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CARABID BEETLES

their evolution, natural history, and classification

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2.37. The American Connection, Past and Present, as a Model Blending Dispersal and Vicariance in the Study of Biogeography

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My reasons for presenting this premature outline of Middle American carabid biogeography are to pose questions and suggest directions for future research, not to provide answers as to how carabid beetles find themselves where they are today. Although I will mention a recent study based on fish, worms, wood lice, and rats, I am mainly concerned with what carabid beetles tell us about past geological and ecological events in the American Connection, that part of the present Western Hemisphere (Figure 1) between the equator and 30° N latitude, that is between the large continents of South America and North America north of Mexico.

Study of carabid biography in Middle America began with the early European collectors—Champion, Sallé, Höge, Bougard, Flohr, Belt, Rogers, and Van Patten. These men tied together for future workers a taxon and a place and stored this information as specimens in museums. Henry Walter Bates (1884) was the first to synthesize carabid distribution of Middle America, coming to the same conclusion as Salvin (cf. Bates, 1884) did for birds—that a demarcation line exists just north of Lake Nicaragua and that this line separates two Neotropical subprovinces. This hypothesis has been tested with geological evidence and distributions of other animals and remains substantially intact.

The first major attempt at some synthetic biogeographic statement for the Antilles was made by Philip Darlington (1937) when he hypothesized the Central American derivation of the carabid fauna of the West Indies. He continued to explore this aspect and presented a summary at the Puerto Rico Symposium (1970).

George Ball (1968) provided data and a discussion of how relatively recent holarctic boreo-montane carabid elements moved southward along the Middle American mountain systems as far as Guatemala, and how these elements were excluded or delayed from further advance, or protected from replacement.

Several recent monographers, including Ball (1975), Ball & Nègre (1972), Noonan (1973), Whitehead (1972), Goulet (1974), Allen (1972), Reichardt (1974), and myself (1970, 1975), have dealt with generic units of the Middle American fauna and have made zoogeographic analyses of the generic components. Several of these people are now engaged in other generic treatments and much additional data is presently in manuscript or note form. However, even with this increased activity on Middle American carabid systematics, there still is not enough known of monophyly, sister group relationships, and distribution to set forth a general Middle American zoogeographic statement, although we are tantalizingly close!

Fig. 1. Distribution of apterous and brachyptery-prone taxa in Middle America and the West Indies. Initials refer to names of islands, Cuba, Hispaniola, Jamaica, Puerto Rico. Quotation marks around presently ill-defined genera.

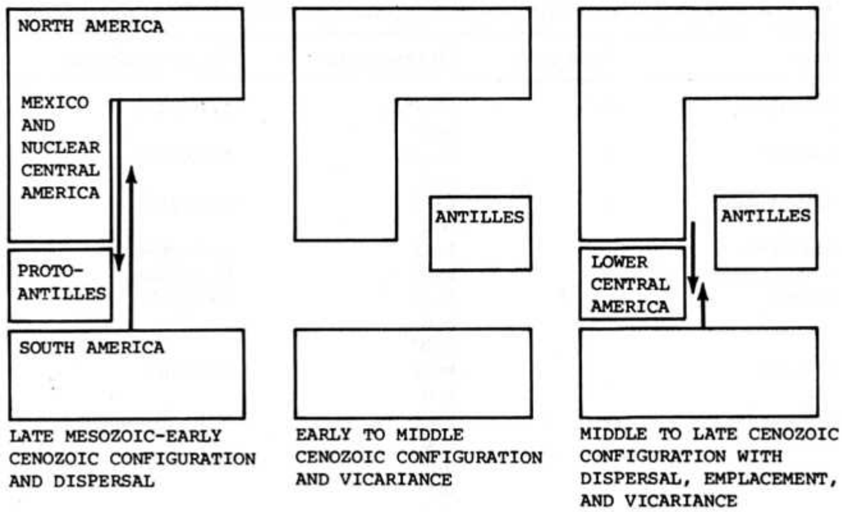

Fig. 2. Graphic configuration of Middle America during the last 80 million years with hypothetical dispersal routes (from Rosen, 1975).

As is often the case, vertebrate zoologists with their well studied animals are among the first to offer general zoogeographic statements about certain areas of the world. Recently Donn Rosen (1975), an icthyologist at the American Museum, presented a general hypothesis concerning the origins of the West Indian and Galapagos faunas based on a survey of some taxonomically "known" vertebrates and invertebrates and recent geological evidence and hypotheses (Figure 2). Because Rosen studies fresh water fish and because he and some of his colleagues at the American Museum and elsewhere are "rediscovering" Leon Croizat's biogeographic contributions, Rosen has accepted the premise that vicariance, as indicated by "tracks" is to be assumed, and dispersal only explains special cases. The major flaw of the entire Croizat school is that their method is no more "general" than that of the dispersal or centrist's school, because biological organisms are not generalists! All groups and subsets of groups have their own unique powers of movement or lack of movement and each group must be dealt with on its own merits with full knowledge of powers of dispersal, passive or active, or lack thereof. Be that as it may, Rosen and the geologists have offered an interesting set of facts and speculation, hypotheses and ideas, that are worth testing with our knowledge of carabid beetles. What we know about carabids is limited at this point and raises more questions than provides answers.

Ground beetle components of the West Indies

Most West Indian carabid beetles (Table I) live in the lowlands and are dispersants of high vagility which commonly fly to lights, are caught by net,

Table 1.
General wing state, disperal type, and habitat preference of the Antillean carabid fauna

Taxa	Wing state	Dispersal type	Habitat preference
Acupalpus	+*	hv-d*	hydrophile
		lv-d*	
Agonum	+	hv-d	hydrophile
		lv-d	
Amblygnathus	+	hv-d	hydrophile
		lv-d	
Anatrichis	+	hv-d	hydrophile
Anchonoderus	+	hv-d	hydrophile
Apenes	+, –*	hv-d	mesophile
		lv-d	
		ul-b*	
Apristus	+	hv-d	xerophile
		lv-d	
Ardistomis	+, –	hv-d	meso, hydrophile
		lv-d	
		ll-b*	
		ul*	
		ul-b	
Aspidoglossa	+	hv-d	hydrophile
Athrostictus	+	hv-d	mesophile
Bembidion	+, –	hv-d	halo, meso, hydrophile
		lv-d	
		ul-b	
Brachinus	+	hv-d	hydrophile
Bradycellus	+	hv-d	meso, hydrophile
		lv-d	
		ul	
Caelostomus	+	hv-d	hydrophile
Calleida	+	hv-d	arboreal
		lv-d	
Calosoma	+	hv-d	meso, xerophile
Chlaenius	+	hv-d	meso, hydrophile
		lv-d	
Cicindela	+	hv-d	hydrophile
Clinidium	+	rafter	wood
Clivina	+	hv-d	hydrophile
Colliuris	+	hv-d	hydrophile
		lv-d	
Coptia	+	lv-d	?mesophile
Coptodera	+	hv-d	arboreal
		lv-d	
Diplochaetus	+	hv-d	halophile
Diplocheila	+	lv-d	hydrophile
Dyschirius	+	hv-d	halo, hydrophile
		lv-d	
Dyschromus	–	ul-a*	mesophile
Elaphropus	+	hv-d	hydrophile
		lv-d	
		?rafter	
Eucaerus	+	lv-d	hydrophile
Euphorticus	+	hv-d	meso, hydrophile
		lv-d	
		ul	

Table I (Continued)

Taxa	Wing state	Dispersal type	Habitat preference
Euproctinus	+	lv-d	arboreal
Galerita	+, −	hv-d	mesophile
		lv-d	
		ul-b	
Gallerucidia	+	lv-d	arboreal
Glyptolenus	+	hv-d	mesophile
		lv-d	
Gynandropus	+	hv-d	hydrophile
		lv-d	
Halocoryza	+	hv-d	halophile
		?rafter	
Harpalus	+	hv-d	xerophile
Lachnophorus	+	hv-d	hydrophile
		lv-d	
Lebia	+	hv-d	arboreal
		lv-d	
Leptotrachelus	+	hv-d	hydrophile
Loxandrus	+, −	hv-d	meso, hydrophile
		lv-d	
		ul-b	
Lymnastis	+, −	hv-d	hydrophile
		lv-d	
		ll-b	
Masoreus	+	lv-d	xerophile
Micratopus	+	hv-d	hydrophile
Microlestes	+	hv-d	meso, xerophile
		lv-d	
Mioptachys	−	ul-a	wood, epiphytes
Megacephala	+	hv-d	subhydrophile
Morion	+, −	lv-d	wood
		ul-b	
		?rafter	
Omophron	+	lv-d	hydrophile
Oodes	+	hv-d	hydrophile
		lv-d	
Oxydrepanus	+, −	hv-d	meso, hydrophile
		lv-d	
		ll-b	
Pachyteles	+, −	lv-d	wood
Panagaeus	+	hv-d	mesophile
Paratachys	+, −	hv-d	meso, hydrophile
		lv-d	
		ll-b	
		ul-b	
Pentagonica	+	hv-d	mesophile, arboreal
		lv-d	
Pericompsus	+	hv-d	hydrophile
		lv-d	
Perigona	+	lv-d	wood
		?rafter	
Perileptus	+	hv-d	hydrophile
Pheropsophus	+	hv-d	hydrophile

Table 1. Continued

Taxa	Wing state	Dispersal type	Habitat preference
Phloeoxena	+, −	hv-d lv-d ul-b ul-a	arboreal
Platynus	+, −	hv-d lv-d ll-b ul-b ul-a	meso, hydrophile, arboreal
Plochionis	+	hv-d lv-d	arboreal
Pogonodaptus	+	hv-d lv-d	hydrophile
Polyderis	+	hv-d lv-d	mesophile
Pseudaptinus	+	hv-d	meso, hydrophile
Pseudomorpha	+	hv-d	ant symbiont
Pterostichus	+	hv-d ul-b	mesophile
Scarites	+, −	hv-d lv-d	meso, hydrophile
Schizogenius	+	hv-d lv-d	hydrophile
Selenophorus	+	hv-d lv-d ul	meso, hydrophile
Stenocrepis	+	hv-d lv-d	hydrophile
Stenolophus	+	hv-d	meso, hydrophile
Stenomorphus	+	hv-d	xerophile
Stratiotes	+	lv-d	hydrophile
Stylulus	−	ul-a	mesophile
Tachys	+	hv-d	halophile
Tachyta	+	hv-d ?rafter	wood
Taeniolobus	−	ul-a	mesophile
Tetragonoderus	+	hv-d lv-d	xerophile
Zuphium	+	hv-d	meso, hydrophile

*Abbreviations and symbols: + means fully winged, − means brachypterous, apterous, or dimorophic with respect to wing length or breadth; hv-d means high vagility dispersant, lv-d means low vigility dispersant, ul-b means upland brachypterous, ll-b means lowland brachypterous, ul means upland winged, ul-a means upland apterous, rafter means in logs across water barriers.

and are hygrophilous in habits. Hereafter these species are referred to as hv-dispersants. Several genera of hv-dispersants with quite small species such as *Perileptus*, *Halocoryza*, *Tachyta*, *Tachylopha*, *Spaerotachys*, and *Lymnastis* are also in the West Indies; these have African affinities and are closely related at or below the species group level. It is likely that dispersal across the Atlantic relatively recently accounts for their distribution. No old African lineages are in Middle America to my knowledge. There are, however, three probably known introduced species in the West Indies

(*Perigona nigriceps*, *Elaphropus yunax*, and *Caelostomus punctifrons*), all of which also occur in Africa and /or elsewhere. These are cosmopolitan hv-dispersants.

There are no holarctic boreal elements in the West Indies. As Ball (1970) showed, only *Notiophilus* and *Loricera* reached Guatemala and probably quite recently. All others are presently stopped much further north in Mexico or not found out of the southern United States.

For zoogeographic purposes, the most interesting of the West Indian groups are the old apterous elements and the aptery or brachyptery-proned elements (coined here to designate those groups such as *Platynus*, *Bembidion*, and *Ardistomis* which are mostly widespread lowland inhabitants with long wings and good powers of flight, but often have upland/brachypterous/apterous subgroups). Brachyptery-proned groups (Figure 1) are common in the West Indies while apterous groups are not. In addition to these common kinds of groups, there are a few apterous species of normally winged groups that rarely lose their wings.

Ground beetle components of mainland Middle America

Several lowland or mid-altitude temperate elements occur in Central America in a pattern of subtraction from north to south including blue *Brachinus*, *Schizogenius*, *Elaphropus*, *Tachyta*, *Amara*, *Pasimachus*, *Bembidion*, *Omophron*, and *Trechus*.

Several South American groups also occur in Central America in a subtraction pattern from south to north, including brown *Brachinus*, *Pericompsus*, *Agra*, *Mioptachys*, *Galerita*, *Apenes*, *Eucaerus*, and probably *Pelmatellus* if Andean forms are really related. Both northward and southward subtractors appear to be groups presently on the move, all are lowland or lowland derived elements, and most are hv-dispersants. Some (Figure 1) are brachyptery-proned.

Another pattern is exemplified by such groups as *Phloeoxena*. These groups have South American affinities at the subtribal level but appear to have had major radiation in nuclear Middle America (Ball, 1975).

Finally, the last major pattern exhibited by carabids in Middle America is that of old apterous elements which center in the highlands of Mexico and Guatemala. This element includes *Pasimachus* in part, *Percolaus*, *Allotriopus*, *Cyrtolaus*, *Paratrechus*, *Dyschromus*, *Geocharidius*, *Mioptachys s. str.*, perhaps *Taeniolobus*, and the non-sulcate *Pelecium*. The rhysodid genus *Clinidium* is a special case because most of its species are Antillean (Bell, 1970). Please note that I have totally ignored the *Platynus* (or "*Colpodes*") complexes. This large and diverse group probably would tell us much about zoogeography if only the classification and relationships were worked out.

Middle American—West Indian shared groups

Aside from the hv-dispersant carabid species mentioned above and