A New

ISLAND BIOGEOGRAPHY
OF THE SEA OF CORTÉS

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8

The Nonavian Reptiles

Origins and Evolution

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Early in the history of systematic biology, scientists were interested in documenting the wonders of "the creation." Specimens procured on expeditions were placed in collections, and spectacular hand-colored plates graced giant monographs, showpieces of discovery and exploration. Darwin's work shifted interests to natural selection and the process of speciation. In addition to Darwin's volumes on evolution, whose main tenets were predicated on observations of island speciation patterns, Alfred Wallace's (1880) *Island Life* explained the great diversity of species on islands. Today, in an expanded concept islands remains the central focus for investigations of speciation and the mechanisms that drive change. Islands come in the form of Petri dish cultures of bacteria, bottles of *Drosophila*, mesic sky islands (mountaintop habitats isolated by intervening desert), and subaerial landmasses (surrounded by water). Evolution has remained the unifying principle of biology, and the concepts and methods associated with it have made their way into virtually all aspects of human culture.

Several groups of islands have been instructional in the development of evolutionary theory. The Galapagos Islands clearly had the greatest impact. However, the islands in the Sea of Cortés have also significantly influenced our understanding of the speciation process. Within herpetology, studies have looked at the evolution of insular gigantism (Case 1978b; Petren and Case 1997), anatomical and genetic variability (Soulé et al. 1973), and species composition (Case 1975, 1983; Murphy 1983a). Others have addressed island biogeography in the manner of MacArthur and Wilson's (1963, 1967) model of colonization and extinction (Case 1975, 1983; Wilcox 1978, 1980) versus historical constraints imposed by plate tectonics (Murphy 1983). Various ecological attributes of insular populations have been compared to those of the found-

ing source (reviewed in Case 1983). Controversies over peninsular effects have been evaluated (Taylor and Regal 1978, 1980; Seib 1980; Murphy 1991), as have the phylogenetic relationships of taxa (reviewed below). These are but a few examples of the herpetological investigations. The intensity of study in the Sea of Cortés has not waned in recent years. To the contrary, it has intensified.

Renewed interest in the evolution of the Baja California herpetofauna owes much to the nature of the peninsula and its associated islands. The peninsula affords the opportunity to study clinal variation or peninsular effects. The geological history provides opportunities to investigate the biological consequences of plate tectonics, especially as our understanding of the paleostratigraphy of the region advances. Clinal variation in climate and plant distributions facilitates investigations of ecological constraints on animal species distributions, and mounting paleoecological data fuel the fire. Isolated mountain regions and the associated islands of the peninsula provide laboratories for evaluating the genetic and anatomical consequences of isolation (i.e., speciation and divergence), both recent and old. Owing to these attributes, the region has recently received much attention from molecular systematists, in part because their data provide explicit hypotheses of genealogical relationships of individuals and the history of female dispersion.

Advances in Methods and Data

Concomitant with an increase in basic knowledge, sophisticated methods of data accumulation and analysis have been developed in the past 20 years. Molecular studies have advanced from gathering small isozyme databases to accumulating large amounts of sequence data (Hillis et al. 1996). More important, application of a rigorous philosophy of systematics (e.g., Popper 1934; Hennig 1966; Brooks and McLennan 1991), and recent refinements in methods of data analysis (e.g., Murphy 1993; Siddall and Kluge 1997; Murphy and Doyle 1998) and computer algorithms (Swofford 2000) have led to a revolution in our approach to evaluating the history of species. Phylogenies have been applied to a binomial taxonomy, a species name (Frost and Hillis 1990; Frost and Kluge 1994), thus allowing the instant retrieval of evolutionary history. Undoubtedly, the greatest impact of cladistic methodology has been the movement from storytelling to the scientific rigor of testing hypotheses using a refutationist philosophy (Popper 1934, 1959; Frost and Kluge 1994; Kluge 1997; Siddall and Kluge 1997). The congruence of phylogenies and models of geomorphic stratigraphic development of the peninsula and islands can now be tested using tools such as Brooks parsimony analysis (Wiley 1988; Brooks 1990).

Since the first publication of *Island Biogeography in the Sea of Cortez*, the number of significant databases has increased. Defendable phylogenetic hypotheses have been developed for a number of reptilian groups. DNA sequence studies have challenged our understanding of the evolution of the biota. Allozyme data evaluated within a phylogenetic framework have furthered our knowledge of the relationships of tree lizards (*Urosaurus*; Aguirre-León et al. 1999) and sand lizards (Murphy and Doyle 1998). They have also led to estimates of gene flow among populations of rock lizards (*Petrosaurus*; Aguilar-S. et al. 1988) and desert spiny lizards (*Sceloporus*; Grismer and McGuire 1996).

Paleoecology has developed as another line of investigation. Packrat midden records (Van Devender 1990; Bell and Whistler 1996) suggest that the distribution of xerophilic species remained constant at times of maximum glaciation in the Pleistocene. In contrast, the ranges of mesophilic species expanded and contracted concomitant with environmental fluctuations, including those associated with Pleistocene glacial events (Murphy 1983a,b, 1991; Grismer and McGuire 1993).

Baja California is not only an attractive area for biological investigations, it is of critical importance to geologists and geophysicists. Because of active plate interactions, the peninsula is the focus of much research on tectonic theory and change (chap. 2, this volume). The general parameters of the tectonic origins of the peninsula and the islands in the Sea of Cortés seem to be reasonably well established. Nevertheless, much controversy still exists, especially regarding the nuances of the stratigraphic history of the peninsula. Because of unresolved issues in the geological development of the region, an essential question emerges: Can phylogenies of organisms help geologists understand the tectonic and stratigraphic development of the area? We believe so.

Paleobiogeography of the Peninsular Archipelago Herpetofauna

Generalized Alternative Models

Because most island populations in the Sea of Cortés originated on the neighboring peninsula, an understanding of the peninsular fauna is critical. Two previous scenarios for the evolution of the peninsular herpetofauna differed significantly. In the first synthesis of data, Savage (1960) concluded that the composition of the fauna was due to waves of north-to-south invasion. Savage's brilliant argument centered on the geological concept of a permanent peninsula and a long existence of the Sea of Cortés. It built upon earlier studies by Matthews (1915), Nelson (1921), and Schmidt (1922, 1943). In contrast, Murphy (1983b, 1991) formed a vicariance scenario based on emerging pictures of plate tectonics: the peninsula broke away from mainland Mexico and it is still evolving tectonically. He correlated genetic-distance calculations with presumed tectonic events for a number of species assuming the dominant stratigraphic hypothesis to be true. However, Murphy merely fitted species to the most current stratigraphic model, and the study lacked rigorous phylogenetic methodology, which then did not exist for allozyme data. A number of subsequent studies have attempted to refine Murphy's scenario (e.g., Grismer 1994a,b). However, as with previous studies, these studies used a particular geological model for the peninsula, and the biological data were merely fitted to it. Their phylogenetic approach did not succeed because of the lack of methodological rigor and consistency. Frequently, one alternative, nonphylogenetic scenario for a species group was chosen, and all genetic data were ignored, including those demonstrating the absence of gene flow, at least within the framework of Mendelian principles (appendix 8.2).

New Databases

Before forming generalized biogeographic scenarios, several sound phylogenies are required (Brooks and McLennan 1991). Fortunately, we now know how to move

beyond just-so storytelling, and we can do so at a very fine level of resolution by tracking female dispersion using mitochondrial DNA. Furthermore, allozyme data yield direct estimates of and evidence for gene flow.

Frequently, major discrepancies occur between molecular and anatomically based phylogenies and taxonomies. For example, dramatically incompatible sets of phylogenetic relationships have been hypothesized for chuckwalla lizards (*Sauromalus*) by Hollingsworth (1998) and Petren and Case (1997; app. 8.1). Equally divergent cladograms have been advanced for orangethroat whiptail lizards, *Cnemidophorus hyperythrus*, by Grismer (1999b) and Radtkey et al. (1997). Some of the problems relate to the use of nonheritable characters such as ecological preferences or, in anatomical studies, to the reliance on and distribution of primitive character states. Other problems are due to the incorporation of meristic and other "numerical" data and questionable methods of data coding (Murphy and Doyle 1998) and philosophically problematic analyses (Siddall and Kluge 1997). These problems exist in most cladistic anatomical analyses. Consequently, we have restricted our databases to molecular characters because of their unquestionable heritability and fine level of resolution, and to unweighted maximum parsimony analyses.

Below we briefly review the accumulated molecular cladograms and population genetics studies for species of reptiles from Baja California to discover common patterns of tree branching. We rely most heavily on DNA sequence data because the sequences yield particulate data amenable to cladistic evaluation and can potentially detail relationships among populations. We then use cladogenic patterns to propose a new hypothesis that best explains the repeating cladogenic patterns observed in the herpetofauna.

Even with greater methodological rigor, we emphasize that a firm synthesis of genetic cladogenic patterns with geological history remains aloof. This synthesis is only speculation due to the absence of data and analyses for many species groups and uncertainties about the stratigraphic and tectonic history of the region.

Interpreting the Cladograms

We can predict how DNA patterns will appear for peninsular populations through time (fig. 8.1). For nonterritorial species, recent linear dispersions appear as sequential bifurcations, with sister taxa spinning off as the species invade new areas (fig. 8.1A).

Figure 8.1 (Facing Page) Expectations of cladogenic patterns derived from mtDNA gene sequences for peninsular populations. (A) Initial cladogenic patterns following colonization at the southern end of the peninsula followed by rapid northward dispersion. A reverse pattern of cladogenesis is expected for southward dispersions. (B–D) Small regions accumulate mutations and eventually obfuscate the original dispersal pattern. Nearby populations become each other's nearest sister species, and (D) multiple haplotypes will eventually accumulate at single localities yielding homoplastic associations. (E) A vicariant division initially results in nonexclusive patterns of the two isolates. (F) In time, the isolates are recognized as exclusive lineages. If the populations reunite, the cladogenic patterns will eventually return to pattern D.
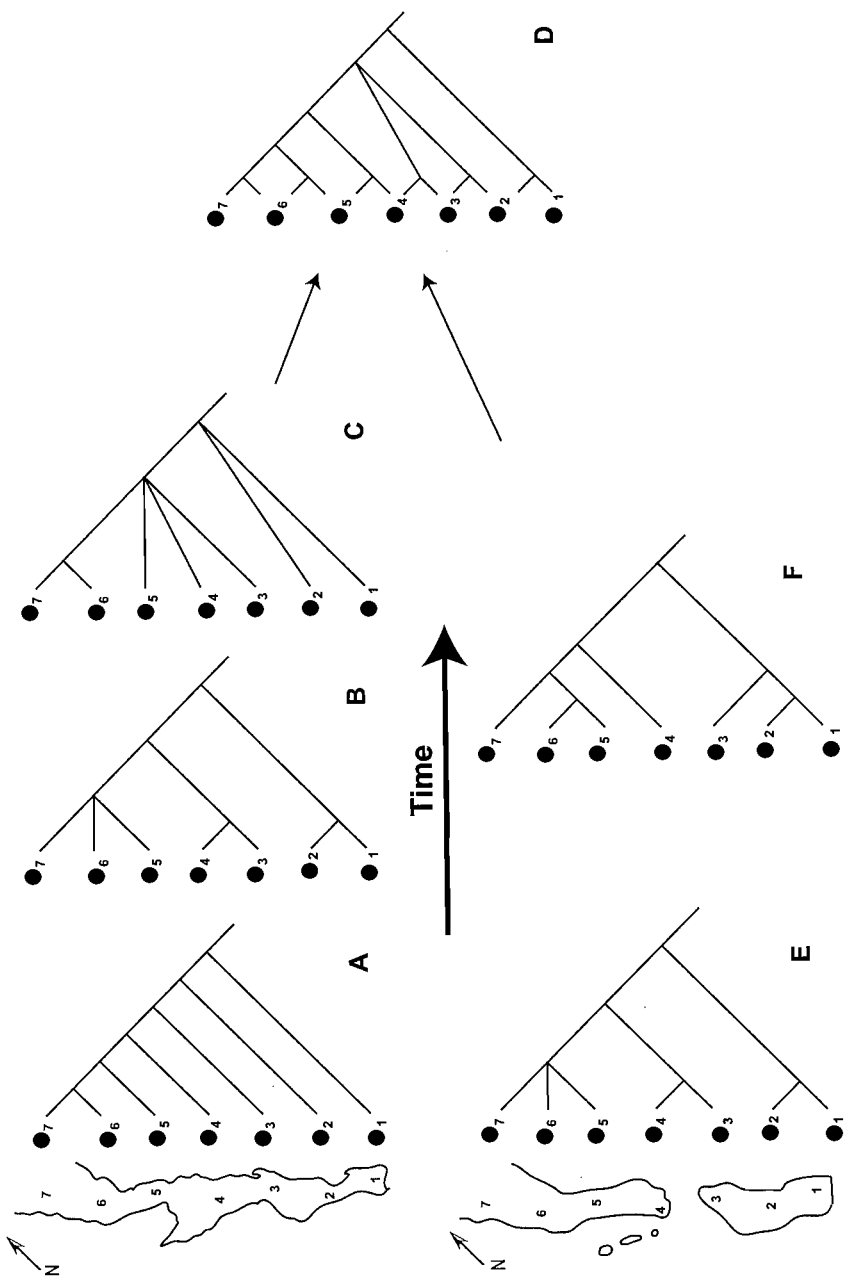
New populations are established in previously unoccupied sites, but the most recent bifurcations occur in areas of more recent cladogenic events. In time, local populations will accumulate mutations, and the genotypes will slowly spread. Dispersions and accumulated mutations will progressively obscure the original dispersal pattern (fig. 8.1B, C). Mutations accumulate over time in territorial species and small regions take on their own genetic identity. Derived genotypes will replace ancestral ones, eventually completely obscuring the original pattern. Nearby populations will be sister groups, and either homoplastic relationships or polytomies among individuals will appear on cladograms (fig. 8.1D). If the population becomes subdivided through a vicariance event, geographically proximal individuals from the two new groups will initially appear as sister taxa, to the exclusion of more geographically distant individuals in the same interbreeding group (fig. 8.1E). In other words, the populations will appear as a polyphyletic (nonexclusive) assemblage of individuals (Graybeal 1995). Time will erase this pattern (fig. 8.1F, D). We evaluate the accumulated data in light of these predictions below.

DNA Sequences

1. Side-blotched lizards, genus *Uta*. Upton and Murphy (1997) gathered 890 homologous nucleotide base pair (bp) sites of sequence data for these small saxicolous lizards from the mitochondrial (mt) DNA cytochrome *b* (cyt *b*) and ATPase 6 genes. They found that the peninsular populations of side-blotched lizards were a monophyletic group exclusive of Chihuahuan Desert populations (*Uta stejnegeri*). The peninsular populations formed two distinctive clades, one on the northern half of the peninsula, and the other on the southern half. The haplotype disconformity was narrowed to a 70-km wide region between San Ignacio and Santa Rosalia. Hollingsworth (1999) extended Upton and Murphy's study. He evaluated 1132 bp from cyt *b* and cytochrome oxidase III and narrowed the peninsular haplotype disconformity to a 10-km wide area near Santa Rosalia. Populations in Sonora arrived from the southward dispersion of more northern populations (fig. 8.2).

2. Chuckwallas, genus *Sauromalus*. Petren and Case (1997; updated in appendix 8.1) gathered 902 nucleotide sites mtDNA cyt *b* sequence data from a series of these large lizards. The peninsular samples of chuckwallas formed a clade separate from those north and east of the Peninsular Ranges. On the peninsula, two distinctive groupings occurred, with the division in the middle of the peninsula.

3. Western whiptail lizards, *Cnemidophorus tigris*. Radtkey et al. (1997) analyzed 887 nucleotide sites of mtDNA cyt *b* sequence data for western whiptails along the length of the peninsula. They observed three major clades for this group of highly vagile, nonterritorial lizards: an extreme northern clade, including Sonora, a mid- to northern Baja California (Norte) clade, and a Baja California Sur clade. The southern clade was further divided into Cape Region lizards and those farther north in the state of Baja California Sur (fig. 8.3).

4. Orangethroat whiptail lizards, *Cnemidophorus hyperythrus*. Radtkey et al. (1997) also evaluated mtDNA sequence data for this peninsula-restricted, highly vagile, nonterritorial species. The cladogram was pectinate in shape, a Hennigean comb, with the older cladogenic events occurring in the south, and the nearest sister populations farthest north. Reeder, Cole, and Dessauer (unpublished data) evaluated 12S and
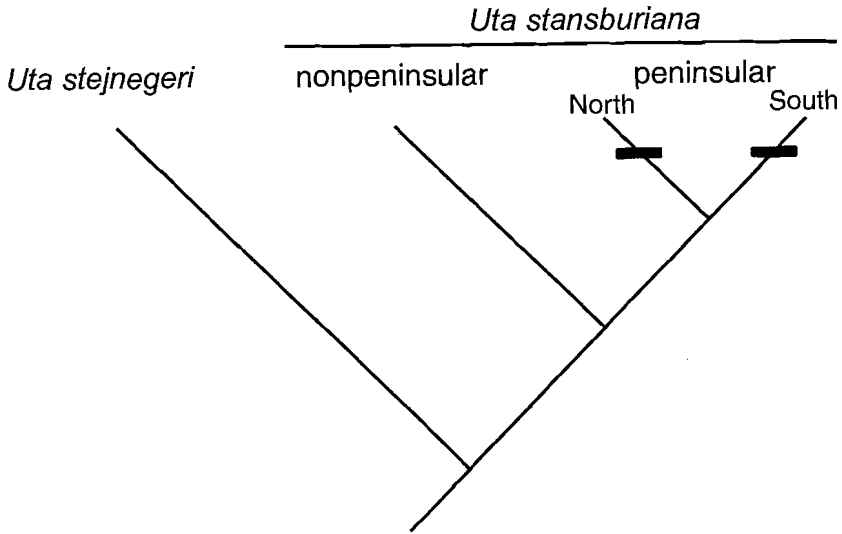
Figure 8.2 Reduced area cladogram for side-blotched lizards, genus *Uta*, on the peninsula of Baja California.
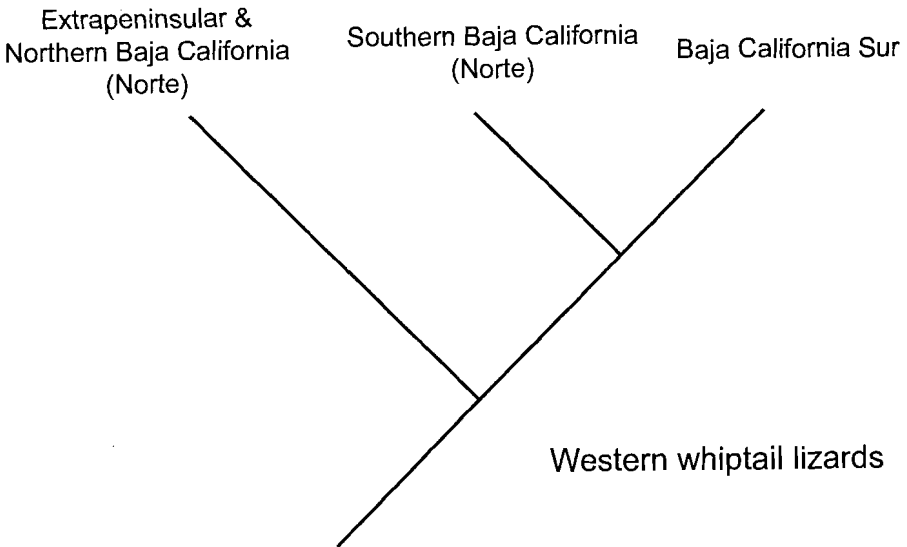

Figure 8.3 Reduced area cladogram for western whiptail lizards, *Cnemidophorus tigris*, on the peninsula of Baja California.

16S gene sequences from a number of whiptail lizards and found that this species is the sister taxon to a clade containing *C. deppei* and *C. guttatus* from mainland Mexico.

5. Pacific gopher snakes, *Pituophis catenifer*. Rodríguez-Robles and De Jesús-Escobar (2000) evaluated 893 nucleotide sites of mtDNA ND4 and 3 tRNA genes, of which 225 were potentially cladistically informative. All species of gopher snakes were examined, including the sister species *P. melanoleucus* and *P. ruthveni*. On the peninsula, *P. catenifer* formed northern and southern clades at the middle of the peninsula (fig. 8.4). Although Grismer (1994b) considers the peninsular snakes to be two species based on color pattern, the geographic distributions of the mtDNA haplotypes significantly conflict with his pattern-class alpha taxonomy.

6. California mountain kingsnakes, *Lampropeltis zonata*. This species occurs in the northern mountains of Baja California. Rodríguez-Robles et al. (1999) evaluated 105 potentially cladistically informative sites from the mtDNA ND4 and 3 tRNA genes. Individuals from the Peninsular Ranges of northern Baja California and southern California up to San Gorgonio Pass formed a distinctive clade. Populations north of San Gorgonio Pass formed a second clade, with two subclades: a coastal clade and an eastern Sierra Nevada clade (fig. 8.5).

7. Rattlesnakes, *Crotalus*. Murphy et al. (in press) gathered 2945 homologous sites of mtDNA sequence data from 5 genes for all but 2 of the 32 species of rattlesnakes. They found that the Baja California rattlesnake, *C. enyo*, was the sister species of the Neotropical rattlesnake, *C. durissus*. Excluding insular species, they confirmed that the western diamondback rattlesnake, *C. atrox*, was the sister species of the red diamond rattlesnake of Baja California, *C. ruber*. The speckled rattlesnake, *C. mitchellii*, which occurs on the peninsula and north, was likely the sister species of the western rattlesnake, *C. tigris*, of southern Arizona to Sinaloa.
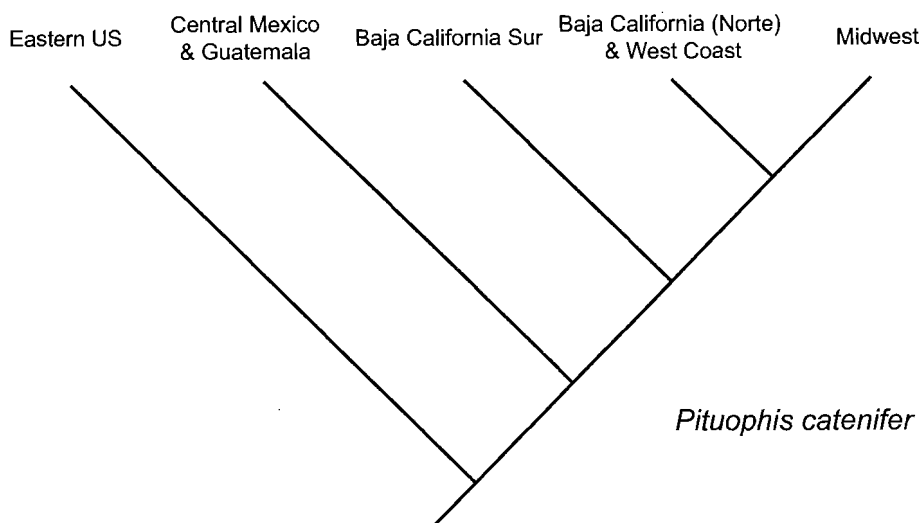

Figure 8.4 Reduced area cladogram for gopher snakes, *Pituophis catenifer*, on the peninsula of Baja California.
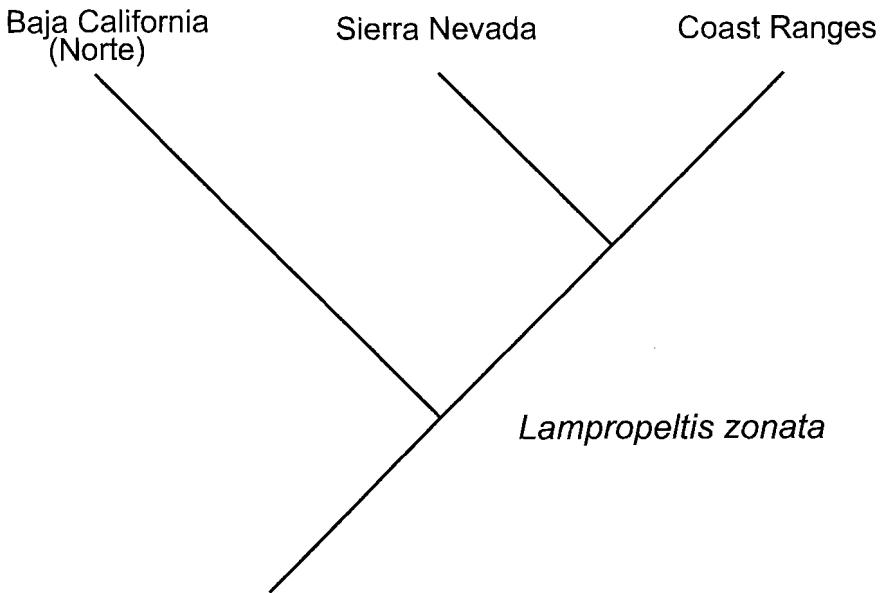
Figure 8.5 Reduced area cladogram for California mountain kingsnakes, *Lampropeltis zonata*, on the peninsula of Baja California.

8. Colorado Desert fringe-toed lizards, *Uma notata*. Trépanier and Murphy (in press) evaluated 1031 homologous sites of sequence data from cyt *b* and ATPase 6 mtDNA genes for 6 populations of these sand-dune–restricted lizards. Lizards around the head of the Sea of Cortés (the only place on the peninsula where they occur) west of the Colorado River are the sister group of *U. inornata* from near Palm Springs, California. In turn, individuals east of the Colorado are the sister group of *U. notata* and *U. inornata*, and lizards from the Mohawk Dunes in Arizona are the basal clade. Populations of Colorado Desert fringe-toed lizards in Sonora are southward dispersers from more northern populations.

9. San Lucan and western skinks, *Eumeces lagunensis* and *E. skiltonianus*. Richmond and Reeder (unpublished data) evaluated the phylogenetic relationships of these skinks using mtDNA ND4 gene sequences. *Eumeces lagunensis*, which occurs in Baja California Sur, is the sister taxon to populations of *E. skiltonianus* from Baja California (Norte) and southern California. In addition, both *E. skiltonianus* and Gilbert's skink, *E. gilberti*, are paraphyletic with respect to each other. *Eumeces lagunensis* is not closely related to *E. brevirostris*, as hypothesized by Grismer (1994b).

10. Iguanid genera. Reeder (1995), Reeder and Wiens (1996), and Schulte et al. (1998) evaluated relationships among the genera of phrynosomatines (Phrynosomatinae sensu Macey et al. 1997; Schulte et al. 1998). The most extensive data set is the total evidence evaluation of Schulte et al., and we use their generic phylogeny (fig. 8.6). The sequence data of both Reeder and Schulte et al. are congruent in finding that *Sator* is the sister group to *Petrosaurus* plus *Urosaurus* and most species of *Sceloporus*. Reeder's sequence data also supported a sister species relationship be-
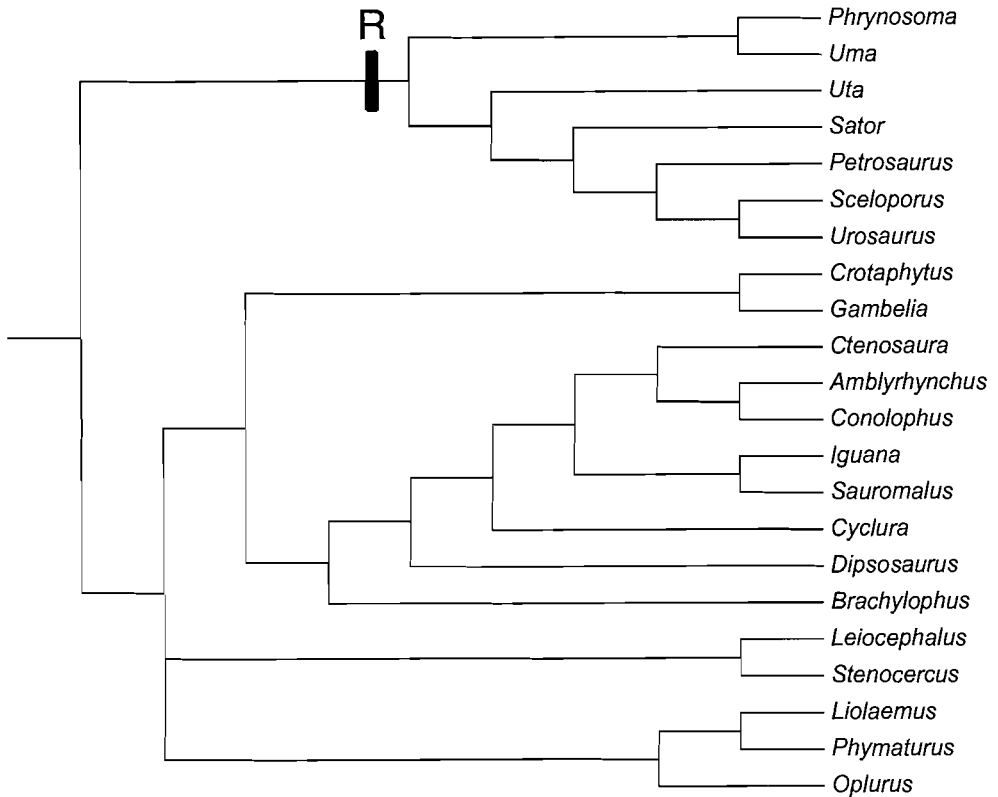
Figure 8.6 Composite phylogeny of iguanid genera based on the evaluations of Schulte et al. (1998) for the major lineages, and node "R" from Reeder (1996) and Reeder and Wiens (1996) for the phrynosomatines.

tween *Sator angustus* and *Sceloporus chrysostictus* + *Sceloporus variabilis*, species that Schulte et al. did not consider. Reeder and Wiens, based on total evidence including anatomical data, found that these two species of *Sceloporus* were members of a larger group that potentially also included *Sceloporus parvus, S. couchii, S. cozumelae, S. utiformis, S. siniferus, and S. squamosus*. Wyles and Gorman (1978) reported a sister relationship between *Sator* and *Sceloporus utiformis*. Given concordance among the sequence data sets, and problems in the evaluation of anatomical data (Murphy and Doyle 1998), the relationships among the critical group of *Sceloporus* remain uncertain. Nevertheless, the genus *Sceloporus* appears to be a paraphyletic assemblage of species. If tropical Mexican species of *Sceloporus* form the sister group of *Sator*, they will need to be placed in *Sator* to maintain monophyly of *Sceloporus*. Here we retain recognition of the genus *Sator* because of its apparent genealogical relationships and to preserve stability of the nomenclature until the required data are accumulated.

Relationships among the iguanine genera are based on the work of Sites et al. (1996) and Petren and Case (1997). The generic relationships have been placed on

the phylogeny of Schulte et al. (1998), who did not evaluate all of the genera. Significantly, chuckwallas (*Sauromalus*), which are restricted to the Peninsular Ranges and areas farther north, but west of the Continental Divide, are the sister taxon of green iguanas (*Iguana*) from tropical America (fig. 8.6).

11. Zebra-tail lizards (*Callisaurus draconoides*). Lindell and Murphy (unpublished data) have sequenced multiple specimens of these lizards from throughout their range on the peninsula, the southwest United States, and northwest Mexico. Peninsular populations formed a monophyletic group exclusive of extra-peninsular populations. The mid-peninsular discontinuity in mtDNA sequences occurs.

12. Sand snakes (*Chilomeniscus*). These fossorial snakes occur throughout the arid regions of Baja California into the southwestern United States. Wong et al. (1998) sequenced a 380 bp segment of cytochrome *b*. They resolved a pectinate set of relationships, as observed in orangethroat whiptail lizards (see paragraph 4 above).

13. LeConte's thrasher (*Toxostoma lecontei*). Zink et al. (1997) evaluated 619 mtDNA sites from cyt *b* and ND6. They observed a large haplotype disconformity between birds from the Sierra Vizcaíno and those farther north.

14. Additional avian reptiles. mtDNA analyses of cactus wren (*Campylorhynchus brunneicapillus*) and verdin (*Auriparus flaviceps*) show a mid-peninsular discordance that is concordant with that reported by Zink et al. for LeConte's thrasher. However, Zink et al. (unpublished ms) found no phylogeographic divisions within the range of the California Gnatcatcher (*Polioptila californica*), although this species spans the same region.

15. See mammalian examples in chapter 12.

Allozymes

Previously, Murphy (1983b) reviewed allozyme studies. Below we note new data sets only.

1. Rock lizards, *Petrosaurus*. Aguilar-S. et al. (1988) evaluated 34 loci for samples of rock lizards on the peninsula, exclusive of *P. thalassinus*. The shortnose rock lizard, *P. repens*, and banded rock lizard, *P. mearnsi*, are genetically very similar in being separated by only two fixed and two nearly fixed loci. Within *P. repens*, gene flow appears to be common.

2. Desert spiny lizards, *Sceloporus magister* group. Grismer and McGuire (1996) presented allozyme data from the doctoral dissertation of Galen Hunsickler (1987), supplemented with anatomical data. They concluded that only a single species, *S. zosteromus*, occurred on the Peninsular Ranges, and that zones of anatomical intergradation occurred in the regions of the transpeninsular seaways. However, Murphy's (1983b) and Aguirre, Morafka, and Murphy's unpublished data do not support Grismer and McGuire's conclusion (app. 8.2).

3. Brush lizards, *Urosaurus*. Aguirre et al. (1999) used allozyme data to investigate nuclear DNA diversity among these lizards. They observed two areas where derived alleles (duplicated loci) appeared to be dispersing along the peninsula: from the Cape Region northward to near Isla San José, and from San Ignacio to south of Santa Rosalia. They further observed that the endemic Baja California brush lizard, *U. lahtelai* of the Cataviña region, central Baja California (Norte), shared derived allelic states with northern populations of blacktail brush lizard, *U. nigricaudus*, exclusive
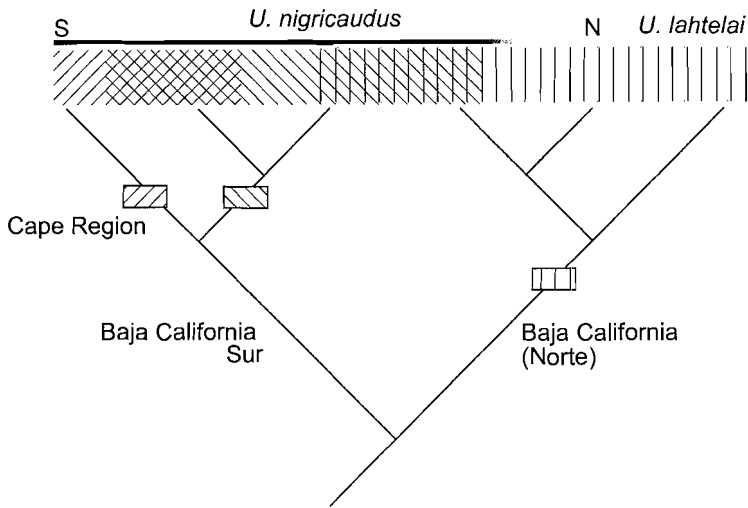
Figure 8.7 Reduced area cladogram for brush lizards, *Urosaurus nigricaudus*, on the peninsula of Baja California. The horizontal bar indicates the integradation of derived character states after reunification of ephemeral isolated populations.

of southern populations (fig. 8.7). (They also mistakenly reported the occurrence of *U. nigricaudus* on Isla Cedros.)

Emergent Patterns of Cladogenesis

From these molecular phylogenetic investigations, six patterns of relationships emerge:

1. Some endemic peninsular taxa have a sister group in tropical Mexico, particularly those species restricted to Baja California Sur (see also Papenfuss, 1982). Examples include chuckwallas and green iguanas, orangethroat whiptail lizards and mainland Mexico whiptail lizards, and Baja California and Neotropical rattlesnakes.

2. Some peninsular taxa share a sister relationship with more easterly taxa in northern Mexico and Arizona, and even more distant relationships to taxa in the Chihuahuan Desert of Texas and north-central Mexico. Examples include side-blotched lizards, fringe-toed lizards, gopher snakes, western diamondback and red diamond rattlesnakes, and speckled and western rattlesnakes.

3. A mid-peninsula genetic discontinuity is common. It occurs in side-blotched lizards, chuckwallas, western whiptail lizards, Pacific gopher snakes, San Lucan and western skinks, zebra-tail lizards, LeConte's thrasher, cactus wren, and verdin. Mammalian examples are reviewed in chapter 12.

4. At least two peninsular species have a comblike set of relationships with their nearest sister taxa occurring in the north, including orangethroat whiptail lizards and sand snakes.

5. A large genetic nonconformity occurs at San Gorgonio Pass. Examples include chuckwallas, Pacific gopher snakes, California mountain kingsnakes, and zebra-tail lizards. See also mammalian examples in chapter 12.

6. Xerophilic lizards at the head of the Gulf of California appear to have southward dispersal patterns with nearest sister relationships located in the south, such as fringe-toed lizards and side-blotched lizards.

A New Scenario for the Peninsular Herpetofauna

The origins of the native peninsular herpetofauna are intimately tied to the origin of the peninsula and to the changing environment. Much of our understanding of the development of the peninsula derives from plate tectonics as associated with strati-graphic information. Murphy (1983b) reviewed the development of the peninsula, and little has changed other than nuances of timing, tectonics, and additional documentation (chap. 2). Nevertheless, we briefly review the paleostratigraphy and paleoecology here.

In the early Miocene the Sea of Cortés had not formed and thus the peninsula of Baja California did not exist (fig. 8.8). A few islands occurred, and these are now part of the peninsula (Durham and Allison 1960; Gastil and Jensky 1973; Gastil et al. 1975; Minch et al. 1976). The continents were drifting northward. Concomitantly, from the Eocene onward, the Madro-Tertiary geoflora (Axelrod 1975) spread south-ward and replaced the tropical and subtropical flora. A mixture of dry tropical forest and tropical scrub likely characterized the flora of the proto-peninsular region (Axel-rod 1979). Oak-pinyon woodlands likely dominated the northern flora because the area was quite moist, as evidenced by numerous, deep, Miocene streambeds (Gastil et al. 1975). Tropical floral elements dominated in the south.
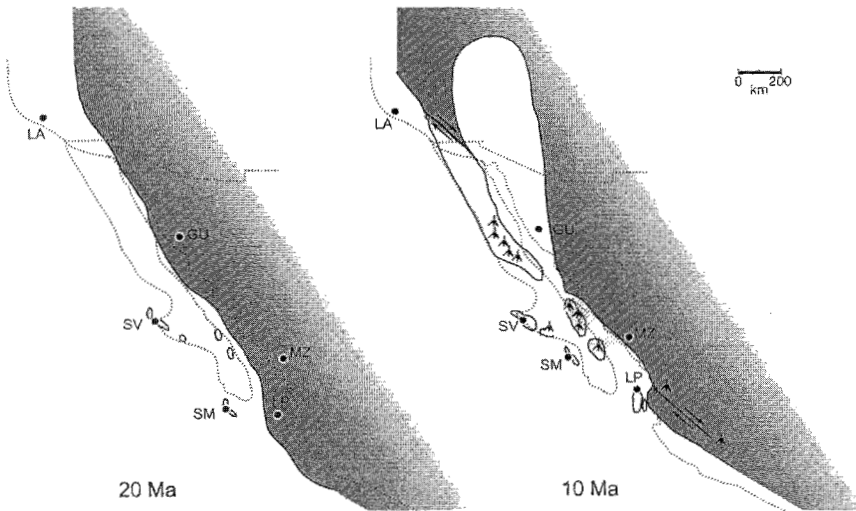

Figure 8.8 Paleographic reconstructions of western North America for the early Miocene (20 Ma) and mid-Miocene (10 Ma). The stippled areas symbolize the temporary formation of the Sea of Cortés. The Cape Region is 50 km farther south of its current position relative to the peninsula. Present locations of LA = Los Angeles; GU = Guaymas; SV = Sierra Vizcaíno; SM = Islas Santa Margarita and Magdalena; MZ = Mazatlán; LP = La Paz.

Around 12.5 million years ago, the southern peninsular region rotated westwardly away from the mainland (Mammerickx and Klitgord 1982; Hausback 1984). The displacement may have been as much as 100–150 km northwest from its original location. A temporary proto-Gulf of California formed (fig. 8.8; Atwater 1970; Atwater and Molner 1973; Gastil and Jensky 1973; Gastil et al. 1975). By the close of the Miocene, the Cape Region was located near the vicinity of the Islas Las Tres Marías (fig. 8.9; Atwater and Molner 1973; Gastil and Jensky 1973), and the proto-Gulf of California extended up to near Tiburón island (Jensky 1975; Gastil and Krummenacher 1977; Stock and Hodges 1989). The northern Peninsular Ranges had attained half the elevation that occurs today (Stock and Hodges 1989). The southern portions of the peninsula existed either as an island archipelago (Murphy 1983b), or as a solid peninsula (Grismer 1994b: fig. 12).

Around 4–5.5 million years ago, plate interactions accelerated, eventually moving the Peninsular Ranges some 300 km farther northwest relative to mainland Mexico. The Sea of Cortés permanently formed, and by 3 million years ago it extended northward at least to the San Gorgonio Pass of southern California and eastward into Arizona (figs. 8.9, 8.10). The southern peninsular regions initially formed as an island archipelago, but most of the landmasses were soon connected along the Peninsular Ranges (Hausback 1984). Although Murphy (1983b) suggested the possibility of a northern seaway connecting the Sea of Cortés and the inundated Los Angeles Basin (fig. 8.9), no geological evidence exists for this proposal (Boehm 1984, 1987). Around 3 million years ago, the Cape Region appeared as two islands (fig. 8.10). Upton and Murphy (1997), in the absence of geological evidence, proposed the occurrence of a
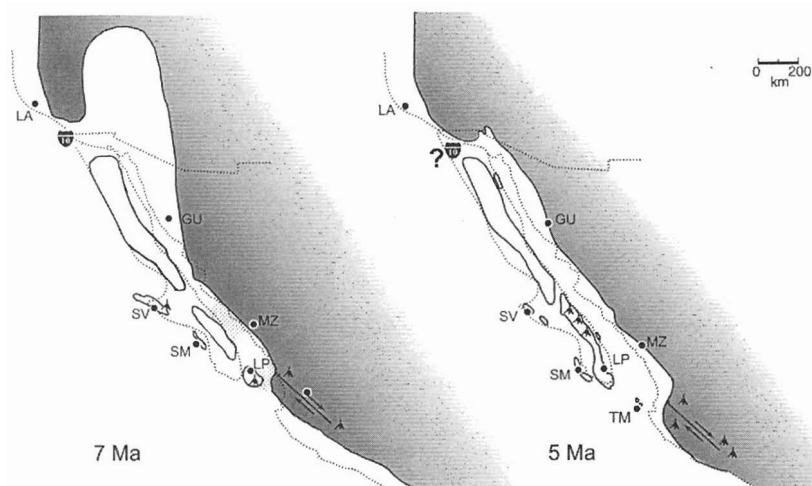

Figure 8.9 Paleographic reconstructions of western North America for the late Miocene (7 Ma) and the Miocene-Pliocene boundary (5 Ma). The stippled areas symbolize the temporary formation of the Sea of Cortés. A proposed seaway occurs at San Gorgonio Pass (Interstate Highway 10), and in the area of the mid-peninsula. Present locations of LA = Los Angeles; GU = Guaymas; SV = Sierra Vizcaíno; SM = Islas Santa Margarita and Magdalena; MZ = Mazatlán; LP = La Paz; TM = Islas Las Tres Marías.

Figure 8.10 Paleographic reconstructions of western North America for the Early Pliocene (4 Ma) and the Late-Pliocene boundary (3 Ma). The mid-peninsula Vizcaíno Seaway temporarily reformed. Present locations of LA = Los Angeles; GU = Guaymas; SV = Sierra Vizcaíno; SM = Islas Santa Margarita and Magdalena; MZ = Maztalán; LP = La Paz; TM = Islas Las Tres Marías.
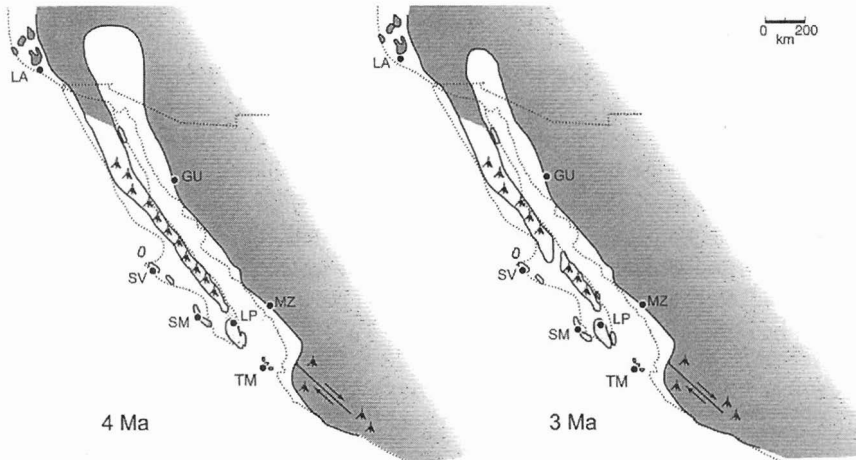
mid-peninsular seaway sometime before 1 million years ago, which we refer to as the Vizcaíno Seaway. Identification of volcanic intrusions in a marine environment near Santa Rosalia (Ochoa-Landin 1998) around 3 million years ago now support the prediction (fig. 8.10), but at an earlier date. Earlier deposits also suggest that the seaway was formed more than one time (figs. 8.9, 8.10).

The late Pliocene to Pleistocene saw the formation of the peninsula as it exists today, including environmental conditions (Morafka 1977). However, the deserts as we know them today did not develop until the end of the last interglacial (Axelrod 1979; Van Devender 1990). By the early Pleistocene, the Cape Island rejoined the peninsula, and the Vizcaíno Seaway dried up. The Peninsular Ranges attained their present great heights. During times of maximum glaciation, islands separated by a depth of less than 150 m were connected to the peninsula, and many embayments, such as Bahía de los Angeles and Bahía Concepción, disappeared.

The accumulated cladogenic patterns can be associated with tectonic events and the paleostratigraphy of the peninsula. Previously, both Murphy (1983b) and Grismer (1994b) associated species with various geomorphic events. Some taxa exhibited cladogenic patterns that fit the previous groups, but not others. The cladograms (e.g., figs. 8.2–8.7) depicted common geographic patterns and thus likely depict the sequence of vicariance events for taxa that share a common speciation history. By associating the cladograms with the tectonic history, three primary faunal associations can be hypothesized.

Transgulfian Vicariance

When the Cape Region and the Peninsular Ranges of Baja California separated from mainland Mexico about 5–12 million years ago, they likely isolated a fauna represen-

tative of mainland Mexico. Some cladogenic patterns derive peninsular species from tropical ancestors, and these are among the oldest representatives in the region. Extant representative taxa include the Baja California rattlesnake, *Crotalus enyo*, sister species to the Neotropical rattlesnake, *C. durissus*. The orangethroat whiptail lizard, *Cnemidophorus hyperythrus*, has the mainland sister species *C. deppei* and *C. guttatus*. The combined data for the genus *Sator* suggest that it was isolated from its sister taxa, *Sceloporus chrysostictus, S. variabilis, S. parvus, S. couchii, S. cozumelae, S. utiformis, S. siniferus*, and *S. squamosus*. The two-legged amphisbaenid, *Bipes biporus*, has two sister species on the mainland, *B. tridactylum* and *B. canaliculatus* (Kim et al. 1976; Papenfuss 1982). It is also possible that the lizards of the genera *Sauromalus* and *Petrosaurus* also had their origins at this time, as might have other species.

The East–West Split

A widespread northern fauna apparently occurred across subaerial regions of the southern United States, as exemplified today by species in the genera *Uta, Crotaphytus, Coleonyx*, and *Pituophis*. These east–west assemblages likely predated the formation of the permanent peninsula. Their subdivision formed two clades, one restricted to the region around the Sea of Cortés, and the other farther east in the Chihuahuan Desert and Mexican Plateau. The mesic, high mountain pass at the Continental Divide is partially responsible for the isolation of these faunal elements during the Pliocene (Morafka 1977). The separation of the east–west assemblage would be further reinforced, if not caused, by the barrier posed by San Gorgonio Pass sometime before 3 million years ago (Murphy 1983b).

The Peninsular Archipelago

Aguirre et al. (1999) summarized early evidence that the peninsula was an island archipelago at least 1 million years ago. Aguirre et al., who coined the term "peninsular archipelago," built on the evidence and hypotheses of Murphy (1983b) and Upton and Murphy (1997).

Unambiguous cladogenic patterns show that peninsular species became isolated from those farther north and east. Upton and Murphy (1997) and Hollingsworth (1999) showed that peninsular populations of side-blotched lizards form a distinct group. Rodriguez-Robles et al. (1999) found a significant mtDNA discontinuity in the California mountain kingsnake, *Lampropeltis zonata*. One group occurs on the northern Peninsular Ranges up to the San Gorgonio Pass, and another clade occurs farther north. The chuckwallas show an identical pattern of relationships: one clade is restricted to the Peninsular Ranges and another north and east (appendix 8.1).

Many species of reptiles have distributions on the Peninsular Ranges up to San Gorgonio, such as leaf-toed geckos (*Phyllodactylus*), rock lizards (*Petrosaurus*), and granite spiny lizards (*Sceloporus orcutti*). Consequently, Murphy (1983b) proposed the occurrence of the "San Gorgonio Filter Barrier" because these animals did not occur farther north. However, this proposal of a narrow mesic region fails to explain a generalized pattern for the isolation of both mesophilic and xerophilic species, as well as the restriction of many species to the Peninsular Ranges. If the San Gorgonio

region were cool and moist (Axelrod 1937, 1950; Frick 1933), then a strong genetic discordance would not be expected in the California mountain kingsnakes (*Lampropeltis zonata*) and western skinks (*Eumeces skiltonianus*). And if the region were more xeric, then the same break would not be expected in side-blotched lizards, collared lizards (McGuire 1996; Murphy and Doyle 1998), and desert spiny lizards (*Sceloporus magister-zosteromus* complex). Many of these species on the Peninsular Ranges are not restricted to desert regions, and they coexist with other species associated with the head of the Sea of Cortés, such as fringe-toed lizards. Consequently, there must have been a universal barrier to dispersion and not just a filter. The most plausible explanation for the strong genetic patterns appears to be yet another temporary seaway at San Gorgonio Pass, appropriately termed the "San Gorgonio Seaway."

The peninsular archipelago developed. While the Vizcaíno Seaway was inundated, southern portions of the peninsula likely became more or less intact. Cladogenic patterns suggest that species dispersed along the developing Peninsular Ranges. Subsequently, the Vizcaíno Seaway and flooding at the Isthmus of La Paz again divided the peninsula. Both extensive genetic data and geological investigations now support the presence of at least these two seaways. The Vizcaíno Seaway formed the genetic discordance observed in both avian and nonavian reptiles. The genetic distinctiveness of the Cape Region whiptail lizard, *Cnemidophorus tigris maximus*, and the San Lucan rock lizard, *Petrosaurus thalassinus*, likely resulted from this more recent peninsular connection and subsequent disruption. It is expected that cladogenic patterns will be identical in other territorial species such as granite spiny lizards (*Sceloporus orcutti* complex), desert spiny lizards (*S. zosteromus* complex), and leaf-toed geckos (*Phyllodactylus xanti* complex) once data have been accumulated and analyzed.

After the formation of the Vizcaíno Seaway, the peninsula rejoined the mainland, forming San Gorgonio Pass. When the Sea of Cortés receded from its northern extension, newly developed habitats were invaded. Peninsular archipelagian species such as side-blotched lizards, *Uta stansburiana*, dispersed around the head of the Sea of Cortés and southward into Sonora, and western whiptail lizards, *Cnemidophorus tigris*, dispersed in the opposite direction. Species associated with the Colorado River, including species such as fringe-toed lizards, *Uma*, and Colorado River toads, *Bufo alvarius*, dispersed southward into the newly created delta.

During the Pleistocene, the peninsular islands reunified, forming the greatest amount of connected landmass in the history of the peninsula. Interestingly, the orangethroat whiptail, *Cnemidophorus hyperythrus*, appears to have originated on a peninsular island north of the Cape Region, likely in the vicinity of Islas Carmen and Danzante (Radtkey et al. 1997). These islands are separated by a channel depth of only 26 m (Gastil et al. 1983). After reunification of the peninsula, this species quickly dispersed northward. Additional evidence of a peninsular archipelago is provided by other taxa. Neither side-blotched lizards (Upton and Murphy 1997; Hollingsworth 1999), nor chuckwallas (appendix 8.1) from Carmen and Danzante cluster with nearby peninsular populations. Moreover, these insular populations cluster together, requiring either one additional peninsular island in the archipelago, or that these islands were joined only to each other. Given the reported ocean-channel depths (Gastil et al. 1983) and that only 10,000–15,000 years have elapsed since the last major continental glaciation, we believe the former explanation is more likely.

Evolution of the Insular Reptiles

The islands in the Sea of Cortés have divergent geological histories. Most are land-bridge islands, and thus the tectonic origin of these islands is likely inconsequential in terms of the composition of the herpetofauna. However, the tectonic history of the remaining deep-water islands is very important. Whereas deep-water islands of continental origin likely carried a complement of mainland faunal and floral elements, islands of oceanic origin must have been colonized by overwater dispersal, sometimes facilitated by humans.

Alternative Models

Few have tried to explain the origin and evolution of the insular herpetofauna. Schmidt (1922) considered the origins of the peninsular species and briefly discussed the problems of the insular populations. Savage (1960) noted that the insular herpeto-
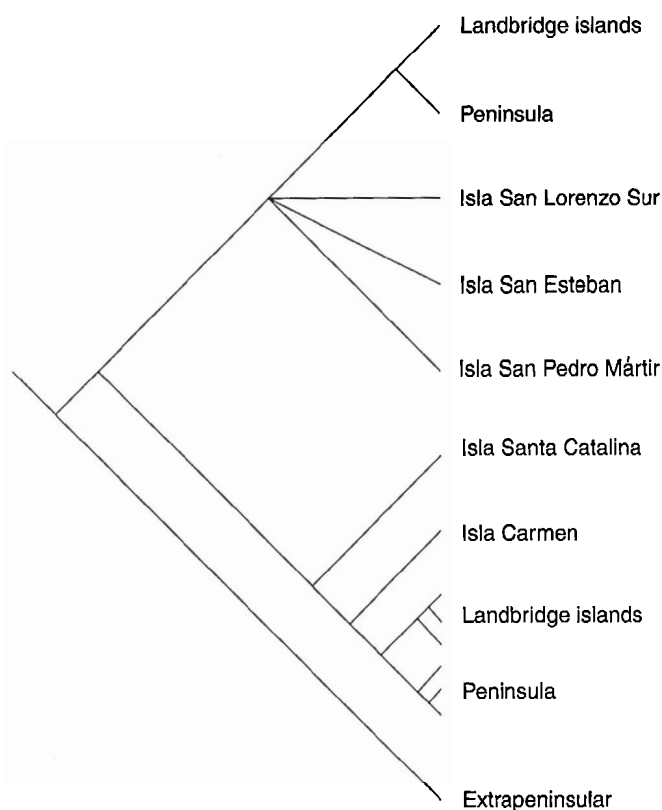

Figure 8.11   Reduced area cladogram for side-blotched lizards, *Uta*, on the islands in the Sea of Cortés based on Upton and Murphy (1997). Unsupported nodes have been collapsed. Although associations at unsupported nodes provide the best explanation of the data, they are considered tentative phylogenetic hypotheses that may change as data accumulate.

fauna formed interesting patterns. Soulé and Sloan (1966) first noted the biogeographic significance of landbridge islands and first considered the correlation between species numbers and island areas. Other treatments dealt with the evolution of particular groups of species (e.g., Robinson 1973; Smith and Tanner 1974). Murphy (1975, 1983a,b) provided the first synthetic reviews of the peninsular and insular herpetofauna. Grismer (1994c) updated Murphy's review of the insular fauna and speculated on alternative origins for a few insular species.

MacArthur and Wilson (1963, 1967) provided a monumental framework for interpreting the distributions of organisms on islands, particularly for oceanic islands. Their colonization and extinction model was applied to the fauna on the islands in the Sea of Cortés by Soulé and Sloan (1966), Case (1983, 1975), and Wilcox (1978, 1980). In contrast, Murphy (1983a) provided an alternative, deterministic argument for the evolution of the insular herpetofauna. Based on genetic-distance coefficients, patterns of species composition, and tectonic development, Murphy proposed that most populations on continental islands were there before isolation. The absence of particular species on these islands resulted from the absence of needed habitat. In contrast, the herpetofauna on oceanic islands (i.e., those islands that never had a terrestrial connection) resulted from somewhat random colonization. Grismer (1994c) haphazardly used phenetic anatomical studies, some of which predated phylogenetic theory and methodology, to conjecture origins of species on the islands. He concluded that all deep-water islands except for Isla San Pedro Mártir contained a mixture of peninsular and mainland species and therefore that these species assemblages were neither completely deterministic, nor generally reflective of colonization and extinction.

All of the above treatments are based on theoretical models and unsubstantiated assumptions; none is based on sound phylogenetic investigations or at the required fine-grained, population level. To demonstrate the insular origin of each species, precise data are required, and these must be evaluated within a phylogenetic framework.

New Databases

DNA Sequences

1. Side-blotched lizards, genus *Uta*. The phylogeny resolved by Upton and Murphy (1997) is shown in figure 8.11. Lizards on the northern deep-water islands in the Gulf of California are the sister group to peninsular and landbridge island populations, although this position is very tenuous. The side-blotched lizard from Isla Santa Catalina, *Uta squamata*, is the sister species to the southern peninsular clade, followed by the population from Isla Danzante. Hollingsworth (1999) observed nearly the same set of relationships as found or predicted by Upton and Murphy. Landbridge island populations generally had a nearest sister species relationship with a nearby mainland population, including *Uta nolascensis* from San Pedro Nolasco, and the three endemic subspecies on the northernmost islands in the Sea of Cortés (Upton and Murphy 1997). Hollingsworth also found that lizards from Carmen and Danzante formed a distinctive clade, and, like Upton and Murphy, observed that lizards on these landbridge islands did not share a sister relationship with nearby peninsular populations.

2. Chuckwallas, genus *Sauromalus*. Petren and Case (1997; app. 8.1) observed that the large chuckwallas from the northern Gulf of California formed the sister group to the northern peninsular populations. The Santa Catalina Island chuckwalla branched off from within the southern peninsular clade, and lizards from Danzante, Carmen, and Monserrat formed a separate clade (app. 8.1). The two giant chuckwallas were sister taxa, and their nearest sister group was the northern peninsular population. Populations of spiny chuckwallas from Isla San Lorenzo Sur branch off from within a clade from Isla Ángel de la Guarda (app. 8.1).

3. Western whiptail lizards, *Cnemidophorus tigris*. Radtkey et al. (1997) found five major clades: (1) northern Sonora plus northern Baja California and the deep-water islands of San Esteban, San Pedro Mártir, San Lorenzo Norte, and Salsipuedes; (2) Santa Catalina; (3) Baja California (Norte) plus associated landbridge islands, and Ángel de la Guarda and Partida Norte; (4) Baja California Sur and associated land-bridge islands exclusive of the Cape Region; and (5) the Cape Region and associated landbridge islands Espíritu Santo and San Francisco. It is surprising that the population from Santa Catalina branched off as the sister taxon to the clade 1. However, reanalysis of these data including all potentially cladistically informative sites plus sites with missing data shows that the Santa Catalina population forms the sister group to all other western whiptail lizards (fig. 8.12). This reevaluation forms a far more plausible explanation of relationships.

4. Orangethroat whiptail lizards, *Cnemidophorus hyperythrus*. Radtkey et al. (1997) found that insular populations were derived in a south-to-north sequence of cladogenic events. The populations that rooted at the base of the tree occurred sequentially on Islas Carmen and Cerralvo. Populations on Islas San Francisco and San José formed the next clade, followed by Isla Monserrat, then a clade containing La Paz and nearby Isla Espíritu Santo, followed sequentially by Isla Coronados, Isla San Marcos, and finally northern peninsular populations. This pattern indicates a recent northern dispersion, one that occurred on the peninsula after the disappearance of the Vizcaíno Seaway, and possibly after the last glacial event (fig. 8.13).

5. Rattlesnakes, *Crotalus*. Murphy et al. (in press) gathered nucleotide base pair data from 2945 sites from 5 mtDNA genes for all but 2 of the 32 species of rattlesnakes. Within the diamondback group, they found that the Santa Catalina Island rattlesnake, *C. catalinensis*, was the sister taxon of *C. ruber*, as proposed by Murphy and Crabtree (1985). The mtDNA sequence cladogram placed the Tortuga rattlesnake, *C. tortugensis*, as a sister taxon to an undescribed species of *Crotalus* allied with *C. atrox*, from Santa Cruz. In turn, these two are the sister groups to the western diamondback rattlesnake from southern California and mainland Mexico (fig. 8.14), although the association is tenuous.

6. Mammalian cladograms are given in chapter 12.

Island Records

An updated checklist for the islands in the Sea of Cortés was recently published (Grismer 1999a). These records, plus two additional records, have been included in appendixes 8.2–8.4 for sake of completeness. However, much of the alpha taxonomy differs from that of Grismer (1999a) in order to reflect genealogical relationships.

Majority Rule

- 100
- 74 San Pedro la Presa / San Ignacio
- 94 Isla Carmen
- Isla San Marcos
- 60 / 62 Isla Espíritu Santo / Isla San Francisco / La Paz
- 94 Punta Abreojos / El Arco / Isla Cedros
- Isla Partida Norte / Isla Ángel de la Guarda
- Isla Tiburon / Cataviña
- 89 Bahia de los Angeles / Isla Smith
- Peñasco
- 97 Isla Salsipuedes / Isla San Lorenzo Norte
- 76 Isla San Pedro Mártir
- Isla San Esteban
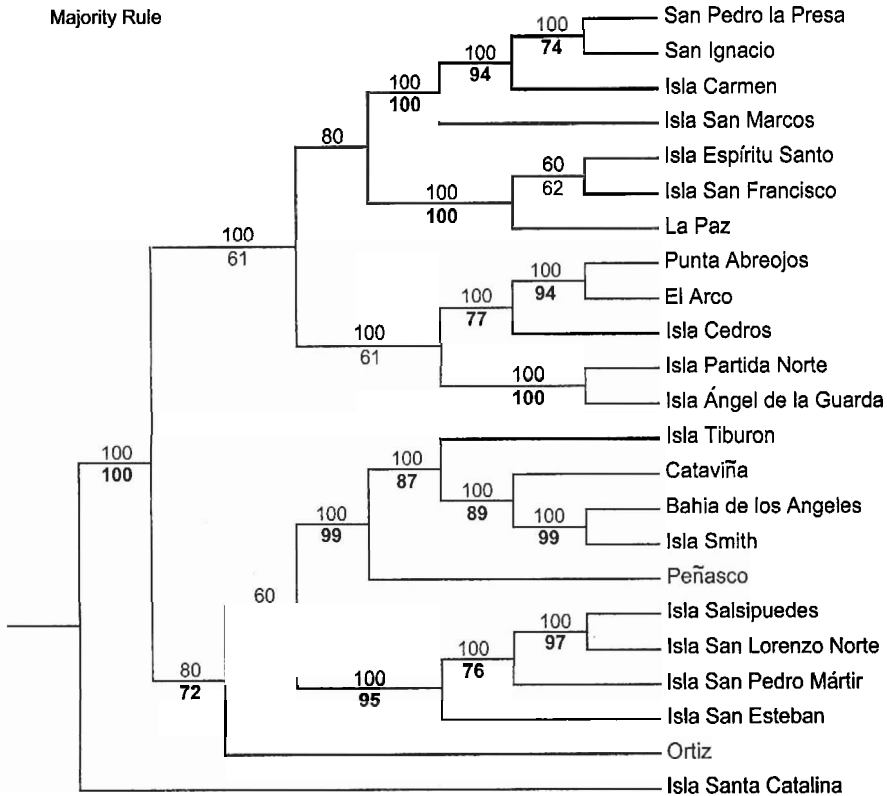- Ortiz
- Isla Santa Catalina

Figure 8.12 Revised cladogram for western whiptail lizards, *Cnemidophorus tigris*, on the islands in the Sea of Cortés based on an unweighted maximum parsimony evaluation of all available mtDNA sequence data, including those with missing information. Numbers above the lines denote frequency of the nodes among multiple most parsimonious trees. Bootstrap proportions are given below the lines; values >70% are in bold.

Interpreting the Cladograms

Most deep-water islands in the Sea of Cortés had a continental origin (chap. 2). The key to whether or not preference is given to a model of colonization and extinction, deterministic history, or a mixture of the two lies in both cladogenic sequences and patterns of species composition. If a deterministic history were responsible for the patterns, then we would expect to observe similar cladogenic patterns for multiple species and a faunal composition that reflects nested groups of species. For example, if the fauna of Isla Santa Catalina was already present when the island was formed, then the cladogenic patterns of relationships should be equivalent for all taxa so long as no recolonization followed extirpation. Using side-blotched lizards as a baseline reference, we would expect all other taxa to have a phylogeny similar to that in figure 8.11, if they had a common origin and equivalent territoriality. The determin-
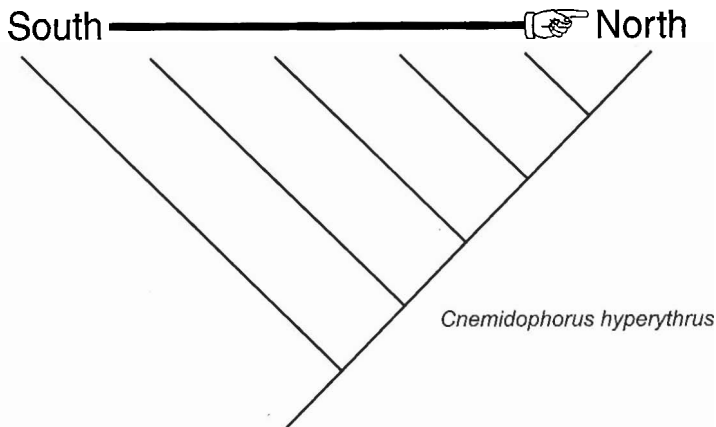
Figure 8.13 Reduced area cladogram for orangethroat whiptail lizards, *Cnemidophorus hyperythrus* group, on the peninsula of Baja California.

istic scenario is rejected by a cladogram depicting alternative relationships, such as a sister relationship with populations in mainland Mexico, with Baja California (Norte), or nested inside a group of landbridge islands (fig. 8.15).

Interpreting Patterns of Species Distributions

The theory of island biogeography (MacArthur and Wilson 1963, 1967) accounts for insular faunas by colonization and extinction, whereas a paleogeographic scenario explains the occurrences from the perspective of the history of the peninsula. Thus, whereas the island biogeography theory has a large stochastic component, the paleogeographic scenario predicts that the faunal elements arrive all at once and that extir-
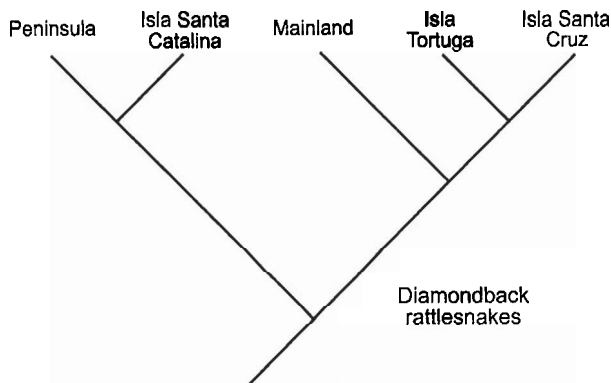

Figure 8.14 Reduced area cladogram for rattlesnakes, *Crotalus*, on the islands in the Sea of Cortés based on 2945 bp of mtDNA sequence data (Murphy et al. in press).
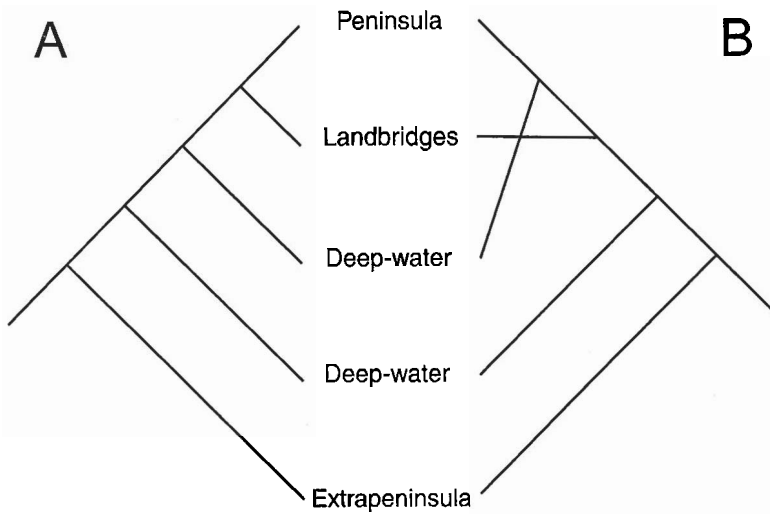
Figure 8.15 (A) Presumed tectonic history of some islands. (B) Hypothetical reduced area cladogram for insular organisms. Crossed lines show how noncorroboration of the tectonic data would look if the origins owed to dispersal or misclassification of islands based on channel depth (age).

pations are deterministic (**Murphy 1983**). If a mixture of the two extreme explanations is responsible for the origin of the faunas, then we still predict a stochastic composition for colonization, although extirpation might remain deterministic. Cladogenic patterns could serve to arbitrate among the scenarios, once additional data sets have been compiled.

A New Scenario?

The new scenario for the evolution of the insular herpetofauna might derive from our reexamination the evolution of the peninsular herpetofauna. The islands can be grouped into those having a continental origin and oceanic islands that were never connected to another landmass. The oceanic islands are Islas Tortuga, Rasa, and Monserrat. Three other islands may have had an oceanic origin: Islas Ángel de la Guarda, San Esteban, and San Pedro Mártir. Given the composition of the herpetofauna on Isla Ángel de la Guarda, a terrestrial connection is strongly indicated. The remaining islands are thought to have had a continental origin or to have been connected to a larger faunal source during the Pleistocene (chap. 2).

The Oceanic Islands and Overwater Colonization

Many species of reptiles colonize by overwater dispersion. Table 8.1 summarizes the distributions of taxa on oceanic islands in the region, and one island thought to be oceanic, Isla Monserrat. Upton and Murphy (1997) proposed that humans recently introduced the population of side-blotched lizards on Isla La Rasa, a Holocene volca

Table 8.1 Successful, possible, and unsubstantiated overwater colonists on islands in the Sea of Cortés

Taxon	Oceanic Island Occurrence	No. of Gulf Islands on Which Taxa Occur
Successful Overwater Colonists		
1. *Phyllodactylus*	La Rasa	42
2. *Sceloporus orcutti* (*sensu lato*)	Tortuga	11
3. *Uta*	Tortuga	
	La Rasa[a]	49
	Revillagigedo	
4. *Hypsiglena*	Tortuga	18
5. *Lampropeltis getula*	Tortuga	12
6. *Crotalus tortugensis* (=*atrox*)	Tortuga	8
7. *Masticophis* (*flagellum* group)	Revillagigedo	11
Possible Overwater Colonists		
1. *Dipsosaurus dorsalis*	Monserrat	12
2. *Sauromalus*[a]	Monserrat	34
3. *Sceloporus* (*zosteromus* group)	Monserrat	6
4. *Cnemidophorus hyperythrus*	Monserrat	8
5. *Chilomeniscus cinctus*	Monserrat	9
6. *Phyllorhynchus decurtatus*	Monserrat	5
7. *Crotalus mitchellii*	Monserrat	11
8. *Crotalus ruber*	Monserrat	8
Unsubstantiated Overwater Colonists		
1. *Callisaurus draconoides*		15
2. *Crotaphytus insularis*		2
3. *Ctenosaura hemilopha*[a]		4
4. *Petrosaurus*		6
5. *Urosaurus microscutatus*		21
6. *Coleonyx variegatus*		10
7. *Cnemidophorus* (*tigris* group)		20
8. *Leptotyphlops humilis*		5
9. *Charina trivirgata*		4
10. *Bogertophis rosalea*		1
11. *Eridiphas slevini*		4
12. *Rhinocheilus ethridgei*[b]		1
13. *Salvadora hexalepis*		3
14. *Sonora mosaueri*		2
15. *Tantilla planiceps*		1
16. *Trimorphodon biscutatus*		6
17. *Crotalus enyo*		9
18. *Masticophis* (*lateralis* group)		3

[a]Possible human-facilitated dispersal.
[b]Not a potential colonizer of Tortuga and Monserrat.

nic island. There are no data on the Rasa Island leaf-toed gecko, *Phyllodactylus tinkeli*, to help determine whether its occurrence may be attributable to humans.

Isla Tortuga, an early Pleistocene volcanic island, contains a mix of species, all of peninsular origin except one from mainland Mexico, the Tortuga Island rattlesnake, *Crotalus tortugensis*. However, mtDNA sequence data associate the Tortuga Island rattlesnake with that from Isla Santa Cruz and very weakly with *C. atrox* from the

mainland (fig. 8.14). Thus, most of the fauna of Isla Tortuga is associated with the nearby peninsula and not with distant mainland Mexico.

Among oceanic islands, Isla Monserrat is the largest and likely among the oldest (chap. 2). Its fauna has of a variety of nonavian reptiles (table 8.1), and apparently all of these have been successful overwater colonists. It is interesting that the chuckwallas from Monserrat were apparently derived from those on Isla Carmen, and not from either Danzante or Santa Catalina (app. 8.1), both of which are geographically closer to Monserrat. Ocean currents may have more influence than proximity in determining distributions.

About 20% of the nonavian reptilian groups have colonized by overwater dispersion, and an additional 20% likely did the same. We have no data on the colonizing ability of the remaining 60% of species groups; we cannot say if they did, could or will colonize by overwater dispersal. Although many species can colonize, one question remains. How frequently does this occur without human assistance?

Ángel de la Guarda Block

The island group with the best documented tectonic origin is the Ángel de la Guarda island chain in the northern part of the Sea of Cortés. The major islands include Islas Ángel de la Guarda, Partida Norte, Salsipuedes, San Lorenzo Norte, and San Lorenzo Sur. Satellite landbridge islands also occur in association with the large islands. Islas San Lorenzo Norte and San Lorenzo Sur are landbridge islands with respect to each other, and the herpetofaunal distributions suggest that Isla Salsipuedes also had a landbridge connection with them. All other large islands appear to have remained isolated after their formation, including during times of maximum Pleistocene glaciation. Figure 8.16 depicts the presumed tectonic history of the island group, which began its isolation about 1 million years ago (Moore 1973) from the peninsula (Phillips 1966). The side-blotched lizards from this group of islands form two distinctive clades, one associated with Ángel de la Guarda (an unnamed species; Upton and Murphy 1997) and the other, *Uta antiqua*, on Salsipuedes, San Lorenzo Norte, and San Lorenzo Sur. Western whiptail lizards also occur on these islands, and the cladograms show two distinctive groupings, although the southern group appears to have had its origin from Sonora. In contrast, the spiny chuckwallas, *Sauromalus hispidus*, on Isla San Lorenzo Sur branch off within the clade of chuckwallas from Isla Ángel de la Guarda indicating a recent colonization. Because Seri Indians moved populations of these large, edible lizards among islands in the Sea of Cortés (Felger and Moser 1985), it seems likely that the species was introduced from Ángel de la Guarda to the smaller Isla San Lorenzo Sur. Unfortunately, we do not know if chuckwallas originally occupied Isla San Lorenzo Sur and neighboring islands before this introduction. However, this seems likely, and, if true, then the original species likely became extinct or was genetically swamped out by introduced animals.

At least one species of rattlesnake may have dispersed over water to Isla Ángel de la Guarda. On the mainland, the red diamond rattlesnake, *Crotalus ruber*, is a much larger species than the speckled rattlesnake, *C. mitchellii*. However, on Isla Ángel de la Guarda, red diamond rattlesnakes are small, and speckled rattlesnakes are large. Insular populations of snakes generally become smaller on islands (Soulé and Sloan 1966). However, Cody (1974) and Case (1978b, 1983 chap. 9) proposed that the
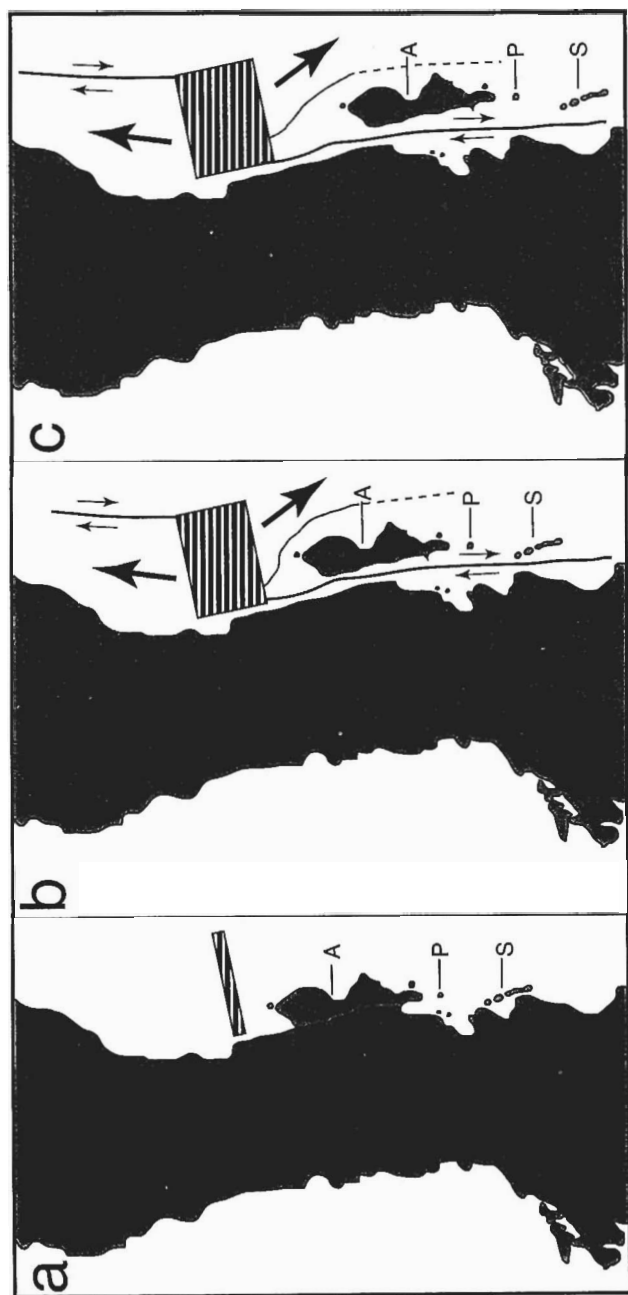
Figure 8.16 Paleogeographic reconstruction showing the formation of the Ángel de la Guarda island chain. (a) about 1 million years B.P. the island chain broke away from the peninsula. Diagonal lines indicate the formation of the Delfín Basin (= spreading center). (b) Reconstruction for about 0.5 million years ago. Arrows indicate relative plate movements. (c) Reconstruction of the present. Islands are indicated as follows: A = Ángel de la Guarda; P = Partida Norte; S = San Lorenzo Norte and San Lorenzo Sur.

speckled rattlesnakes became large on Ángel de la Guarda in order to feed on giant chuckwallas, and later the red diamond rattlesnake arrived, and to avoid competition, dwarfed. This explanation for the differences in body length is extremely interesting, particularly for studies of competition, but it remains to be tested from the perspective of cladograms.

The leaf-toed gecko on Isla Partida Norte, *Phyllodactylus partidus*, is an apparent sister species of the Sonoran gecko *P. homolepidurus*. Given that the species does not occur on other islands in the Sea of Cortés, it is possible that Seri Indians introduced the species. However, cladogenic data are required to confirm the species' genealogical relationships. In terms of Ángel de la Guarda and its associated islands, all available evidence points to a peninsular origin for the herpetofauna, including the origin of the giant chuckwallas. No cladogenic data suggest otherwise. In contrast, the more southern group of islands on the block appears to have a mixture of species. Whereas side-blotched lizards came from the peninsula and chuckwallas from Isla Ángel de la Guarda, the western whiptails appear to have their nearest sisters on other midriff islands, and then in Sonora (fig. 8.12; Radtkey et al. 1997). Additional data, both additional sequences from different genes and from more species, are required to clarify the history of the herpetofauna on this island group.

San Esteban

The tectonic history of San Esteban is not detailed, although it is thought to be of continental origin (Gastil et al. 1983; chap. 2, this volume). The island contains a mixture of peninsular and mainland species. The endemic piebald chuckwalla, *Sauromalus varius* (shown in fig. 16.1), had an origin from the peninsula (app. 8.1). Upton and Murphy (1997) and Hollingsworth (1999) found that San Esteban side-blotched lizards were the sister group of a large clade containing northern Baja Californian populations. The taxonomy of leaf-toed geckos (Dixon 1964; Murphy 1983b) suggests a peninsular origin. Spiny tail iguanas appear to have been introduced onto San Esteban by the Seri Indians who once lived on the island (Felger and Moser 1985); their presence is historically uninformative. The evolutionary relationships of western whiptail lizards are problematic. Apparently, they had an origin from mainland Sonora (fig. 8.12). They form the sister group to other insular populations, including those on deep-water Islas Salsipuedes, San Lorenzo Norte, and San Lorenzo Sur. Given the apparent introduction of the chuckwallas to Isla San Lorenzo Norte, it is also possible that western whiptails were also introduced, accidentally or intentionally. Finally, the blacktail rattlesnake, *Crotalus molossus*, appears to have arrived by overwater dispersal from Sonora. Nevertheless, given that the majority of the fauna of the island was derived from the peninsula, if the island had a continental origin it should have been with the peninsula.

San Pedro Mártir

This probably continental island had its origin from mainland Mexico (Henyey & Bischoff 1973; Bischoff & Henyey 1974). All nonavian reptilian species on this island are also thought to have their derivation from the mainland, and there is no apparent mixing of origins with the peninsula (Murphy 1983a; Grismer 1994a).

Santa Catalina

This continental island had an origin from the peninsula, but its age is unknown (Gastil et al. 1983). Based on tectonics, Murphy (1983a) proposed that the herpeto-fauna of this island was entirely representative of the peninsula. Grismer (1994c) challenged this assumption for both the side-blotched lizards and western whiptail lizards. The Santa Catalina Island side-blotched lizard, *Uta squamata,* belongs to the southern peninsular clade (Upton and Murphy 1997; Hollingsworth 1999). For the western whiptail lizards, the tree presented by Radtkey et al. (1997) conflicted with Murphy's proposal. However, our total evidence reevaluation of the sequence data does not conflict (fig. 8.12). Furthermore, the association of the Santa Catalina Island whiptail lizard at the base of the clade is not supported by significantly covaried character states (Fu and Murphy 1999). Some randomizations of the data yield a more parsimonious solution than the unrandomized data. We are confident that additional sequence data will clarify the conundrum in favor of a southern peninsular origin. The only other species thought to have had a mainland origin is the Santa Catalina Island kingsnake, *Lampropeltis catalinensis* (Blaney 1977). However, given the absence of a phylogenetic analysis Blaney's study does not provide evidence for a mixture of faunas.

Santa Cruz

This is one of the most biologically enigmatic islands in the Sea of Cortés, owing to the presence of the phrynosomatine lizard *Sator angustus,* and the western diamond-back rattlesnake, *Crotalus atrox.* Boulder-dwelling *Sator* apparently exclude all other phrynosomatine lizards from occurring sympatrically through competitive exclusion and aggressive behavior (Case 1983), except for the sand-dwelling zebra tail lizard, *Callisaurus draconoides* (on Isla Cerralvo). This is also evident from the absence of other phrynosomatine lizards on landbridge Isla San Diego. The occurrence of *Sator* on deep-water Isla Santa Cruz and landbridge Isla San Diego has been attributed to both plate tectonics (Murphy 1975, 1983a,b) and extinction of a once widespread southern peninsular population (Grismer 1994c) leaving insular relicts. The peninsular extinction scenario seems unlikely given that other phrynosomatines apparently cannot coexist with *Sator* (chap. 9), and many of these species have had a long presence on the southern peninsula as evidenced by cladogenic patterns. The vicariant origin is also problematic. There are two insular species in the genus *Sator,* and they do not occur on nearby islands: one occurs on Islas San Diego and Santa Cruz, and the other on Isla Cerralvo, and yet they are sister species. They could have been derived from a single species of *Sator* on mainland Mexico, which has since become extinct. Any number of stories can be told but, at present, they are just stories even though we believe overwater colonization from one island to another remains the least problem-atic explanation. This conundrum may never have an irrefutable explanation.

The species of rattlesnake on Santa Cruz also has an enigmatic distribution. If its occurrence results from overwater dispersal from mainland Mexico, then more than 140 km of swimming or rafting is required. The distance is much greater if it dispersed from Isla Tortuga, or vice versa. Alternatively, if it was derived from a vicariant event

(Murphy 1983a), then its relationships should lay with the peninsula and not mainland Mexico. mtDNA sequence data (Murphy et al. in press) are equivocal as to whether the insular populations *C. atrox* are the sister clade to mainland *C. atrox* or the sister group of the peninsular *ruber* group. Thus, the origin of the herpetofauna remains enigmatic for Santa Cruz.

Cerralvo

The herpetofauna of Cerralvo appears to have a close relationship with the peninsula, an association that even includes two species of amphibians (app. 8.3). However, there are two exceptions. The lizard genus *Sator* is known from this island, and the problem of its occurrence was previously noted. The other enigmatic species is the Cerralvo longnose snake, *Rhinocheilus etheridgei*. Grismer (1994c) believes that it is a recent overwater colonist from mainland Mexico. Cerralvo may have formed 2–5 million years ago (Gastil et al. 1983), which coincides with the Cape Region breaking away from mainland Mexico (chap. 2). If Cerralvo is 5 million years old, then it could have carried nearby mainland representatives as it broke away from mainland Mexico. However, a more recent age of island formation seems likely given the extent of shared faunal elements, and the likelihood that the two amphibians did not arrive by overwater colonization, at least without human assistance. Another alternative explanation is that the southern peninsular population of longnose snake went extinct after the formation of the Vizcaíno Seaway was formed; this can be tested by cladogenic patterns.

Landbridge Islands

With only one exception, the landbridge islands in the Sea of Cortés have a subset of reptiles from the nearest larger landmass, be it the peninsula of Baja California, mainland Mexico, or a larger island. The exception is the occurrence of the leaf-toed gecko, *Phyllodactylus nocticolus*, on Isla Tiburón. If the current taxonomy reflects genealogical relationships, then the population must have arrived by island hopping. Given travel among the islands by Seri Indians, it seems likely that an accidental introduction occurred. This is being tested using a phylogenetic analysis of sequence data.

In terms of cladogenic patterns, all landbridge islands appear to have their closest genetic relationships with the nearby mainland populations, except for those on Carmen and Danzante. On these islands, the orangethroat whiptail lizard, Slevin's chuckwalla (*Sauromalus slevini*), and side-blotched lizard (*Uta*) do not have nearest sister relationships with adjacent peninsular populations. Furthermore, the highly vagile, nonterritorial orangethroat whiptail lizard, *Cnemidophorus hyperythrus*, appears to have undergone a recent, rapid northward dispersal that erased the nearby island–peninsula historical patterns (fig. 8.13). This pattern may owe to either a range shift or extinction of the former peninsular population, or to the peninsular genotype being swamped out by that of the insular-evolved lizards. In this case, as in several others noted above, we can only speculate about the possible explanations for the patterns owing to the absence of data and cladistic analyses.

Paleogeography or Equilibrium?

Colonization

If colonization were stochastic, we would expect to see divergent patterns of phylogenetic relationships expressed among cladograms. With few exceptions, the available cladograms are highly congruent, and we must assume that this congruence is due to identical origins. A few insular herpetofaunas are undoubtedly a mix of mainland and peninsular elements (apps. 8.2–8.4). However, many of the problematic occurrences may be due to human introductions and not to the animals arriving via overwater dispersal. Most insular occurrences appear to reflect a historical land connection. Consequently, colonization on the Sea of Cortés islands appears to be largely deterministic and not stochastic as proposed early in the development of equilibrium theory (Case 1983, 1975; Wilcox 1978, 1980). If colonization is not stochastic except for some occurrences on the three oceanic islands, then is extinction stochastic as predicted by island biogeographic theory (MacArthur and Wilson 1963, 1967)?

Patterns of Extinction

Murphy (1983a) reviewed patterns of extinction on islands in the Sea of Cortés and concluded that they were deterministic. His findings were based on a series of assumptions about the origins of the insular forms. Some of these assumptions have changed. Therefore, we briefly review the extinctions in light of new information.

Stochastic patterns of extinction should appear as random subsets of faunas on islands. In contrast, deterministic patterns of extinction should appear as nested subsets of co-occurring species. No information about extinction can be gained from evaluating oceanic islands because, in the absence of fossil data, it is impossible to determine which, if any, species have become extinct. Consequently, we can only examine landbridge and deep-water islands of continental origin to obtain data on extinction. Furthermore, even when connected to a larger faunal source, small islands may not have had suitable habitat for a full complement of mainland species. Thus, in explaining extinction we are limited to those taxa for which suitable habitat occurs on particular islands.

The species composition north of the Vizcaíno Seaway differs from that south of the area (Murphy 1991; Grismer 1994b). Given that the islands north and south of the seaway had different species pools, potential species compositions are not equivalent. The situation is further complicated by rainfall patterns. Islands in the northern Sea of Cortés are subject to extremes in temperatures and rainfall; the seasonal average of rainfall is <15 cm per year and highly unpredictable. In contrast, islands associated with the southern half of the peninsula have more predictable and equitable rainfall, averaging >15 cm per year (Soulé and Sloan 1966). The activities of the Seri Indians have also likely complicated historical analyses. Finally, although many of the islands are well surveyed for diurnal lizards, the occurrence of nocturnal species, especially snakes, is probably not well documented.

Considering these variables, we divided the islands into four more or less homogeneous groups: northern landbridge islands, northern deep-water continental islands, southern landbridge islands, and southern deep-water islands of continental origin

(table 8.2). Among these groups, the southern islands form the most suitable group for examining potential patterns of extinction because, unlike for the northern islands, human-facilitated introductions have not been documented.

Table 8.3 shows distribution patterns for lizards on southern continental islands in the Sea of Cortés that have at least three species of diurnal lizards. The table also summarizes distribution data for lizards on oceanic islands. Taxa are ranked in order of decreasing number of insular occurrences. Islands are grouped by age and origin, and ranked in descending order of number of lizard species. Island areas are noted in parentheses. Table 8.3 shows a general trend for loss of species richness with decreasing island area, particularly for landbridge islands. Given a significant correlation in ranking ($p < .01$), most losses do not appear to be random, and thus occurrences are not stochastic. If extinction were simply stochastic, then we might expect some of these islands to have random subsets of the original species pool. However, this is not observed. The nested subsets of landbridge island species imply a regular, deterministic pattern of extinction.

Some exceptions to the pattern of extinctions occur. Western banded geckos, *Coleonyx variegatus*, have not been reported from Isla Carmen and San Francisco. However, these geckos are rare on some islands, such as Danzante, where there is only a sight record (Murphy and Ottley 1984). Thus, we believe the species likely occurs on the large island Isla Carmen, and possibly on smaller San Francisco, as appropriate habitat is available. The granite spiny lizard, *Sceloporus orcutti*, is not found on Isla

Table 8.2 Islands in the Sea of Cortés categorized into northern and southern distributions and into landbridge or deep-water status

Landbridge		Deep Water	
Island	Area (km^2)	Island	Area (km^2)
Northern Islands			
Tiburón	1225.53	Ángel de la Guarda	936.04
Mejia	2.26	Partida Norte	1.36
Estanque (Pond)	1.03	Salsipuedes	1.16
Miramar (El Muerto)	1.33	San Lorenzo (N & S)	37.29
Encantada Grande	6.85	San Esteban	40.72
		San Pedro Mártir	2.90
		San Pedro Nolasco	3.45
Southern Islands			
Espíritu Santo-Partida			
Sur	106.84	Santa Catalina	40.99
San José	187.16	Santa Cruz	13.06
Carmen	143.03	Cerralvo	140.46
San Marcos	30.07		
Los Coronados	7.59		
San Francisco	4.49		
Danzante	4.64		
San Ildefonso	1.33		
San Diego	0.60		

Islands with fewer than three species of diurnal lizards are not shown.

Table 8.3 Distribution of lizards on southern islands once connected to the peninsula of Baja California and southern oceanic islands in the Sea of Cortés

	Continental Islands												Oceanic Islands	
	Landbridge							Deep Water					Oceanic	
	Espíritu Santo-Partida Sur (107)	San José (187)	Carmen (143)	Coronados (7.6)	San Marcos (305)	San Francisco (4.5)	Danzante (4.6)	San Diego (0.6)	San Ildefonso (1.3)	Cerralvo (140)	Santa Catalina (40.9)	Santa Cruz (13.1)	Monserrat (19.9)	Tortuga (11.4)
Phyllodactylus	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Uta	●	●	●	●	●	●	●	○	●	○	●	○	●	
Sceloporus (*orcutti* group)	●	●	●	●	●	●	○	○		○		○		
Sauromalus	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Cnemidophorus (*tigris* group)	●	●	●	●	●	●	●			○	●			
Urosaurus	●	●	●	●	●	●	●			●				
Callisaurus	●	●	●	●	●	●	●							
Coleonyx variegatus	●	●	●	●	●		●							
Cnemidophorus hyperythrus	●	●	●		●	●				●			●	
Dipsosaurus	●	●	●		●	●				●	●		●	
Sceloporus (*zosteromus* group)	●	●	●	●			●						●	
Petrosaurus	●							●		●		●		
Sator											●			
Ctenosaura										●				

Islands with fewer than three species of lizards are not considered. Taxa are shown in order of decreasing number of insular occurrences. Islands are in order of decreasing number of lizard species. Island areas are in parentheses. Filled circles indicate species occurrences. Open circles indicate species likely eliminated by competitive exclusion.

Danzante. However, the Baja California rock lizard, *Petrosaurus repens*, occurs on Danzante, and given a 71.8 percent niche overlap (Case 1983), it is likely the ecological replacement of the granite spiny lizard. The island is likely too small to support both species (Case 1983; Murphy 1983a). Because no other missing records exist for the southern landbridge islands, except for San Diego (see below), the patterns of extinction do not appear to have been random, at least during the last 10,000–15,000 years.

Wilcox (1978) suggested that the landbridge islands were supersaturated. This was based in part on island area and distance estimates. Unfortunately, these estimates were not accurate (app. 1.1). We can empirically evaluate this possibility by examining the fauna on older continental islands. Cladogenic patterns revealed that Carmen and Danzante are older than the channel depths indicate, and yet they still display the fauna expected for landbridge islands (table 8.3). Thus, these data alone provide no indication of supersaturation. However, the lizard fauna of Isla Santa Catalina tells an alternative story. The presence of both the desert spiny lizard (*Sceloporus lineatulus*, a sister species of *S. monserratensis*) and the desert iguana (*Dipsosaurus catalinensis*) on Isla Santa Catalina indicates that the herpetofauna was once equivalent to that on Islas San José, Carmen, and Coronados (table 8.3). If true, then Santa Catalina has lost 5 of an original 11 species of lizard inhabitants, including a granite spiny lizard (*Sceloporus orcutti*), brush lizard (*Urosaurus*), zebra tail lizard (*Callisaurus*), western banded gecko (*Coleonyx variegatus*), and orangethroat whiptail (*Cnemidophorus hyperythrus*). Suitable habitat for all of these species appears to be present on Isla Santa Catalina. (If *Cnemidophorus hyperythrus* had an insular origin, as the cladogenic data suggest, then it is not a possible vicariant colonizer.) The nested subsets of landbridge islands do not predict this pattern of extinction. If Santa Catalina carried a representative fauna when it was formed, which seems likely given the presence of the fossorial western blind snake, *Leptotyphlops humilis*, then two important conclusions follow. First, if all species on the landbridge islands were available for colonization of Isla Santa Catalina, then extinction may have been a random event as predicted by island biogeography theory (MacArthur and Wilson 1963, 1967). Second, the landbridge islands are supersaturated (i.e., they have not reached equilibrium).

Islas Cerralvo, Santa Cruz, and San Diego appear to be special cases. Table 8.3 lists phrynosomatine lizards likely displaced by *Sator*, which occurs on these islands. San Diego is a landbridge island, and its complement of lizards is identical to nearby Isla Santa Cruz, which is a deep-water island. If *Sator* was absent, and the displaced phrynosomatines present, then both San Diego and Santa Cruz would have the expected complement of lizards (table 8.3). Therefore, extinction here appears to be deterministic via competitive exclusion or predation (Case and Cody 1983).

Cerralvo appears to be about 2–5 million years old. After considering the exclusion effects of *Sator* (table 8.3), two species appear to be randomly missing: the western banded gecko, *Coleonyx variegatus*, and the Cape Region whiptail lizard, *Cnemidophorus tigris maximus*. The absence of the western banded gecko could reflect insufficient collecting efforts, as noted above. However, on many islands, this species appears to be rare and could just be susceptible to extinction, particularly on older islands, because of low population densities. Nevertheless, these data also support the concept of supersaturated landbridge islands. The absence of *Cnemidophorus tigris maximus* is unexpected.

The oceanic islands are the final group to evaluate from southern Baja California. There is no evidence that humans introduced any of these insular species. Therefore, species must have arrived by overwater dispersal. Whether occurrences are randomized or not depends on each species' adaptation for colonizing. Amphibians are extremely poor oversea colonizers because of their permeable skin. Some ecological attributes of nonavian reptiles may predispose them to overwater travel. These might include an affinity for sleeping in trees and logs and ability to survive upon landing, such as relatively low metabolic rates, a high tolerance for salt, or a high tolerance for desiccation. If successful, overwater colonizers are exapted for insular survival, then they ought to be the best survivors. They should be the last species to become extinct on older islands, although limited empirical evidence suggests that long-term survival is also deterministic. Of six lizard species on Isla Santa Catalina, five have successfully colonized Isla Monserrate, presumably by overwater dispersal (table 8.3). Those absent from Santa Catalina are also absent from Monserrat. These data also suggest a predetermined ability to colonize (i.e., that colonization, like extinction, is deterministic).

Previously, Murphy (1983a) performed a similar evaluation of the northern midriff islands. However, as reviewed above, the available cladograms suggest that Seri Indians introduced some of the herpetofaunal species. In light of this new information, a similar evaluation would be futile.

Epilogue

We can now return to the original question. Is a new scenario required? Absolutely. Not only have sequence data significantly changed our perspective of the peninsula's evolution, they have also dramatically affected our understanding of the insular biota. Advances in tectonics have detailed the mechanics of the peninsula's origin, but they have not significantly impacted on its stratigraphic development. More than the geological data, the combined sequence data allow us to make predictions about how the peninsula must have evolved. Early predictions are being born out by corroborative paleostratigraphic data.

The concept of the peninsular archipelago, now better defined and more explicit, is most exciting for us. Although the peninsula might teach us about genetic clinal variation and linear transformations, this now appears to be rare. New data indicate that the peninsula will be more informative in terms of understanding the role of isolation in evolution and the evolutionary consequences of reunited populations and faunas. With additional data from key herpetological species and other comparative taxonomic groups, the peninsular archipelago and the associated islands provide us an invaluable vision of history, an understanding of the present, and a window to the future.

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