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COMMENTARY

[Commentary is a section of *Quaest. Ent.* that appears from time to time, and will contain expressions of opinions about general items, controversial or otherwise, that ought to be of interest to many of our readers. These contributions will not be refereed because they are intended to be free expressions of opinion. Changes by the Editor might be made to the form of presentation, but not to its substance. Remarks that are deliberately abusive or insulting will not be published. Rebuttals to previously expressed views will be considered, but the journal is under no obligation to publish them.

The Editor]

Following is an extended book review. Because of the potentially controversial nature of some of the comments, it seems more appropriate to place the review in a section of the journal that invites dialogue--hence its location in "Commentary".

LIEBHERR, J. K. (Editor). 1988. Zoogeography of Caribbean Insects. Comstock Publishing Associates, Cornell University Press, Ithaca and London. xi + 285 pp. Price, \$39.95 (U.S.)

Printed on acid-free paper, this volume is attractively hardbound, with dark green covers. On the front cover is a figure illustrating the geographical distribution and reconstructed phylogeny of the drosophilid genus group *Pseudiastata* and an adult of the West Indian *Mayagueza argentifera*, a member of this taxon. It is an excellent illustration and provides a focus on the subject matter of the book. The lighter green end-papers inside the covers contain a useful map of the Caribbean Basin, including the islands of the West Indies and adjacent portions of the North, Middle, and South American mainland, complete with scale and indications of longitude and latitude.

The volume includes a preface, list of contributors, and 11 chapters. Subject and taxonomic indices end the volume. Chapter 1 is a general discussion of Caribbean zoogeography. Chapter 2 treats geological aspects; and Chapter 11 is a critique of biogeographical methods in general, and of work of the other authors of this volume, in particular.

Chapters 3 to 10 contain analyses of taxa, as follows: Lygaeidae, by J.A. Slater; auchenorrhynchous Homoptera of the Greater Antilles, by J.A. Ramos; scaritine Carabidae, by S.W. Nichols; platynine Carabidae, by J.K. Liebherr; polycentropodid caddisflies, by S.A. Hamilton; relict Drosophilidae, by D.A. Grimaldi; ants, by E.O. Wilson; and halictid bees, by G.C. Eickwort. Each taxon-based chapter is a rich source of clearly presented information, containing extensive lists of included taxa and their distributions. Most of the chapters contain very well executed illustrations of the insect group treated, or of their work, and maps and diagrams are also provided that amplify the text. The chapter by Ramos is not illustrated, and overall seems rather perfunctory.

As a carabid specialist, I was impressed especially with the execution of the distribution maps in Nichols' chapter: each with a photograph illustrating habitus of one or more species whose range is indicated by dots, etc. Much care went into the preparation of these figures, and collectively they are a valuable source of data.

Recurrent themes in the text are: occurrence of old relicts on Puerto Rico (noted by Slater, Nichols, Liebherr, and Grimaldi); and incomplete knowledge of the biota, because of insufficient collecting by appropriate specialists.

The analyses of various taxonomic groups are inconsistent in delimitation of the study area. In his concept of the West Indian Biogeographic Region, Nichols includes the Greater and Lesser Antilles, the Bahamas, Barbados (as a separate entity), South Florida, and the Yucatan Peninsula of Mexico. Wilson does not include the mainland in his treatment of the ants, but does include Trinidad and Tobago. This inclusion increases the size of the ant fauna of the West Indies by about a third. The other authors confine their study areas to the Bahamas, and Greater and Lesser Antilles, with Barbados included in the last-named island group. Such differences in definition of study area must be taken into account by those who might wish to compare taxonomic diversity of the various taxa in the West Indies.

The Editor claims in the title of the Introduction (Chapter 1) that the Caribbean area is a "fertile ground for zoogeography". He provides a clear, even-handed discussion of the history of ideas about assembly of the West Indian biota; first, postulation of land bridges to make possible movement of the ancestral terrestrial biota from mainland to islands; second, carefully reasoned dispersal theory, without invocation of land bridges; and third, plate tectonic theory, with its pieces of land, originally close to mainland Central and South America, that drifted eastward, and brought an essentially mainland biota to the development of the present Greater Antilles.

Liebherr indicates that this basic question of the mechanism of faunal assembly has not been settled, and maintains (p. 10) that "geologic data often cannot provide unequivocal answers about the history of areas, making biological data of utmost importance in the interpretation of faunal histories". He advocates use of vicariance biogeography in this endeavour. However, I doubt that conclusions drawn from biological data can be more compelling than geological data, by whatever means the former are interpreted.

The Editor makes a convincing case that the Caribbean area is fertile ground for zoogeographers. He concludes his opening chapter by indicating the great potential of data derived from insects, as follows:

1. Insects are apt to help clarify old patterns of faunal relationships, because the West Indies have a fair number of taxa that exhibit relations with Africa rather than with New World taxa, and this implies Gondwanian connections. Liebherr implies that such relationships are direct, *i.e.*, without extinct New World mainland intermediates, or even

intermediates that have yet to be discovered.

2. Many taxa in the Antilles are conspecific with or very closely related to mainland Neotropical species. These taxa indicate overwater dispersal between mainland and islands.
3. There is a rich endemic fauna in the islands, which provides an “extensive potential data base for intra-island analyses”.

He notes, however, that the insect fauna of the Antilles is not well known, and that much field work is required to elucidate “species distributions and habitat requirements”. Mindful of the destruction of habitats that is taking place in the islands and the effect that such will have on distribution patterns before there is the chance to study them, he advocates activity in protection of the biota.

Thomas W. Donnelly, a geologist and dragon fly specialist with extensive experience in the Caribbean area, and thus sympathetic to the requirements of biogeographers in interpreting geological history, provides important background information in his chapter entitled “Geologic Constraints on Caribbean Biogeography”. Reviewing the evidence on the basis of plate tectonic theory, Donnelly argues that an island arc formed between Central and South America, providing a tenuous connection between these land masses. In latest Cretaceous and early Cenozoic times, this arc was broken into fragments as a “flood basalt moved eastward” (p.33). These fragments, or terranes, formed the present Greater Antilles, but some (such as proto-Jamaica) were totally submerged for extended periods. Cuba was formed in the late Cretaceous by diverse terranes that were “swept northward” with the opening of the Yucatan Basin. In the Middle Cenozoic (Oligocene to early Miocene), the continued eastward movement of the Caribbean Plate closed the gap that separated Central and South America and another island arc system served as a limited filter bridge for terrestrial organisms, between the two continents. The lesser Antilles, during mid-Cenozoic, was a series of separate fragments more distant from South American than from the Greater Antilles. The volcanic arc that formed during the late Cenozoic provided a filter bridge for dispersal from South America, but geological evidence minimizes the probability of an earlier Cenozoic connection of the mainland and the Lesser Antillean arc.

For most of late Mesozoic and Cenozoic time, faunal movements into the proto-Antilles and Greater Antilles would have required overwater dispersals in the order of tens of kilometers. For brief periods, the water gaps might have been “relatively narrow”, and there could have been terrestrial connections with northern Central America, and between the islands. Overwater dispersal must be emphasized, though geologists are beginning to find evidence for “limited vicariant interchange”.

Donnelly emphasizes that changing climatic conditions during the Cenozoic must have had profound influence on distribution of the biota. Using evidence of lateritic soils in the Greater Antilles, he postulates less moderate climates during the middle Cenozoic than at present, with markedly alternating wet and dry periods. The

development of the Central American isthmus during the Pliocene must have led to profound climatic change, and during the Pleistocene there is strong evidence for aridity during the glacial maxima.

The main point of all this is that biogeographers must be very cautious about invoking interruptions of continuous land connections to explain present-day vicariant distributions of related taxa.

One might think that Donnelly's paper would have caused all of the other symposiasts to emphasize dispersal theory in explaining extant distribution patterns. In fact, this did not happen, with the resulting biogeographic analyses forming two groups: those postulating dispersal theory as the principal means of explaining extant distribution patterns; and those postulating elimination of former land connections and subsequent establishment of new connections as the basis for vicariant patterns.

Of course, vicariant distribution patterns result, whatever mechanism gives rise to geographically isolated descendants of an originally continuously distributed ancestral stock. Consequently, it is incorrect to use "vicarism" as a term for a process. However, for want of a better term, I will use vicarism as is accepted by some biogeographers to designate postulation of interruptions of continuous parental ranges as the normal cause of subsequent vicariant distribution patterns of descendants.

Authors adopting dispersal as the principal cause of vicariant distributions in the Caribbean area are Slater, Nichols, Wilson, and Eickwort. Vicarists are Liebherr, Hamilton, and Grimaldi. Wilson hardly acknowledges the existence of the vicarist school, and interprets the Antillean ant fauna mainly in terms of island biogeographic theory.

An interesting age correlation emerges. Of the dispersalists, three (Slater, Wilson, and Eickwort) are appreciably older than the vicarists. Nichols is the exception. As the youngest and least experienced of the symposiasts, perhaps he was the most inclined to pay attention to Donnelly. The older individuals had their ideas formed before the heyday of the vicarists, whereas the others have been developing their careers during the vicarism period, and thus perhaps they were influenced by recent events, not to mention forceful protagonists.

Slater argues that congruence of distribution patterns of different groups may not be applicable in establishing vicariance explanations to islands located relatively close to different source areas. Taking exception to the late D.E. Rosen's expressed antipathy to using dispersal to explain biotic complexity, Slater (p.39) notes that "if wind patterns, ocean currents, similarity of habitats, and relative proximity of areas persist over a reasonable period of time, congruent patterns could be developed by dispersal as well as by vicariance". He proceeds to establish the high probability of several mainland-Greater Antillean faunal connections being the result of over-water dispersal. He concludes by noting the need for improved analyses using cladistic methods and having more complete collections with which to work.

Wilson's analysis is a generally satisfying outline of the geographical history of the West Indian ant fauna. Based on fossil as well as living taxa, dynamic principles involving dispersal and possible radiation *in situ* of certain dispersants, the only discordant element in Wilson's account seems to be the presence of the poor - dispersing Ectoninae in the fossil record of Hispaniola.

Wilson points out as defects in knowledge of West Indian ants the probable under-collecting of some islands, particularly Cuba and Jamaica, as well as lack of knowledge of certain West Indian taxa that are markedly speciose. To this list of imperfections must be added the absence of phylogenetic analysis of the West Indian ants. Without this information, the details of geographical history of the relatively luxuriant Antillean ant fauna will remain obscure.

Nichols supports the argument that the Greater Antilles function as oceanic islands, using three arguments: first, values derived from Preston's Similarity Index indicate that the islandic scaritine fauna is "in a state of flux": second, the genus *Pasimachus* (adults are large, flightless scaritines) is confined to Middle and North America, with a few species in South Florida and the Yucatan Peninsula: and third, many of the endemic genera of Coleoptera in the West Indies are borers or live under bark. Had there been land connections between the islands and mainland, presumably *Pasimachus* would be represented in the Greater Antilles. Similarly, because a preponderance of endemic and thus older genera of the West Indies live in situations suitable for transport by rafting (*i.e.*, logs) their disproportionate representation in the islands is argument for overseas dispersal. The "state of flux" argument based on the Preston Similarity Index seems to indicate that faunal composition is being determined by forces working on an ecological time scale, and if so, strength is added to Nichols' more general argument. However, the pattern might be an artifact of the method of analysis. As Connor points out (p. 258) this index emphasizes the effects of forces working on an ecological time scale, and these may outweigh historical relationships. Thus, the disturbance of the general order in the fauna implied by its being "in a state of flux" or kaleidoscopic, may not reflect an older underlying reality. Be that as it may, the present pattern of scaritine distribution does seem to me to be rather unordered.

Evidence presented by the vicarists for their hypotheses is interesting but less than convincing. In fact, Hamilton shows, in his phylogenetic reconstruction of the *Polycentropus nigriceps* group (Figs. 7-9, notes G and H, p. 159), that only the terminal clades fit the pattern required by the Rosen model. He concludes that "this cladistic analysis....gives no clear evidence of disjunct inter-island patterns of relationship", and calls for cladistic analyses of other Greater Antillean groups to search for a common pattern. Taken at face value, however, the data presented do not fit the Rosen model, and the author is left in the uncomfortable position of having to question the value of the data presented, thus: "A cladistic analysis of the *nigriceps* group based on the semaphoront [read holomorph] (not just adult male)...would undoubtedly test and enhance the results I have presented here".

Accepting the analysis presented as preliminary, therefore, I would be more encouraged to test the Rosen model further if it were supported by the preliminary data. It seems to me that the pattern of *Polycentropus* is suggestive of inter-island dispersal, and accordingly, it is a dispersalist hypothesis that ought to be tested with a more complete set of data about the species of this genus.

Grimaldi's reconstruction of the geological history of the Greater Antilles calls for a close connection of the proto-Antillean land mass with Africa, following near separation of the former from the American mainland. This seems to be required because of the relationships of some old lineages of Drosophilidae with Old World, rather than with New World, extant lineages. On two counts, I find the argument unconvincing: first, Donnelly's account of Caribbean geological history does not support Grimaldi's hypothesis (in fact, there is no reference to it), and second, just because relicts with African affinities occur in the West Indies, it is not necessary to postulate a direct former connection between the two areas. Puerto Rico could be the last area in the New World where a former widespread lineage has been able to survive. Of the larger Antillean islands, that one is farthest from the mainland, and thus might be expected to accumulate relicts, under the strictures of a dispersalist hypothesis as developed by P. J. Darlington, Jr.

In Liebherr's treatment of *Platynus*, the fauna of each island is discussed, with emphasis on cladistic relationships, and problems therewith. The major problem with the phylogenetic analysis is lack of characters in which one can have confidence. Liebherr recognizes one assemblage (the wingless group) that is based on wing loss (character 40) and displacement of the setae of the posterior angles of the pronotum (character 14). Neither of these features is very reliable as an indicator of relationships, and for the setal feature, this instability is highlighted by the necessity to hypothesize a reversal within the wingless clade, at the base of the *P. jaegeri* group (Figs. 6-7 and 6-8). In that same clade, character 17 (width of pronotal margins) is used to relate the *P. cinchonae* and *P. jaegeri* groups. I have no doubt about the value of this character for determining relationships of similar adjacent allopatric taxa that differentiated comparatively recently, but I am skeptical that such a feature is useful to establish relationships of geographically widely separated clades including a total of 18 species.

Nonetheless, Liebherr uses the hypothesized relationships of the flightless clade in his geographical analysis, suggesting that Rosen's vicariance model "adequately explains taxon relationships among species on Cuba and south and central Hispaniola, and implying that island vicariance and hybridization have been at work along the northern edge of the Caribbean plate". If, in fact, the extreme mobilist hypothesis were established, or if relationships of the *Platynus* species involved in testing the model were more convincingly demonstrated, one would have cause to accept the underlying theory of vicariance biogeography as applied to the West Indies. Under the circumstances, I find little basis for use of Rosen's model in interpreting the history of the West Indian biota.

By accepting at face value the result of the numerical analysis that relates several montane lineages with brachypterous adults, Liebherr is not in a position to consider the possibility that each of these lineages came from lowland winged ancestors which invaded montane habitats on their respective islands, with subsequent extinction of the lowland ancestors and loss of wings among the upland survivors. Such an interpretation may be contrary to the principle of parsimony as practiced by numerical cladists, but the resulting picture might make at least as much sense biogeographically as the interpretation based on the Rosen vicariance model.

Although I am not persuaded of the Rosen model of vicariance nor of the details of relationships and historical interpretation of the distribution pattern of the *Platynus* taxa as presented by Liebherr, I am impressed by the clarity of the presentation and appreciate the value of this contribution in highlighting phylogenetic and zoogeographic areas for further investigation. Discussion of causal relations between brachyptery and diversity, and between climatic change and origin of the bromeliad-inhabiting fauna of Jamaica are insightful, valuable contributions to the more general aspects of West Indian biogeography.

The concluding chapter (No. 11), by Edward F. Connor, outlines mathematically acceptable procedures for inferring historical biogeographic relationships. His principal conclusions are two: first, none of the other authors of this volume used methods acceptable to mathematicians for inferring historical biogeographic relationships: two, "it is best to examine the biogeographical evolution of the Caribbean biota independently of geologic hypotheses concerning area relationships". I suppose that systematists should pay attention to the pronouncements of their more mathematically inclined brethren, and in a logical sense, I can appreciate why one might want to analyze biogeographical data independently of geological hypotheses. However, I believe that, in the absence of the required mathematical precision that plagues most types of biogeographical data, Hennig's principle of reciprocal illumination can be applied to the available geological and phylogenetic biogeographic data, with reasonable approximations to the truth thus being obtained. I suspect it will be more useful for biogeographers to improve the quality of their taxonomic and phylogenetic information than to invest too much effort in elaborate statistical treatment of what is now available.

Connor's negative assessments aside, based on study of this volume I conclude that in view of clear evidence of past crossing of sea barriers by insects, flying or otherwise, and in the absence of clear evidence for the geologic basis of a vicariance hypothesis, little is to be gained by developing a research program to test further the tenets of that hypothesis. Gains are to be made, first by improving the data available for analysis (i.e., more complete collections of the islandic faunas; better information about way of life and local distribution of the species), and second by undertaking phylogenetic analyses of the taxa, to be interpreted using a dispersalist theory, which takes into account the tenets of the theory of island biogeography and the Darlington-Wilson-Erwin theory of taxon cycles or pulses. If such analyses fail

to provide a satisfactory account of the biota and its history, then it will be time to seek other explanatory means.

In conclusion, I found this volume to be enlightening and interesting, and a valuable contribution both to entomology and to the growing knowledge of the West Indian biota. My principal negative comment about the presentation, as such, is the lack of a concluding chapter that could have discussed and perhaps attempted to resolve the different interpretations of biotic history by the various authors. It would have been desirable for each author to have used the same definition of the study area, so that the resulting data could be compared more easily.

This volume ought to be owned and studied by anyone interested in West Indian biogeography. Otherwise, various chapters can be read with profit by taxonomists interested in the taxa treated therein, though not interested in the West Indian fauna, as such.

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