

# GENERAL PATTERNS IN WEST INDIAN INSECTS, AND GRAPHICAL BIOGEOGRAPHIC ANALYSIS OF SOME CIRCUM-CARIBBEAN *PLATYNUS* BEETLES (CARABIDAE)

JAMES K. LIEBHERR

Department of Entomology, Comstock Hall, Cornell University,  
Ithaca, New York 14853-0999

**Abstract.**—The relationships of the Antillean terrestrial arthropodan and onychophoran taxa are reviewed using track analysis, in which tracks are considered the connected areas of endemism of cladistically unresolved monophyletic groups. The West Indian fauna is shown to be of complex affinities, with elements related to Central and South America, North America, Africa, Asia, and Australia. Numerous taxa in a variety of insect orders exhibit Antillean-African relationships, suggesting that resolved cladistic analyses of such groups will allow testing of vicariance hypotheses of Antillean geohistory. Relationships among taxa on Cuba, Hispaniola and Puerto Rico support a geologic reconstruction in which proto-Hispaniola is composed of eastern Cuba, central and northern Hispaniola and Puerto Rico during the early Tertiary.

Cladistic analysis of a clade within the carabid beetle genus *Platynus* is used to generate taxon-area cladograms. The clade is composed of 32 species, 8 from the mainland, 14 from Hispaniola, 4 from Jamaica, 4 from the northern Lesser Antilles, and 2 from Cuba. Fitch optimization is used to generate area transformation series from the taxon-area cladograms. Of the 39 equally parsimonious character cladograms generated in the cladistic analysis, two taxon-area cladograms most parsimoniously account for the area relationships of the *Platynus* species. These are compared to two contrasting geologic hypotheses of area relationships: a mobilist geologic hypothesis and a stabilist geology/taxon dispersal hypothesis. Using component analysis and a graphical representation of the area transformation series, called closed biogeographic graphs, the mobilist geologic hypothesis is shown to better account for the area relationships of the *Platynus* clade. These area relationships include: 1) a relatively earlier association of portions of the northern Lesser Antilles with the Greater Antilles; 2) a hybrid origin for Hispaniola, with the central and northern cordilleras related to eastern Cuba, and the southern Haitian peninsula related to Jamaica; 3) a relatively later relationship of Jamaica and northern Central America. The techniques of biogeographic graph analysis are compared to recent attempts at track analysis and to the methods of cladistic biogeography. The biogeographic graphs are shown to be a useful adjunct to component analysis, but suffer from a loss of directed component information. [Biogeography, Caribbean, Carabidae, *Platynus*, beetles, vicariance.]

Elements of the Caribbean biota exhibit affinities with taxa in many other parts of the world. The most obvious relationships of the Antillean island biotas are to the adjacent Central and South American mainland. Early monographers and biogeographers were content to compare overall faunal similarity of the Caribbean biota to the mainland, proposing hypotheses of biotic dispersal to account for the similarity (Darlington, 1938, 1957). The development of knowledge in three areas—organismal taxonomy, systematic theory, and geology—has shown such simple procedures as pairwise estimates of similarity between adjacent geographic regions to be inadequate as the basis for hypothesizing historical area relationships. Increased

taxonomic knowledge of the world biota repeatedly illustrates taxonomic affinities among presently disjunct taxa. Replacement of local faunal and floral studies with taxonomic revisions of worldwide scope has enhanced the ability to recognize affinities among disjuncts. The use of cladistic methodology (Hennig, 1966) and the subsequent development of cladistic biogeography (Platnick and Nelson, 1978; Rosen, 1978; Nelson and Platnick, 1981) have provided an operational method for analyzing relationships of areas of endemism definable by biotic distributions, based on the phylogenetic relationships of taxa determining those areas. Geologic science, with the recognition of plate tectonics as a dynamic phenomenon that has alter-

nately united and divided geographic regions of the world, has corroborated early biologists' (e.g., Hooker, 1853) contentions that present-day biotas were conceived under geologic-area relationships much unlike those observed today. Moreover, the relative disagreements among geologists regarding the history of geographic areas such as the Caribbean (Rosen, 1975, 1985; Donnelly, 1988) suggest that elucidation of biotic history will provide data for understanding geologic history.

The development and synthesis of knowledge regarding the affinities of the Caribbean biota has been of long duration. Jeannel (1942) was among the earliest biogeographers to adopt a Wegenerian (Wegener, 1915) view of earth history, recognizing that elements of the Neotropical biota bore affinities to Old World taxa. Croizat (1958) also believed some Caribbean taxa could have diverged from Old World or New World taxa through vicariance, not dispersal across water gaps. Rosen's (1975) synthesis of geologic and biotic data, using Croizat's track analysis for the illustration of biotic distributions of monophyletic groups, pointed to four geographic regions that exhibit affinities to the Antilles: North America, South America, the eastern Pacific, and the Old World tropics including equatorial Africa (Rosen, 1975:444, fig. 6). Among terrestrial Arthropoda and Onychophora, phyla to which I will restrict myself in this paper, two basic patterns of area relationships are consistent with a vicariant origin of the Antillean fauna. The first pattern, called the northern element by Rosen (1975), and old northern by Savage (1982), includes taxa exhibiting the taxon-area relationships: Antilles + (North America + (Central America + northern Central America)). South American affinities are shown by the relationship Antilles + (South America + (Central America + northern Central America)). I will show below that many of these patterns implicate the Old World, usually Africa, and can be expressed as Africa + Antilles + (South America + (Central America + northern Central America)), the basal addition of Af-

rica unresolved. Antillean groups with African affinities would be predicted to be old groups, isolated by Cretaceous disjunction of Africa, and South and North America (Anderson and Schmidt, 1983).

Many taxa exhibit patterns of distribution suggesting late arrival on the Antilles. As proposed by Darlington (1938), such dispersal events are supported by Antillean groups exhibiting affinity with an adjacent mainland source, with the added cladistic proviso that such a mainland source also be more closely related to the island than any other area. Recasting a dispersal hypothesis in the context of a cladistic statement, we might suspect dispersal if we observe the cladogram northern Central America + (Central America + (Antilles + South America)). This set of relationships would indicate a disjunction between Antillean taxa and their South American allies subsequent to the colonization of the trans-American Isthmus in the Mio-Pliocene (Savage, 1982). Based on common elements in various geologic hypotheses (Donnelly, 1988), such relationships would indicate that the groups are too young to supply information regarding the formation of geologic barriers associated with the Antilles, having radiated subsequent to such formation. Whereas many taxa exhibit distributional patterns that are not informative regarding Caribbean geologic history, many taxa exhibit concordant taxon-area relationships that agree with independent hypotheses of earth history. It is these latter examples I review below.

Following review of the present state of knowledge of arthropod distributions and relationships in the Caribbean, I present an analysis of one clade of the carabid beetle genus *Platynus*, a genus containing 66 Antillean species of which 63 are single-island endemics. The analysis expands that of Liebherr (1988a) by including Central American and Mexican members of what I have called the wingless clade, a lineage of *Platynus* characterized by heavy cuticle, loss of flight wings associated with metathoracic reduction, and several shared-derived setational characters. I first derive

most-parsimonious character cladograms for the 32 species of this group. A graphical optimizing criterion, based on Mickevich's (1981) biogeographic map procedure, is then used to choose those cladograms which most parsimoniously summarize both the character data and relationships among areas of endemism. The optimized cladograms are then compared to vicariant-geologic (Rosen, 1985) and dispersal (Darlington, 1938) hypotheses of area relationships. The area relationships of the *Platynus* wingless clade are shown to be more congruent with a geologic hypothesis based on the mobilist models of Caribbean history (Sykes et al., 1982; Rosen, 1985; Donnelly, 1988).

#### RELATIONSHIPS OF THE CARIBBEAN FAUNA

Many arthropod taxa are old enough, based on fossil evidence, to have been influenced by a vast array of events during earth history. Having cladograms of taxa composed of Antillean, American and African taxa, for example, would allow tests for concordance of those cladograms. For most groups we lack such knowledge of hierarchical relationships, necessitating less informative track analysis. In track analysis, a line joining a series of taxa comprising a monophyletic group can be considered an unresolved cladogram. If a track contains only two taxon-areas, it cannot be resolved as a cladistic statement. Tracks comprised of three or more taxon-areas are resolvable given cladistic analysis, and track analysis may be considered a preliminary stage of analysis, suggesting groups for which cladistic analysis should be conducted. The following review assumes taxa such as genera to be monophyletic, and may be construed as a call for cladistic analysis of taxa comprised in part by Antillean species, possessing distributions likely to shed light on Caribbean history.

#### *Antillean-South American Track*

The Onychophora, near relatives of Annelida and Arthropoda, are first known from the Cambrian. The family Peripatidae, subfamily Peripatinae, comprises eight

genera: *Mesoperipatus* from tropical Africa, and seven other genera distributed in South America, Central America, and all of the Antilles except Cuba and St. Lucia (Brues, 1923; Peck, 1975). Peck described an eyeless, depigmented Jamaican cave species, placing it in the monotypic genus *Speleoperipatus*. Its relationships are obscure, due to possession of numerous primitive character states, and/or possible character convergence due to cave habitation.

The pseudoscorpion *Pseudochthonius squamosus*, described by Schwaller (1980) from Oligocene Dominican amber, belongs to a genus also distributed on the Galapagos, in Central and South America, and west-central Africa. The theridiosomatid spider genus *Wendilgarda* is distributed in the neotropics and Africa, with *W. mexicana* known from mainland Mexico to Honduras and Cuba; *W. clara* found in Central and South America, Hispaniola, and Puerto Rico; and *W. atricolor* distributed on the African coastal islands of Principe and São Tomé (Coddington, 1986). The collembolan genus *Troglopedetes* comprises 16 species known from Jamaica, Cuba, Hispaniola, Puerto Rico, and mainland Central and South America (Christiansen and Culver, 1987). The affinities of the genus are said to be African, again suggesting a distribution consistent with a vicariant origin.

In the Insecta, taxa among at least six orders exhibit Antillean-American-African relationships. The Hispaniolan damselfly genus *Phylolestes* (Odonata) is a member of the Synlestidae, otherwise distributed in Southern Africa and tropical Asia (Flint, 1978). The caddisfly genus *Antillopsyche* (Trichoptera) is restricted to Cuba, Hispaniola, and Puerto Rico, and is the only Neotropical member of the Polycentropodidae: Pseudoneureclipsinae, otherwise distributed from tropical Africa to Indonesia (Flint, 1978).

Among Coleoptera, the Carabidae and Scarabaeidae offer a number of examples of an Antillean-African connection. The carabid genera *Barylaus* (Liebherr, 1986) and *Antilliscaris* (Nichols, 1986b) both comprise

flightless, montane, relict species of Hispaniola and Puerto Rico. Both are most closely related to African taxa. *Barylaus* is a sister group to the Old World taxa of the carabid subtribe Caelostomi (tribe Pterostichini), with the mainland Central American genus *Cyrtolaus* sister to *Barylaus* plus the Old World taxa. *Antilliscaris* is most closely related among the scaritine lineages to *Prodyscherus* of Madagascar. Based on larval morphology, the sister group to this sister pair of genera is Madagascan.

Two genera of Scarabaeidae each include an Antillean species, with all other species Ethiopian or Asian (Matthews, 1966). *Oniticellus cubiensis* is distributed on Cuba, Jamaica, and the Bahamas, with 14 Ethiopian, 4 Palaearctic and 3 Oriental species comprising the remainder of the genus. *Drepanocerus reconditus* of Jamaica is congeneric with 18 Ethiopian and 9 Oriental species. Both species are taxonomically isolated in their respective genera, leading Matthews to reject introduction into the Caribbean from the Old World as a means to explain the distributions.

*Canthochilum*, a scarab genus endemic to the Antilles, is composed of 8 Cuban and 3 Puerto Rican species (Matthews, 1966). The most likely sister group is the South American *Ipsellissus*, with these two genera potentially related to an Old World tropical complex including *Panelus*, *Pycnopanelus* and *Cassolus*.

Members of several taxa of Antillean butterflies (Lepidoptera) exhibit Antillean-African affinities. The nymphalid genus *Archimestra*, restricted to Hispaniola, is a member of a group of nymphalid genera distributed in the neotropics, Africa, and Asia (Munroe, 1949). The lycaenid genus *Brephidium* is comprised of one species from South Africa and two or three in the New World, distributed from Venezuela to the southern United States including Cuba, Hispaniola, Jamaica, and the Caymans (Clench, 1963; Shields and Dvorak, 1979). Shields and Dvorak also list the genus *Libythea* (Libytheidae) as a probable Atlantic vicariant, with taxa in Africa, South Africa, the Antilles, and Central American north to the southern United States.

One of the major insect radiations on the Antilles has occurred in the wood satyr genus *Calisto* (Lepidoptera: Satyridae). The genus is restricted to the West Indies; one Jamaican species, one Puerto Rican species, two on Cuba, one on the Bahamas, and 15 species on Hispaniola (Munroe, 1950). This genus is of obscure relationships, but the South American *Eretris* has been proposed as most closely related (Brown and Heine-man, 1972). Of the Hispaniolan species, nine are restricted to either the southern peninsula of Haiti or the more northern island block composed of the Cordilleras Central and Septentrional (Fig. 1). Based on Munroe's classification, the Bahamian and Cuban species are most closely related to Hispaniolan species groups.

Saether (1981) studied the subfamily Orthoclaadiinae of the dipteran family Chironomidae, concluding that the Lesser Antillean fauna contained several taxa of close relationship to Africa. The admittedly poor sampling of South American habitats precludes any firm hypotheses of relationships including South America.

In the true bug order, Hemiptera, the seed bug *Pachygrontha singularis* (Lygaeidae), restricted to Cuba, is more closely related to congeneric African species than to congeners from Central and South America (Slater, 1988). As in the above examples of Scarabaeidae, dispersal via human agency is not implicated as an explanation for the distribution.

#### *Antillean-North American Track*

There are many Antillean insect taxa that appear most closely related to Central American and Mexican lineages. Fewer Antillean groups exhibit affinities to Florida, and those that do possess ecological requirements suggesting that they are good colonizers. In the Carabidae, examples of such patterns include closely related marine beach species of *Scarites* s.s. distributed in Florida and Cuba (Nichols, 1986a), and the Floridan species *Agonum elongatulum*, most closely related to Antillean populations of the widespread *Agonum decorum* (Liebherr, 1985).

The *Polycentropus nigriceps* species group,

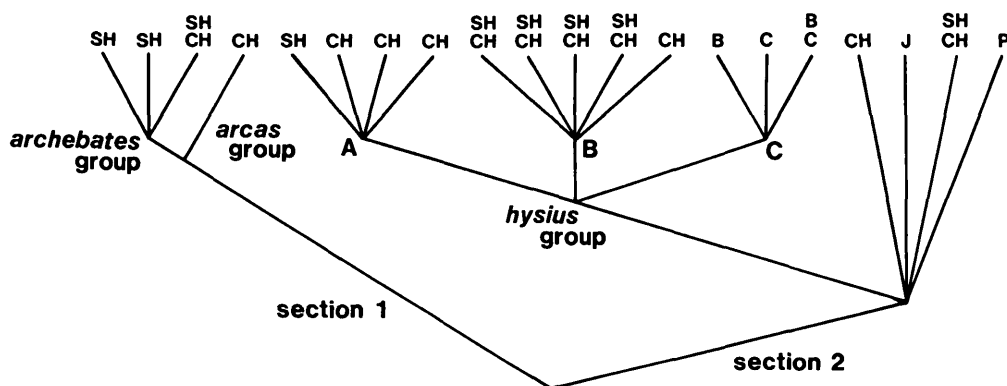


FIG. 1. Area cladogram derived from classification of *Calisto* butterflies (Munroe, 1950). *C. hysius* group is divided into three subgroups (A, B, C). In addition, section 2 contains four monotypic species groups. Area designations are: SH = southern Hispaniola; CH = central and northern Hispaniola; B = Bahamas; C = Cuba; J = Jamaica; P = Puerto Rico.

of the trichopteran family Polycentropodidae, comprises 10 Greater Antillean species, and is sister group to the eastern North American *confusus* group (Hamilton, 1988). These groups contain no Mexican or Central American species. For this pattern to be compatible with a vicariant origin of the *nigriceps* group, extinction of taxa in Mexico and Central America must be assumed.

The nominate subgenus of the carabid genus *Phloeoxena* is comprised in part by an Antillean clade of seven species that is sister to species in southern Mexico, the Chiapas-Guatemala highlands, and the Costa Rica-Panamá lowlands (Ball, 1975). Two other subgenera are included in *Phloeoxena*, both found in mainland Mexico to Panamá. The *Phloeoxena* s.s. pattern is compatible with a hypothesis of vicariant origin. Jamaica lacks *Phloeoxena*, suggesting that the Antillean clade vicariated through the breakup of the superisland proto-Hispaniola—eastern Cuba, central Hispaniola, plus Puerto Rico (Sykes et al., 1982). The cladogram for this group provides partial support for such a contention; the Puerto Rican species is sister to a Hispaniolan-Cuban species, and another Hispaniolan species, although from the southern peninsula, is sister to an eastern Cuban species.

The genus *Euxenus* of the fungus weevil family Anthribidae is distributed from

Canada to the Panamanian isthmus, with species on Cuba, Hispaniola, and Puerto Rico (Valentine, 1979). A specialized relative is the monotypic *Apteroxenus* of Jamaica. Cladistic analysis of taxa in these genera would allow comparison to patterns compatible with a vicariant origin.

#### Greater Antillean-Lesser Antillean Affinities

Although the Greater and Lesser Antilles are generally considered separate geographic entities, biotic distributions of some taxa do not recognize such a distinction. This is especially true for the northern Lesser Antilles—Guadeloupe, Dominica, Martinique, and St. Lucia—which have undergone two cycles of volcanism starting in the Miocene (Fink, 1970).

Based on cladistic biogeography and track analysis, Matile (1982) concluded that Lesser Antillean taxa of the fly family Keroplatidae were related to taxa in Central America, the Andes, and Jamaica. For example, cladistic relationships within the genus *Neoditomyia* show the Dominica species, *N. spinosa*, to be sister to a Jamaican species, whereas the Cuban *N. trogliphila* is sister to the Colombian *N. andina*.

Fennah (1955) revised the Lesser Antillean lanternflies (Homoptera: Issidae), remarking on the strong affinities to Puerto Rican and Jamaican taxa observed in all

three Lesser Antillean genera—*Colpoptera*, *Acanalonia*, and *Thionia*.

#### *Anomalous Disjunctions*

In more than several cases, Antillean insect taxa have been shown to be related to Asian taxa, with Ethiopian and sometimes South American representation lacking from such lineages. More than anything, such distributions point to the great age of elements of the Antillean fauna, and to the confounding effect of extinction.

Among Coleoptera, Antillean taxa with Asian affinities include the monotypic Jamaican fungus weevil genus *Cyptoxenus* (Anthribidae) (Valentine, 1982), the Greater Antillean scarabaeid genus *Canthonella* (Matthews, 1966), and the tenebrionid genus *Archaeoglenes* (Watrous, 1982). Whereas the first two examples appear most closely related to Asian taxa, *Archaeoglenes* is comprised of nine species distributed in Australia, the Solomon Islands, New Zealand, Hawaii, Panamá (three species), Jamaica, and Puerto Rico (M. Ivie, pers. comm.). *Canthonella* comprises four single island endemics found on Cuba, Hispaniola (two species), and Puerto Rico.

Two genera of ants exhibit Antillean-Asian-Australian disjunctions. *Gnamptogenys* is currently found on the Greater Antilles excluding Puerto Rico, in Central and South America, and in the Indomalayan region (Baroni Urbani, 1980b). Two species have been described from Early Miocene Dominican amber. The extant distribution of *Leptomymex* ants includes New Guinea, Australia, and New Caledonia, but Baroni Urbani (1980a) described a species from Dominican amber.

Grimaldi (1988) reported on several disjunct distributions of fruit fly taxa. He found the Puerto Rican endemic drosophilid fly genus *Mayagueza* to be the sister to the Indo-Australian genus *Acletoxenus*, with the Neotropical *Pseudiastata* sister to the *Mayagueza* + *Acletoxenus* clade. The drosophilid genus *Paramycodrosophila* exhibits a similar disjunct distribution, with three species on the Greater Antilles, one in the southeastern United States, and seven in the Indo-Pacific and northern Australia.

Thirdly, one lineage within the predominantly Neotropical genus *Zygothrica* is comprised of the South American *bilineata* group, and the Indo-Pacific *samoensis* group.

Slater (1988) classified the endemic Antillean lygaeid bug genera *Abpamphantus*, *Neopamphantus* and *Pamphantus* in the Bledionotinae, the subfamily otherwise known only from the eastern Mediterranean and Australia. These three genera are restricted to Cuba, Hispaniola, and Puerto Rico. *Abpamphantus* is a monotypic Cuban genus. *Neopamphantus* has three species, one Cuban and two Hispaniolan. *Pamphantus* comprises nine species—five Cuban, three Hispaniolan, and one Puerto Rican.

#### *Summary of Patterns*

Based on this review, it is clear that the Antillean insect fauna is of complex origins. Nonetheless, the above examples suggest faunas to be studied in the search for sister taxa to Antillean groups. Based on already recognized patterns, that list would include: 1) Central America, 2) Mexico and southern North America, 3) the Andes and northern South America, 4) tropical Africa, 5) south temperate Africa, 6) Indomalaya and 7) New Guinea and Australia. This sequence traces both increasing geographic disjunction and increased duration since vicariant events (Smith et al., 1981; Anderson and Schmidt, 1983). The occurrence of 3-area relationships such as ((Antilles-Africa) Central America) (*Barylaus* in Liebherr, 1986), and ((Antilles-Asia) Central America) (*Mayagueza* in Grimaldi, 1988) suggests that only a worldwide search of lineages related to Antillean taxa will ensure complete understanding of Antillean affinities, especially for taxa of relictual distribution.

Within the Antilles, some patterns of relationship of the islands appear more general than others. The relationship of Eastern Cuba, Hispaniola, and Puerto Rico as a cohesive land mass is supported by *Antillopsyche* (Flint, 1978), *Barylaus* (Liebherr, 1986), *Antilliscaris* (Nichols, 1986b), *Canthochilum* (Matthews, 1966), *Calisto* (Munroe,

1950), the *Polycentropus nigriceps* group (Hamilton, 1988), *Phloeoxena* (Ball, 1975), *Canthonella* (Matthews, 1966), and the bledionotine lygaeid genera *Abpamphantus*, *Neopamphantus*, and *Pamphantus* (Slater, 1988).

Based on phylogenetic affinities of its endemic taxa, Jamaica is less closely related to proto-Hispaniola than the latter's constituent parts. Antillean taxa such as *Calisto* (Satyridae) possess Jamaican species that appear distantly related to those on the other three Greater Antilles. Jamaican endemics exhibit a wide variety of affinities: *Drepanocerus* (Scarabaeidae) has African affinities (Matthews, 1966), *Apteroxenus* (Anthribidae) is related to the North American-Antillean *Euxenus* (Valentine, 1979), *Cyptoxenus* (Anthribidae) has Asian affinities (Valentine, 1982), and *Archaeoglenes* (Tenebrionidae) has other species on Puerto Rico, in Panamá and in the Austro-Pacific region (Watrous, 1982).

Whereas the Lesser Antillean fauna is usually distinguished from that of the large islands, several taxa suggest a relationship between the northern islands of Guadeloupe, Dominica and Martinique, and Puerto Rico and Hispaniola.

#### BIOGEOGRAPHIC ANALYSIS OF *PLATYNUS*

Among Antillean taxa, the carabid beetle genus *Platynus* stands as one of the more speciose, with 66 species known from the islands (Liebherr, 1987). The tribe Platynini contains lineages that have undergone extensive speciation radiation in montane tropical regions of the world: over 400 species in Mexico and Central America (unpubl. data), over 300 species on Madagascar (Basilewsky, 1985), over 100 species described from New Guinea (Darlington, 1952), and 111 species described from the Hawaiian Islands (Sharp, 1903; Csiki, 1931). Many of these species exhibit flight-wing reduction, and have only limited geographic ranges. Among insects, these carabids are excellent subjects for the estimation of hierarchical relationships among areas of endemism.

#### MATERIALS AND METHODS

*Taxa*.—A cladistic analysis of West Indian *Platynus* (Liebherr, 1988a) resulted in recognition of a lineage called the wingless clade. This clade contains species with vestigial metathoracic flight wings, reduced metathorax, variable position and occasional absence of the laterobasal prothoracic seta, and heavy elytral cuticle, with the elytral intervals often broadly convex or costate. These species were classified in the Cuban-Hispaniola *jaegeri* group (11 species), Jamaican *cinchonae* group (4 species) and Hispaniolan *laeviceps* group (5 species) (Liebherr, 1987). Allied to these groups is the Lesser Antillean *ellipticus* group, four species from the northern Lesser Antilles. The *ellipticus* group species are brachypterous, and share the derived placement of the laterobasal pronotal seta. Based on this analysis, the above species groups have been united as a redefined *jaegeri* species group (Liebherr, 1988b).

Study of the major collections of Mexican and Central American *Platynus*<sup>1</sup> has resulted in recognition of nine mainland taxa that share derived character states with the West Indian taxa. Eight of these species are wingless, the ninth (UASM-154) possesses wings, but is phenetically similar to the others, and is included in the analysis as a likely member of the mainland sister group to the other 32 species. Seven of the nine mainland species are undescribed, and are identified by collection acronyms and taxon number (see Acknowledgments). These species are described in Liebherr (1988b).

*Character analysis*.—Seventy characters were scored for the 33 species. Characters and associated identifying numbers correspond to Liebherr (1988a), with the addition of four characters. These include: character 11a—one midlateral pronotal seta (primitive = 0), versus two or more lateral setae on apical half of pronotal margin (derived = 1); character 16a—prothorax cor-

<sup>1</sup> University of Alberta, Strickland Museum of Entomology, Edmonton, Alberta, and National Museum of Natural History, Smithsonian Institution, Washington, D.C.

date, the base constricted (0), versus prothorax pedunculate, the lateral margins strongly constricted in basal half (1); character 48a—anterodorsal area of metafemoral apex glabrous (0), versus anterodorsal area bearing one or more setae (1); character 67—median lobe of aedeagus with acuminate apex (0), versus apex of median lobe hook-like, recurved ventrally (1). Of the 70 characters, 47 are informative, and analysis is based on these characters. The character-state matrix is presented in Appendix 1. Character-state polarity is based on out-group comparison using a variety of other Neotropical *Platynus* lineages as out-groups.

*Cladistic analysis.*—The character data were analyzed using Swofford's (1986) 2.4.1 version of PAUP (Phylogenetic Analysis Using Parsimony). Based on the recommendations of Platnick (1987), 20 analyses were run, varying the hold trees option (hold trees = 5, 10, 15, 20, 25) and the addseq option (addseq = closest, simple, rootless, asis). The simple and rootless options performed best, giving the shortest trees found, for hold trees of 10 or more. The basic analysis of all taxa was run using the following options: addseq = simple, hold trees = 25, opt = deltran, swap = global, mulpars, maxtree = 100, and root = ancestor. A hypothetical ancestor of uniform zero character states was used to root the cladogram. Deltran favors derived parallelisms over sequential advances and reversals, and was used because many of the setal characters transform by derived losses.

As the initial run with all taxa produced more than 100 equally parsimonious representations of the character data, of at least 39 different cladogram topologies, a modification of the biogeographic map concept (Mickevich, 1981) was used to choose among cladograms.

Biogeographic maps are area transformation series derived from taxon-area cladograms using the rules of transformation series analysis (Mickevich, 1982). In this study, Fitch (1971) optimization was used to construct area transformation series because TSA incorporates two rules judged unsuitable for biogeographic anal-

ysis—the median rule and the nearest terminal taxon rule (see the example below). Because Fitch optimization produces more general, and in some cases numerous area transformation series, the results are called biogeographic graphs.

Biogeographic graphs were derived for cladograms output by the initial PAUP analysis of the entire data set. One group of cladograms, all of which contained a specific subclade, or area-component, produced the shortest biogeographic graphs. It was assumed that the most parsimonious hypotheses of area relationships are preferable, given that the taxon-area cladograms being compared can be derived from equally parsimonious character cladograms. By this use of parsimony, a more restricted analysis based on cladogram topologies producing the shortest biogeographic graphs was undertaken. In this secondary analysis, a dummy taxon possessing the basal synapomorphies of the subclade present in all cladograms transformable to the shortest biogeographic graphs in the initial analysis was used in place of the taxa of that subclade. This substitution allowed all possible cladograms for the remaining portion of the cladogram to be output by the PAUP program, given the limitation of the maxtrees = 100 option. The secondary analysis was run using addseq = simple, hold trees = 25, swap = global, mulpars, and four HTU optimizing algorithms: acctran, deltran, Farris, and min f. The resultant cladogram topologies that were most defensible based on multistate character transformation series and missing data were compared to area cladograms derived from specific hypotheses of geologic and biotic history.

*Comparison of cladograms.*—The primary purpose of this analysis is the derivation of taxon-area cladograms that can be compared to area cladograms derived from models of geologic and biogeographic history (Darlington, 1938; Rosen, 1985). Given the character-based taxon cladograms, areas were assigned to the apical terms based on species' distributions. Areas of endemism were chosen such that no species was found in more than one area. Because the *Platynus*



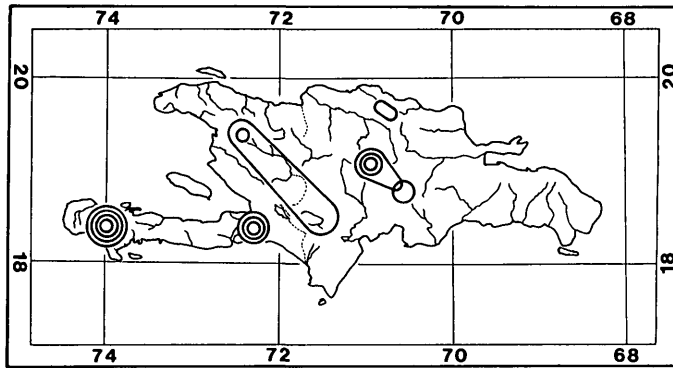


FIG. 2. Species distributions for 14 species of Hispaniolan *Platynus* included in the wingless clade.

species studied are all of very restricted distribution, this assumption required only minimal fusion of species ranges into geographically defined areas of endemism. For this analysis, two levels of resolution for areas of endemism were used. For the coarse resolution the areas of endemism were: mainland Central and North America (M); Jamaica (J), Cuba (C), Hispaniola (H), and Lesser Antilles (L). Based on geologic data (Rosen, 1985), a more finely resolved analysis recognized two subareas of Cuba (eastern Cuba and western Cuba), two subareas of Hispaniola (the Cordilleras Central and Septentrional as central Hispaniola, and the Peninsula du Sud and Sierra Baoruco as southern Hispaniola), and central America defined as Panamá and Costa Rica, as distinct from northern Central America and Mexico.

One could argue that species distributions should strictly define areas of endemism. In this study, where species distributions are very limited, this would result in many more areas of endemism. For example, the Hispaniolan species alone would reside in five areas of endemism (Fig. 2). The practical decision was made to define areas of endemism based on joint distributional and geographic data, with the hope that the analysis would provide a low resolution view to the biogeographic history of this group, and allow a more general hypothesis to be used in comparison with other hypotheses.

Biogeographic graphs were generated from taxon-area cladograms using the

method of Fitch (1971). Fitch optimization was used for two reasons: 1) it was assumed that area relationships have no intrinsic order that can be determined a priori, or by arbitrary rules assigned based on cladogram topology (as used by Mickevich, 1981, 1982); 2) Fitch optimization allowed the most parsimonious area transformations series to be visualized.

Because the use of Fitch optimization for constructing biogeographic graphs differs from Mickevich (1981), and because the biogeographic graphs were used in two different manners in this study, an example of the procedure is provided below.

Given the cladogram of taxa 1-9 distributed in the six areas A-F (Fig. 3A), we wish to assign area states to the nodes of the cladogram to form an area tree. Pass downward through the cladogram from paired apical terms (sister species) toward the root. The nodes joining sister groups are considered the intersection of their area-state sets if a common area is held between sister groups. If no area is held in common between sister groups, the area-state set of the node is considered the union of the area-state sets of both sister groups. The results of this preliminary phase are presented without parentheses (Fig. 3A).

For the second or final phase of optimization, pass upward on the area tree from root to terms. Starting at the node above the root, if the preliminary area-state set contains all states present at the root, eliminate any other states present at the second node not present at the root. Optimization

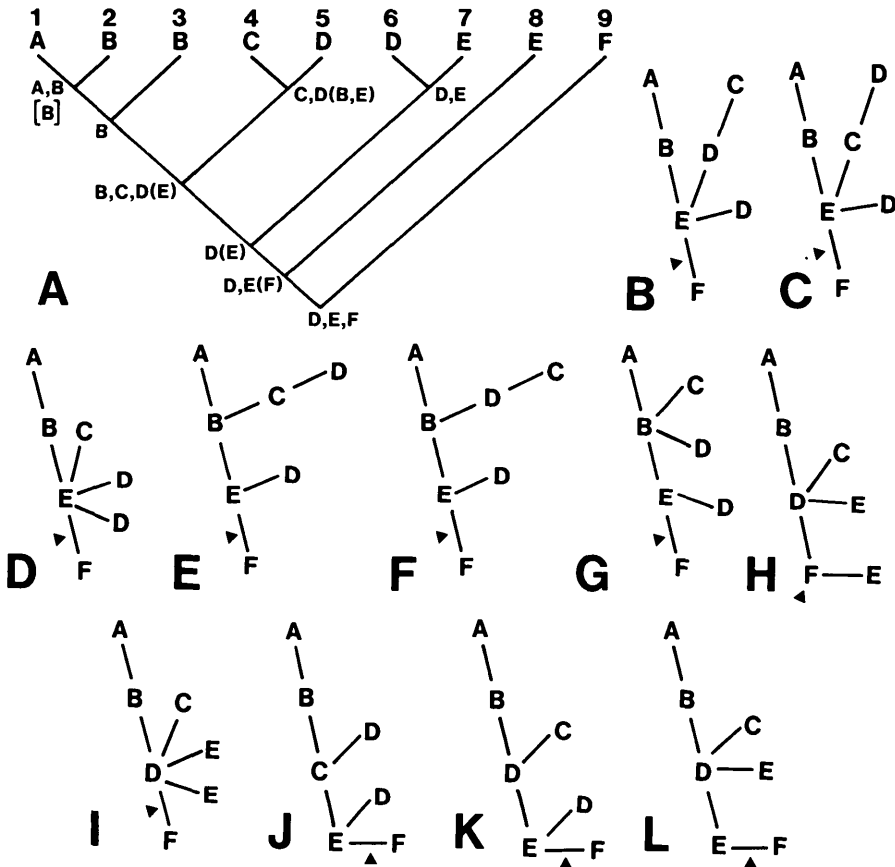


FIG. 3. A. Exemplar cladogram in which taxa 1-9 inhabit six areas A-F. Nodes of cladogram are assigned area states according to Fitch (1971) optimization procedure. Preliminary nodal area assignments are naked, areas added in final optimization phase are in parentheses, area in brackets the result of final optimization with other area excluded. B-L. Eleven equally parsimonious transformation series derived from nodal area assignments of the taxon-area cladogram using Fitch optimization. Transformation series L is the single solution obtained using the rules of transformation series analysis (Mickey, 1982). Root may be placed at state on either side of triangle, except for series H, in which root is state F.

is finished at this node. If the second node does not contain all area states of the root, and the nodal area-state set was formed by a union (Fig. 3A), add any states present in the root but absent from the second node. If the second node does not contain all states of the root, and the second node's states were determined by intersection of its apically adjacent nodes, add to the preliminary nodal set for the second node any areas present in both the root and at least one of the two more apical nodes. After completing this procedure for the antebasal node, iteratively repeat the procedure upwards along all stems of the tree,

considering the next most basal node to be the root, and the node in question to be the second node. For Figure 3A, those area states added to nodes during the final phase of optimization are indicated by parentheses. For the single instance of an area being subtracted, the final area designation is shown in brackets. This procedure is derived directly from Fitch (1971), with two exceptions: 1) areas are substituted for nucleotides; 2) Fitch's trees read from top to bottom.

Based on the polarity of the cladogram, a root may be assigned to biogeographic graphs (Fig. 3B-L). In the example, place-

ment of the root may be ambiguous because of ambiguity in the assignment of area states to the root of the cladogram. The root will always reside at the basal area state of the basal clade, or at its next-most apical state on the graph (e.g., states E or F, Fig. 3B). Transformations may be ordered sequentially from the root toward the apices of the transformation series, providing a relative sequence of events within each continuous series of state transformations. Relative times on parallel lines of the transformation series need not have occurred at times relative to their distance from the root for a variety of reasons; e.g., later dispersal from area E to D than divergence of C and D (Fig. 3B, C). Nonetheless, events along any one pathway from the root to a term may be sequenced. If a graph is found consistent with a vicariant origin for a fauna, the sequence of divergence events can be read directly off the biogeographic graph. Such rooted graphs can be considered the "orientated phylogenetic tracks" of Page (1987).

As emphasized by Mickevich (1981), Fitch optimization offers the unfortunate result of creating some very poorly resolved transformation series (Fig. 3D, I). An alternative is to adopt arbitrary optimization rules, such as used in transformation series analysis (Mickevich, 1982). The use of Farris (1970) optimization is precluded in this instance, because Farris optimization assumes an intrinsic order among states of a character. When sister groups do not share a common state, the state set of their common ancestor is defined as the two most closely related states, one taken from each state set (Farris, 1970: 91, rule R-2). Unless we wish to propose an order of areas a priori, or allow the structure of the cladogram to determine the nodal state using criteria such as the state of the nearest real taxon, or the median state of the nodes surrounding an ambiguous node (Mickevich, 1982), the structure of the transformation series will remain ambiguous.

In the above example, transformation series analysis offers a single unambiguous transformation of areas (Fig. 3L). The root

state (F) and second state (E) are determined by the areas of adjacent extant taxa 9 and 8, respectively. The inner nodes joining sister groups of taxa 1-5 and 6-7, and sister groups 1-3 and 4-5, are determined as state D by the "median rule" of Mickevich. This rule is stated: "it can be deduced that when two of three surrounding nodes of a node of a cladogram have the same state, the inner node should be assigned that state (Mickevich, 1982:463). Once these two nodes are assigned state D, the nodes joining taxa 4 and 5 and taxa 6 and 7 are both assigned state D. The median rule also assigns state B to the node joining taxa 1 and 2. This unambiguous result can be seen as arbitrary, as 10 other equally parsimonious solutions exist. For the analysis that follows, the generation of many equally parsimonious area transformation series by Fitch optimization is not considered disadvantageous, as only the length of the area transformation series is used to judge the suitability of a particular cladogram for biogeographic analysis.

Given many equally parsimonious character cladograms, we can choose for biogeographic analysis those cladograms that result in the most parsimonious transformational relationships among areas. Such a choice strives to minimize hypotheses of divergence events necessary to account for the biogeographic patterns of taxa. These events could be vicariant, or dispersal/founder events. As will be shown, selecting for concentrated study only those character cladograms that produce the shortest biogeographic graphs in this study has the ancillary benefit of allowing examination of all cladogram topologies, given the output characteristics of PAUP.

Whereas I am advocating the use of biogeographic graphs for selecting cladograms supporting the most general biogeographic hypotheses, character weighting, where unambiguous, can also be used to evaluate competing equally parsimonious cladograms (Wheeler, 1986). In the analysis of *Platynus* data, a return to the character data is used after the biogeographic graph analysis. In several cases, species are grouped by PAUP based on a synapomor-

phy whereby one species in the group lacks data for that character. Rejection of such topologies is considered appropriate, with the proviso that the analysis be reexamined when more complete data become available.

*Testing biogeographic hypotheses.*—The area cladograms chosen as most parsimonious representations of the taxon-area relationships, and best supported by the character data, were tested against two hypotheses of the area relationships of the Antilles. A mobilist geologic hypothesis (Rosen, 1985; Donnelly, 1988) and a stabilist geology/taxon dispersal hypothesis (Darlington, 1938) were converted to area cladograms, and what I term closed biogeographic graphs. Above, we have derived open biogeographic graphs, in which areas may be represented more than once. In closed biogeographic graphs, each area occurs once on the graph, and graphs need not be minimally connected.

Multiple transformations associated with an area on a closed biogeographic graph may be interpreted in several ways. The area may support a fauna that has been derived partly via vicariant events, and partly via dispersal from another source area. Alternatively, the area may be of geologically hybrid origin, with vicariance and hybridization of two areas resulting in the interdigitation of two lineages. Of course, two separate dispersal sources could also produce such a pattern. Finally, an area connected to two other areas on a transformation series may host a paraphyletic biota, i.e., one derived from taxa in a cladistically more basal source area, and serving as the ancestor to more derived taxa in a third area. The transformation sequence numbers assignable when an open graph is rooted may be used to interpret area relationships on the closed graph.

The taxon-area cladograms were also converted to closed biogeographic graphs. In this way, comparisons could be made among closed biogeographic graphs based on taxonomic and geologic hypotheses. Similarity among graphs was determined using Jaccard's similarity coefficient (Sneath and Sokal, 1973), which compares

the number of matching area connections out of all connections observed in both graphs.

Area cladograms were also compared using component analysis (Nelson, 1979). Taxon-area cladograms were compared to the two competing geologic hypotheses, and the best fit of the taxonomically defined area relationships with the available geologic hypotheses, based on shared component and total term information, was accepted as the best currently available explanation for past events.

#### RESULTS AND DISCUSSION

*Cladistic and graphical analysis.*—The initial PAUP analysis reported 180 equally parsimonious trees, of 142 step length. The only modification made to all trees was the assumption that character 6, reduction of the width of the eyes, was irreversible. The assumption that eye reduction is a common parallelism adds one step in the clade comprising *P. biramosus* to *P. tipoto* (Fig. 6). Of the 100 trees output under the maxtree option, there were 39 cladograms of five basic topologies (Fig. 4). Six cladograms grouped an apical Hispaniola-mainland-Jamaica component (Fig. 4A), and placed the Lesser Antillean species in a paraphyletic group near the base of the cladogram. Four cladograms placed two of the Lesser Antillean species as sister to the Hispaniola-Cuba clade (Fig. 4B), or at an unresolved trichotomy at the base of that clade. Thirteen cladograms broke up the apical Hispaniolan clade, placing the mainland *P. robustus* in its midst (Fig. 4C, compare to Fig. 6). The last two classes of cladograms included the Lesser Antillean *P. pseudellipticus* in the apical Hispaniola-mainland clade, far separated from its putative sister species *P. ellipticus* (Liebherr, 1987). Class D contained 4 cladograms and class E contained 12 cladograms (Fig. 4D, E).

Biogeographic graphs were derived for the five classes of cladograms. For class A only one biogeographic graph is possible under Fitch optimization (Fig. 4A). Under the other four classes of cladograms more than one topology can be derived, of which only one is shown for each cladogram type

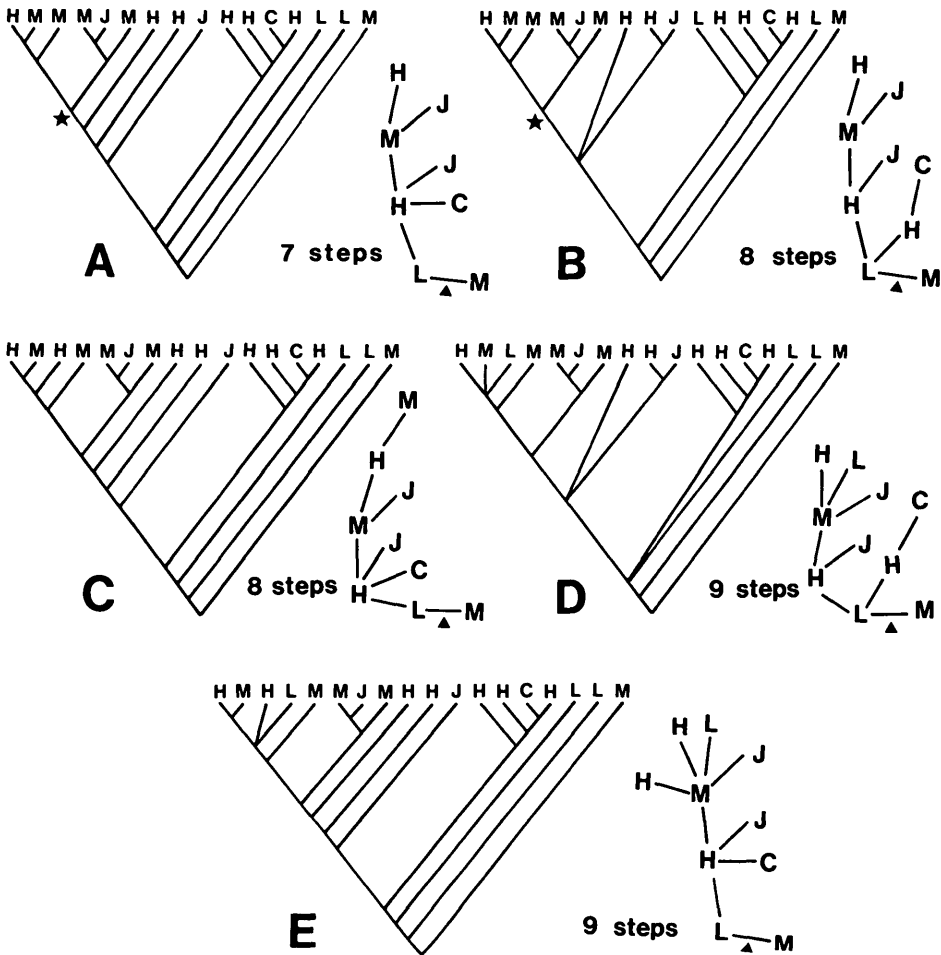


FIG. 4. A-E. Five classes of cladograms output using PAUP with maxtree option = 100, and areas substituted for *Platynus* taxa. Monophyletic groups from single areas of endemism have been reduced to a single area term. Area cladograms have been grouped by possession of identical topologies within the clade defined by the (M(J-M)) area taxon and its sister group (see \* of A and B). Representative biogeographic graph optimized using Fitch (1971) optimization shown to right of area cladograms. Area cladogram A has only one transformation series solution, cladograms B-E have more than one solution. Area designations are: H = Hispaniola; M = Mainland; J = Jamaica; C = Cuba; L = Lesser Antilles.

(Fig 4B-E). Unresolved trichotomies (e.g., Fig. 4B, D, E) were dealt with using the Fitch algorithm by placing the unresolved taxa in the three possible resolved relationships, and calculating the Fitch tree for all three positions.

Because cladograms of class A possessed the shortest biogeographic graphs, the search for all possible topologies of this preferred class of cladograms was conducted by reducing the data set through substitution of the apical starred clade (Fig.

4A) with a dummy taxon possessing the synapomorphies at that node, given class A cladogram topologies. This dummy taxon was represented with synapomorphies for characters 17, 26, 34, 39, 40, 41, 43 (Fig. 6), those synapomorphies determined using the CSPOSS option of PAUP. The basal mainland taxon, UASM-154, was also eliminated, and a dummy ancestor with synapomorphous characters 34 and 43 used to root the resulting cladogram of the basal paraphyletic assemblage of taxa. For this

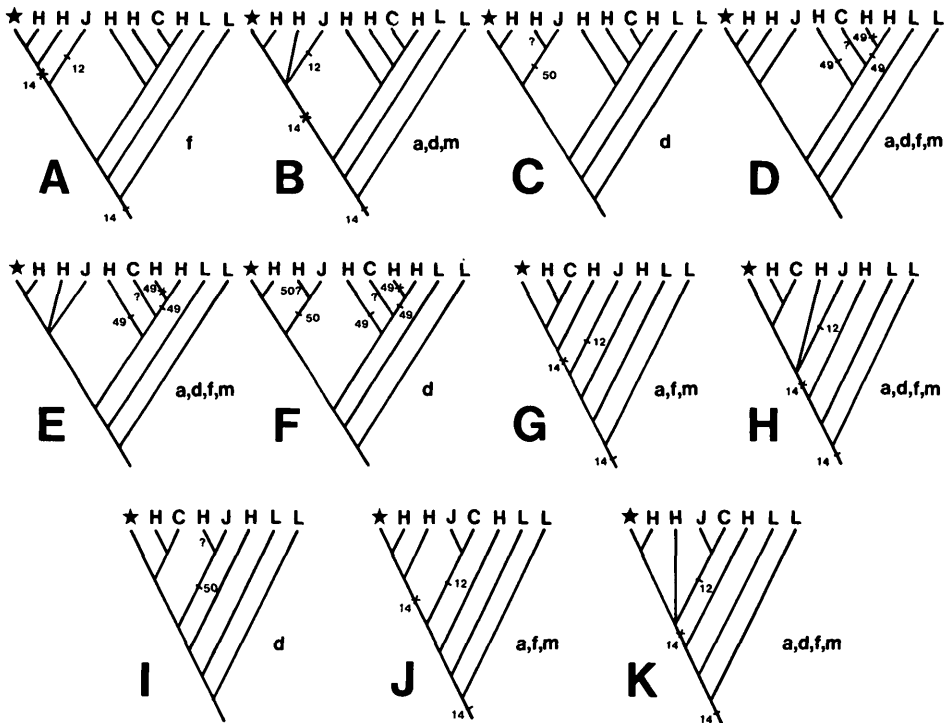


FIG. 5. A–K. Eleven cladograms resulting from reduced PAUP analysis in which apical clade is replaced with a dummy taxon (Fig. 4A). Taxon-area assignments are reduced so that monophyletic groups from a single area are represented by a single term. Optimization algorithms of PAUP under which topologies were derived shown at right of each area cladogram: a = acctran; d = deltran; f = Farris; m = min f. Character advances are shown as slashes, reversals as “Xs”, missing data as “?” See text for discussion of character transformations. Area designations as in Figure 4.

reduced run, PAUP found 11 cladograms (Fig. 5). Four optimization algorithms were used (acctran, deltran, Farris, and min f), none of which found all cladograms. Choosing among these cladograms was based on examination of character transformations implied by each topology. The deltran optimizing algorithm, in which character-state transformations are delayed, resulting in more parallelisms at the expense of reversals, grouped the Hispaniolan *P. constricticeps* and Jamaican *P. cinchonae* on the basis of character (50), apical gonocoxite of the female with normally proportioned lateral setae (0), or with short peg-like setae (1) (Fig. 5C, F, I). As females of *P. constricticeps* are not known, this grouping requires prediction that a derived state for character 50 will be found when females are studied. Rather than make this prediction, it was judged best to

group only on known synapomorphies, resulting in exclusion of cladograms C, F, and I from further consideration.

Missing data in character 49 in the Cuban *P. acuniai*, apical female gonocoxite with 2–3 lateral setae (0), or with 4 or more (1), leaves three cladograms (Fig. 5D, E, F, 6) unstable. *P. cubensis* lacks the synapomorphy for character 49, requiring a topology in which character 49 alone supports the monophyly of the apical clade of Hispaniolan species (*P. wolla*, *P. laeviceps*, *P. marcus* and *P. ramoni*) under the topology of Figure 5D–F. In addition, *P. marcus* lacks this synapomorphy. Should the female of *P. acuniai* possess this derived state, it will be most parsimonious to assume a character advance basal to *P. amone* (Fig. 6) and separate losses in *P. cubensis* and *P. marcus*. Such a finding will require switching to the topology of Figure 6 for this clade. Should

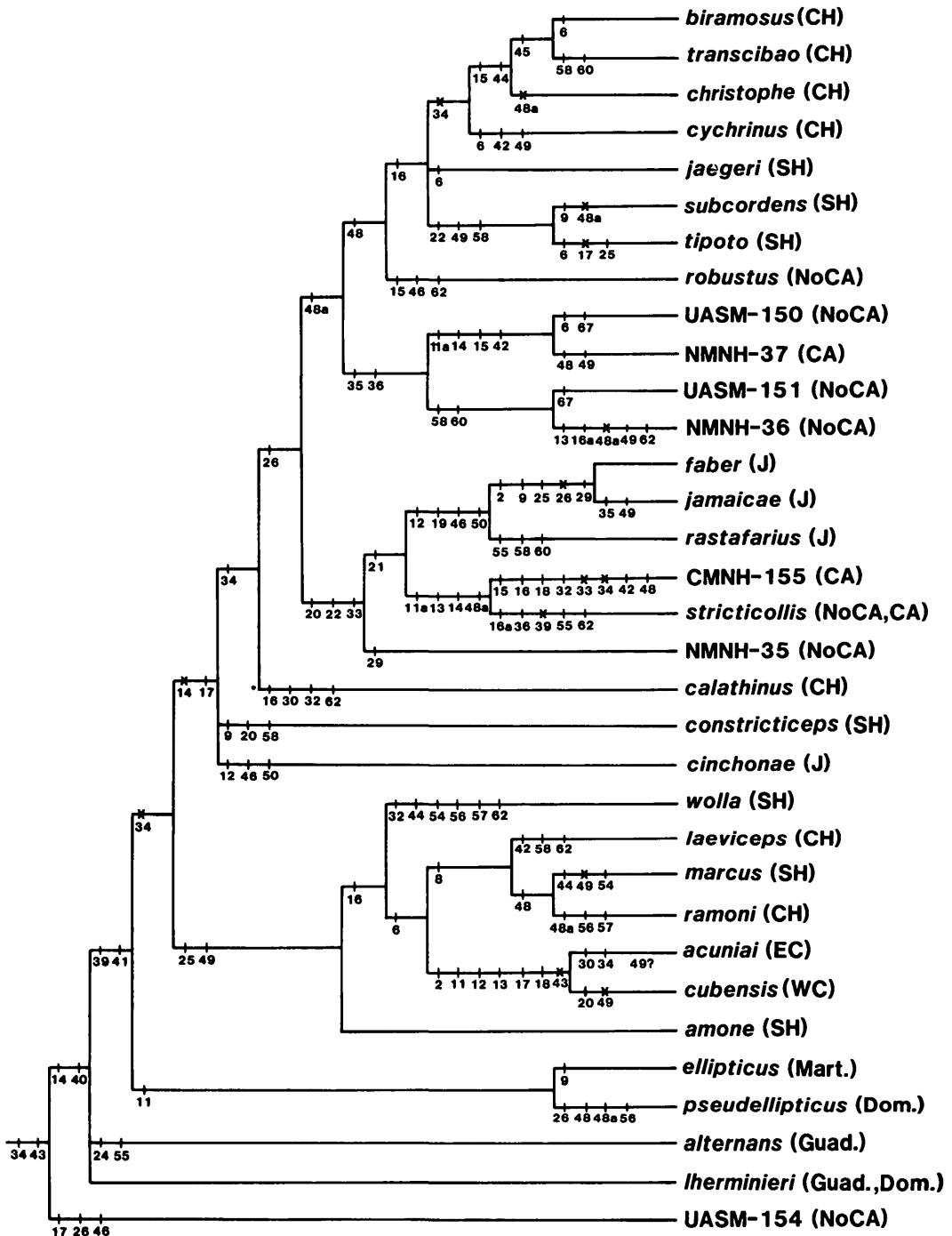


FIG. 6. Representative taxon-area cladogram of topology in Figure 5B. Taxa shown by museum acronym and identification number are described in Liebherr (1988b). Character state advances shown by slashes, reversals by "Xs", missing data by "?". Area designations are: CH = central and northern Hispaniola; SH = southern Hispaniola; J = Jamaica; EC = eastern Cuba; WC = western Cuba; NoCA = northern Central America, the Chiapan highlands and southern Mexico; CA = Central America from Panamá to Costa Rica; Mart. = Martinique; Dom. = Dominica; Guad. = Guadeloupe). Total length is 143 steps, a consistency ratio of .329.

*P. acuniai* lack the synapomorphy, the topology of Figure 6 would be just as parsimonious as that posited in Figure 5D–F, as *P. acuniai* and *P. cubensis* would possess a shared loss for this character (Fig. 6).

The remaining six cladograms (Fig. 5A, B, G, H, J, K) differ in placement of the Cuban species, and in the transformation of characters 12 and 14. Characters 12 and 14 are both derived states associated with the hind, or laterobasal, seta of the pronotum, or prothoracic dorsum. As character 12, the seta is either present (0) or absent (1). Character 14 involves placement of the seta at the pronotal hind angle (0) or well before the hind angle (1). In cladograms, A, G, and J of Figure 5, a reversal of character 14 resolves the cladogram, and taxa lacking the seta are hypothesized to have lost it from the derived state. There is no reason to prefer this transformation over that of cladograms B, H, and K, in which the seta is lost from the primitive state. Moreover, it is argued that ambiguity in this case should be reflected in lack of resolution on the cladograms. By this criterion, cladograms B, H, and K are the only ones of Figure 5 that should be considered both 1) compatible with the most parsimonious transformation of this clade in the areas it occupies, and 2) the best supported by the morphological character data.

*Biogeographic hypotheses.*—Two taxon-area cladograms were tested against two geographic hypotheses. The taxon-area cladograms included one of topology B (Fig. 5B, 6, 7C), and the Adams (1972) consensus of topologies H and K (Fig. 5H, K, 7D). The geographic hypotheses included a vicariance hypothesis modified from Rosen (1985) (Fig. 7A), and a stabilist geology/taxon dispersal hypothesis (Darlington, 1938) (Fig. 7B).

Rosen (1985) based his model of Caribbean vicariance on a number of geologic cladograms for various periods of Caribbean geology, ranging from the early Cenozoic to present. Based on Rosen's model, two of the current Greater Antilles are hybrid islands. Hispaniola is composed of a northern portion with relationships to eastern Cuba, Puerto Rico and the north-

ern Lesser Antilles, and a southern peninsula, which separated from the mainland much later. The eastern movement of the southern peninsula is associated with lateral movement of Jamaica during expansion of the Cayman spreading center, with vicariance of both fragments from the mainland placed in Oligocene to Miocene time much later than the initial vicariance of the mainland and proto-Hispaniola (eastern Cuba and northern Hispaniola and Puerto Rico) in the Eocene.

Cuba is also hypothesized to be of hybrid origin; an eastern portion with affinities to Hispaniola, and the central and western portions with affinities to the Yucatán Peninsula. Based on Sykes et al. (1982), proto-Cuba was situated at the northern end of an island arc during Eocene, and with northern Hispaniola, Puerto Rico, the Virgin Islands and the northern Lesser Antillean islands, joined Yucatán to South America. Rosen hypothesized western Cuba to have mid-Cenozoic aged affinities to Jamaica and southern Hispaniola. However, the geologic hypotheses (Sykes et al., 1982; Wadge and Burke, 1983) do not specify this, and these relationships are not assumed in the area cladogram for the Antilles used in this analysis (Fig. 7A). Instead, the western portions of Cuba are assumed to have separated from Yucatán during the formation of the Yucatán basin (Donnelly, 1988). This vicariance would predate the vicariance of Jamaica and southern Hispaniola from the mainland during expansion of the Cayman spreading center. Eastern Cuba was originally associated with central Hispaniola, with vicariance between them dating from Eocene to Miocene, prior to fusion of eastern and western Cuba in Miocene (Hedges, 1982; Rosen, 1985). Puerto Rico is considered the sister area to central Hispaniola and eastern Cuba, with vicariance considered early Eocene (Hedges, 1982). The Lesser Antilles are considered the earliest vicariant region of the island arc running from proto-Hispaniola to the northern Lesser Antilles (Donnelly, 1988).

In the Puerto Rico–Cuba–Hispaniola component (Fig. 7A, component 5), south-



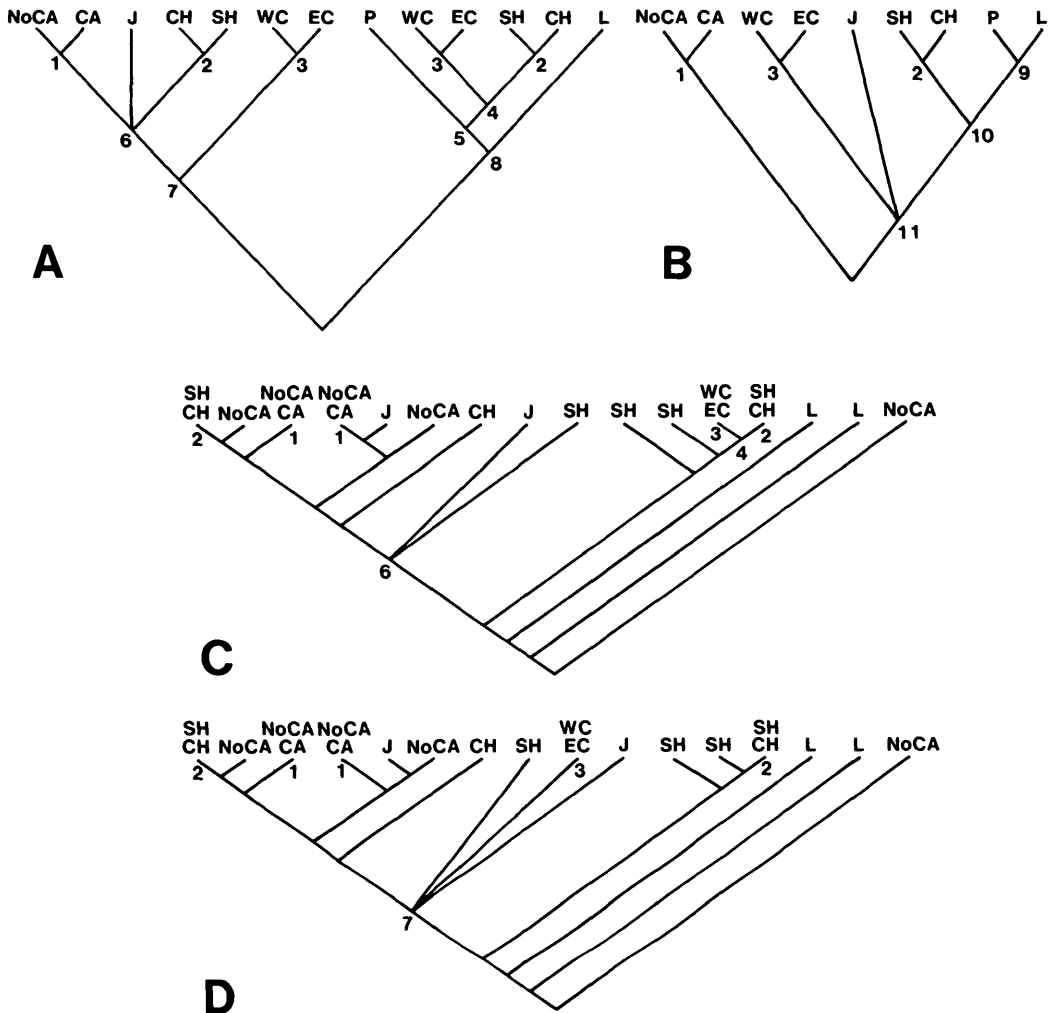


FIG. 7. A. Area cladogram derived from Rosen (1985) for the Caribbean. Components are numbered 1-8. Area designations are: NoCA = northern Central America, the Chiapan highlands and southern Mexico; CA = Central America from Panamá to Costa Rica; J = Jamaica; CH = Central and Northern Hispaniola; SH = southern Hispaniola; WC = western Cuba; EC = eastern Cuba; P = Puerto Rico; L = Lesser Antilles. B. Area cladogram derived from area relationship formula of Darlington (1938) (Fig. 8B). Components are numbered 1-3 and 9-11, area designations as above. C. Area cladogram derived from topology in Figure 5B. Components and areas labeled as above. D. Area cladogram derived from Adams consensus of topologies in Figure 5H and K. Components and areas labeled as above.

ern Hispaniola has been colonized from central Hispaniola, and western Cuba has been colonized from eastern Cuba, both in the Miocene. In the northern Central America-Central America-Jamaica-Hispaniola component (Fig. 7A, component 6), the Central American region comprises the mountains of Costa Rica and the Chiriquí region of Panamá, Talamancan Cen-

tral America of Savage (1982). This area was colonized from a Chiapas-Guatemalan source during emergence of the trans-American isthmus in the Pliocene. Also in this clade, colonization of central Hispaniola would have originated from the tectonically rafted biota of southern Hispaniola, sometime in the Miocene (Sykes et al., 1982). Western Cuba bears an older rela-

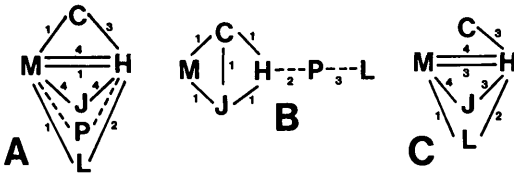


FIG. 8. A–C. Closed biogeographic graphs in which areas are represented only once on graph, and multiple connections indicate non-monophyly of an area's fauna. Numbers correspond to patristic distance from root to edge on open graph. Area designations are: M = mainland; C = Cuba; J = Jamaica; P = Puerto Rico; L = Lesser Antilles; H = Hispaniola. A. Graph derived from Rosen's (1985) model of Antillean vicariance. Puerto Rico connected by dashes and its connections unnumbered because of lack of Puerto Rican species of the wingless clade. B. Formula of area relationships proposed by Darlington (1938), with addition of Puerto Rico as suggested by Darlington (1957:510–517, fig. 63), and northern Lesser Antilles as would be predicted based on dispersal/founding of taxa on these islands with Greater Antillean affinities. C. Graph derived from area cladograms judged most general based on area transformations, and best supported by character data (Fig. 7C, D). The open graph this is derived from (Fig. 4A) has ambiguous root; either state M or L. For purposes of assigning sequence numbers, root was assumed to be M.

tionship to the mainland (Fig. 7A, component 7), and would serve as a source for Miocene colonization of eastern Cuba. Thus the Cuban and Hispaniolan areas occur twice on this vicariance area cladogram.

The dispersal hypothesis area cladogram (Fig. 7B) is derived from an area-relationship formula presented by Darlington (1938) (Fig. 8B). Based on the width of water gaps given present-day geography, Darlington proposed area relationships that would be reflected in the overall faunal similarity of Cuba, Jamaica, and Hispaniola. Based on his view that the Antillean arc served as a filter bridge (Darlington, 1957:fig. 63), Puerto Rico is shown to derive its fauna exclusively from its western neighbor. The Lesser Antillean element is connected to Puerto Rico, even though Darlington believed all Lesser Antillean taxa to be derived over-water from adjacent South America. This change is justified in this specific analysis based on the lack of any *Platynus* allied to the wingless clade in northern South America. The most recent sister-area relationships of Rosen (1985) are

included in the dispersal-area cladogram (components 1, 2, 3, Fig. 7B).

Comparison of area and taxon-area cladograms using component analysis shows the recurrence of several trivial components, called incontrovertible elements by Patterson (1981). These include sister-area relationships between northern Central America and Central America (component 1), southern and central Hispaniola (component 2), and western and eastern Cuba (component 3). These components can be considered trivial in this instance because they are predicted by both geologic hypotheses. Beyond these matches, cladograms A and C show the best concordance, with shared components 4 and 6 (Fig. 7A, C). As *Platynus* have not been recorded from Puerto Rico, component 5 should be excluded from comparison. For the same reason, components 10 and 11 would be acceptable, if present, even were they to lack Puerto Rico as a term. As it is, they do not occur on the taxon-area cladogram. If it is assumed that the ancestral distribution of the two Cuban species was eastern Cuba, component 7 need not be represented on the taxon-area cladogram. Thus, the taxon-area cladogram of topology C unambiguously lacks only component 8 in comparison with the area cladogram A. Of course, areas are represented more times on the taxon-area cladogram, suggesting more extensive biotic diversification during the geologic history of the Antilles. Taxon-area cladogram D contains trivial components 1, 2, and 3, plus a highly unresolved component 7. Based on component information, cladogram C has one more component predicted by the vicariance hypothesis than does cladogram D. The term information is also greater for cladogram C. Totaling the area-terms for only those components predicted by the vicariance hypothesis, cladogram C totals 26 terms, whereas cladogram D totals 24.

The dispersal hypothesis shares only trivial components with taxon-area cladograms C and D (Fig. 7B–D). Even were the Lesser Antillean taxa considered most closely related to South American taxa, placing this term as the sister to the Central

American term (assuming Pleistocene dispersal implicit in most dispersalist biogeography), cladogram B would share no components other than trivial components with the taxon-area cladogram.

The concordance of Rosen's mobilist vicariance scenario with the taxon-area relationships expressed by the present *Platynus* cladogram is much greater than that found in a previous analysis (Liebherr, 1988a). That analysis differed by the lack of any mainland taxa, and by the use of four fewer characters. The inclusion of the eight mainland species changes the cladistic relationships of the Antillean taxa somewhat, the major alteration being a change in the hypothesized relationships of the two Cuban species. Previously these species were placed at the node basal to *P. jaegeri* (Liebherr, 1988a:133; Fig. 6–10). Based on Rosen's vicariance scenario, I interpreted this placement to require over-water dispersal of the ancestor of the Cuban species plus their cladistically more derived Hispaniolan relatives. The vicariance of central Hispaniola and eastern Cuba would have then isolated the Cuban species from their sister group. The current analysis places the two Cuban species within the *laeviceps* species group of Liebherr (1987). This placement is consistent with vicariance of the ancestor of the Cuban species plus the *laeviceps* group (Fig. 6), after vicariance of the ancestors of the Antillean taxa, but before vicariance involving Jamaican and southern Hispaniolan ancestors. The relative cladistic similarity between the mainland *P. robustus* and species of its Hispaniolan sister group (Fig. 6), suggests that Antillean-mainland vicariance has operated throughout much of the diversification of this group.

The lack of Puerto Rican *Platynus* of this group was interpreted as a primary absence by Liebherr (1988a) because over-water colonization of proto-Hispaniola was assumed. Based on more complete data, it is hypothesized that *Platynus* were primitively present on Puerto Rico, and if absent today, the absence is due to extinction. If species are discovered on Puerto Rico, based on this vicariance hypothesis they should

exhibit affinities to the Lesser Antillean taxa, or species of the *laeviceps* clade of Figure 6.

*Biogeographic graphs.*—The biogeographic data may also be tested using a modification of the Mickevich (1981) map procedure. Fitch (1971) optimization can be used to generate open biogeographic graphs for taxon-area cladograms C and D (Fig. 7C, D), assuming hybrid areas to be single areas. Only one topology is obtained, that identical to the topology obtained in the initial sorting of cladograms (Fig. 4A). When this open graph is closed, that is, areas are represented only once with the network not minimally connected, we obtain a graph in which Hispaniola is connected to all other areas of interest, and twice to the mainland (Fig. 8C). The numbers adjacent to each connection represent the transformation series distance from the root (Fig. 4A).

The closed biogeographic graph may be compared to graphs derived via geologic or geographic methods. Darlington's stabilist geology/dispersal formula shows no hierarchy of sequences among the mainland, Jamaica, Cuba, and Hispaniola, with subsequent colonization of Puerto Rico and the Lesser Antilles. When the mobilist geologic hypotheses are presented as closed graphs, they show an initial breakup of the Lesser Antilles, Puerto Rico (not numbered), central Hispaniola, and western and eastern Cuba from the mainland (step 1). Subsequently, the Lesser Antilles are isolated from Hispaniola (step 2), Puerto Rico is isolated (not numbered), and eastern Cuba is isolated from Hispaniola, then fused with western Cuba (step 3). Finally, southern Hispaniola and Jamaica vicariate from the mainland, and southern Hispaniola fuses to central Hispaniola (step 4).

Comparison with the taxon-area graph (Fig. 8C) shows the vicariant graph (Fig. 8A) to be a better match than the dispersal graph (Fig. 8B). As shown by component analysis, Hispaniola can be considered a hybrid island. It is also of central importance in biotic diversification, exhibiting affinities with all other areas included in this analysis. Quantifying the similarity of

graphs A and C using Jaccard's similarity coefficient, we obtain 7 matches out of 8 connections present in both. Comparing graphs B and C we obtain a similarity coefficient of 4 matches out of 8 connections present in both. Reducing the taxon-area cladograms (Fig. 7C, D) to transformation series eliminates component information, resulting in identical graphs that are very similar to the mobilist geologic graph. As stated by Mickevich (1981), such graphs are more general hypotheses, but such generalization results in lost information.

The closed graphs may also be used to compare the sequence of area relationships among hypotheses. Comparing graphs A and C, there are two differences. The Hispaniolan fauna appears to bear later relationships to the mainland based on the biotic data than based on the geologic hypothesis. Also, whereas this *Platynus* clade shows asynchrony in the connections of the Jamaica biota (Figs. 4A, 8C), indicating a hybrid area of endemism, or perhaps vicariance and dispersal events in its history, the geologic hypothesis suggests concurrent breakup of the mainland, Jamaica, and Hispaniola. For the former case, the paraphyly of the Lesser Antillean taxa, which places L between H and M on the open graph (Fig. 4A), causes this disparity. Few synapomorphies support this relationship, and the disparity may be due to the character data. For the latter, indication of a hybrid Jamaican biota may be due to Jamaica's earlier geologic association with southern Hispaniola, and a later association with the mainland due to a subaerial Nicaraguan Rise (Donnelly, 1988). In this case, a hybrid biota would exist on a purebred geologic area, with secondary dispersal from the Nicaraguan Rise to Jamaica leading to the hybrid biota. We cannot be certain of the relative timing of divergence events along parallel edges of open graphs (Fig. 4A, H-J, M-J) unless we can ascertain that the geologic area is a hybrid and all divergence events have been vicariant. Introductions of dispersal arguments requires independent tests of the timing of the vicariant and dispersal/founding events.

#### SUMMARY

Placing the results obtained from the analysis of the *Platynus* wingless clade into the context of the general, albeit mostly unresolved, patterns exhibited by other Antillean insects suggests several things. We should not be surprised to find close biotic relationships among Cuba, Puerto Rico, and Hispaniola. If portions of these areas formed part of an early island arc (Donnelly, 1988), we should not be surprised to find relicts on these land masses with affinities to the Old World, especially Africa. In the case of the above *Platynus*, the close relationship between the island fauna and that of the Central American mainland is certain. Based on taxon-area relationships inherent in the wingless clade data, diversification of this group has proceeded in tandem with Eocene vicariance of the proto-Antillean island arc, and subsequent hybridization of Hispaniola and Cuba. There is evidence that the older Lesser Antilles may bear affinities to the Greater Antilles. That these islands contain basement rocks dating to the Cretaceous and the breakup of South America, North America and Africa is well supported (Fink, 1970). In this case, biotic affinities may prove more informative than geologic data. Certainly for *Platynus*, the existence of two clades in the Lesser Antilles, one allied to the north and one to the south (Liebherr, 1988a), supports the contention of two tracks in this island arc.

The history of Jamaica is enigmatic, and the *Platynus* fauna does little to elucidate its relationships except to say it bears affinities to Hispaniola and the mainland. An Eocene association with the mainland and southern Hispaniola (Sykes et al., 1982) is one explanation for such a pattern.

The approach taken in this analysis has been to work from taxonomic character data, to taxon-area cladograms, and then to various modified graphical presentations of such cladograms. Area cladograms and their attendant graphs, derivable both from vicariance and dispersal models, can be compared to the taxon-area cladograms and graphs, with concordance used as a

measure of corroboration. Dispersal hypotheses need not assume random colonization, and where the hypotheses differ from vicariant hypotheses, the relative explanatory value of the two types of hypotheses can be evaluated.

Craw's (1982) contention that cladistic biogeography cannot deal with hybrid areas is clearly false, as in this instance the hybrid origin of *Hispaniola* is suggested by the area cladograms. The concept of the biogeographic map (Mickevich, 1981) or graph is a useful adjunct to the taxon-area cladogram, although its construction eliminates information contained in the cladogram. Orientation of these graphs should be based strictly on data obtainable in the cladogram. Use of extrinsic geographic data for graph construction is unnecessary, and is likely to lead to spurious hypotheses based on incomplete knowledge of past geography and present-day distributions. To argue that Croizatian panbiogeography (Craw, 1983; Page, 1987) is superior to vicariance biogeography sensu Croizat et al. (1974) seems to be so much arguing over the body. Use of various techniques based on newly synthesized data, as exemplified by Rosen (1978), is the surest means of advancing a science of biogeography.

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APPENDIX 1. Taxon-character matrix of species in the *Platynus* wingless clade. Character numbers are based on Liebherr (1988a), or are presented in the text (character numbers modified with an "a" postscript, and character 67). Plesiomorphic character states are indicated as 0, advanced states by 1, missing data by 9.

Species	Character number																					
	2	6	8	9	11	11a	12	13	14	15	16	16a	17	18	19	20	21	22	25	26	29	30
<i>biramosus</i>	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0
<i>christophe</i>	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0
<i>constricticeps</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
<i>cychrinus</i>	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
<i>jaegeri</i>	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
<i>subcordens</i>	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0
<i>tipoto</i>	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0
<i>transcibao</i>	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0
<i>calathinus</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
<i>acuniaii</i>	1	1	0	0	1	0	1	1	9	0	1	0	1	1	0	0	0	0	1	0	0	1
<i>cubensis</i>	1	1	0	0	1	0	1	1	9	0	1	0	1	1	0	1	0	0	1	0	0	0
<i>cinchonae</i>	0	0	0	0	0	0	1	0	9	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>faber</i>	1	0	0	1	0	0	1	0	9	0	0	0	1	0	1	1	1	1	1	0	1	0
<i>jamaicae</i>	1	0	0	1	0	0	1	0	9	0	0	0	1	0	1	1	1	1	1	0	1	0
<i>rastafarius</i>	0	0	0	0	0	0	1	0	9	0	0	0	1	0	1	1	1	1	0	1	0	0
<i>amone</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>laeviceps</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
<i>marcus</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
<i>ramoni</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
<i>wolla</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
<i>alternans</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>ellipticus</i>	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>lherminieri</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>pseudellipticus</i>	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>robustus</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
UASM-150	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0
UASM-151	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
UASM-154	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
CMNH-155	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	1	1	0	1	0	0
<i>stricticollis</i>	0	0	0	0	0	1	0	1	1	0	0	1	1	9	0	1	1	1	0	1	0	0
NMNH-35	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0
NMNH-36	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0
NMNH-37	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0



APPENDIX 1. Continued.

Character number																								
32	33	34	35	36	39	40	41	42	43	44	45	46	48	48a	49	50	54	55	56	57	58	60	62	67
0	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	9	9	9	0	0	0	0	1	0	0
0	0	0	0	0	1	1	1	1	1	0	0	0	1	1	1	0	0	9	9	9	9	9	9	9
0	0	1	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	1	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
0	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0
1	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	9	9
0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
0	1	1	0	0	1	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
0	1	1	1	0	1	1	1	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
0	1	1	0	0	1	1	1	0	1	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0
0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0
0	0	0	0	0	1	1	1	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0
0	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1
1	0	0	0	0	1	1	1	0	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	1
0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9
0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0
0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9
0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0
0	1	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9
0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0
0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0