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Geographic isolation in southwestern North American butterflies (Lepidoptera, Rhopalocera)

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Abstract: Several cladistic studies of western United States butterflies have geographically isolated taxa as basal within their clades. Here various southwestern North American butterfly species and subspecies are identified as geographic isolates that could be tested by future cladistic and genetic studies to determine if this pattern is a general rule. In the punctuated equilibrium model, comparatively rapid speciation rates occur when small, isolated populations adapt to new, stressful environments. The isolated butterfly taxa are shown to largely conform to this constraint. Their Neogene history is partially reconstructed from their zoogeographic affinities, Bering landbridge availability times, paleoclimatology, paleobotany, mountain range uplift times, and sealevel oscillations.

Geografische Isolation bei Tagfaltern des südwestlichen Nordamerikas (Lepidoptera, Rhopalocera)

Zusammenfassung: Kladistische Studien an Tagfaltern der westlichen Vereinigten Staaten ergaben für verschiedene Verwandtschaftsgruppen basale Verzweigungen zu isolierten Taxa. Weitere hier vorgestellte geografische Isolate im südwestlichen Nordamerika könnten in zukünftigen kladistischen und genetischen Studien darauf getestet werden, ob es sich dabei um eine generelle Erscheinung handelt. Im „Punctuated Equilibrium"-Evolutionsmodell wird eine vergleichsweise schnelle Artbildungsgeschwindigkeit vorausgesagt, wenn kleine, isolierte Populationen sich an neue, „streßvolle" Habitate anpassen müssen. Die aufgeführten Fallbeispiele entsprechen größtenteils diesen Vorhersagen. Ihre neogene Historie wird mit Hilfe von zoogeografischen Affinitäten, den Perioden einer durchgängigen Bering-Landbrücke, paläoklimatischen und paläobotanischen Daten, den Hebungsperioden der Gebirge und den Meeresspiegelschwankungen zu erklären versucht.

Introduction

Modern evolutionary theory views some species as originating allopatrically in a very small, isolated population at the margin of the ancestral species range or on oceanic islands in geographic isolation from the mainland population. These founder, satellite populations occupy new, often harsh environments that are stressful, such as seacoasts, local semiarid or arid sites, once active volcanoes, mountain summits, canyon bottoms, marshes, or glacial refugia (nunataks), i.e. specialized habitats that are greatly restricted in distribution. Isolating barriers include lowland deserts, high mountain rain shadow effects, lava flows, glaciations, and oceans. This is the punctuated equilibrium model of evolutionary change when extended to geological time (cf. AXELROD 1967, GOULD & ELDREDGE 1977, STANLEY 1979, VRBA 1980, BROWN & GIBSON 1983, HAMMOND 1990, COLLINS 1991). A number of examples are discussed by GOULD & ELDREDGE (1977). Perhaps the clearest examples are several rapid speciation events that abruptly occurred in Wyoming early Eocene condylath mammals at faunal turnover times that were not connected by intermediates, based on nearly 1400 fossil specimens in dense chronological sequence (GINGERICH 1985). In contrast, a peripheral population that occupies a relatively non-stressful habitat evolves very slowly and would thus remain plesiomorphic, not apomorphic, relative to the large central population over time (cf. FREY 1993).

Geographically isolated populations may be founded by only a few individuals that have been cut off from the main population for gene flow and thus possess only a small fraction of the parental species genetic variability (founder effect). Mutations have a much better chance of becoming homozygous in small isolated populations than in large panmictic ones, while genetic drift and catastrophic selection become very important to small populations in the initial shifting of characteristics away from parental populations. Great random fluctuations in gene frequencies especially occur when a small population undergoes maximal contraction in size, producing chance fixation or loss of alleles (KING 1962). The spatial isolation is geographical, ecological, and reproductive, with the resulting evolutionary changes proceeding at a much faster rate than in larger populations. For geographically isolated subspecies, however, reproductive isolation has not yet been fully achieved. Environmental stress creates opportunities for new forms to become established by strongly selecting against all those particular individuals that are stress-intolerant (DIMICHELE et al. 1987). The isolated population's seasonal fluctuations in numbers will affect their genetic variation much more so than in the larger parent populations (FORD 1949). Survival of a geographically isolated population involves specialized adaptation to the new, local habitat that eventually leads to taxonomic divergence and adaptive radiation (LOVTRUP 1982).

Allopatric speciation by gradual divergence of races or subspecies now appears unlikely due to the difficulties of sufficient enough gene flow and uniform directional selection (Levin 1993, Rieseberg & Brouillet 1994). However, allopatric vicariant speciation of a widespread ancestral species may be the common method of speciation (Rosen 1978, Cracraft 1982).

In butterflies, another method of species formation occurs in sibling species, i.e. young species-pairs that have fairly recently evolved within already-existing clades. Here the speciation can be either parapatric (e.g. *Erynnis telemachus* Burns 1960 and *E. juvenalis* (Fabricius 1793)) or sympatric (in *Lethe* Hübner 1819, *Celastrina* Tutt 1906, and *Celotes* Godman & Salvin 1899) (cf. Burns 1960, 1974, Cardé et al. 1970, Clench 1972, Heitzman & dos Passos 1974). The common denominator in these examples is reproductive isolation by male genitalia modification, although this lock-and-key hypothesis has recently been questioned (see Shapiro & Porter 1989). In a species-pair of *Tatochila* Butler 1870 from Patagonia, a difference in the sclerotization of the female genitalia is not enough to prevent intergradation where their ranges come into contact (Shapiro 1986), although there is some question that these are in fact two different species since they readily hybridize in the lab.

Cladistics

The most primitive species of a clade is probably closer to the area once occupied by the ancestral species than are the more synapomorphic members, with environmental constancy maintaining primitiveness (Horton 1973). The most plesiomorphic (least apomorphic) taxon of a clade occupies a part of what was once the ancestor's distributional range (Bremer 1992). The immediate ancestor, which has invariably long since become extinct or modified, is morphologically most similar to its immediate descendant taxon and possesses only plesiomorphies relative to all of its descendants. The ancestor itself is the stem species of the clade and is a paraphyletic taxon relative to the clade (Nelson & Platnick 1984, Ax 1985). It is also conceivable, however, that during drastic environmental changes in the past, the ancestral species itself became restricted to a localized relictual environment (Axelrod 1948), which might explain why no immediate ancestral species seemingly survive. If this is the case, the geographically isolated populations themselves would be surviving ancestors (stem species) and would occupy the closest outgroup position for the clade.

Polarization of character states is determined by the outgroup selected, but unfortunately many cladograms are generated without choosing the most appropriate outgroup for the analysis, resulting in errors (Mooi 1989). Stratigraphy provides the time dimension and can confirm or deny morphologically based cladograms by testing for congruence (Laws & Fastovsky 1987) but is of limited use in butterflies where the fossil record is decidedly poor.

Cladistic methods are capable of testing to see if the species or subspecies with a restricted, isolated distribution occupies the most plesiomorphic or basal position within that clade. One such example is in the *Lycaena rubidus* (Behr 1866) complex (Johnson & Balogh 1977, Pratt et al. 1991). *Lycaena ferrisi* K. Johnson & Balogh 1977 is confined to only several localities in the White Mountains of Arizona and is cladistically basal to *L. rubidus* which contains five subspecies all having slightly (*monachensis* K. Johnson & Balogh 1977) to much wider distributions in western United States. Another is in *Argynnis (Speyeria) callippe* (Boisduval 1852), where *A. c. callippe* and *A. c. comstocki* (Gunder 1925) basally split off before the other 11 subspecies in the cladogram (Hammond 1990, fig. 3). Nominate *A. callippe* has the most restricted range of any of the subspecies, existing only on the San Francisco Peninsula (Howe 1975, Hammond 1985) and the Berkeley Hills (R. A. Arnold, pers. comm.). Cladistic analysis of western North American butterflies has not as yet been performed on other genera or species complexes that contain isolated taxa, so it is too early to know if this is a general pattern. There is, of course, at least the possibility that an isolated taxon could be very recent in origin (Cook 1961), especially for subspecies.

One cladogram does not identify the most isolated taxon as basal in Nearctic *Colias* Fabricius 1807 species (Ferris 1993), a position held by *C. johanseni* Troubridge & Philip 1990 instead of *C. philodice* Godart 1819 or *C. eurytheme* Boisduval 1852. However, the most appropriate outgroup may not have been selected since *Zerene* Hübner [1819] is likely more advanced than is *Colias* (C. D. Ferris, in litt.), and some character states were unfortunately scored as separate characters in the analysis.

Methods and materials

A literature survey was conducted of taxonomic and distributional studies on southwestern North American butterflies to determine which species and subspecies are the most restricted in distribution of their respective clades. To qualify as a geographically isolated taxon, an arbitrary distributional range limit of 70 km or less was imposed. Their habitats were subsequently analyzed to see how well they fit the criteria for founder taxa occupying stressful, specialized environments. Zoogeographic affinities for some of the taxa were then determined from the literature to sort out Neotropical from Palearctic elements. Finally, their paleobiogeographical history in Neogene times was partially reconstructed, based largely upon Palearetic source areas, Bering landbridge crossing-times, and the Neogene vegetation and climatic history in the Bering Strait vicinity.

A thorough analysis of all geographically isolated butterfly taxa in southwestern North America proved impractical, so only those that are reasonably assurred of being so are reported. Some groups contain several to many isolated taxa such that determining which one is the most isolated is problematic. These taxa include *Agathymus* H. A. FREEMAN 1959, *Megathymus coloradensis* C. V. RILEY 1877, *Polites sabuleti* (BOISDUVAL 1852), *Papilio indra* REAKIRT 1866, *Parnassius clodius* MÉNÉTRIES 1855, *Coenonympha tullia* MÜLLER 1764, *Argynnis (Speyeria) atlantis* (W. H. EDWARDS 1862), *A. mormonia* (BOISDUVAL 1869), *Boloria (Clossiana) improba* (BUTLER 1877), *Euphydryas chalcedona* (DOUBLEDAY 1847), *Plebeius icarioides* (BOISDUVAL 1852), *Glaucopsyche lygdamus* (DOUBLEDAY 1841), *Callophrys (Incisalia) fotis* (STRECKER 1878), and *Apodemia mormo* (C. & R. FELDER 1859). Also, a few taxa originally described as isolated are now known to be wider-ranging, such as *Euchloe guaymasensis* OPLER 1986, *Oeneis nevadensis iduna* (W. H. EDWARDS 1874), *Coenonympha tullia yontocket* PORTER & MATTOON 1989, *Argynnis (Speyeria) hydaspe viridicornis* (J. A. COMSTOCK 1925), *Lycaena arota nubila* (J. A. COMSTOCK 1926), and *Pseudocopaeodes eunus alinea* SCOTT 1981. *Pyrgus ruralis lagunae* SCOTT 1981 is known only from the Laguna Mountains and Palomar Mountain in California but may eventually turn up in several northern Baja California ranges (BROWN et al. 1992) and so was not included.

If the theory that a peripheral, isolated population is a founder of a subsequent clade holds true, with few exceptions the following taxa should be closest in relationship to their respective immediate ancestors, something future cladistic and genetic analyses could readily test for, i.e. they should prove to be the most plesiomorphic types in their respective clades.

Results

Islands

Isla de Cedros adjacent to the west coast of Baja California Norte has *Euphilotes bernardino garthi* MATTONI 1990 and *Callophrys (Mitoura) loki cedrosensis* (J. W. BROWN & FAULKNER 1990) as local endemics. A highly isolated, unnamed subspecies of *Anthocharis cethura* C. & R. FELDER 1865 occurs on Isla Magdalena on the west coast of Baja California Sur (BROWN et al. 1992), the southernmost representative of *A. cethura*.

A few subspecies are endemic to the California Channel Islands. These include *Euphydryas editha insularis* T. & J. EMMEL 1975 (Santa Rosa Island), *Cercyonis sthenele* unnamed subspecies near *silvestris* (W. H. EDWARDS 1861) (Santa Cruz Island), and *Anthocharis cethura catalina* MEADOWS 1937, *A. sara gunderi* INGHAM 1933, and *Strymon avalona* (W. G. WRIGHT 1905) (Santa Catalina Island). (*S. avalona* is known to occasionally hybridize in the wild with *S. melinus* HÜBNER [1818].) The Channel islands were likely colonized from the mainland during the lowering of sealevels ca. 11-20 ka ago, with their endemics evolving *in situ* in isolation when sealevels subsequently rose (cf. EMMEL & EMMEL 1974, GALL 1979, LANGSTON 1979, MILLER 1984, GORELICK 1986, MATTONI 1988, BROWN & FAULKNER 1988), though *S. avalona* may be a Pliocene endemic. Cedros, however, is the southernmost outpost for *Euphilotes bernardno* (BARNES & MCDUNNOUGH 1917) and *C. loki* (SKINNER 1907), so their clades may have originated there in Holocene isolation from the mainland. Another subspecies of *C. loki, C. l. thornei* (J. W. BROWN 1983), is endemic to Otay Mountain in San Diego County, California, and may be an evolutionary stage toward *C. nelsoni muiri* (Hy. EDWARDS 1881) (cf. BROWN 1982, SHIELDS 1984).

Seacoasts

Aside from *Euphydryas editha insularis,* of the multitude of *E. editha* (BOISDUVAL 1852) subspecies, the one with the most restricted range is *E. editha baroni* (W. H. EDWARDS 1879) from the coast at several locations in Mendocino County, California (cf. HOWE 1975, DORNFELD 1980, MURPHY 1982, MURPHY & EHRLICH 1983).

Plebeius (Lycaeides) idas lotis (LINTNER 1878) is restricted to several coastal locations in Mendocino County (R. A. ARNOLD, pers. comm.). Supposed records from the Warner Mountains are dubious. It appears to have the most limited distribution of the 12 *P. idas* LINNAEUS 1761 subspecies in North America. *P. idas* is the correct species name for North American material, not *P. argyrognomon* (BERGSTRÄSSER 1779) (HIGGINS 1985).

Cercyonis sthenele sthenele (BOISDUVAL 1852) once flew commonly on the sand dunes of the city of San Francisco, California (e.g. Golden Gate Park and Lone Mountain). The other two mainland subspecies of *C. sthenele* have much wider distributions. *Argynnis (Speyeria) callippe* has already been mentioned.

Satyrium auretorum fumosum J. EMMEL & MATTONI 1990 is confined to the Santa Monica Mountains, while the other two *S. auretorum* (BOISDUVAL 1852) subspecies have much more extensive Californian distributions. It is the darkest subspecies, probably an adaptive response to a moist coastal climate (EMMEL & MATTONI 1989).

Hypostrymon margaretae CLENCH 1975 is restricted to the vicinity of Mazatlan, Mexico, along the coast, while the other two *Hypostrymon* CLENCH 1975 species have more extensive distributions in westernmost Mexico (CLENCH 1975).

Canyon bottoms

Philotes sonorensis extinctis MATTONI 1991 was confined to upper San Gabriel wash at the mouth of San Gabriel Canyon (MATTONI 1989). Several other *P. sonorensis* (C. & R. FELDER 1865) geographic segregates are more widely distributed within the California Floristic Province.

Philotiella speciosa bohartorum (TILDEN 1968) is confined to the bottom of the Merced River gorge at one location in Mariposa County, California (SHIELDS 1974, 1987). Nominate *P. speciosa* (Hy. EDWARDS 1876) is much more widespread, occurring mainly in the deserts of southeastern California, western Nevada, extreme western Arizona, and Baja California Norte. Interestingly the plant *Clarkia lingulata* LEWIS & LEWIS (Onagraceae) also is restricted in distribution to this same gorge, on the periphery of the broader range of its closest relative, *C. bilobata* (DURAND) NELSON & MACBRIDE (LEWIS & ROBERTS 1956).

Alkali sinks

Cercyonis pegala wheeleri (W. H. EDWARDS 1873), a pallid, fairly distinctive phenotype, was found only by Owens Lake, California, while eight other related but weakly differentiated Great Basin *C. pegala* (FABRICIUS

1775) subspecies have wider distributions (AUSTIN 1992). Similarly, *Cercyonis oetus pallescens* T & J. EMMEL 1971 is the most pallid and restricted of the four *C. oetus* (BOISDUVAL 1869) subspecies, occurring only on alkali flats in several central Nevada locations (cf. EMMEL & EMMEL 1971, AUSTIN & MURPHY 1987). *Cercyonis meadii alamosa* T. & J. EMMEL 1969, another pallid subspecies from alkali flats of the San Luis Valley of southern Colorado, has the narrowest distribution of the three *C. meadii* (W H. EDWARDS 1872) subspecies (EMMEL 1969, EMMEL & EMMEL 1969).

Mountains of Kern and Tulare Counties

Melitaea minuta monache (J. A. COMSTOCK 1918) is confined to about a dozen high valley locations in southeastern Tulare County, California, at ca. 2300–2750 m (J. F. EMMEL, pers. comm.). It has the most restricted distribution of the *M. minuta* W. H. EDWARDS 1861 subspecies. *Melitaea* FABRICIUS 1807, not *Poladryas* BAUER 1961 is the correct genus name (cf. HIGGINS 1941, 1960).

EMMEL & EMMEL (1973) and DAVENPORT (1983) call attention to a number of montane subspecies endemic to Kern County, California. These include *Argynnis (Speyeria) egleis tehachapina* (J. A. COMSTOCK 1920) and *Euphilotes battoides comstocki* (SHIELDS 1975) from the Tehachapi and Piute Mountains, *Plebeius lupini chlorina* (SKINNER 1902) from the Tehachapi and Tejon Mountains, and *Argynnis (Speyeria) adiaste atossa* (W. H. EDWARDS 1890), *A. (S.) coronis hennei* (GUNDER 1934), and *Lycaena heteronea clara* Hy. EDWARDS 1880 from the Tehachapi and Tejon Mountains to Mount Pinos. All of these have the most restricted distributions of their respective subspecies assemblages. SIMS et al. (1979) have shown that *Speyeria adiaste* (W. H. EDWARDS 1864) and *egleis* (BEHR 1862) are genetically distinct species.

Spring Mountains

The Spring Mountains in Clark County, Nevada, harbor a few endemics including *Speyeria zerene carolae* (DOS PASSOS & GREY 1942), *Euphydryas anicia morandi* GUNDER 1928, and *Plebeius shasta charlestonensis* AUSTIN 1980, as well as *Limenitis weidemeyerii nevadae* BARNES & BENJAMIN 1924 which extends to the nearby Sheep Range (AUSTIN 1981). These are the most isolated subspecies within their respective species (cf. MOECK 1957 PERKINS & PERKINS 1967, HOWE 1975, FERRIS 1976 a, AUSTIN 1980, DORNFELD 1980, AUSTIN & MULLINS 1983). *E. anicia morandi* is fairly widespread in the range, mostly above 3050 m. *E. anicia cloudcrofti* (FERRIS &

HOLLAND) (FERRIS & HOLLAND 1980), which does have a more restricted range than *morandi,* is probably a synonym of *capella* (BARNES 1897) (SCOTT 1986). *S. z. carolae* was once erroneously placed in *S. coronis* (BEHR 1864) but it "pretty surely belongs within *zerene* (BOISDUVAL 1852)" (GREY & MOECK 1962). It and *L. weidemeyerii nevadae* are fairly widespread in the range at moderate elevations (AUSTIN & AUSTIN 1980). *P. shasta charlestonensis* occurs mostly above 2450 m in the range (AUSTIN & AUSTIN 1980).

Baja California Norte Mountains

Habrodais poodiae J. W. BROWN & FAULKNER [1982] is known only from three locations in the Sierra Juarez and three locations in the Sierra San Pedro Martir of Baja California Norte at higher elevations (BROWN & FAULKNER 1982, BROWN et al. 1992). The other Nearctic *Habrodais* SCUDDER [1876] species, *H. grunus* (BOISDUVAL 1852), is found in California, extreme northwestern Nevada, western Oregon, southwestern Idaho, and central Arizona. The Sierra San Pedro Martir populations may represent an undescribed subspecies of *H. poodiae*. The species differs from *H. grunus* in phenotype and in male genitalia.

Mexico

The most isolated population of Nearctic *Parnassius phoebus* (FABRICIUS 1793) is an undescribed subspecies from one locality (457 m elevation only) in west-central Tamaulipas, which is certainly less widely distributed then are the other eight subspecies of non-arctic North American *P phoebus* (FERRIS 1976 b). It appears to be a Pleistocene introduction from the Palearctic.

Argynnis (Speyeria) nokomis wenona (DOS PASSOS & GREY 1945) at 3660 m on Cerro Potosi in Nuevo Leon has the most restricted range of any of the five *A. nokomis* (W. H. EDWARDS 1862) subspecies (cf. DOS PASSOS & GREY 1945 b, 1947, MCHENRY 1964, FERRIS & FISHER 1971). The small size, reduced black spots, and the brown coloration in both sexes readily distinguish *wenona* from the other subspecies.

Hesperia uncas gilberti MACNEILL [1964], from a foothill location in the Sierra Volcanica Transversal, is the most isolated subspecies of *H. uncas* W. H. EDWARDS [1863] (MACNEILL 1964). MACNEILL indicates that it could well be a full species, in which case it possesses the most restricted range of any of the other 18 Nearctic *Hesperia* FABRICIUS [1793] species.

Erynnis mercurius (Dyar 1926) is known only from several locations in the Valley of Mexico and has a much narrower range than any of the other 17 Nearctic *Erynnis* Schrank [1801] species (cf. Burns 1964, Beutelspacher 1980).

Of the four species of *Paramacera* Butler [1868], two (*P. chinanteca* L. D. Miller [1972] and *P. copiosa* L. D. Miller [1972]) occur only in montane Cerro Pelon of Oaxaca, with *P chinanteca* likely the most primitive species in the genus. The other two species (*P. xicaque* (Reakirt 1867) in Mexico, *P. allyni* L. D. Miller [1972] in southeastern Arizona) have wider distributions (Miller 1972).

Zoogeographic affinities

For the taxa under consideration that are not represented in the Palearctic, the source area appears to be the Neotropical realm. These include *Paramacera, Hypostrymon,* and *Callophrys (Mitoura)* Scudder [1872]. Genera that are highly diversified in the Nearctic with comparatively few Palearctic representatives are also likely to be Neotropical in origin (*Hesperia, Erynnis*). Morphologically, *Hesperia* arose from the primarily Neotropical genus *Atalopedes* Scudder [1872], and *Erynnis* has close morphological ties with two Neotropical groups of genera under Evans' *Erynnis* and *Telemiades* Hübner [1819] (cf. de Jong 1975, Burns 1989). This would mean that their Palearctic representatives originated from stock that crossed the Bering landbridge from North America into Asia. Morphologically, *E. mercurius* and *H. uncas* belong to species groups that are considered basal in their respective genera (cf. Burns 1964, MacNeill 1964).

In clades that are much more diverse in the Palearctic than in the Nearctic, the Neogene route travelled was most likely over the Bering landbridge, from Asia into North America. These taxa include *Parnassius* Latreille [1804], *Euphydryas* Scudder [1872], and *Melitaea.* Others, such as *Plebeius (Plebeius)* Kluk 1780 and *Plebeius (Lycaeides)* Hübner [1819], probably also crossed in that direction since they are not in close proximity to the Neotropics and do not appear to have any close relatives in the Neotropics.

It should be noted that Higgins (1978) split *Euphydryas* (14 species, Holarctic) into four different genera and elevated the group to new tribe status (Euphydryini Higgins). However, their genitalic variation is more on a par with that found in, e.g., *Euphilotes* Mattoni 1977 In my opinion, these HIGGINS "genera" are only subgenera at best and should be downgraded accordingly. On genetic similarity, *Euphydryas editha* is the basal member of the subgenus *Occidryas* HIGGINS 1978 which also contains *E. anicia* (DOUBLEDAY & HEWITSON 1848) ard *E. chalcedona* (BRUSSARD et al. 1985). Later it was found, also on genetic similarity, that *E. anicia* is a subspecies of *E. chalcedona* (BRUSSARD et al. 1989). *Euphydryas gilletti* (BARNES 1897) from montane western Wyoming, central Idaho, northwestern Montana, and southwestern Alberta is genetically the most basal member of Nearctic *Euphydryas* and closely resembles *E. maturna* (LINNAEUS 1758) in markings and male genitalia from France (Paris), southern Sweden and eastern Europe to the Altai Mountains and eastern Siberia (cf. HIGGINS 1978, BRUSSARD et al. 1985, WILLIAMS 1988). The subgenus *Occidryas,* however, may have been a separate introduction. In male valve and aedeagus, *E. editha* is closest to *E. alexandrina* (STAUDINGER 1887) (cf. HIGGINS 1950, figs. 32–33; HIGGINS 1978, figs. 8–9) from south-central Asian mountains, in Kirghizia, Tyan Shan, Alexander Mountains, Tekes, Ala Tau, and Semirechensk.

The following provides some detail on other Nearctic taxa that most likely originated in the Palearctic.

In the argynnids, the harpe digitus is peculiar only to *Argynnis (Speyeria)* SCUDDER 1872 and *Argynnis (Mesoacidalia)* REUSS 1926, which also share similar valvae and female genitalia, such that they may be one subgenus within the same genus (cf. WARREN 1955, GREY 1957). No doubt *Speyeria* arose directly from *Mesoacidalia* (WARREN 1955). REUSS separated *Argynnis (Mesoacidalia)* into two subgenera, with *M. clara* (BLANCHARD 1844) going into *Proacidalia* REUSS 1926 (WARREN 1944). *A. vitatha* (MOORE 1874) is a separate species from *A. aglaja* LINNAEUS 1758 (= *A. charlotta* (HAWORTH 1802)), and its unique genitalic features are not matched by *A. (Speyeria)* (WARREN 1955). The male genitalia of *A. (S.) nokomis* is fairly close to *A. (M.) clara* but not to *A. (M.) aglaja* (cf. DOS PASSOS & GREY 1945 a); however, *A. (S.) mormonia* was not illustrated for comparison. *A. mormonia* is basal in the dendrogram of genetic similarity of the western Nearctic *Speyeria,* with *A. nokomis* the next most primitive member (BRITTNACHER et al. 1978). Both *A. (S.) mormonia* and *A. (M.) clara* are colonial, fly in wet meadows at high elevations, and strongly resemble one another in facies. *A. clara* is found at 3050–4875 m from the NW Himalaya (Garhwai, Kashmir, Pir Panjal Range) to Nepal, Sikkim, and northeastern Tibet, as well as Amdo in Singhai, China.

Limenitis weidemeyerii nevadae is phenotypically a fairly close match for *L. trivena hydaspes* MOORE 1874 from NE India (Sind and Liddar Valleys, Kashmir, Lahoul, Pangi, Sutlej Valley) (cf. WYNTER-BLYTH 1917, PERKINS & PERKINS 1967). *L. trivena* MOORE 1864 ranges from NW Nepal to Kashmir, Chitral, the Pamirs, and Tadzhikistan.

Genitalic morphology of *Melitaea minuta* is closest to *M. collina* LEDERER 1861 from Israel, Lebanon, Syria, south Turkey, and parts of Iraq, and to *M. turkmanica* HIGGINS 1940 of Askhabad in extreme southern Turkestan (cf. HIGGINS 1941, figs. 188-191; HIGGINS 1960, figs. 3-6; LARSEN 1974). WILTSHIRE (1957) regards *turkmanica* as a subspecies of *collina*, along with *M. consulis* WILTSHIRE 1941 from Iran.

Structurally, *Cercyonis* SCUDDER 1875 is a member of Maniolini HAMPSON 1918 (MILLER 1968), perhaps closest to the Palearctic *Hyponephele* MUSCHAMP 1915 or *Maniola* SCHRANK 1801 in phenotype. *Cercyonis* probably originated from Palearctic stock since all the other genera of Maniolini have Palearctic distributions.

Preliminary morphological indications are that *Philotiella* MATTONI 1977 arose from *Praephilotes* FORSTER 1938 of the Turkestan Desert to the northeastern Iranian Desert and Tyan Shan (SHIELDS & REVEAL 1988). The Scolitantidini certainly achieve their greatest development in the Palearctic.

Nearctic *Anthocharis* BOISDUVAL 1833, *Philotes* SCUDDER 1876, *Lycaena*, and *Habrodais* also appear to have originated in the Palearctic, not from the Neotropics.

Discussion

The analysis demonstrates that southwestern North American butterfly taxa in geographic isolation generally closely correspond with founder species criteria for stressful, specialized environments, such as seacoasts, volcanoes, canyon bottoms, isolated semiarid mountain ranges, and mountain summits. An additional stressful environment may be alkali sinks. Some that do not fit neatly into these categories reside in isolated foothills, valleys, or offshore islands. Though these islands certainly provide geographic isolation, their habitats do not appear to be especially stressful. Tho areas of California that contain isolated butterfly taxa are also areas where relict plant species are frequently encountered (STEBBINS & MAJOR 1965, fig. 2). Most of these butterfly taxa are at the periphery of the clade's total range, mostly at the southern end but sometimes along the western margin. Exceptions are *C. meadii alamosa, H. margaretae,* and *P. sonorensis extinctis,* which are at the precise geographic center of their respective ranges, where the range is narrowest. The only taxa found along the clade's eastern margin are *A. (S.) nokomis wenona* and *C. meadii alamosa,* and none occur along the northern margin of a clade's distribution. It should also be mentioned here that a distinctive, isolated subspecies of *Ochlodes yuma* (W. H. EDWARDS 1873) from Taos County, New Mexico, on the easternmost margin of the species' wide range, has recently been described as subspecies *anasazi* (see CARY & STANFORD 1995). The highest representation is from isolated mountain ranges, followed by islands and seacoasts, and extend in elevation from sealevel to mountain summits. Many of the taxa are strongly colonial.

The clades range from those with only two subspecies (*P. speciosa, H. poodiae*) to large numbers of subspecies (e.g. *A. (Speyeria), E. battoides* (BEHR 1867)), and from only two species (*Habrodais*) to fairly large numbers of species (*Hesperia, Erynnis*). In some clades the most isolated taxon is obviously the most distinctive of the entire clade (e.g. in *A. (Speyeria), Cercyonis, P. chinanteca, P. sonorensis extinctis, L. ferrisi, H. poodiae*).

Areas where isolated subspecies are particularly concentrated are the Tehachapi Mountains and the Spring Mountains. Kern County mountains are uniquely endowed with a concentration of *Argynnis (Speyeria)* that are xeric endemics (*A. adiaste atossa, A. coronis hennei,* and *A. egleis tehachapina*). Based upon the genetic similarities of 10 *A. (Speyeria)* taxa (BRITTNACHER et al. 1978, fig. 2), an early diversification from the *A. zerene carolae* ancestral line probably first evolved in that area.

Marginal populations near the environmental limits of the species, that initially are minimal in size, will be strongly homozygous from inbreeding, becoming closely adapted to a specialized niche (REMINGTON 1968). Low genetic variability probably applies to many of these isolated butterfly taxa, e.g. in the melanic forms (*A. callippe callippe, A. auretorum fumosum*), the pallid forms (*A. adiaste atossa, Cercyonis*), and one having reduced spots (*P. speciosa bohartorum*). *P. sonorensis extinctis* was exceptional, however, in exhibiting large genetic variability in phenotypic expression (polymorphisn), known to occur by population size increase from a more homozygous small colony during population size fluctuations (FORD 1971).

If overall size is a genetic expression, some isolated taxa are noteably the smallest (*A. (S.) nokomis wenona, Callophrys (Mitoura), E. mercurius*) or the largest (*A. (S.) zerene carolae, A. (S.) adiaste atossa, P. speciosa bohartorum*) of their respective clades.

During the past century, some of these taxa in California have become totally extinct (*A. adiaste atossa, C. pegala wheeleri, C. sthenele sthenele, P sonorensis extinctis*) or substantially reduced in population size (*A. callippe callippe, P. (L.) idas lotis*). The rate is obviously far greater than what would occur naturally and can be directly attributed to destruction or alteration of their habitats by man. Fortunately many of the remaining taxa reside in remote areas, though some of these exist only as small colonies of very limited extent.

In the Great Basin, the pluvial lakes rapidly dried up during the Hypsithermal interval of the Holocene (8–4.5 ka B.P.) under hot climatic conditions (REVEAL 1979). The alkali sink *Cercyonis* likely evolved at that time, its ancestor having crossed the Bering landbridge in the late Wisconsin dry cycle when there was an abundance of *Artemisia* LINNAEUS, grasses, *Ephedra* LINNAEUS, and chenopodes mixed with tundra in Siberia and Alaska during lowered sealevels (HOPKINS 1959, 1967). The San Francisco bay area was largely submerged during the Pleistocene interglacial stages, so *Cercyonis sthenele* also probably dates from the Wisconsin stage. Crucifers were present 11.5 ka B.P. at Goodnews Bay, Alaska, suggesting a similar pattern may apply to *Anthocharis*. The Bering landbridge was open during Pleistocene glacials but was occupied by tundra except for the drier parts of the Illinoian and Wisconsin when steppe-adapted vegetation was mixed with tundra. Sealevels again rose during the Holocene, preventing any landbridge passage from Asia. *L. idas* appears to be a late Pleistocene southward dispersal into coastal Mendocino County (SHAPIRO 1992). Uplift on the San Francisco Peninsula and the Berkeley Hills occurred shortly after early Pleistocene time, when *A. callippe* probably became established. Lowland tundra and arctic climate existed in Beringia as early as 2.4 to 2.5 Ma B.P. (MATTHEWS 1980). The Bering landbridge again became available at various other times during the Pliocene (REPENNING 1980).

E. editha baroni may be at least late Pliocene since the present flora near Fort Bragg is like that at Santa Rosa ca. 3.5 Ma B.P., then located at sealevel (Axelrod 1976). Similarly, *P. sonorensis extinctis* may have first become isolated when the Los Angeles basin was uplifted above sealevel ca. 2.2–3.5 Ma B.P.

With improvements in Neogene dating in recent years, what used to be known as early to middie Pliocene has now become latest Miocene time (cf. AXELROD 1980, CANDE & KENT 1992). This affects fossil floral dates but not radiometric or mammalian age evidence. The following discussion incorporates this dating change.

Xeric vegetation at central California sites 4–7 Ma B.P. is very similar to species living today in central and southern California, with *Prunus turlockensis* AXELROD 1980 having an Asiatic affinity (AXELROD 1980). A similar pattern is found in latest Miocene-Pliocene xeric floras of northwestern China that have close relatives living today in the same region (CHANEY 1936). The Bering landbridge was open during the late Miocene, and a summer dry climate was present in latest Miocene-Pliocene in the Pacific Northwest (cf. HOPKINS 1959, WOLFE 1969). Late Miocene-Pliocene coniferous forests in Alaska were depauperate, with herbs showing an increased diversity (WOLFE 1972). By late Pliocene the coniferous forest disappeared and herbs and shrubs dominated the region. In all likelihood, the arid-semiarid latest Miocene was when many of the Asiatic-derived butterfly taxa under consideration first crossed the Bering landbridge into North America (see SHIELDS 1986), though more Beringian floras for that time are needed. Tertiary climate in western North America was warmest and driest during mid-Hemphillian (Messinian) time (ca. 5–7 Ma B.P.). There was rapid speciation of floras then, probably followed in the early Pliocene by selective differentiation of their taxa in more localized environments (AXELROD 1948, 1980). Butterfly speciation in western North American *Euphydryas*, *Argynnis (Speyeria)*, *Hesperia*, and *Erynnis* seems to fit this pattern as well.

Besides the Rocky Mountains, the earliest uplifting of mountains in the southwestern North America study area were the Sierra Juarez, San Pedro Martir, and Sierra Madre Occidental in Miocene time. Close to the Miocene/Pliocene boundary ca. 5 Ma B.P, a small clockwise rotation of the Pacific plate began (COX & ENGEBRETSON 1985), initiating San Andreas Fault displacement and concurrent seafloor spreading in the Gulf of California. A short time later in the early Pliocene (ca. 3.6–5.3 Ma B.P.), mountain range uplift occurred in the Santa Monica, Tejon, Tehachapi, Sierra Nevada (renewed uplift), Spring, Sierra Madre Oriental, and Trans-Mexican Volcanic Axis ranges, likely isolating the butterfly taxa *in situ* that presently are found in them as relictual populations in refugia. The great climatic fluctuations of the Pleistocene glacials and interglacials, and especially the Holocene desert development, perhaps eliminated these ancestral species from other parts of their range while allowing their diversification northward as new species and subspecies with the contracting and expanding vegetational migrations.

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