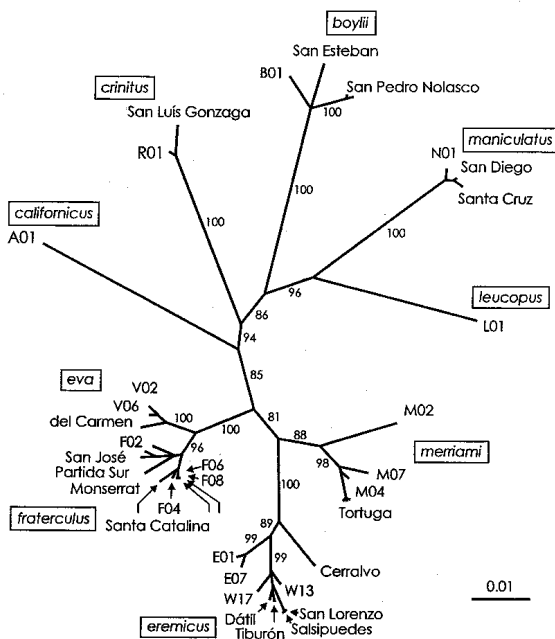
FIG. 2.—Unrooted neighbor-joining tree comparing 16 insular populations of *Peromyscus* (indicated by island name) to 18 populations of 9 mainland species of *Peromyscus*, based on corrected pairwise estimates of sequence divergence among variable haplotypes from a 699-base-pair fragment of the mitochondrial DNA COIII gene. Nonparametric bootstrapping values (percentage of 500 replications) summarize relative levels of branch support on the neighbor-joining tree. Representative reference sequences are indicated by haplotype number (from Riddle et al. 2000a); scale bar represents 0.01 substitutions/site.

tion summarizing patterns of sequence variation in the mainland taxa examined in this study are provided in Riddle et al. (2000a). Maximum parsimony analysis produced 4 most-parsimonious trees (length = 587; consistency index = 0.51; retention index = 0.83); a consensus tree (not shown) indicated affinities between island and mainland haplotypes that were identical to those indicated by the neighbor-joining tree.

Most island populations exhibited little sequence divergence from mainland populations: addition of individuals from island populations generally did not produce long branches on the neighbor-joining tree, with the exception of *P. eremicus avius* (from

Isla Cerralvo). The 2 samples of *P. eremicus avius* joined the mainland *P. eremicus* haplotypes (Fig. 2), but as a basal branch of that clade and at an average of 4.4 percent sequence divergence from remaining haplotypes in that clade. Elsewhere within the *P. eremicus* species group, *P. dickeyi* (Tortuga) nested within the known range of variation within *P. merriami*, demonstrating close affinities to 1 of 2 relatively divergent clades in that species; samples of *P. interparietalis* (San Lorenzo and Salsipuedes) represented an identical haplotype that, along with *P. eremicus* from Tiburón and Dátil, fell within the range of variation in the Sonoran lineage of *P. eremicus*; *P. eva* (del Carmen) grouped with peninsular *P. eva*; and *P. eremicus* from Partida Sur and San José, *P. slevini* from Santa Catalina, and *P. caniceps* from Monserrat clearly were aligned with *P. fraterculus*. All other island individuals examined in this study were aligned closely with species outside of the subgenus *Haplomylomys* (sensu stricto): *P. crinitus* from San Luís Gonzaga grouped with mainland *P. crinitus*; *P. stephani* from San Esteban and *P. boylii* from San Pedro Nolasco represented different haplotypes in the *P. boylii* clade; and samples of *P. sejugis* from San Diego and Santa Cruz grouped closely with *P. maniculatus* of the peninsula.

DISCUSSION

Estimated times and sources of origin.—For 10 of the 16 populations sampled, mtDNA analysis (Fig. 2; Table 1) indicated a relatively recent (late Pleistocene) origin from the species that currently occurs on the adjacent mainland: these include 1 population of *P. crinitus*, 2 of *P. boylii*, 2 of *P. maniculatus*, 2 of *P. eremicus*, 1 of *P. eva*, and 2 of *P. fraterculus*. Of the remaining 6 populations, 5 also seem to be recent in origin, either via vicariance associated with submergence of glacial-age land bridges or overwater dispersal. However, the source of these populations apparently is not from the currently nearest mainland species: islas

San José and Partida Sur harbor *P. frater-culus* instead of *P. eva*; *P. interparietalis* on Salsipuedes and San Lorenzo are derived from the Sonoran *P. eremicus* rather than *P. fraterculus* of the nearby peninsula; and the population on Tortuga, nearest to the peninsula, is a derivative of the Sonoran *P. merriami*. Finally, the single population that may be of more ancient origin (indicated by more extensive sequence divergence) is the derivative of *P. eremicus* on Isla Cerralvo, only 8.7 km from the peninsula (which harbors *P. eva* and *P. frater-culus*).

Peromyscus stephani.—Townsend (1912) initially compared *P. stephani* (Isla San Esteban) morphologically to *P. eremicus* (subgenus *Haplomylomys*); Hall and Kelson (1959) and Hooper (1968) tentatively followed this provisional allocation to *Haplomylomys*. Hooper and Musser (1964) and Lawlor (1971b) instead considered it morphologically similar to *P. boylii* (subgenus *Peromyscus*), an assignment followed by Hall (1981). Avise et al. (1974b) initially placed *P. stephani* within a broad cluster representing the subgenus *Haplomylomys* (sensu lato) based on allozyme similarity. However, inclusion of members of the *P. boylii* species group in the allozyme analysis (Avise et al. 1974a) indicated a close relationship between *P. stephani* and *P. boylii*, and further inclusion of members of the *P. maniculatus* species group (Avise et al. 1979) reinforced assignment of *P. ste-phani* to the *P. boylii* species group. Based on mtDNA sequence data, *P. stephani* is no more differentiated from a single mainland sample of *P. boylii* than is *P. boylii glasselli* of Isla San Pedro Nolasco.

Peromyscus caniceps.—Lawlor (1971b) considered similarities in bacular characters to suggest a close affinity between *P. can-iceps* and *P. eva*. Hall (1981) listed *cani-ceps* in the *crinitus* species group without explanation. Allozyme data (Avise et al. 1974a, 1974b, 1979) placed *caniceps* vaguely in the subgenus *Haplomylomys*, without close affinity with any other spe-

cies. Based on mtDNA sequence data, *P. caniceps* (occurring on Isla Monserrat, a deep-water "oceanic" island < 14 km from the peninsula) clearly is derived from *P. fraterculus,* which occurs on the adjacent mainland.

Peromyscus sejugis.—Assignment of the 2 insular populations of *P. sejugis* to the subgenus *Peromyscus* has never been questioned (Avise et al. 1979; Hogan et al. 1997; Hooper and Musser 1964). In agreement with Hogan et al. (1997), mtDNA sequence data from the COIII gene also indicated little differentiation from a single mainland sample.

Peromyscus interparietalis.—The west-ernmost midriff islands of the northern Sea of Cortéz (from north to south: Mejía, Granito, Ángel de la Guarda, Estanque, Partida Norte, Raza, Salsipuedes, Ánimas, and San Lorenzo) are all part of the Ángel de la Guarda block, which formed about 1 million years ago (Moore 1973). This block apparently has migrated about 50 km south relative to the peninsula (R. P. Phillips, in litt.) after Isla Ángel de la Guarda was torn away from the peninsula (Murphy 1983a). The islands of this block currently are separated from the peninsular mainland by the narrow (12- to 20-km) but deep (≤1,400-m) Salsipuedes basin or channel, which is characterized by "vigorous tidal currents" (Maluf 1983:28). *P. guardia* (not included in this study) is known from Ángel de la Guarda and 2 small, nearby islands (Mejía and Granito); *P. interparietalis* is known from the southern 3 islands in the block (Salsipuedes, Ánimas, and San Lorenzo). No *Peromyscus* are known from the intermediate islands (Partida Norte and Raza— Banks 1967). Based on an analysis of cranial characters, Banks (1967:217) suggested that *guardia* and *interparietalis* represented separate colonization events from a common *eremicus* stock (presumably from the peninsula; = *P. fraterculus*), because "they are each more like *eremicus* [= *fraterculus*] than either is like the other." Brand and Ryckman (1969) examined morphology

and blood serum and conducted breeding experiments among *guardia, interparietalis*, and *eremicus* (from a site where *P. eremicus* and *P. fraterculus* come into contact). They concluded that the 3 were distinct species, and that "protein data appear to indicate a closer relationship between *eremicus* and *interparietalis* than is suggested by morphological characteristics" (Brand and Ryckman 1969:501). Lawlor (1971a) compared *guardia* and *interparietalis* with peninsular (= *fraterculus*) and Sonoran *eremicus* and *merriami*, based on a variety of morphologic and genetic characters. He supported Banks' (1967) contention of separate origin of *guardia* and *interparietalis* and further concluded that *guardia* derived from an earlier ancestral stock in common with *merriami*, whereas *interparietalis* "evidently is more recently derived from a mainland *eremicus* [= *fraterculus*]-like form" (Lawlor 1971a:121). Although Avise et al. (1974b:231) concluded that *guardia* and *interparietalis* "are genetically more similar to each other than either is to any other *Haplomylomys* considered" (in direct conflict with the conclusions of Banks [1967] and Lawlor [1971a]), inspection of their allozyme data (Avise et al. 1974b:230, table 2) reveals that the single-island samples of each species share no unique alleles, and their coupling seems to be an artifact of the clustering technique employed.

Assignment of *P. interparietalis* as a derivative of Sonoran *P. eremicus* suggests that *interparietalis* probably colonized the southern islands of the Ángel de la Guarda block from the Sonoran mainland via Isla Tiburón and possibly Isla San Esteban. The maximum sea-way gap between San Esteban and San Lorenzo is about equal to that between Salsipuedes and the peninsula (17 km), but the more "vigorous tidal currents" are found between Salsipuedes and the peninsula (Maluf 1983:28). Although *P. eremicus* is found today on Isla Tiburón, no derivatives of *Haplomylomys* occur on San Esteban, located between Tiburón and San Lorenzo. Lawlor (1971a) speculated that

this absence might be due to competitive presence of *P. stephani*, a derivative of *P. boylii*, on San Esteban. He cited as circumstantial evidence the apparent extinction of *P. pembertoni* (*Haplomylomys*) from Isla San Pedro Nolasco, where *P. boylii glasselli* is thriving. Thus, overwater colonists of *P. eremicus* from the Sonoran mainland once may have occupied the entire chain of islands (Tiburón, Dátil, San Esteban, San Lorenzo, Ánimas, and Salsipuedes) and subsequently been extirpated from San Esteban because of competition with *P. stephani*.

Peromyscus dickeyi.—Isla Tortuga, on which *P. dickeyi* is the only native mammal, is the barren top of an active volcano that rises >300 m above the Sea of Cortéz, 25 km off the peninsula. *P. dickeyi* has long been recognized as a member of the subgenus *Haplomylomys* (Hall and Kelson 1959; Hooper and Musser 1964). Based on a phenetic analysis of allozyme data and a resulting similarity value (S = 0.99) that indicated a close relationship to *P. merriami* (which occurs on the Sonoran coast), Avise et al. (1974b:231) somewhat ambiguously stated that *P. dickeyi* "is genetically similar to *P. eremicus* (S = 0.91), particularly to the western subspecies of *P. eremicus* [= *P. fraterculus*], and is most similar to *P. merriami* (S = 0.99)." Coupling of *P. dickeyi* and *P. merriami* based on allozyme data persisted after inclusion of additional species of *Peromyscus* (Avise et al. 1974a, 1979). Diagnosis of *P. dickeyi* as a derivative of *P. merriami* based on mtDNA sequence data indicates that the allozyme similarity between the 2 is not spurious; despite the island's closer proximity to the peninsula (25 km), *P. dickeyi* evidently dispersed overwater to Isla Tortuga from the Sonoran mainland (≥100 km).

Isla Santa Catalina.—As summarized by Hogan et al. (1997), *P. slevini* from Isla Santa Catalina has been considered as a member of either the subgenus *Haplomylomys* (allied with *P. californicus*; Maillaird 1924) or allied with *P. maniculatus* of the

subgenus *Peromyscus* (based on cranial morphology—Burt 1934; Lawlor 1983). Hooper (1968) questioned placement of *P. slevini* in the *P. maniculatus* species group, considering morphology of its supraorbital shelf to be similar to that of the *P. mexicanus* species group. Carleton (1989) judged assignment of *P. slevini* to the subgenus *Peromyscus* to be tenuous. Based on mtDNA sequence data (Hogan et al. 1997; this study), *P. slevini* seems clearly to be outside of the *P. maniculatus* species group and to be closely related to *P. fraterculus* (*Haplomylomys*). Although original assignment to *Haplomylomys* was based on body size and molar morphology (Maillaird 1924), Lawlor (1971a) has shown that insular populations of *Peromyscus* in the Sea of Cortéz frequently exhibit great variation in molar morphology. Until specimens for which mtDNA sequence data are available are compared with all available specimens of *Peromyscus* from Santa Catalina, the possibility exists that 2 species occur on the island, and that specimens identified as *P. slevini* include a mixture of derivatives of both *P. maniculatus* and *P. fraterculus*.

Isla Cerralvo.—Identification of *P. eremicus avius* of Isla Cerralvo as a derivative of *P. eremicus* of the Sonoran mainland, rather than *P. eva* or *P. fraterculus* of the peninsula, might appear to parallel distribution of the lizard genus *Sator* in the southern Sea of .Cortéz (Murphy 1975, 1983a). According to Wyles and Gorman (1978), the nearest extant relative of this endemic insular genus (which occurs on islas Santa Cruz, San Diego, and Cerralvo) is *Sceloporus utiformis,* a subtropical species of mainland Mexico. Murphy (1975) interpreted the distribution of *Sator* as resulting from entrapment of the genus on islands during initial formation of the Gulf during the Miocene. Murphy (1983a) listed 2 other reptilian candidates of a possibly similar origin: the Cerralvo Island orangethroat whiptail (*Cnemidophorus ceralbensis*) on Cerralvo (Murphy 1983b; Robinson 1973) and the western diamondback rattlesnake (*Cro-*

talus atrox) on Santa Cruz. However, Murphy (1983a) cautioned that distributions of these latter 2 species might have resulted instead from immigration from the peninsular or Sonoran mainlands (respectively) or misidentification of the rattlesnake. *P. eremicus avius* seems to be a somewhat distant relative of Sonoran *P. eremicus,* with a sequence divergence greater than that between Sonoran and Chihuahuan clades of *P. eremicus* (E and W haplotypes of Fig. 2—Riddle et al. 2000a). However, divergence values between *P. e. avius* and Sonoran *P. eremicus* are less than that between peninsular (*eva* + *fraterculus*) and Sonoran (*merriami* + *eremicus*) species in the subgenus, indicating a separation of *P. e. avius* subsequent to formation of the Gulf. Thus, a more likely explanation for the origin of *P. e. avius* on Cerralvo is overwater dispersal from mainland Sonora (currently a distance of at least 150 km) during the Pliocene or early Pleistocene. The apparent origin of *P. dickeyi* (Isla Tortuga) via overwater dispersal from *P. merriami* on the Sonoran coast (≥100 km; see above) renders the hypothesized origin of *P. e. avius* via 150 km of rafting from the Sonoran mainland to Isla Cerralvo less improbable. If *P. e. avius* did originate via rafting from the Sonoran coast, the genetic identity of an isolated population of *Peromyscus* from near Las Cruces, immediately adjacent to Cerralvo, is of heightened interest. Lawlor (1971b) considered this population to be *P. eremicus* (= *P. fraterculus*?) instead of the surrounding *P. eva* of the southern peninsula. Instead, this population may represent secondary invasion of the peninsula from *P. e. avius* of Cerralvo.

Islas San José and Partida Sur.—The occurrence of *P. fraterculus* on islas San José and Partida Sur (both of which are nearshore, land-bridge islands) probably reflects a northward withdrawal in distribution of the species on the peninsula since the last full glacial, when *P. fraterculus* presumably occupied the adjacent mainland and spread via land-bridge connections. The isolated

population of *P. eremicus* (= *P. fraterculus*?) from Las Cruces described by Lawlor (1971b) also may represent a relict of this previous, more-widespread distribution.

Taxonomic recommendations.—Inspection of branch lengths depicting levels of sequence divergence (Fig. 2) indicates that divergences of these island populations from their mainland counterparts are generally on a scale with that among multiple samples of mainland species. Thus, no justification seems obvious for elevating any insular populations that currently are considered subspecies (*P. boylii glasselli, P. crinitus pallidissimus, P. eva carmeni,* and 5 subspecies of *P. eremicus*) to species status. Moreover, continued recognition of *P. stephani, P. caniceps, P. interparietalis,* and *P. dickeyi* would render *P. boylii, P. fraterculus, P. eremicus,* and *P. merriami,* respectively, paraphyletic. Therefore, we recommend that each of these former insular endemic species be included as subspecies of the respective mainland species (Table 1). We consider it likely that additional mainland samples of *P. maniculatus* will demonstrate that *P. sejugis* should be included as a subspecies of *P. maniculatus,* based on the minimal degree of sequence divergence between those taxa.

Although it is clear that a derivative of *P. fraterculus* presently occurs on Isla Santa Catalina (based on this study and Hogan et al. 1997), it is not certain that specimens included in these genetic analyses represent the same population (referred to as *P. slevini*) described in earlier morphologic studies (Burt 1934; Carleton 1989; Hooper 1968; Lawlor 1983; Maillaird 1924). It is possible that either 2 species occur on the island (derivatives of *P. maniculatus* and of *P. fraterculus*), or that the derivative of *P. fraterculus* subsequently colonized the island and replaced the other species. We consider it most likely that there has been but a single colonization event by *Peromyscus* on Santa Catalina of a *P. fraterculus* that subsequently evolved external and cranial traits somewhat intermediate between the sub-

genera *Haplomylomys* and *Peromyscus,* and that this intermediate morphology accounts for the historical difficulty in assigning the population to a subgenus or species group. However, we prefer to postpone any taxonomic changes pending a comprehensive morphometric review of all available specimens.

Recognition of *P. fraterculus* apart from *P. eremicus* (Riddle et al. 2000a) necessitates reassignment of populations on Isla San José and Isla Partida Sur to *P. fraterculus.* The fact that Isla Partida Sur and the larger Isla Espíritu Santo "are separated only by a narrow, steep-sided channel that is very shallow and rocky, navigable only at high tides to dingies and canoes" (Dickey 1983:184) leads us to recommend that populations of *Haplomylomys* on Espíritu Santo also properly are considered as *P. fraterculus insulicola.* Similarly, ample evidence documents that the 3 island populations currently considered as *P. interparietalis* are conspecific (Banks 1967; Brand and Ryckman 1969; Lawlor 1971a). Thus, we recommend that *P. i. lorenzi* (not included in this study) be included with the other 2 populations under *P. eremicus* (as *P. e. lorenzi*). Taxonomic review of the 3 remaining insular endemic species (*P. pseudocrinitus, P. guardia,* and *P. pembertoni*) awaits comparative genetic analysis.

Summary.—Recognition of deeper phyletic divisions within *Haplomylomys* surrounding the Sea of Cortéz (Riddle et al. 2000a, 2000b, 2000c) and reassignment of insular taxa based on mtDNA sequence data (herein) have altered significantly the overall view of evolution on the Baja California peninsula and islands in the Sea of Cortéz. Previous consideration of *P. eremicus* as continuously distributed around the Gulf seriously underestimated the impact of pre-Pleistocene and early Pleistocene geologic events on small mammals of the regional deserts, and recognition of insular populations at the species level overestimated the antiquity of these populations. Although analysis of the morphologic char-

acters among island populations has revealed significant and often unexpected differentiation between even very close islands (e.g., islas Ánimas and San Lorenzo—Lawlor 1971a), it is critical to consider these levels of differentiation in the proper temporal perspective to separate impacts of founder effect and genetic drift from those of lengthy isolation. This morphologic differentiation likely resulted from rapid fixation of characters in a small founding population rather than gradual differentiation during long periods of isolation.

RESUMEN

Se compararon para el género *Peromyscus* 9 especies del continente contra 16 poblaciones de las islas del Mar de Cortés, México. Se secuencio un fragmento de 699 pares de bases del gen COIII del ADN mitocondrial (mtDNA). Con base en estimaciones corregidas de la divergencia de secuencia por pares, entre los haplotipos variables de mtDNA, se construyó un árbol sin raíz por el método de vecinos-ligados. El que indica un origen reciente (Pleistoceno tardio) en el continente para 10 linajes que se presentan las islas, representadas por: *P. boylii, P. crinitus, P. eremicus, P. eva, P. fraterculus,* y *P. maniculatus.* Otras 5 poblaciones son recientemente derivadas de linajes que se relacionan actualmente con poblaciones del continente, lo que indica un proceso de dispersión sobre del mar o cambio en las distribuciones en el continente después la perdidad de las conexiones de tierra. En Isla Cerralvo, en las margenes de la Península de Baja California, se obtuvo que la población tiene posiblemente el origen más antiguo, inducido por disperción a través del Golfo de California desde Sonora. Basado en estos resultados, 4 especies insulares (*P. stephani, P. interparietalis, P. caniceps,* y *P. dickeyi*) deben ser consideradas como subespecies de *P. boylii, P. eremicus, P. fraterculus,* y *P. merriami,* respectivamente. La visión en conjunto que resulta por las relaciónes evolutivas dentro del subgénero *Haplomylomys* en la región, refleja los acontecimientos de la historia filogeográfica más profunda en el continente que rodea el Golfo, y el origen más reciente de poblaciones de islas.

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