1995

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Recommended Citation

Ramirez, M. G. & R. D. Beckwitt. (1995) Phylogeny and historical biogeography of the spider genus *Lutica* (Araneae, Zodariidae). *Journal of Arachnology* 23: 177-193.

1995. The Journal of Arachnology 23:177–193

PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF THE SPIDER GENUS *LUTICA* (ARANEAE, ZODARIIDAE)

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ABSTRACT. Spiders of the genus *Lutica* from 19 populations in southern California and Baja California, including all the California Channel Islands except Anacapa, were compared electrophoretically on the basis of variability at 15 gene loci. Fixed allelic differences clearly define two species: new species A [Santa Barbara and Ventura Counties, northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz), southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina)] and new species C [Guerrero Negro, central Baja California], while morphological features define two others: new species B [Los Angeles, Orange and San Diego Counties, northern Baja California] and *clementea* [San Clemente Island]. Phylogenetic analysis of the electrophoretic data using a variety of methods revealed that evolutionary rates among the populations sampled have been very unequal. The phylogenetic relationships among populations consistently supported by the electrophoretic cladograms generally correspond with the geological history of the Channel Islands and adjacent mainland and suggest certain likely colonization events involving some of the islands.

Genetic similarities and differences among populations can be used to assess specific hypotheses about biogeography and evolution. Populations on islands are especially useful because they frequently are discrete entities with little gene flow among islands; for some islands the geologic history also is known. This type of analysis is especially powerful for sedentary species in which chances for dispersal among populations are minimal (Carlquist 1981).

The California Channel Islands are an excellent system for addressing questions of evolutionary and biogeographic history. These eight islands vary in size, topography and physical isolation (Fig. 1). While the geologic history of the islands and their surroundings is complex, it has clearly involved the northward transport of these island landmasses on crustal blocks (terranes) caught in the tectonics of the Pacific/North American plate margin (Hornafius et al. 1986). It has also involved extensive changes in sea level which have repeatedly submerged some islands while possibly leaving the highest areas of others continuously above water since the Oligocene (Vedder & Howell 1980; Haq et al. 1987). Biogeographic studies of biologically old taxa on the Channel Islands need to consider both vicariance and dispersal as factors in producing contemporary distributional patterns.

The spider family Zodariidae and many of its genera have existed since at least the Oligocene (Petrunkevitch 1942, 1952) and they have been exposed to the geological and climatic changes of the last 30 million years. Worldwide, 47 genera have been described, mainly from the tropical and temperate regions of the Old World (Jocqué 1991). Spiders of the genus *Lutica* are the only native representatives of the Zodariidae in the continental United States and they live in restricted insular and coastal dune communities in southern California and Baja California, including all the California Channel Islands except Anacapa (Ramirez 1995). Their preferred habitat is a sand dune covered by native beach vegetation located well behind the high tide line and the influence of sea water (Gertsch 1961; Ramirez 1995). On Santa Barbara Island, typical coastal dunes do not exist and these spiders live in the sandy soil and debris below vegetation growing on a sea cliff (Ramirez 1995). They live in silk-lined burrows they construct in the sand, emerging only at night to feed and, during August–October, to mate (Gertsch 1961; Ramirez 1995). When dislodged from their burrows, these

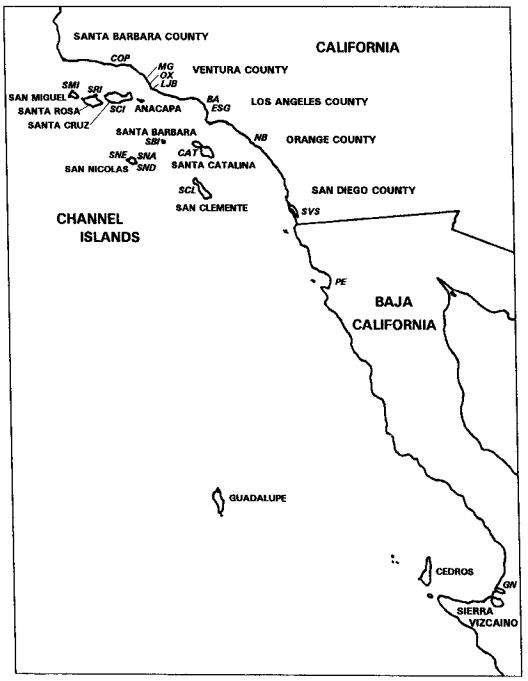

Figure 1.—Map of southern California and Baja California, including Channel Islands, showing *Lutica* sample sites. Population abbreviations follow Table 1.

spiders actively burrow into the loose sand and are quickly lost from sight. *Lutica* does not use ballooning (aerial transport on wind blown silk threads) as a means of dispersal at any point in its life cycle; ballooning is rare in other fossorial spiders (Decae 1987) and has never been recorded in the family Zodariidae (Jocqué 1993). Non-reproductive terrestrial dispersal may be minimal (Ramirez 1995). Males wandering in search of females can be found in great numbers in September; how far they actually range is not known. *Lutica* is thought to have a lifespan of two to three years (Gertsch 1961; W. Icenogle pers. comm.).

In this study, we present the results of a survey of allozyme variation among *Lutica* populations from the Channel Islands and mainland of southern California and Baja California. The primary objective was to use allozyme variation to identify valid species of *Lutica* and to determine their phylogenetic relationships. A second objective was to use the phylogenetic relationships indicated by the electrophoretic data to discuss the historical biogeography of this genus, with particular attention to estimating probable patterns of colonization among island and mainland populations.

METHODS

Systematic background.—George Marx first described the genus *Lutica* from Klamath Lake, Oregon (Marx 1891). Gertsch (1961) corrected the type locality of *Lutica maculata* to Santa Rosa Island, California, and also described three new species: *nicolasia* (San Nicolas Island), *clementea* (San Clemente Island) and *abalonea* (Oxnard, Ventura County). Additional species have been described from India (Tikader 1981), but these taxa are clearly misplaced (Jocqué 1991).

Collections.—During 1985 and 1987, we collected *Lutica* from 19 sites in southern California and Baja California, covering a range of 865 km (Fig. 1). Sample sizes ranged from 20–50 spiders per population for a total of 812 spiders (Table 1). In the laboratory, they were starved for at least a week and then frozen at −70 °C until they were prepared for electrophoresis.

Electrophoresis.—A survey of 60 enzymes on 2–7 buffer systems revealed consistently scorable activity for 15 loci on three buffer systems; electrophoretic techniques and staining protocols are described in Ramirez (1990). No significant differences in the banding patterns of spiders of different ages or sex were ever detected, making it possible to examine spiders of all instars. All genotypes were inferred from the appearance of the staining patterns and the known subunit structure of the enzymes (Harris & Hopkinson 1976; Richardson et al. 1986).

Species identification.—In this study, the detection of fixed allelic differences was the criterion for species identification, in accord with the biological species concept [i.e., a fixed difference reflects the separate gene pools of two non-interbreeding taxa (Mayr 1970)] and following the recommendations of Farris (1981) and Richardson et al. (1986). Since it has been shown that a sample of three individuals each from two different populations is sufficient to reveal a fixed allelic difference between the populations (Richardson et al. 1986), the mean sample sizes per locus in this study, which ranged from 33–46 for 16 populations and 19–22 for three populations, were certainly adequate for the detection of fixed differences and the identification of species. In cases where diagnostic loci could not be found for a group of populations, reference was made to the morphological taxonomy of Gertsch (1961, pers. comm.) for evidence that might suggest val-

Table 1.—Summary of collections of *Lutica*. Samples include spiders of all instars.

Locality (abbreviation)	Sample size	Dates of sampling
Coal Oil Point Reserve (COP) (Santa Barbara County)	48	May 12, 1985
McGrath State Beach (MG) (Ventura County)	48	June 11 & August 15, 1985
Oxnard Beach (OX) (Ventura County)	36	June 11, 1985
La Jolla Beach (LJB) (Ventura County)	48	May 27, 1985
San Miguel Island (SMI) Cuyler Harbor	48	August 13, 1985
Santa Rosa Island (SRI) Southeast Anchorage	48	July 1, 1987
Santa Cruz Island (SCI) Johnstons Lee	48	August 17, 1985
Santa Barbara Island (SBI) Cliffs south of Signal Peak	48	July 9–10, 1987
San Nicolas Island		
Army Camp Beach (SNA)	24	July 31, 1985
Dutch Harbor (SND)	22	July 30, 1985
Red Eye Beach (SNE)	20	July 31, 1985
Santa Catalina Island (CAT) Little Harbor	48	August 23, 1985
San Clemente Island (SCL) Flasher Road Dunes	48	August 21, 1985
Ballona Wetlands (BA) (Los Angeles County)	48	June 9, 1985
El Segundo Dunes, LAX (ESG) (Los Angeles County)	36	April 15, 1985
Balboa Beach (NB) (Orange County)	48	April 14, 1985
Silverstrand State Beach (SVS) (San Diego County)	48	July 13, 1985
Punta Estero (PE) (Baja California Norte, Mexico)	48	October 15, 1985
Guerrero Negro (GN) (Baja California Sur, Mexico)	50	October 18, 1985

id groupings. Gertsch has recently reviewed morphological variation in this genus and all references to morphological differences are based on personal communication with him.

Phylogenetic analysis.—The problem of estimating phylogenetic trees from electrophoretic data has generated a wealth of divergent opinion, some of it couched in very strong language (reviewed by Felsenstein 1982; Buth 1984). While many methods for phylogenetic tree construction from electrophoretic data have been proposed (Felsenstein 1982; Swofford & Olsen 1990), none has been universally accepted (Quicke 1993; Avise 1994). Because of this lack of agreement, we used a variety of methods to analyze the electrophoretic data set for *Lutica*, using allele frequencies, alleles as discrete characters and genetic distances. These methods are based on the two main approaches that do not assume a constant rate of molecular evolution across all taxa being compared, maximum parsimony (Edwards & Cavalli-Sforza 1963) and maximum likelihood (Edwards & Cavalli-Sforza 1964; Felsenstein 1981). Comparison of the trees generated by the various methods indicates those portions of the phylogeny that are unaffected by the different assumptions of each method (i.e., different methods may yield similar branching patterns for some or all taxa) and which therefore may be assumed to represent more accurately actual evolutionary relationships (Lanyon 1985; Avise 1994). Computer programs to carry out each of these methods are readily available. The particular programs/packages and specific computational procedures which were used are as follows:

Maximum parsimony: FREQPARS (version 1.0) (Swofford 1988) was used to conduct frequency parsimony analysis (Swofford & Berlocher 1987) of alleles at all loci, except those which were monomorphic across all populations (n) or $n - 1$ populations and therefore were phylogenetically uninformative. FREQPARS 1.0 has a very limited ability to search for the most parsimonious tree(s), so 19 runs of the data set were performed, with each OTU (operational taxonomic unit) in turn being placed first in the input file (following Rohlf & Wooten 1988). The shortest (i.e., most parsimonious) tree generated was retained.

HENNIG86 (version 1.5) (Farris 1988, 1989) was used for Wagner parsimony (Kluge & Farris 1969; Farris 1970) analysis of alleles as discrete characters, using presence/absence (1/0) coding for both complete (all alleles at frequencies > 0) and reduced (all alleles at frequencies ≥ 0.05) data sets (following Mickevich & Mitter 1981; C. Griswold pers. comm.), for all informative loci. The implicit enumeration (IE*) option of HENNIG86 was used to generate all most parsimonious trees for the complete and reduced

data sets, and then a strict consensus tree (Nelson 1979; Rohlf 1982) was computed for each set of most parsimonious trees.

BIOSYS-1 (version 1.7) (Swofford & Selander 1981, 1989) was used to perform distance Wagner analysis (Farris 1972; Swofford 1981) on a matrix of Rogers (1972) genetic distances for the *Lutica* populations; since Nei (1972, 1978) distances are non-metrical, which can result in negative branch lengths (Farris 1972; Nei 1987), they are not appropriate for use with distance Wagner analysis (Swofford 1981). Specifically, the DISWAG step call was invoked, with the multiple addition criterion (Swofford 1981) (maxtree = 30), Prager & Wilson's (1976) *F* goodness of fit criterion and outgroup rooting (Farris 1972) [with Guerrero Negro (GN) as outgroup] options. The shortest (i.e., most parsimonious) tree generated was retained.

Maximum likelihood: PHYLIP (versions 3.1 and 3.2) (Felsenstein 1988, 1989a, b) was used to generate maximum likelihood trees from the allele frequency data for the 19 *Lutica* populations using the CONTML program, with the G (global branch swapping), J (jumble addition, i.e., each OTU is added to the developing tree in random order) and O [outgroup rooting, with Guerrero Negro (GN) as outgroup] options invoked. Since CONTML does not perform exhaustive enumeration and evaluation of all possible tree topologies, the data set was run 19 times, with different random number seeds for the J option, following Felsenstein's (1981, 1989b) recommendation. Of the trees generated, the tree with the greatest likelihood was kept and the others were discarded.

Congruence.—Congruence among the phylogenies generated by the different methods was determined by the construction of consensus trees (reviewed by Rohlf 1982; Mickevich & Platnick 1989). In the present study, consensus trees were constructed for multiple trees generated by a single method (i.e., Wagner parsimony analysis of alleles as discrete characters with HENNIG86), as well as among the cladograms representing the best or consensus tree for each method. Because methods which generate multiple, equally likely trees might lead to misleading results with Adams (1972) consensus, strict consensus (Nelson 1979; Rohlf 1982) was used in such cases. On the other hand, in an effort to maximize taxonomic information, Adams consensus was used to determine congruence among the final (best or strict) trees produced by each method. To quantitatively assess congruence among the phylogenies generated by the different methods, two consensus measures were calculated (following Rohlf 1982 and Rohlf et al. 1983): the normalized consensus fork (CF) index of Colless (1980) and the CI_1 index of Rohlf (1982). Both congruence measures can range from 0.0 (totally dissimilar topologies) to 1.0 (identical topologies). The CONTREE program included with the PAUP (version 2.4.1) (Swofford 1985) computer package was used to generate consensus trees and calculate the consensus indices.

RESULTS

There were 43 alleles identified at the 15 genetic loci; two loci (APK-2 and G-3-PDH) were monomorphic across all populations and one locus (TPI-2) was autapomorphic (variable in only a single population) (Table 2). Tables of interpopulation genetic distances, mean genetic distances within and between *Lutica* species, and the data matrix of alleles coded as character states, which were used as the basis for some of the analyses reported herein, are available on request from the senior author.

Species identification.—The most striking feature of the allelic data (Table 2) is the genetic distinctness of the Guerrero Negro (GN) population: there are fixed differences at the FUM, HK and LDH loci; nearly fixed differences at the GPI (frequency of GPI-A = 0.990), IDH (frequency of IDH-C = 0.990) and PGM (frequency of PGM-A = 0.940) loci; and unique alleles at the AAT (AAT-A) and IDH (IDH-D) loci. In addition, the IDH-B allele, appearing at a frequency of 0.021 in only one other population [San Cruz Island (SCI)], is found at a frequency of 0.796 at Guerrero Negro. In light of the three fixed and three nearly fixed differences, the population of Guerrero Negro clearly represents a distinct species, our new species C. Spiders from this region are also a distinct group morphologically. Due to its genetic distinctness and the lack of certainty about which zodariid taxon would serve as an suitable outgroup for *Lutica*, Guerrero Negro was used as the outgroup in the phylogenetic analyses reported here.

In analyzing the data for the remaining populations for valid phylogenetic groups, the fixed difference at the NP locus is clearly indicative of common ancestry (and is not contradicted by data at other loci): populations 1–12 are fixed for NP-A and comprise our new species A. These are the mainland populations of Santa Barbara

and Ventura Counties, as well as the populations of the northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz) and three of the southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina). With the exception of Santa Barbara and Santa Catalina Islands, this is also a valid group morphologically.

As for the remaining populations (13–18), the electrophoretic data provide little basis for species decisions. The population of San Clemente Island (SCL), representing *clementea*, was not characterized by any fixed differences (Table 2) but did possess two unique alleles, though one was very rare: APK-1-A was found at a frequency of 0.132 and TPI-1-A was found at a frequency of 0.031. Among the mainland populations of southern California and northern Baja California, there were likewise no fixed differences that would conclusively indicate species status for any of these populations, though one locus indicated a close relationship between the populations of the Ballona Wetlands (BA) and El Segundo Dunes (ESG): at the PGM locus, the PGM-B allele was found at frequencies of 0.696 and 0.750 respectively and is found in only two other populations at frequencies of less than 0.05. Since the electrophoretic data are neutral with regard to the status of *clementea*, it will be accepted as a valid species. Likewise, while there are no allelic differences that would unite the mainland populations of southern California and northern Baja California as a group, morphological features define these populations as a distinct group (see also Thompson 1973). As such, they will be accepted as a valid species, our new species B.

Phylogenetic analysis.—We produced five estimates of the phylogeny of *Lutica* using methods which make no assumptions about evolutionary rates among taxa (i.e., frequency parsimony, distance Wagner, Wagner parsimony analysis of alleles as discrete characters and maximum likelihood). Trees generated by these methods have branch lengths which are proportional to the amount of evolutionary change which has occurred along each branch (Nei 1987; Swofford & Berlocher 1987). The trees generated by these methods for *Lutica* had branch lengths which were very unequal among the populations being compared. The distance Wagner tree (Fig. 2) is typical of the branch length variability which was present in all the trees; some populations (i.e., COP, MG, OX, LJB) have undergone considerable differentiation, while others (i.e., PE, NB) have changed much less. The unevenness of the branch lengths indicate that allelic evolution in *Lutica* has certainly not been clocklike.

In order to simplify comparisons among the phylogenies produced by the four rate independent methods, they are presented as cladograms in which only the branching patterns are shown (following Richardson et al. 1986) (Figures 3–7). These cladograms are consistent in the definition of two monophyletic groups: A) the large group A (= new species A) appears in all the cladograms [in that based on Wagner parsimony analysis of alleles as discrete characters using the complete data set (alleles > 0.0) (Fig. 5), the population of San Clemente Island (SCL) is also included in this group]; B) the Los Angeles County populations of the Ballona Wetlands (BA) and the El Segundo Dunes (ESG) form a clade that appears in all the cladograms. Within group A, two clades are found in all the cladograms: one consisting of the population of Coal Oil Point Reserve (COP), Santa Barbara County, and the Ventura County populations of McGrath State Beach (MG), Oxnard Beach (OX) and La Jolla Beach (LJB) [reflecting their common possession of the PEP-C allele at frequencies ranging to fixation (Table 2)]; and the other comprised of the populations of San Nicolas Island [Red Eye Beach (SNE), Dutch Harbor (SND), Army Camp Beach (SNA)] and at least one of the northern Channel Islands, usually Santa Rosa (SRI) [reflecting their common possession, except for Santa Cruz Island (SCI), of the LDH-C allele in frequencies ranging to fixation (Table 2)]. These relationships are accurately represented in the Adams consensus tree for these cladograms (Fig. 8).

The populations of new species B (including the BA - ESG clade) and *clementea* are placed in various positions among the five cladograms, with no consistent pattern of relationship, not surprising given the inconclusiveness of the electrophoretic data for these populations. San Clemente Island (*clementea*) is placed as the sister group to new species A in two cladograms (Figs. 3, 7); as sister group to new species A along with the populations of Balboa Beach (NB) and Punta Estero (PE) in one (Fig. 4); and as sister group to new species A along the with populations of the Ballona Wetlands (BA) - El Segundo Dunes (ESG) clade, Balboa Beach (NB) and Punta Estero (PE) in another (Fig. 6). As mentioned earlier, the remaining cladogram (Fig. 5) places San Clemente as part of new species A. The Adams consensus tree (Fig. 8) reconciles these differences by placing SCL, NB and PE as sister group

Table 2.—Allele frequencies in 19 populations of *Lutica* in California and Baja California. Species abbreviations are: CLE, *clementea*; NSP C, new species C. Population abbreviations follow Table 1.

Locus	New species A												CLE	New Species B					NSp C
Allele	COP	MG	OX	LJB	SMI	SRI	SCI	SBI	SNE	SNA	SND	CAT	SCL	BA	ESG	NB	SVS	PE	GN
Mean *n*	45	45	33	44	44	44	44	44	22	21	19	45	45	45	33	44	45	45	46
AAT																			
A																			0.010
B							0.021												0.796
C	1.000	1.000	1.000	1.000	1.000	0.979	0.979	1.000	1.000	1.000	1.000	0.948	1.000	1.000	1.000	1.000	1.000	1.000	0.194
D						0.021						0.052							
APK-1																			
A													0.132						
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.971	1.000	1.000	1.000	1.000	0.868	0.971	1.000	0.969	1.000	1.000	1.000
C								0.029						0.029		0.031			
APK-2																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
FUM																			
A								0.152											
B						0.011		0.152							0.044				
C	1.000	1.000	1.000	1.000	1.000	0.924	1.000	0.696	1.000	1.000	1.000	1.000	1.000	1.000	0.941	1.000	1.000	1.000	
D						0.065									0.015				1.000
G-3-PDH																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI																			
A								0.010	0.042			0.021		0.010			0.083	0.021	0.990
B	0.417	0.021			0.958	0.979	1.000	0.990	0.958	1.000	1.000	0.969	0.990	0.990	1.000	1.000	0.917	0.979	0.010
C	0.583	0.979	1.000	1.000	0.042	0.021						0.010	0.010						
HK																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
B																			1.000
IDH																			
A	0.010																		
B	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.979	1.000	1.000	0.875	1.000	1.000	1.000	1.000	0.865	1.000	
C									0.021			0.125					0.135		0.990
D																			0.010

Table 2.—Continued.

Locus	New species A												CLE	New Species B					NSp C
Allele	COP	MG	OX	LJB	SMI	SRI	SCI	SBI	SNE	SNA	SND	CAT	SCL	BA	ESG	NB	SVS	PE	GN
Mean *n*	45	45	33	44	44	44	44	44	22	21	19	45	45	45	33	44	45	45	46
LDH																			
A																			1.000
B	1.000	1.000	1.000	1.000	0.587	0.011	0.967	1.000				1.000	1.000	1.000	1.000	1.000	1.000	0.969	
C					0.413	0.989	0.033		1.000	1.000	1.000							0.031	
MDH																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.958	1.000	1.000	0.500	1.000	0.990	0.972	1.000	1.000	1.000	1.000
B									0.042					0.010	0.014				
C												0.500			0.014				
NP																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.021						
B													0.979	1.000	1.000	1.000	1.000	1.000	1.000
PEP																			
A	0.177	0.362	0.277																0.490
B	0.760	0.170	0.168		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.290
C	0.063	0.468	0.555	1.000															0.220
PGM																			
A														0.011					
B									0.042		0.025			0.696	0.750				
C																	0.219		
D	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.958	1.000	0.975	1.000	1.000	0.293	0.250	1.000	0.781	1.000	0.060
E																			0.940
TPI-1																			
A													0.031						
B	1.000	0.969	0.500	0.187	1.000	0.969	1.000	1.000	1.000	1.000	1.000	1.000	0.969	1.000	1.000	1.000	1.000	1.000	1.000
C		0.031	0.500	0.813		0.031													
TPI-2																			
A					0.098														
B	1.000	1.000	1.000	1.000	0.902	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

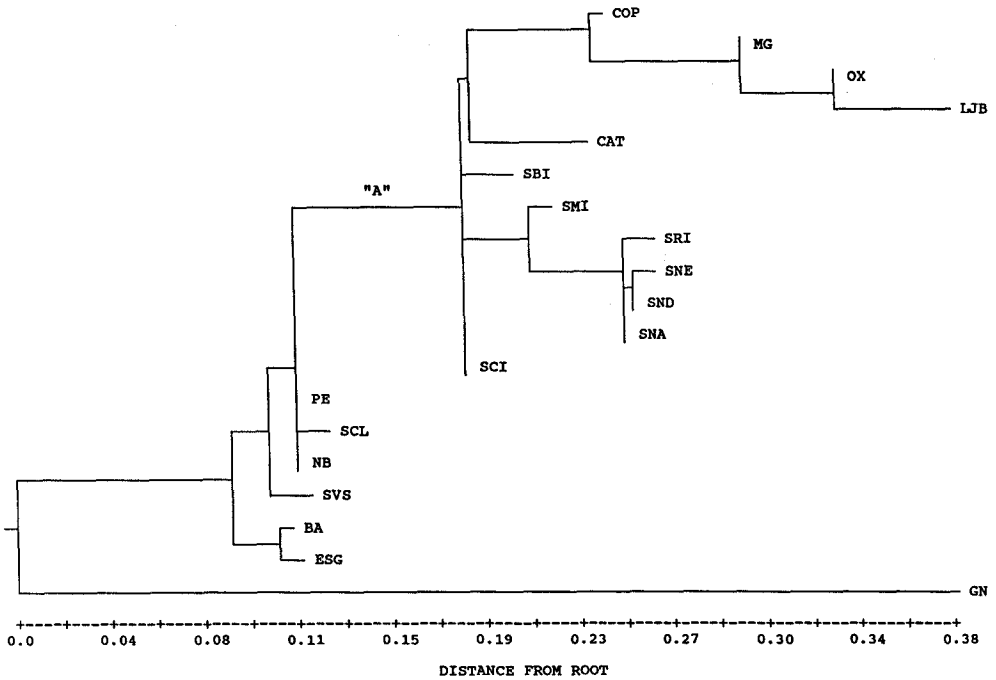

Figure 2.—Phylogenetic tree generated using distance Wagner method (Farris 1972; Swofford 1981) with multiple addition criterion (Swofford 1981) and outgroup rooting (Farris 1972), with Guerrero Negro (GN) as outgroup. The distance measure used is Rogers (1972). Total length of tree = 0.984 and Prager & Wilson's (1976) $F = 4.985$.

to new species A. Finally, in four of the five cladograms (Figs. 3, 5–7), the population of Silverstrand State Beach (SVS) is placed as the sister group to all other ingroup populations, while in the one exception (Fig. 4), the BA - ESG clade is placed in this position. The consensus tree resolves this difference by placing both SVS and the BA - ESG clade as sister group to all other populations (Fig. 8). This last feature of Fig. 8 illustrates one of the problems with Adams consensus trees: in none of the original cladograms is a clade comprised of SVS and BA - ESG placed as the sister group to all other ingroup populations. Given the differences in topology among these cladograms, it is not surprising that consensus indices for the Adams consensus tree are not high: Colless' (1980) CF = 0.471 and Rohlf's (1982) $CI_I = 0.400$.

To focus specifically on the phylogenetic relationships of the species themselves, the population data for new species A and B were combined into single species samples and the analyses reported above were repeated for the four OTUs (new species A, B, C, *clementea*), with the sole exception that Wagner parsimony of alleles as discrete characters was not performed for the reduced data set (alleles ≥ 0.05), due to the exclusion of practically all alleles under such a restriction. The cladograms produced by each method are shown in Fig. 9, A–D and the Adams consensus tree is shown in Fig. 9E. For three OTUs, there are three possible relationships [A(BC), C(AB), B(AC)] and all three are seen for the ingroup taxa among the cladograms in Fig. 9, A–D, although those produced by frequency parsimony (A) and maximum likelihood (D) are identical and place new species B and *clementea* as sister groups, as might be expected given their minimal genetic distance [Nei (1978) unbiased genetic distance: 0.017 (Ramirez 1990)]. Since the topologies of these cladograms covered all the possibilities for a three taxon statement, the Adams consensus tree presents the relationships among the three ingroup species as a unresolved trichotomy, although the consensus indices for this tree were fairly good [Colless' (1980) CF = 0.500 and Rohlf's (1982) $CI_I = 0.667$], reflecting the perfect agreement between two cladograms. Thus, while two of the cladograms agreed in the placement of new species B and *clementea* as sister groups, these results were contradicted by the topologies of the other two cladograms, so

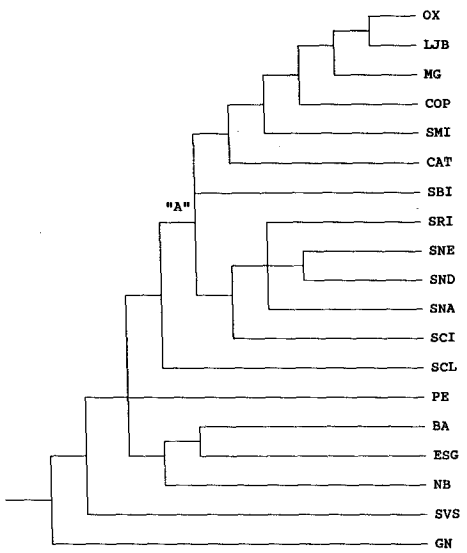

Figure 3.—Cladogram for *Lutica* based on the shortest tree generated using the frequency parsimony method (Swofford & Berlocher 1987) and outgroup rooting (Farris 1972), with Guerrero Negro (GN) as outgroup. The frequency parsimony method minimizes tree length in the Manhattan metric (Sneath & Sokal 1973); total length of shortest tree = 29.509. Alphabetic designation "A" denotes new species A.

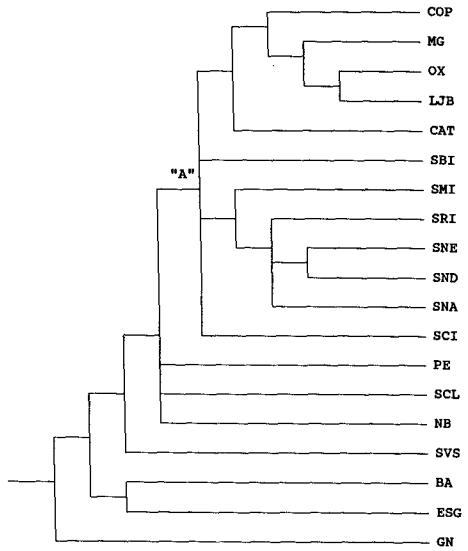

Figure 4.—Cladogram for *Lutica* based on the shortest tree generated using the distance Wagner method (Farris 1972; Swofford 1981), which is shown in Fig. 2. Alphabetic designation "A" denotes new species A.

the electrophoretic data were not able to conclusively determine phylogenetic relationships among the ingroup species.

DISCUSSION

Electrophoresis and morphology.—The genus *Lutica* occupies a long geographic range (approximately 1857 km) yet is relatively invariant morphologically. Gertsch (pers. comm.) uses features of the male palpi to discriminate species and only in *clementea* and the populations of central and southern Baja California are the differences in these structures clearly distinct. An analysis of variation among *Lutica* specimens involving 23–29 morphological characters (Thompson 1973) did not find statistically significant differences (M. Thompson pers. comm.).

The genus *Lutica* is also relatively invariant genetically: Ramirez (1990) found low levels of genetic variability among *Lutica* populations, as well as a general trend toward within population homozygosity. As a presumably old genus (Ramirez 1990), the existence of low genetic variability was unexpected and an analysis of the genetic structure of each species suggests that inbreeding, a spatial Wahlund effect due to local probabilities of random mating and environmental homogeneity associated with a subterranean existence in coastal dune ecosystems may be the most likely causes of low variability in *Lutica* (Ramirez 1990).

The electrophoretic data define an outgroup [Guerrero Negro (GN), new species C] and two nested ingroups: first, populations 1–18, and nested within that, populations 1–12 (new species A). Morphological data indicate the specific distinctness of the population of San Clemente Island (*clementea*) (Gertsch 1961, pers. comm.), whereas the electrophoretic data were neutral. The electrophoretic data were likewise inconclusive with regard to the status of the mainland populations of southern California and northern Baja California but since they are morphologically a valid group, they are assigned to new species B. Future electrophoretic studies involving more loci (only 12 of the 15 loci were phylogenetically informative) may eventually result in the discovery of diagnostic loci for these mainland populations (new species B), as well as for *clementea*.

The morphological systematics of the genus *Lutica* has been in a state of flux for many years (M. Thompson pers. comm.; W. Gertsch pers. comm.) and electrophoretic variation (particularly fixed allelic differences) is probably a more

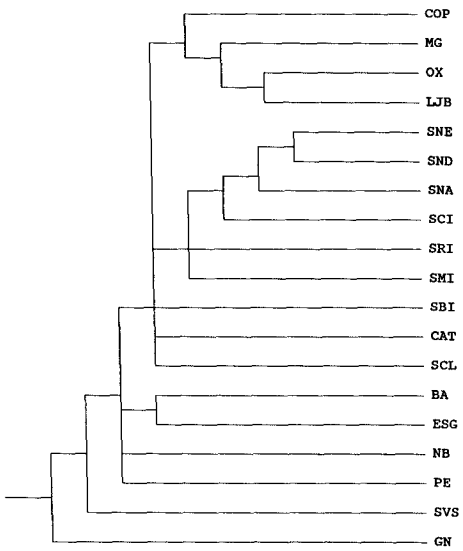

Figure 5.—Cladogram for *Lutica* based on strict consensus tree (Nelson 1979; Rohlf 1982) of 10 trees of 43 steps each with consistency indices of 0.442 generated using Wagner parsimony (Kluge & Farris 1969; Farris 1970), with alleles treated as characters with frequency greater than 0 = present. Consistency index = 0.410.

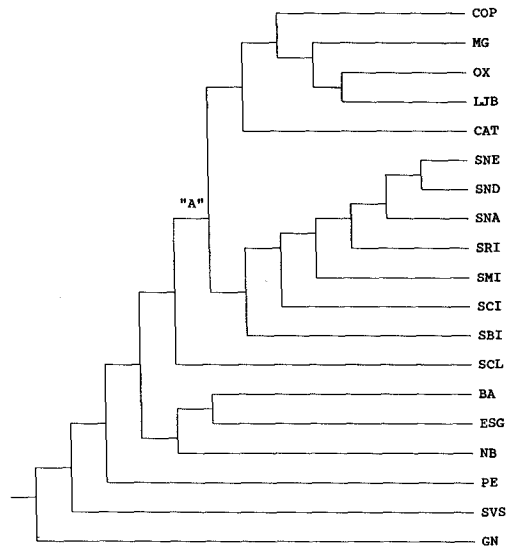

Figure 7.—Cladogram for *Lutica* based on the tree of highest likelihood generated by the restricted maximum likelihood method (Felsenstein 1981) and outgroup rooting (Farris 1972), with Guerrero Negro (GN) as outgroup. Ln Likelihood = 879.074. Alphabetic designation "A" denotes new species A.

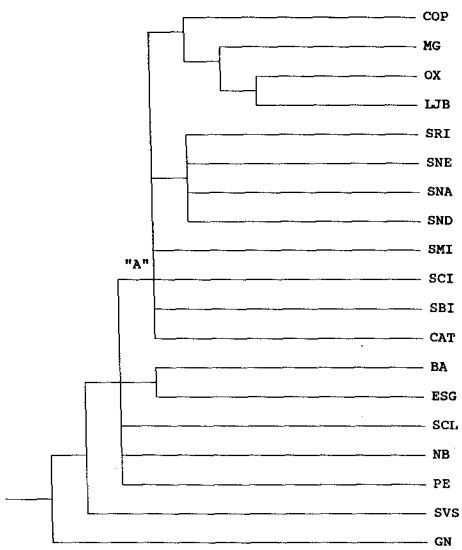

Figure 6.—Cladogram for *Lutica* based on strict consensus tree (Nelson 1979; Rohlf 1982) of eight trees of 21 steps each with consistency indices of 0.610 generated using Wagner parsimony (Kluge & Farris 1969; Farris 1970), with alleles treated as characters with frequency greater than or equal to 0.05 = present. Consistency index = 0.590. Alphabetic designation "A" denotes new species A.

reliable indicator of taxonomic relationships than morphological features for this genus. An obvious disagreement between our species assignments and those of Gertsch (1961) concerns the status of the populations of San Nicolas and Santa Rosa Islands and Oxnard, Ventura County: each is considered a distinct species (*nicolasia*, *maculata* and *abalonea*, respectively), while we place them all in new species A. Due to the fixed difference at the NP locus, the assignment of these populations to new species A is unambiguous on genetic grounds. Gertsch (pers. comm.) began a revision of *Lutica* prior to his deteriorating health and so a detailed comparison of the population groupings indicated by morphological and electrophoretic characters will have to await its completion and publication.

Phylogeny and speciation in *Lutica*.—The fact that the genetic distance between new species B and *clementea* (0.017) is several orders of magnitude less than the other inter-specific estimates [0.138–0.796, all Nei (1978) unbiased distances (Ramirez 1990)] would suggest that these taxa were originally a single species that only recently diverged. If this is the case, one would predict that these species should be placed as sister groups in any phylogeny, as a clade that is the sister group to new species A. However, while this was

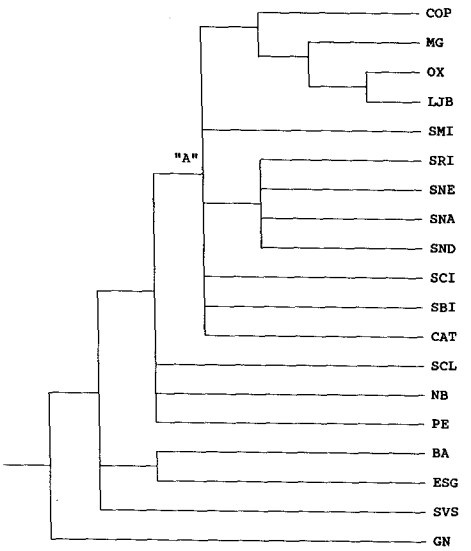

Figure 8.—Adams (1972) consensus tree based on cladograms of Figs. 3–7. Consensus indices for this tree are: Colless' (1980) CF = 0.471 and Rohlf's (1982) CI_I = 0.400. Alphabetic designation "A" denotes new species A.

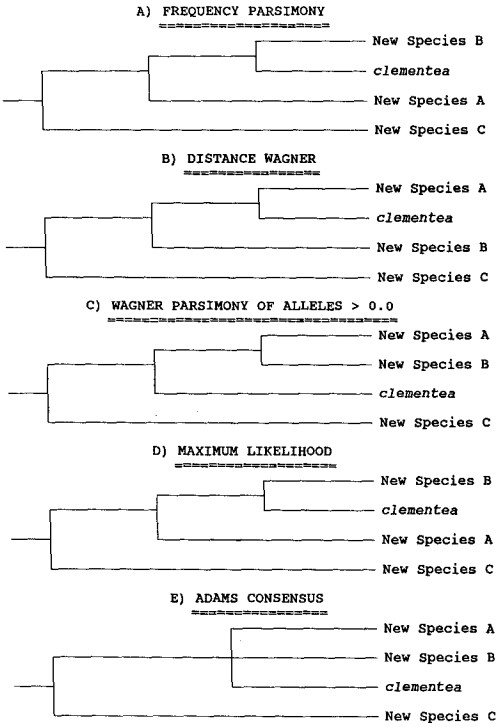

Figure 9.—Cladograms for *Lutica* species. (A) Cladogram based on the shortest tree generated using the frequency parsimony method (Swofford & Berlocher 1987) and outgroup rooting (Farris 1972), with new species C (Guerrero Negro) as outgroup. The frequency parsimony method minimizes tree length in the Manhattan metric (Sneath & Sokal 1973); total length of shortest tree = 18.160. (B) Cladogram based on the shortest tree generated using the distance Wagner method (Farris 1972; Swofford 1981), with multiple addition criterion (Swofford 1981) and outgroup rooting (Farris 1972), with new species C (Guerrero Negro) as outgroup. The distance measure used was Rogers (1972). Total length of shortest tree = 0.616 and Prager & Wilson's (1976) $F = 1.857$. (C) Cladogram based on the shortest tree generated using Wagner parsimony (Kluge & Farris 1969; Farris 1970), with alleles treated as characters with frequency greater than 0 = present. Total length of shortest tree = 16 steps and consistency index = 0.680. (D) Cladogram based on the tree of highest likelihood generated by the restricted maximum likelihood method (Felsenstein 1981) and outgroup rooting (Farris 1972), with new species C (Guerrero Negro) as outgroup. Ln Likelihood = 53.788. (E) Adams (1972) consensus tree based on cladograms presented in A–D. Consensus indices for this cladogram are: Colless' (1980) CF = 0.500 and Rohlf's (1982) CI_I = 0.667.

the case in two of the species cladograms (Fig. 9A, D), these relationships were contradicted by the topologies of the other two cladograms (Fig. 9B, C).

It should be noted that the two cladograms which depict new species B and *clementea* as sister groups (Fig. 9A, D) are the products of phylogenetic methods (frequency parsimony and maximum likelihood) which use allele frequency data directly. Methods which use allele frequencies may be superior because they avoid the loss of phylogenetic information and the procedural/theoretical complexities associated with the reduction of such data to distances or characters (Berlocher 1984; Swofford & Berlocher 1987). On the other hand, allele frequencies are subject to the effects of random drift and/or selection and can vary over time, and so may not provide reliable information for analysis (Crother 1990). Given the continuing controversy about allele frequencies and the potential superiority of phylogenetic methods which make direct use of them (e.g., Shaffer et al. 1991; Jones et al. 1993), a firm conclusion concerning the relationship of new species B and *clementea* within *Lutica* will have to await a future phylogenetic analysis.

Biogeography of *Lutica* in southern California and Baja California.—The phylogenetic relationships among the populations consistently

supported by the electrophoretic cladograms and depicted in the Adams consensus tree (Fig. 8) reflect the evolutionary relationships of these fossorial spiders and suggest probable scenarios for the historical colonization of some of the Channel Islands. In most instances, the electrophoretic data correspond well with the known geological history of the islands and adjacent mainland. During the late Pleistocene, eustatically lowered sea levels united the four northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa) into a single land mass, Santarosae (Orr 1968). Santarosae began its final breakup only about 16,000 years ago (Vedder & Howell 1980; Johnson 1983). The former physical connection of San Miguel, Santa Rosa and Santa Cruz Islands appears to be reflected in the close genetic relationship of the *Lutica* populations of these islands: all three island populations are members of new species A and in four of the five cladograms (Figs. 3–5, 7), at least two of these three islands are placed in the same clade within new species A. In contrast, the southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina, San Clemente) were never physically connected (Vedder & Howell 1980; Johnson 1983). Since two of these islands (San Nicolas and Santa Barbara) were submerged during the middle Pleistocene (Johnson 1983), they derived their biota from other sources since that time. The fact that the *Lutica* populations of the two southern islands which were not submerged, Santa Catalina and San Clemente, are considered to be very different on both electrophoretic and morphological grounds is indicative of the absence of significant gene flow that would have been provided by an inter-island connection and may reflect the fact that these islands were originally far apart, prior to San Clemente's arrival at its present location due to terrane transport (Crouch 1979; Hornafius et al. 1986).

The mainland populations of new species A and B are only about 57 km apart at their southern and northern boundaries respectively [between La Jolla Beach (LJB), Ventura County and the Ballona Wetlands (BA), Los Angeles County] yet spiders from these regions are members of different taxa. This disjunction may simply reflect the fact that there are no relatively continuous dune systems in the intervening coastal area between Ventura County and Los Angeles (Cooper 1967; Powell 1981) which might act as a corridor for gene flow between these species. On the other hand, this disjunction may be associated with geologic changes that occurred in this region beginning in the Pliocene. During this time the Los Angeles basin was flooded (Murphy 1983a), which, coupled with the northward extension of the Sea of Cortez, caused complete isolation or severe restriction of the movements of organisms to and from Baja California at its northern end (Durham & Allison 1960), a situation which lasted till the Pleistocene (Murphy 1983a). This so called San Gorgonio Barrier has been implicated as a historic biogeographic obstacle for the movement of certain xeric-adapted reptiles (Murphy 1983b) and may be at least partly the cause of the disjunction between the mainland populations of *Lutica* from its northern (new species A) and central (new species B) mainland regions.

The Vizcaino Peninsula has alternately been united with and separated from Baja California by sea level changes since the Eocene (Durham & Allison 1960; Murphy 1983a). Since an arid desert lies between this region and the northern portion of Baja (Crosswhite & Crosswhite 1982), it is probable that the divergence between the *Lutica* populations of the Vizcaino Peninsula and those of northern Baja California is an ancient one, as has been shown for the vegetation of these regions (Axelrod 1979, 1980). The considerable genetic and morphological differences between the population of Guerrero Negro (new species C) and populations to the north is consistent with the geologic history outlined above and indicates a long absence of gene flow between spiders of these two regions.

Patterns of colonization.—Some of the genetic relationships are indicative of certain likely colonization events involving the Channel Islands. These will be reviewed for each island or group of islands in the sections which follow.

Northern Channel Islands, Santa Barbara and San Nicolas Islands: The populations of San Nicolas Island were consistently most closely grouped with one of the northern Channel Islands (usually Santa Rosa), indicating probable colonization of this formerly submerged southern Channel Island from the islands 80 km to the north. Santa Barbara Island was also submerged in the Pleistocene and is also a member of new species A. Since there is no particular population(s) with which it is consistently grouped, all that can be deduced is that colonists of Santa Barbara were derived from one of the new species A populations, most of which are located to the north. In the case of both San

Nicolas and Santa Barbara, rafting colonists from the north would have been aided by south flowing ocean currents and prevailing northwest winds that have been implicated in the dispersal of other organisms in this region (examples in Power 1980; Cowen 1985), as well as the south flowing longshore current (Ledig & Conkle 1983). However, the ocean current patterns in this region are not invariant and the southward flowing California Current is known to reverse its direction during El Niño events (Cowen 1985), perhaps making it possible for propagules to drift northward from Santa Catalina Island to Santa Barbara Island.

The fact that the *Lutica* populations of the northern Channel Islands and adjacent mainland of Santa Barbara and Ventura Counties are members of the same species is typical of the close relationships that have been reported for island and mainland populations of other organisms in this region (e. g., sand crickets, Rentz & Weissman 1973; Weissman & Rentz 1976; deer mice, Ashley & Wills 1987). Indeed, 89% of the orthopteran fauna of the northern Channel Islands also occurs in the Santa Monica Mountains (Rentz & Weissman 1981). While the general interpretation of such distributions and relationships has been that colonists from the adjacent mainland founded the island populations (Rentz & Weissman 1981; Ashley & Wills 1987), the geologic relationships among the islands and mainland were considerably different in the past, rendering considerations of dispersal among what may be recent subdivisions possibly suspect. For example, the northern Channel Islands were situated as much as 8° to the south of their present locations during the middle Miocene, prior to northward transport on a terrane (Kamerling & Luyendyk 1985). The southern origin for these islands may mean that the actual colonists of these islands came from mainland populations of southern California or Baja California. On the other hand, the populations of these islands and the adjacent mainland were perhaps established at more or less the same time by colonists from San Clemente Island or mainland populations of new species B. While these and other colonization scenarios may be plausible, the electrophoretic data do not allow one to determine directions of colonization between the island and mainland populations of new species A, nor do they establish the actual sister group of this species, rendering consideration of mainland-island colonization scenarios involving populations of this species unwarranted at this time.

Santa Catalina Island: Since Santa Catalina Island (along with Santa Rosa and Santa Cruz Islands) may have been continuously above water since the Oligocene (Vedder & Howell 1980; Haq et al. 1987), has remained relatively stationary during this period (Luyendyk et al. 1985) and is close to the southern California mainland, one would expect that its closest biotic relationship should be with populations from the adjacent Los Angeles–San Diego coastal strip. However, we have shown that the *Lutica* population of Santa Catalina is most closely related to new species A populations rather than populations on the southern California mainland. The most parsimonious explanation for such a relationship is that spiders from the adjacent mainland never colonized Santa Catalina and so new species A spiders were the first and only colonists. On the other hand, such a pattern of relationships may be due to the extinction of an original insular form derived from the mainland prior to colonization by new species A spiders or because new species A spiders proved to be superior in competition with the native insular form. Separate colonizations of Santa Catalina Island from the northern Channel Islands and southern California mainland have been proposed for Channel Island deer mice, *Peromyscus maniculatus*, due to mitochondrial DNA restriction fragment polymorphisms found among Santa Catalina Island mice (Ashley & Wills 1987). Extinction has also been suggested to explain the distribution of the island night lizard, *Klauberina*, which is found on San Clemente, San Nicolas and Santa Barbara Islands but not on Santa Catalina Island (Crother et al. 1986; Bezy & Sites 1987).

San Clemente Island: A biogeographic relationship between San Clemente Island and Baja California has been proposed by Crother et al. (1986), based on a cladistic study of morphology and karyology within the lizard family Xantusiidae and a vicariance model based on terrane movement linking San Clemente and central Baja California. Based on geophysical evidence (Crouch 1979; Hornafius et al. 1986), it is clear that San Clemente Island was in close proximity to central Baja California up to about 18 million years ago, when the terrane on which it is situated started moving north along the San Clemente Island Fault, eventually reaching its present position about 5–8 million years ago. Crother et al. (1986) hypothesize that relatively sedentary taxa

(like xantusiid lizards) which occupied San Clemente Island and the adjacent mainland of Baja California prior to the time of northward movement (and whose descendants continue to occupy these areas today) should be closely related.

Since *Lutica* is clearly sedentary and has distinct species which occupy San Clemente Island (*clementea*) and central Baja California (new species C), we hoped to be able to test Crother et al.'s (1986) vicariance hypothesis using the electrophoretic data reported herein. However, given the need to use Guerrero Negro (new species C) as an outgroup in our phylogenetic analyses, in the absence of an appropriate zodariid taxon, it was not possible to determine whether *clementea* is indeed most closely allied with new species C of central Baja California. As such, a final decision concerning *Lutica*'s involvement in the biogeographic hypothesis of Crother et. al. (1986) will have to await a future phylogenetic analysis using an actual outgroup taxon.

SUMMARY

The geological history of the California Channel Islands and mainland of southern California and Baja California involves extensive sea level changes and the movement of terranes. These geomorphic changes may have influenced the evolution of taxa in this region, particularly if they are sedentary and biologically old.

Analysis of the results of an electrophoretic survey of populations of the spider genus *Lutica* from much of its range revealed fixed allelic differences that clearly define two species: new species A [Santa Barbara and Ventura Counties, northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz), southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina)] and new species C [Guerrero Negro, central Baja California]. While diagnostic loci were not found for the population of San Clemente Island (*clementea*) or the mainland populations of southern California and northern Baja California, they are morphologically recognizable units according to Gertsch, so *clementea* was accepted as valid, while the mainland populations were assigned to new species B.

Phylogenetic analysis of the electrophoretic data using a variety of methods revealed that evolutionary rates among the 19 populations sampled have been very unequal. The phylogenetic relationships among populations consistently supported by the electrophoretic cladograms generally correspond with the geological history of the Channel Islands and adjacent mainland and suggest certain likely colonization events involving some of the islands.

A future electrophoretic study of *Lutica* involving more loci and a zodariid taxon as an outgroup (chosen in light of Jocqué 1991) is needed to A) genetically validate the species status of the mainland populations of southern California and northern Baja California, as well as of *clementea*, and B) to resolve the phylogenetic relationships among the four species (new species A, B, C, *clementea*). Further systematic studies of other monophyletic taxa (particularly those which are biologically old and poor dispersers) occupying the California Channel Islands and mainland of southern California and Baja California are needed to better understand the geologic and biogeographic evolution of this region. Given the lack of even basic knowledge concerning many taxonomic groups in this area, particularly among the invertebrates, this will be a fruitful area for the conduct of systematic and biogeographic studies.

ACKNOWLEDGMENTS

We are particularly indebted to W. Gertsch for sparking our initial interest in *Lutica* and to M. Thompson for sharing with us his field notebooks and maps based on his own *Lutica* collecting efforts in the 60's and 70's. C. Cutler, C. Drost, W. Icenogle, M. Wilson and members of the Arachnologists of the Southwest provided assistance in the field. K. Akiyama, A. Jimenez and M. Sandoval, participants in the National Institutes of Health Minority High School Student Research Apprentice Program, were expert co-workers in the lab in the summer of 1987, while R. Garthwaite was a continuing source of technical advice concerning electrophoretic procedures. T. Cranford and K. Huie provided general computer advice and D. Wake and M. Frelow helped with analysis of our data using BIOSYS-1. R. Bennett, J. Cronin, J. Estes, L. Fox, C. Griswold and D. Potts offered many constructive comments on various drafts of this manuscript.

For providing collecting permits and access to various mainland localities, we thank: S. Clarke, Marine Science Institute, University of California, Santa Barbara; P. Principe, Department of Airports, City of Los Angeles; and the California Department of Parks and Recreation. For providing collecting permits and access to the California Channel Islands, and for providing lodg-

ing and transportation while on the islands, we are grateful to: W. Ehorn and F. Ugolini, Channel Islands National Park; S. Clarke, Marine Science Institute, University of California, Santa Barbara; L. Laughrin, Santa Cruz Island Reserve; A. Propst and T. Martin, Santa Catalina Island Conservancy; S. Bennett and R. Turner, Catalina Island Marine Institute; J. Estes, U.S. Fish and Wildlife Service; R. Dow, J. Larson and L. Salata, U.S. Navy. Financial support was provided by grants from a variety of sources at the University of California, Santa Cruz (Div. of Natural Sciences, Graduate Studies and Research, Dept. of Biology, Patent Fund, Minority Biomedical Research Support Program) and by a grant from the Exline-Frizzell Fund for Arachnological Research (Grant No. 10).

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Manuscript received 26 November 1994, revised 6 September 1995.