APPENDIX A. (Cont.)

		Mainland		Northern Channel Islands	
		Fossil	Living[2]	Fossil	Living
Gopher snake	*Pituophis melanoleucus*	+	+		+
Common kingsnake	*Lampropeltis getulus*	+	+		
California mountain kingsnake	*L. zonata*		+		
Kingsnake	*Lampropeltis* sp.	+			
Long-nosed snake	*Rhinocheilus lecontei*		+		
Common garter snake	*Thamnophis sirtalis*	+	+		
Western terrestrial garter snake	*T. elegans*		?		
Western aquatic garter snake	*T. couchi*		+		
Garter snake	*Thamnophis* sp.	+			
Western black-headed snake	*Tantilla planiceps*		+		
California lyre snake	*Trimorphodon vandenburghi*		+		
Spotted night snake	*Hypsiglena torquata*		+		+
Red diamond rattlesnake	*Crotalus ruber*		+		
Speckled rattlesnake	*C. mitchelli*		+		
Western rattlesnake	*C. viridis*	+	+		
Rattlesnake	*Crotalus* sp.	+			

[1] Fauna compiled from Savage (1967, pers. comm. 1979), von Bloeker (1967), White (1966), Voy (*ca.* 1893), Johnson (1972, 1978), McKeown (1974), McLaughlin (1959), Dixon (1967), Brattstrom (1953, 1955), Miller (1971), Marcus (1960), Stock (1958), P. Walker (unpubl. ms., pers. comm. 1978), W. Ackersten (pers. comm. 1978), Wilson (1936), Ingles (1965), and E. Anderson (pers. comm. 1978).

[2] "Living" includes those species known to have been present within historic time.

[3] A small piece of skull bone of *Sorex ornatus* and several *Odocoileus hemionus* elements have been found in Indian middens on the Northern Channel Islands. It is probable that these species did not live on the Northern Channel Island group, but were brought in by birds of prey (in the case of *S. ornatus*) or humans (in the case of *O. hemionus*) (Walker 1978).

[4] Extinct.

[5] May not be a valid species.

Biogeography and Distribution of Three Parapatric Salamander Species in Coastal and Borderland California

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INTRODUCTION

Evolutionary biologists since Darwin have assumed that study of geographic variation provides clues to the history of the evolution of taxa. Such studies often lead to hypotheses concerning the historical and phyletic basis for the distributional patterns that are observed (see Ball 1975). Attempts at reconstruction have been hampered by a lack of objective data concerning the time and rate of phylogenetic events. Starch gel electrophoresis has provided quantitative data on genic differentiation between many taxa (see Ayala 1975); many workers have attempted to reconcile genetic distance information with geological characteristics that may have influenced the divergence of taxa. I am aware of no studies that attempt to reconcile genetic distance with evolution of complex intrageneric patterns of distribution.

Slender salamanders of the genus *Batrachoseps* comprise a morphologically and ecologically specialized group of lungless salamanders that is endemic to the west coast of North America. Within this region they are widely distributed and are one of the most common vertebrates. Although there are several species with particularly localized ranges and relatively generalized morphologies, most of the range of the genus is occupied by a single attenuate form previously assigned to a single species, "*B. attenuatus*," that was thought to be highly variable (Stebbins 1951, Hendrickson 1954, Brame and Murray 1968). Forms living in southern California and on the four Northern Channel Islands are distinctive; Campbell (1931) described sympatry between *B. pacificus* and "*attenuatus*" on Santa Cruz Island and between *B. p. major* and "*attenuatus*" in southern California.

In a recent revision of the genus based on an electrophoretic study, I demonstrated that the attenuate form comprises a complex set of taxonomic units of three sibling species that are distributed through the coastal mountains and the Sierra Nevada of California (Yanev 1978). The distributions of the taxa recognized by me are shown in Figure 1, and the major conclusions from that study were as follows. (1) Populations from the Transverse Ranges and the foothills of the southern Sierra Nevada, formerly referred to *B. attenuatus*, are a distinct species for which the name *B. nigriventris* Cope (1869) is available. (2) The name *B. pacificus* Cope (1865) has priority for a superspecies composed of six semispecies. Two of these, *B. p. pacificus* and *B. p. major*, were formerly regarded as full species. One semispecies (centered in the Gabilan and southern Diablo Ranges) was formerly part of *B. attenuatus*. Three of the four allopatric units that were originally included in *B. relictus* by Brame and Murray (1968) are referred to semispecies of *B. pacificus*; the population on Santa Cruz Island is referable to *B. nigriventris*. In addition to the attenuate complex, several relatively generalized members are recognized in the genus: *B. wrighti*, *B. stebbinsi*, *B. simatus*, *B. aridus*, and an undescribed species from the Inyo Mountains (Marlow *et al.* 1979).

The most striking feature of the distributions of the species of *Batrachoseps* is their parapatric geographic ranges. The three sibling species, *B. attenuatus*, *B. nigriventris*, and *B. pacificus*, are parapatric both in coastal and in Sierran regions. Each of these species is composed of allopatric subunits. *B. attenuatus* and *B. nigriventris* have subunits in the Coast

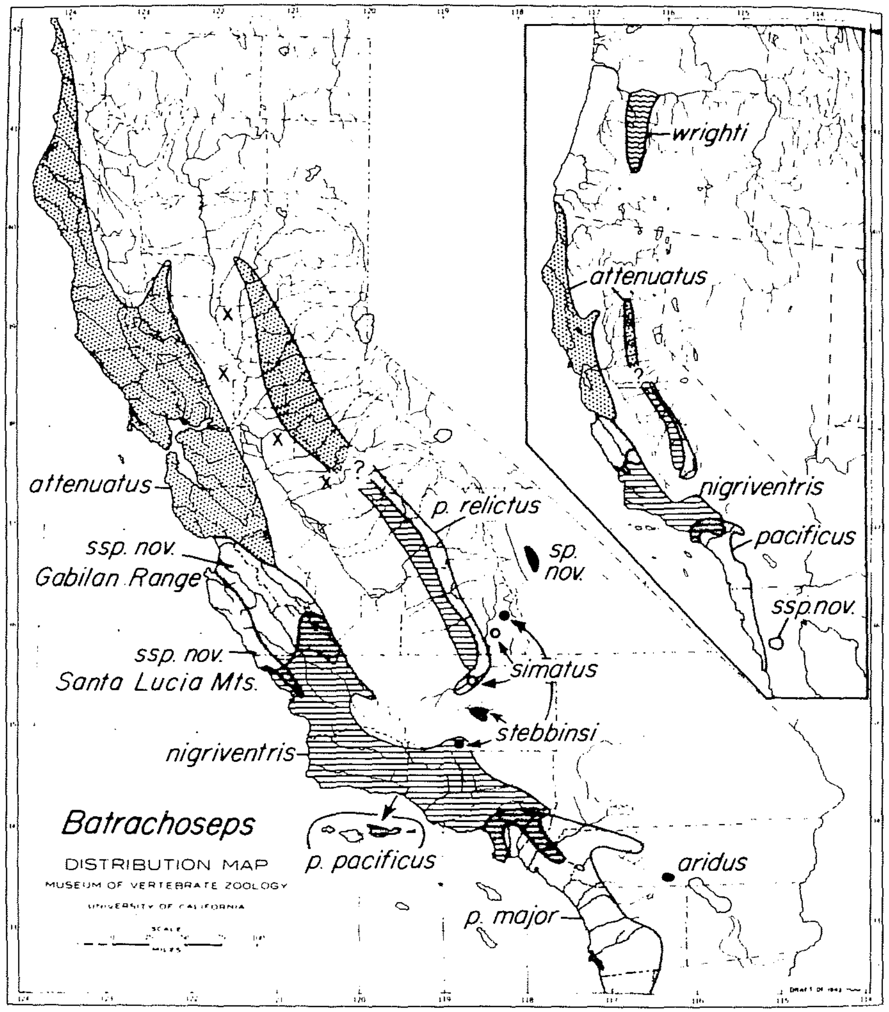

FIGURE 1. *Distribution of* Batrachoseps *in western North America. Map based on data from Yanev (1978). Insert shows isolated position of southern semispecies of* B. pacificus *and northern location of* B. wrighti.

Ranges and in the Sierra Nevada. Four of the six semispecies of *B. pacificus* are allopatric (*B. p. relictus, B. p. pacificus, B. p. major,* and the semispecies in the Sierra San Pedro Mártir) and two are parapatric in the central Coast Ranges (the Santa Lucian semispecies and the Gabilan semispecies). Thus, four parapatric taxonomic units are found in the Coast Ranges—*B. attenuatus,* the Santa Lucian semispecies, the Gabilan semispecies, and *B. nigriventris. Batrachoseps p. major* is a fifth parapatric unit in the Peninsular Range to the south. Populations in the Sierra Nevada form three parapatric units—*B. attenuatus, B. nigriventris,* and *B. p. relictus.*

Species of *Batrachoseps* are morphologically and ecologically specialized for subterranean life. They have elongated bodies with large numbers of vertebrae, markedly reduced limbs and feet, and elongated tails. *Batrachoseps* limit their surface activity to periods of favorable temperature and moisture conditions during the rainy months of winter. They cannot actively burrow and, in order to escape inhospitable surface conditions, rely on passages and spaces excavated by other organisms or produced by agents such as root decay and soil shrinkage. This semifossorial habit allows species of *Batrachoseps* to occupy habitats ranging from moist coastal and montane streamsides to oak and pine savanna and even desert springs.

All *Batrachoseps* are sedentary. Two studies of the movements of marked individuals have been conducted on *B. attenuatus.* Hendrickson (1954) found that adult salamanders moved within a range of 1.5 meters over the two years of his observations, and 59 per cent were found repeatedly under the same cover object. Maiorana (1978) also found evidence of individuals favoring a single cover object during a season of activity. Furthermore, populations of *Batrachoseps* seem to have survived in isolated patches of suitable habitat even though surrounding habitats became unsuitable. For example, *B. aridus* is known from a single spring in the southern California desert (Brame 1970); *B. stebbinsi* is known from several small, scattered localities in the southern California interior; and a recently described species, *B. campi,* is known from isolated springs in the arid Inyo Mountains (Marlow *et al.* 1979).

Stable parapatric distributions of species have been commonly associated with fossorial vertebrates, particularly rodents (see Patton and Yang 1977 for references). Parapatric distributions are also observed in plethodontid salamanders in the eastern United States (see Highton 1972 for closely related species of *Plethodon*). The regular pattern of parapatric distributions among taxa of *Batrachoseps* suggests that this phenomenon is stable and biogeographically significant. Maiorana (unpubl. ms.) has suggested that *Batrachoseps* might face competition for the burrows it needs in order to avoid dry surface conditions. Competition for burrows or other resources may limit the sympatry of closely related congeners. Competition, however, explains neither why there should be so many parapatric units in the genus nor why the units should be distributed as they are.

The thesis of this paper is that the present diversity of the parapatric taxa is related to historical changes in the geographic ranges of their respective ancestral lines. Various factors that may have influenced the establishment of the ranges will be examined in the following sections. Interrelated patterns of variation between the ranges and (1) the amount of genetic differentiation between the taxa and (2) the historical paleogeomorphology of California are described. It is hypothesized that the reconstruction of the evolutionary patterns from the present distributions and genetic relationships of the taxa requires simultaneous examination of the relative tectonic movements of landmasses, shifts in the locations and elevations of seas, mountain building episodes, and changes in paleobotanical and paleoclimatic conditions. I therefore constructed a set of maps showing a time-series of historical reconstructions of the geographical, botanical, and climatic history of California, and then worked backwards from the present patterns of distribution of taxa, superimposing on these maps a scenario of the "potential" divergences of groups inferred from genetic distances between those groups. It is assumed that speciation in salamanders occurred by allopatric mechanisms and that the divergence events occurred in the sequences suggested by the magnitude of the genetic distances between the taxa. A reasonable scenario is sought for the development of the complex parapatric patterns that are observed in *Batrachoseps,* based on the available estimates of the timing and sequence of geological and genic changes. Specific hypotheses concerning the relationship between taxonomic borders and historical geomorphic features may be tested in future studies by examining the concordant or discordant patterns of geographic variation in other genera of amphibians and reptiles.

EVOLUTIONARY HISTORY

Age and Estimates of Divergence Times in the Genus *Batrachoseps*

Batrachoseps is believed to be an old genus. On the basis of osteological and distributional characteristics, Wake (1966) proposed that the ancestors of the tribe Bolitoglossini—which includes *Batrachoseps*, its presumed closest relative, *Hydromantes*, and the Neotropical genera—reached the west coast of North America sometime in the early Tertiary via terrestrial forest corridors from source areas in the Appalachian Mountains. *Hydromantes* and *Batrachoseps* evolved in western North America, while the supergenus *Bolitoglossa* radiated from the northern tropics. Subsequent analyses continue to support the assignment of great age to these groups. Wake *et al.* (1978) report an immunological distance of 75 units between *Batrachoseps* and *Hydromantes*. They estimate that the separation of these lineages occurred around 50 million years (m.y.) ago in the early Eocene. Fossil material for these small animals is scant. A fossil trackway (Peabody 1959) and numerous fossil vertebrae (in the collection of the University of California Museum of Paleontology) from the Miocene of the Sierra Nevada suggest that an attenuate *Batrachoseps* of essentially modern form was present at that time.

In addition to estimating dates from fossil evidence, workers have attempted to infer divergence times from genetic distance. Nei (1972) proposed that genetic distance determined by starch gel electrophoresis is related to time, if it is assumed that most of the observed biochemical changes are effectively neutral or relatively neutral. Studies that examine a diversity of loci with differing evolutionary rates presumably average the discrepancies in evolutionary rates among individual loci. One method of estimating divergence times between taxa as a function of Nei's genetic distance (*D*) involves albumin immunological distance (for references and full development of this argument see Sarich 1977). Albumin immunological and electrophoretic genetic distances between the same pairs of taxa are highly correlated. On the basis of studies on a variety of taxa, Sarich showed that a genetic distance of 1.0 was approximately equivalent to an immunological distance of 35, which, in turn, predicts a divergence time of 20 m.y. ago; time in m.y. equals 20 *D* for an average selection of loci. This method of estimating divergence time from genetic distance has been employed by several workers, including Gorman *et al.* (1976, and references) and Wake *et al.* (1978), who cite geological data supporting the magnitude of their estimates.

Estimates of divergence times within *Batrachoseps*, calculated from genetic distances by Sarich's formula, are large. Mean genetic distances and predicted divergence times between the 15 taxonomic units which I examined (Yanev 1978) are shown in Figure 2. The predicted divergence time between the morphologically generalized species (*B. wrighti* and *B. campi*) and the more derived, attenuate species is on the order of 40 m.y. ago—an early event in the presumed history of the genus. The genetic distances in the original distance matrix from which the dendrogram was derived predict divergence times of 20 to 35 m.y. ago between the three species *B. attenuatus*, *B. nigriventris*, and *B. pacificus*, and 8 to 10 m.y. ago between the allopatric taxa of *B. nigriventris* and of *B. pacificus*. Identical distances are observed between each of the two isolated taxa on Santa Cruz Island and their mainland relatives (*D* equals 0.20 between island and mainland populations of *B. nigriventris* and between *B. p. pacificus* and *B. p. major*). These distances predict that separation between the mainland and the island forms occurred on the order of four million years ago.

Paleogeography of California

The topography of California has changed considerably since the genus *Batrachoseps* evolved and its lineages diverged. The late Tertiary was an active geological period and its paleogeography differed from the present geography in several significant respects.

Global tectonic forces have had a primary influence on the geographic history of western

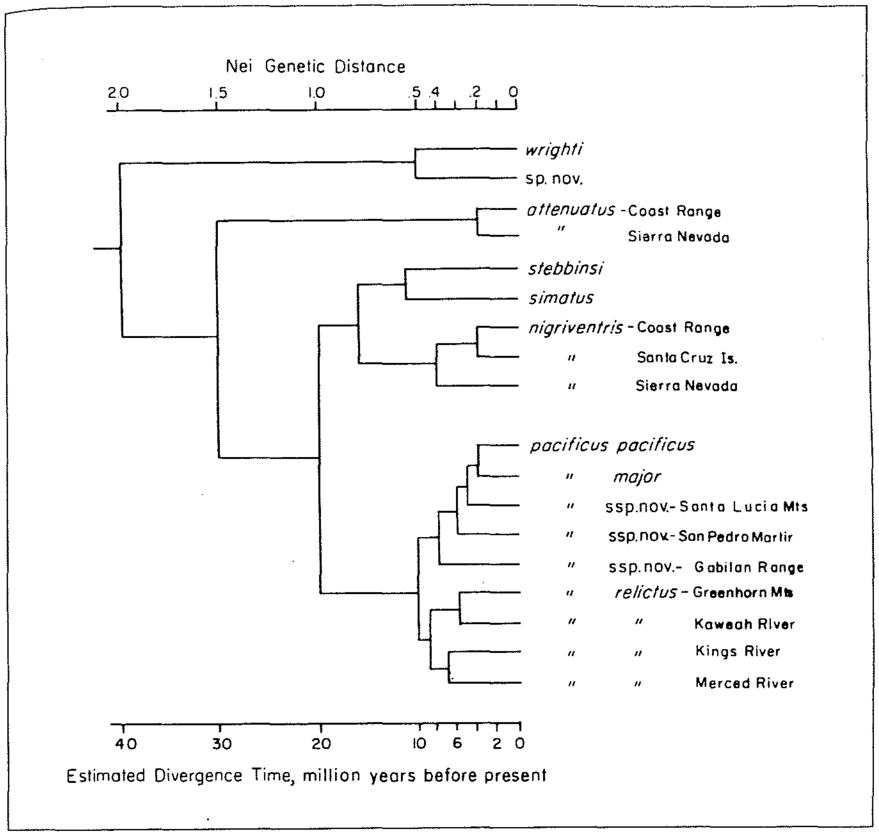

FIGURE 2. *Phenogram of genetic distance between taxonomic units of* Batrachoseps. *Clustering of Nei's* D *is by the unweighted pair-group method for arithmetic averages.*

North America (Atwater 1970). The recent geologic character of California is governed by the uneasy junction between the Pacific and North American plates that is presently expressed as the San Andreas fault. There have been many studies concerning the historic geology of California with respect to petroleum resources and, more recently, with respect to movement of the major fault systems. These studies report lateral displacements of diverse geologic markers representing a continuum of ages. They indicate that the land to the west of the San Andreas fault, which slices through the central coastal region of California, as illustrated in Figure 3, has moved northwest with respect to the mainland North American plate 190 miles (305 km) during the 12 m.y. since the middle Miocene. (Figure 4 *in* Nilsen and Clarke 1975 is an excellent summary of the movement indicated by these studies.) Some workers have proposed offsets of 350 miles (560 km) or more. However, such movements are now thought to be associated with earlier slipping along the fault system of 135 to 260 miles (220 to 420 km) during the Cretaceous. A thorough bibliography and specific documentation are available in Nilsen and Clarke (1975) and Howell (1976).

Several significant changes in sea-level elevations have occurred during the evolutionary

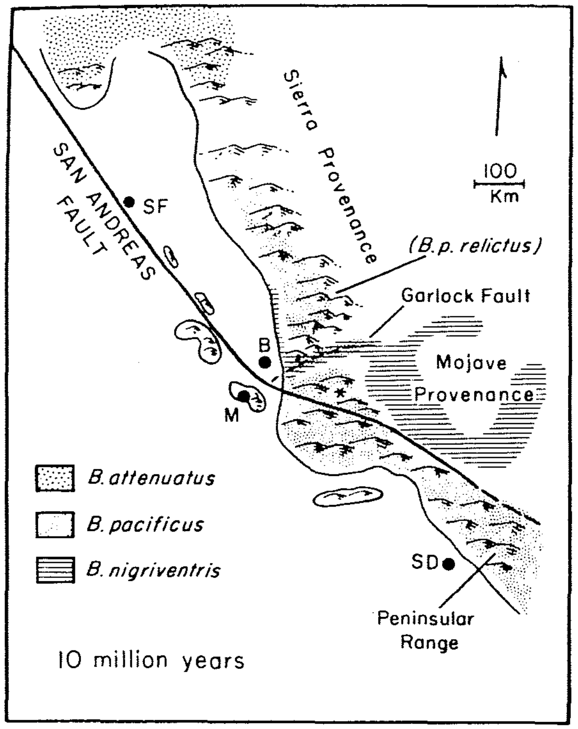

Figure 4. *Hypothetical reconstruction of geography of California and distribution of* Batrachoseps *at 10 million years ago. Circles indicate sites of present cities of San Francisco (SF), Monterey (M), Bakersfield (B), and San Diego (SD). Asterisk indicates site of Transverse Ranges at 10 million years ago.*

Sometime around 10 million years ago (corresponding to a genetic distance of 0.5), a barrier arose between the populations of *B. p. relictus* in the Sierra Nevada and the rest of *B. pacificus*. The existence of lowland basins in the present zone of the Garlock fault suggests that the region may have been geologically active (Nilsen and Clarke 1975). Dibblee (1967) suggests that these basins represented long, continuous, and linear lowlands that separated upland areas to the north and south. The upland areas could potentially harbor populations of mesic-adapted salamanders (*B. pacificus*), while the lowlands could be occupied by arid-adapted salamanders (*B. nigriventris*).

Geography and the distribution of **Batrachoseps** *at 8 m.y. ago.*—The second reconstruction in Figure 5 illustrates the central and southern coast of California as it may have looked two million years later, or at 8 m.y. ago. Relative motion has occurred along the San Andreas fault. The land to the west of the fault has begun to form a peninsula, or archipelago, which separated into an island several million years later. The seas approached their maximum spread, and there were still a few land-positive areas on the east side of the fault in the vicinity of the incipient Diablo Range.

Differentiation of the semispecies which centered in the Gabilan Range from the rest of *B. pacificus* may have occurred at this time, together with differentiation of the allopatric taxa of *B. nigriventris*. The ancestors of the Gabilan semispecies, in the Gabilan Range west of the San Andreas fault, might have become isolated from other *B. pacificus* by a combination of restriction of populations to mesic upland sites during the drying conditions of the Pliocene and increasing distance of those upland areas from each other as the blocks of land where they were

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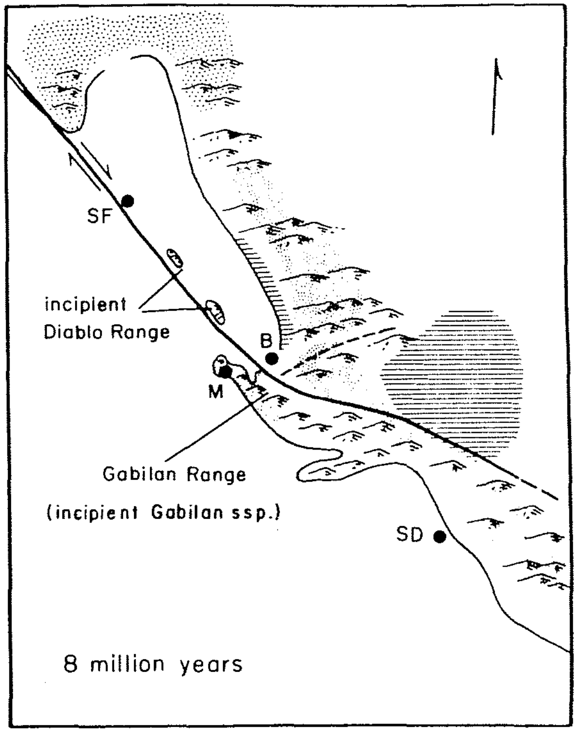

Figure 5. *Hypothetical reconstruction of geography of California and distribution of* Batrachoseps *at 8 million years ago.*

located moved farther apart. Paleobotanical evidence indicates that oak associations were present in the Gabilan region. Freed from genetic contact with the "mainland" *B. pacificus*, those populations in the Gabilan Range may have been under strong selective pressure to adapt genetically to the new conditions. At approximately the same time, the formerly continuous range of *B. nigriventris* may have been split into two disjunct segments in the Mojave region and in the Sierra Nevada foothills.

Geography and the distribution of **Batrachoseps** *between 6 and 5 m.y. ago.*—The geographical changes that occurred by 5 m.y. ago are illustrated in the third reconstruction in Figure 6. Motion continued along the San Andreas fault. The Santa Lucia Range, the Gabilan Range, and the southern Diablo Range landmasses were fully isolated by seas to the east and west and by wide straits to the north and south. The southern strait is that implicated by Peabody and Savage (1958) in preventing dispersal of the herpetofauna to the south from their hypothetical corridor. It has been known that the major drainage from the inland sea or San Joaquin embayment was through the lowland north of the Santa Lucia and Gabilan Ranges, but the importance of this northern strait as a barrier has been underestimated. Throughout much of its history it was a wide seaway, not merely the present continental river valley.

During this time, the Gabilan semispecies became fully isolated on the offshore landmass and drying trends are believed to have been most severe. The most significant geologic event of this mid-Pliocene period was the rise of the Transverse Ranges. The presence of these mountains created a sharp floral boundary between central and southern California by preventing northern storms from reaching southern areas. This climatic stress and the resultant habitat

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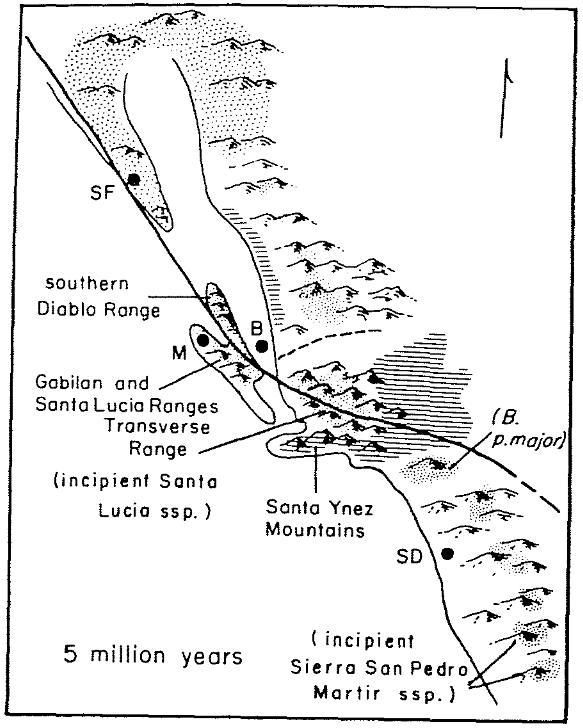

FIGURE 6. *Hypothetical reconstruction of geography of California and distribution of* Batrachoseps *at 5 million years ago.*

stress further split the extensive population of *B. pacificus* into a semispecies in the Transverse Ranges (incipient Santa Lucian semispecies) and populations which ranged south in coastal highlands through the Peninsular Range, into northern Baja California, and perhaps far south along the coast of mainland Mexico. Mesic habitats would still have been available for the Santa Lucian semispecies in the Transverse Ranges and for populations of *pacificus* that happened to be stranded on peaks and ridges to the south (for example, the Sierra San Pedro Mártir). The lowland populations that lived in the rain shadow of the new Transverse Ranges, however, would have been under severe stress to adapt to the increasing aridity. *Batrachoseps p. major* presumably evolved in arid savannas in the lowland basins in the vicinity of Los Angeles. When an arid-adapted form had evolved, it could have begun to spread southward along the coast in similar lowland habitats. With increasing aridity, the mesic habitats in the Transverse Ranges shifted toward the coast, carrying with them the populations of the Santa Lucian semispecies. Similarly, the oak-savanna zones that were inhabited by *B. nigriventris* shifted coastward from the Mojave region into increasingly arid regions of the Transverse Ranges.

Geography and the distribution of* Batrachoseps *at 4 m.y. ago.—The paleogeographic map of the late Pliocene of California changed little from the previous map. The landmass that was occupied by the Gabilan semispecies was still isolated by seas and continued to approach the northern Coast Ranges that were occupied by *B. attenuatus*. In the Transverse Ranges, the Santa Lucian semispecies was further restricted by drying conditions to habitats near the coast. *Batrachoseps nigriventris* was abundant throughout the Transverse Ranges and into the Santa

Ynez Mountains, but it no longer inhabited the increasingly arid Mojave province. *Batrachoseps p. major*, which is tolerant of dry and unpredictable habitats, continued to expand southward along the coast. It contacted *B. nigriventris* at the southern edge of the Transverse Ranges, where the present parapatric distributions of the two taxa seem to correlate with their habitat preferences. While *B. p. major* presently lives in open, low-elevation grasslands, *B. nigriventris* lives in oak woodlands.

The genetic distance of populations of *B. attenuatus* in the northern Coast Ranges as compared with the northern Sierra Nevada suggests separation at this time, perhaps as cooler temperatures forced populations to move south and into disjunct ranges in the two regions. Forested valley corridors may have maintained limited genetic contact between populations in the two areas.

Establishment of the taxa on the Channel Islands.—The most significant event in the history of *Batrachoseps* at approximately 4 m.y. ago was the establishment of the taxa on the Channel Islands. Excluded from this discussion are populations on Santa Catalina, Los Coronados, and Todos Santos Islands that are referred to *B. p. major*. Presently, populations of *B. p. pacificus* occur on the four Northern Channel Islands, and populations of *B. nigriventris* occur on Santa Cruz Island. I (Yanev 1978) have demonstrated that the two taxa on Santa Cruz Island are most closely related to the two mainland taxa whose present ranges are geographically closest to the islands. Both island taxa have the same genetic distance (D = 0.2) from their mainland relatives, which predicts a common divergence time of 4 m.y. ago. Thus, it is inferred that *B. nigriventris* was isolated on Santa Cruz Island and diverged from mainland *nigriventris*, and *B. p. pacificus* from *B. p. major*, at approximately the same time.

These island populations of *Batrachoseps* could have arisen in two ways: (1) by terrestrial range expansion over a land connection which became submerged approximately 4 m.y. ago, or (2) by over-water rafting of the two taxa at approximately the same time. Many geological studies have been conducted recently on the borderlands of southern California (Howell 1976, Vedder and Howell 1980, Junger and Johnson 1980), and there is no support for the hypothesis of a Pliocene land connection between these islands and the mainland. Such a connection has often been erroneously hypothesized in the past, primarily by biologists to explain the presence of terrestrial faunas on the islands (see Wenner and Johnson 1980).

In accordance with these views, Savage (1967) suggested that the modern herpetofauna of the Channel Islands is a depauperate random sample of the herpetofauna of the adjacent mainland and was established during the Pleistocene by over-water distribution of waifs. Circumstantial evidence is in agreement with this hypothesis. Over-water rafting is certainly possible for *Batrachoseps*. Individual salamanders could have been washed out to sea on clumps of debris from mainland rivers, perhaps during periods of torrential rains at the onset of Pleistocene cooling periods. (The power of such storms and their ability to disperse organisms is illustrated by a recent news service report [Anonymous 1978] that a large quantity of fruit was observed floating 10 miles offshore in the Santa Barbara Channel. The fruit, which had been knocked from trees in orchards of central Ventura County by "fierce thunderstorms" the previous week, had floated 20 miles downriver to the ocean.) The minimum distance between the islands and the mainland is believed to have been 7 to 10 km (Junger and Johnson 1980), which is about a quarter of the present distance. In addition, *Batrachoseps* is notably tolerant of saline conditions. Licht *et al.* (1975) report that *Batrachoseps* is one of the most euryhaline amphibians. Furthermore, rafting does not always provide a complete sample of neighboring faunas, which would explain why such generalists as *Ensatina* and *Eumeces* are absent from the islands. The Farallon Islands lie approximately the same distance off the shore of northern California as the Channel Islands do off southern California. Only *Aneides lugubris* is established on the Farallon Islands, even though *Batrachoseps* and other salamanders are

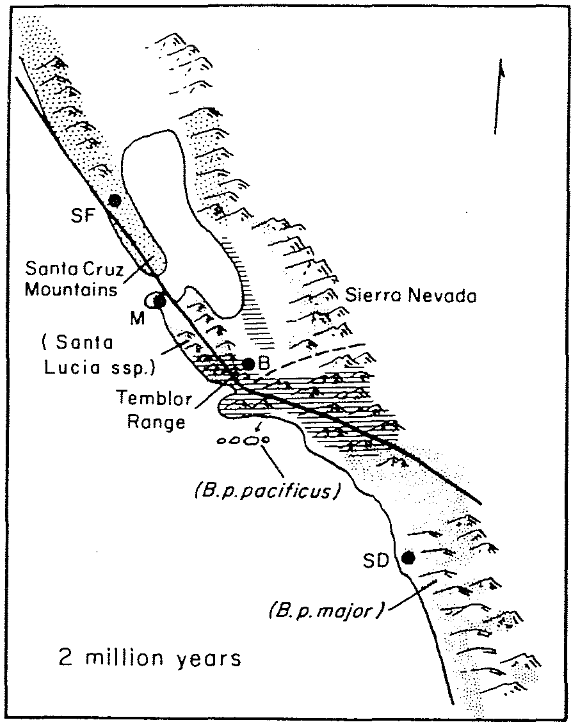

FIGURE 7. *Hypothetical reconstruction of geography of California and distribution of* Batrachoseps *at 2 million years ago.*

abundant on the mainland.

The hypothesis that the island herpetofaunas were established by over-water rafting from the mainland may be tested by comparing the degree of genetic differentiation between other terrestrial island taxa and their mainland relatives. If island populations of different species were established by the submergence of a land bridge, then the genetic distances and the predicted divergence times should be concordant for all pairs of taxa. If the faunas were established by a stochastic process such as rafting, the genetic distances would be expected to be heterogeneous. A parallel test would be to compare the genetic differences between the populations of *B. p. pacificus* on the four Northern Channel Islands with each other and with mainland *B. p. major.* The four northern islands are believed to have been interconnected during the Pleistocene. Thus, these island populations are expected to show small, uniform genetic distances from each other, distances that correspond to divergence times in the late Pleistocene. Analysis of these populations is in progress.

Geography and the distribution of* Batrachoseps *at 2 m.y. ago.—The Pleistocene of two million years ago, illustrated in Figure 7, was a time of cyclical cooling with increased moisture. Forested areas spread inland, and temperate areas shifted southward and downslope. The present configuration of the mountain ranges began to emerge. The Sierra Nevada was uplifted rapidly. The uplift of the Temblor Range at the southern end of the Coast Ranges expelled the San Joaquin Embayment from the central valley (through the shrinking seaway north of the Gabilan and Santa Lucia Ranges) and closed the southern seaway that had for so long prevented geographical contact between the Gabilan semispecies of *B. pacificus* on the "moving island" and the Santa Lucian semispecies living in the Transverse Ranges to the south.

The Santa Cruz Mountains at the southern terminus of the northern Coast Ranges also uplifted rapidly and created habitats for populations of *B. attenuatus* in close proximity to populations of the Gabilan semispecies of *B. pacificus*. The ranges of these two taxa remained separated by the major drainage from the Sierra Nevada through the former northern seaway, which is now the Pajaro River; this river was alternately a major river in cool times of low sea level and high continental runoff and a swampy bay in warm times of high seas.

The tectonic and floristic perturbations had several effects on the taxa. Populations of *B. p. relictus* in the Sierra Nevada, and particularly in the northern drainages, were isolated when colder conditions forced them to move lower into river valleys that were separated by arid ridges. This isolation may be responsible for the large genetic heterogeneity that is observed between these populations today. The southerly spread of mixed evergreen and redwood forests along the coast provided a habitat corridor by which the Santa Lucian semispecies of *B. pacificus* may have moved north along forested coastal slopes to occupy its present range in the Santa Lucia Mountains. *Batrachoseps attenuatus* moved south through continuous habitat from the northern Coast Ranges into the Santa Cruz Mountains. *Batrachoseps nigriventris* expanded onto the new geographic connections between the Transverse Ranges and the southern Coast Ranges and occupied the more arid oak-savanna sites surrounding the mesic pockets preferred by the Santa Lucian semispecies. In the southern Diablo Range, the range of *B. nigriventris* contacted the range of the Gabilan semispecies of *B. pacificus* and the two taxa became seemingly microsympatric over the limited area in which they behave as full species. Nothing is known of their interactions, although their overlap is the most extensive between any of the parapatric units of the genus. Populations of *B. p. major* expanded both inland and southward and recontacted the populations of *B. pacificus* that had been left on cooler, wooded ridges of the Peninsular Range by earlier episodes of drying conditions. *Batrachoseps p. major* also spread inland through the San Gabriel and San Bernardino Mountains; *B. aridus* may have been isolated subsequently and may have become a relict of this distribution.

When two taxa of *B. pacificus* came into secondary contact, reproductive isolation does not appear to have developed, and the taxa intergrade despite some accumulated genetic and morphological differences. Intergradation is presently observed where the Santa Lucia semispecies contacts the Gabilan semispecies in the southern Coast Ranges; it also may have occurred where trans-valley migrants may have passed between the Gabilan semispecies and the relatively isolated populations of *B. p. relictus* in the central Sierra Nevada (see Yanev 1978). Intergradation may have occurred where populations of *B. p. major* in the southern California lowlands came into contact with the *B. pacificus* populations on the ridges of the Peninsular Range. Populations in this area are morphologically intermediate and have been taxonomically ambiguous—they have been referred to "*B. attenuatus leucopus*" (Dunn 1926); "intergrades between *B. pacificus* and *B. attenuatus*" (Hendrickson 1954); and "*B. major* Camp" (Brame and Murray 1968, and see maps *in* Brame 1970 and Lowe and Zweifel 1951).

Geography and the distribution of* Batrachoseps *in the late Pleistocene.—By the late Pleistocene, the geography of California had assumed its present pattern. The major drainage from the Sierra Nevada shifted to the north, to exit from the valley through San Francisco Bay; this shift brought the ranges of *B. attenuatus* and the Gabilan semispecies into contact. However, this contact is limited and occurs primarily at the base of the Santa Cruz Mountains, where *B. attenuatus* remains in the evergreen forest of higher elevations and the Gabilan semispecies has invaded the alluvial lowlands that support savanna-woodland vegetation. The ranges of these two taxa approach each other at the northern end of the Gabilan Range, but probably do not contact at all in the central Diablo Range. Their potential contact zone in the central Diablo Range is dominated by sterile serpentine outcrops and derived, highly toxic soils that support only limited vegetation (Griffin 1975); no salamanders have been collected there.

DISCUSSION AND PREDICTIONS

A second method of estimating divergence times between taxa, as a function of Nei's genetic distance, was suggested by Nei (1972). Nei and Roychoudhury (1974), in a study of races of man, estimated the parameters necessary to predict that time in m.y. equals $5 \times 10^6 D$. This method predicts divergence times that are lower by a factor of four than those calculated by Sarich's formula which was based on a larger number of taxa of greater and more diverse ages. If a scenario for the evolution of the distribution of *Batrachoseps* is constructed using the shorter time scale, it is not possible to resolve the distributions of the taxa with the geologic data.

Several specific testable hypotheses follow from the predictions of the scenario that was developed for the evolution of the complex distributions observed in *Batrachoseps*. Most significantly, if paleogeographic borders exert a relevant influence on taxonomic diversity, then taxonomic borders ought to be concordant in species of appropriate historical age. Either other species inhabiting the same areas will show electrophoretic evidence of genetic discontinuities at the same paleogeographic borders that were observed in *Batrachoseps*, or the other species will have recently dispersed across the region, which will be apparent in very low levels of genetic differentiation. Appropriate species for this analysis are those with distributions through the coastal and montane regions of California. Such species include *Aneides lugubris*, *Taricha torosa* and *T. granulosa*, *Rana boylei*, *Gerrhonotus coeruleus* and *G. multicarinatus*, and particularly the subdivided species *Ensatina eschscholtzii* and *Diadophis punctatus*. Studies on *Ensatina*, *Aneides*, *Diadophis*, and *Gerrhonotus* are in progress.

Few genetic distance comparisons are presently available for other taxa over this geographical region, and none directly concern the paleogeographic borders. The most relevant comparisons involve *Taricha*. The ranges of *Taricha granulosa* and *T. torosa* contact each other in the vicinity of the (former) seaway between the northern and southern Coast Ranges that is hypothesized to have limited the ranges of *B. attenuatus* and the Gabilan semispecies of *B. pacificus*. The hypothesis predicts that taxonomic borders of *Taricha* ought to reflect this biogeographical boundary or demonstrate the low levels of genetic differentiation that would be compatible with recent dispersal across the region. Hedgecock and Ayala (1974) present genetic distance comparisons between five populations of the two species. The range of *T. granulosa* is exactly concordant with this hypothetical boundary, while *T. torosa* ranges primarily to the south but also across this boundary into the southern part of the northern Coast Ranges. The mean genetic distance between the two species equals 0.44, which corresponds to a predicted separation of 8.8 m.y. ago; the seaway may have been a barrier between them. *Taricha torosa* may be regarded as having recently dispersed across this boundary; the genetic distance observed between two populations of *T. torosa* from the northern and southern Coast Ranges equals 0.11, which corresponds to a Pleistocene divergence time within *torosa*.

Some other, more specific predictions from the hypothetical scenario are also testable. (1) The scenario predicts that taxa occupying the southern Coast Ranges will have southern rather than northern affinities. (2) I expect that upland populations in the Peninsular Range will show electrophoretic evidence of past intergradation between *B. p. major* and the undescribed semispecies of *B. pacificus* presently living in the Sierra San Pedro Mártir. (3) The scenario proposed that the present Santa Lucian semispecies of *B. pacificus* moved with shifting mesic habitats from the Transverse Ranges to occupy the Santa Lucia Mountains. The upland Transverse Ranges have not been well sampled. I predict that populations genetically related to the Santa Lucian semispecies and to *B. p. major* may be found and recognized electrophoretically from localized areas. (4) In light of the complex pattern of distribution observed in the semispecific taxa of *B. pacificus*, the distribution of *B. aridus* seems logical for a relict of *pacificus*; I predict that these forms will be found to be close genetic relatives.

SUMMARY

In a recent revision of *Batrachoseps* (slender salamanders) that was based on an electrophoretic survey, it was demonstrated that the attenuate form of the genus comprises a complex set of taxonomic units of three sibling species that are distributed throughout the borderland, the coastal mountains, and the Sierra Nevada of California. The sibling species *B. attenuatus*, *B. nigriventris*, and *B. pacificus* are genetically very different from each other; Nei's genetic distance ranges from 1.0 to 1.5 between them. The superspecies *B. pacificus* is composed of six primarily allopatric semispecies that have genetic distances ranging from 0.2 to 0.5.

The most striking aspect of the distributions of the taxa that were recognized in the revision is the parapatric replacement of morphologically similar taxonomic units. It is proposed in this paper that the present diversity of these parapatric taxa is related to historic changes in the geographic ranges of their respective lineages and that these ranges are predicted by paleogeographic boundaries. A scenario is presented for the evolution of the complex parapatric patterns that are observed in *Batrachoseps*. Divergence times between the taxa are inferred from genetic distance to be 20 to 35 million years ago between the sibling species, and 8 to 10 million years ago between the semispecies. Working backwards from the present patterns of distribution, the possible divergences of lineages are superimposed on a set of maps showing a time-series of reconstructions of the geologic, botanic, and climatic history of California.

Several specific testable hypotheses follow from the predictions of the scenario that is developed for the evolution of the distributions of the taxa of *Batrachoseps*. The relationship between taxonomic borders and historical geomorphic features may be tested in future studies by examining the concordant or discordant patterns of geographic variation in other genera of amphibians and reptiles. Several specific predictions concerning genetic and geographic relationships within *Batrachoseps* also arise from the scenario.

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Species Number, Stability, and Equilibrium Status of Reptile Faunas on the California Islands

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INTRODUCTION

Island biogeography is the study of species distribution among islands. Its purpose is to develop principles that explain patterns of species distribution and species composition of island biotas through ecological, evolutionary, and historical mechanisms.

The most notable feature of the biogeography of the islands off the coast of southern California and Baja California, Mexico is the paucity of land vertebrate species, especially on the northernmost islands. This pattern was especially noted for reptiles and amphibians in an earlier analysis of the herpetofaunas of these islands by Savage (1967). No causal explanation was offered, save the suggestion that previous land bridge connections to the mainland were nonexistent. At the time of Savage's analysis, our understanding of island biogeography was, in general, poorly developed. The primary purpose of this paper is to re-evaluate the depauperate status of the reptile faunas of the California Islands in light of what is now known of the mechanisms controlling species diversity on islands, and to discuss the significance of the findings in terms of current island biogeographic theory.

THE THEORY OF ISLAND BIOGEOGRAPHY

In the interval between Savage's analysis and the present study, major advances have been made in our understanding of island biotas. Whereas in the past most of the emphasis was on dispersal, many recent studies emphasize the importance of extinction in determining the composition of island faunas. Extinction is apparently not an uncommon event, at least among island vertebrate populations (see Diamond and Jones 1980, Wilcox 1978). Thus, present species distribution on islands may only partially reflect the previous status of land bridge connections or successful over-water colonization events. From a consideration of the processes of extinction and immigration of species on islands, and the characteristics of insular biotas influencing their rates, a general theory of island biogeography has emerged.

The theory of island biogeography centers on the concept of an equilibrium between the rate of addition of new species to an island biota, immigration, and the rate of species loss through extinction (Preston 1962, MacArthur and Wilson 1963, 1967). These authors further proposed that the immigration rate should be dependent on the degree of isolation of an island, which is usually quantified as the shortest distance from an island to the mainland. They proposed that the other important variable, extinction, should be dependent on the size of an island. This is because, on smaller islands with limited habitats, population sizes may be so small that typical population fluctuations imposed by environmental vagaries are more likely to result in extinction. Thus, an island's area and its degree of isolation from other landmasses may largely define the equilibrium number of species. A relationship between species number and area and mainland distance has been established for numerous biotas (see Diamond and May 1976 for the

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