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ON THE FORMATION OF SPECIES AND GENERA IN THE INSECT FAUNA OF THE LESSER ANTILLEAN ARCHIPELAGO

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The Lesser Antilles, if certain small islands lying off Venezuela are excluded, comprise all the islands which lie north of Trinidad (10° 40′ N.) and south of the Virgin Islands (18° 28′ N.). The islands lie spaced at more or less regular intervals on a submarine ridge some 500 miles long, which curves westward at its northern end to join the main east-to-west axis of the Greater Antilles.

Most of the islands are approximately oval in outline with a median ridge of high land running from north to south. This ridge varies in altitude from 1500 to 5000 feet. The coast area of each island has a dry scrub flora and the uplands a rain-forest: these two plant associations stand in marked contrast to one another and each may harbour its own endemic species of insects.

The affinities of an overwhelming part of the insect fauna of the Lesser Antilles lie with the tropical portion of Central America, and it is clearly from this area that immigration originally took place.

In Grenada, and to a lesser extent in St. Vincent, immigrant species from the Brazilian subregion, or their modified descendants, are to be found, but they are proportionately very few. It would seem that migration northward from Trinidad has been impeded by the double barrier of the Northern Range—a wall of mountains 2000–3500 ft. high which bounds the island on the north—and of nearly a hundred miles of sea beyond it.

Through this gap between Trinidad and Grenada the zoogeographer might draw a line of faunal division similar to "Wallace's Line" of the Malay Archipelago. Such a line, though by far the more important, is not the only one which may be drawn; a distinct break in faunal continuity also occurs between the island of Guadeloupe and the Leeward Islands which lie to the north of it. Here the stretch of intervening sea is abnormally large, being about fifty miles. The islands lying between these two lines, namely Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent and Grenada, have a more oceanic character than might be inferred from the existing literature on their fauna.

From the point of view of the student of evolution the Lesser Antillean fauna may be divided into four categories. The first includes recent immigrant species and native species of relatively high genetic stability; the second includes forms and varieties of widespread species; the third, a much smaller category, includes species occurring only in the Lesser Antilles; while the fourth includes only endemic genera.

Members of the first category exhibit merely trivial variation between individuals and need not concern us here. The forms and varieties in the second show slight but more stable differences than in the preceding, and these are appreciable only in the adult stage. Variation is found in the pigmentation of the integument, to a much lesser degree in the shape or length of unimportant dermal processes, and in habits. The pigmentation of the epidermis or its setae may vary in three ways: firstly in the intensity or vividness with which a definite specific or generic pattern is developed, secondly in the replacement of the normal pigmentation by a definite alternative form, which usually intergrades with the original, and thirdly in a change of the pattern itself. Such variation is usually most pronounced on, if not actually confined to, the fore-wings in the Hemiptera and Coleoptera from which I have drawn most of my examples.

The first type of pigmentary change, that which concerns the vividness of the colour-pattern, appears as a variable character among individual specimens of the Scutellerine Pentatomid *Augocoris illustris* (Fabricius) and of several species of the Achilid genus *Catonia* Uhler (Fulgoroidea).

Rather more interesting, and confined no longer to individuals but to an upper montane district population, is the pigmentary variation shown by an undescribed species of *Acanalonia* Spinola (Fulgoroidea: ACANALONIIDAE). This insect lives in the mountain rain-forest of Dominica and is of a pure jade green at altitudes around 1000 ft., where it commonly feeds on *Simaruba amara* or *Clusia* sp. At altitudes above 2000 ft. its habitat is modified by the presence over all the woody vegetation of a dense coat of yellowish-green and brown fern-like moss; specimens taken in this formation are all yellowish-green sprinkled with brown. The distribution of this colour-form is coextensive with that of the mossy type of forest.

The second type of pigmentary change—the abrupt appearance of a pigmentation widely different from what might be considered the standard pattern is illustrated by a Flatid, *Petrusa marginata* Brunnich, which occurs in the Leeward Islands and in the Greater Antilles. This insect is usually dark in colour with a pure white submarginal band on the anterior part of the fore-wings. In the alternative form the whole insect is greenish-white, sometimes with a trace of orange around the apical margin of the fore-wings. (This pale form was described, and for long accepted, as a separate species, *P. pygmaea* (Fabricius).) In a long series of specimens a complete set of intergrades can be recognised. It should be added that this pale form does not represent a teneral adult of the dark form, nor is its appearance correlated with sex, time of year, or, as far as samples have indicated, with any constant proportion of the population.

The examples so far quoted are of insects which vary within a single island; an example of the first type of pigmentary change involving whole adult populations from different islands is provided by one of the CIXIIDAE, namely *Bothriocera eborea* Fennah, in which the fuscous pattern on the transparent fore-wings is dark in the St. Lucian strain and pale in that from St. Vincent. Similar modification is found on the lower side of the wings of certain Lycaenid butterflies, such as *Leptotes cassius* (Lucas).

Variation involving a change in pattern is seen in forms of the weevil *Diaprepes abbreviatus* L., in which the elytra are covered with ashy grey scale-like setae interrupted by smooth black longitudinal ridges. The length and number of the smooth denuded ridges vary constantly between the populations of different islands, and each arrangement is representative of its locality. In St. Lucia and in Puerto Rico (Greater Antilles) two or more forms may appear: in St. Lucia the two forms are linked by intergrades. The modification of the ridges is a morphological change, as the length of the smooth area depends on where the setiferous area is developed, and not on the colour of the setae themselves. In addition to this incipient morphological variation, a difference occurs in the colour of the setae: as already indicated, these are ashy grey, but in the populations of two widely separated islands, Tortola in the British Virgin Islands and St. Vincent in the Windward Islands, they are bright yellow in colour.

Subspecific variation in the shape of unimportant epidermal processes is not easy to demonstrate, and the student must be thoroughly familiar with the degrees of specific variation in his group before he can evaluate with confidence trivial degrees of morphological difference. The Fulgoroidea sometimes show variation in the shape of processes of their complex male genital armature at subspecific level. For example, the phallobase of *Petrusa marginata* possesses a subvertical appendage on each side. This process when examined in a long series of specimens from within a single island is found to be either acuminate or broadly bifid at the upper end.

An example of inter-island variation along the same lines is provided by an undescribed species of the Flatid genus *Euhyloptera.* In this species a lateral process on each side of the phallobase is distinctly longer—though by very little—in specimens from St. Vincent than in others from Grenada. The subspecific nature of this variation is made evident by the well-defined differences which separate the Grenadan species from its nearest ally, *E. corticalis* Fennah in Trinidad. These examples will suffice to show that the earliest kind of morphological change can involve both shape and size.

The last type of subspecific variation, which can only be observed in the field, concerns the population habits. One of the most obvious of such modifications in habit is the preference shown by certain Lepidoptera for a single plant species out of a wide range of hosts as a site for oviposition. The principle which governs such selection on the part of the female is well known, but the limitation of a specific preference to the population of a definite area is not so widely recognised. An interesting phenomenon of this class occurs in the Lesser Antilles: in all islands the developing seed-pods of pigeon pea (*Cajanus indicus*) are subject to infestation by the moths *Etiellus rubedinellus* Zeller and less commonly *Ancylostomia stercorea* Zeller. In St. Lucia, and here only, there is added to these the Noctuid *Heliothis virescens* (Fabricius) as a major pest. *H. virescens* is present in all the other islands but confines its attentions to other hosts. To cite another example from a wider area, it may be mentioned that in Florida, U.S.A., the Southern Green Stink-Bug, *Nezara viridula* L., is a recognised pest of citrus. In the Lesser Antilles, in the course of five years' work on the pests of citrus, the author never encountered *Nezara viridula* breeding on any type of citrus or feeding on the fruit, while the total number of times that I have seen one of these insects resting on citrus must be less than a score, and this notwithstanding the fact that *Nezara* abounds in the West Indies.

Such are the subspecific variations detectable in the natural environment. Now we may briefly review the types of differentiation observed between endemic species. In the Lesser Antilles the specific level (though always arbitrary), in the orders of insects from which the examples are taken, may conveniently be established for the groups of most closely similar forms which are separated from one another by bridgeless gaps in morphological characters and which show evidence of being reproductively isolated.

Endemic species may contrast with each other markedly in pigmentation, the contrast involving in the Issid genus *Colpoptera* Burmeister even colour-pattern of the eyes: it is usually in the fore-wings that such differences are best displayed, as illustrated by the weevil genus *Cholus* Germar or the *hemigrammus* group of *Diaprepes* Schoenherr. Differences in size begin to become appreciable: *Cholus spinipes* Fabricius from Grenada is larger than *C. adspersus* Fahringer from St. Vincent or *C. zonatus* Swederus from St. Lucia. Morphological differences in genital structure are almost universal in most orders of the Pterygota, and in the Homoptera Fulgoroidea include the shape of the anal segment of the male, of the non-muscled processes of the ninth abdominal segment as well as of the phallus and harpagones, and in the female the shape of the sclerites in the wall of the vagina, the shape of the spermatheca and the armature of the bursa copulatrix. In some groups the shape of the vertex shows plasticity at specific level, as in the Achilid genus *Catonia* Uhler or the Tropiduchid *Remosa* Distant, while the shape of the fore-wings may vary markedly, as in the Flatid genera *Cyarda* Stål and *Euhyloptera* Fennah, and in many of the subfamily Flatoidinae.

Differences in behaviour, possibly correlated with habitat, are occasionally discernible: for example, the coast-dwelling Flatid *Antillormenis contaminata* Uhler is not particularly agile at any time, and during the day shelters low on the plant or even among leaves on the ground, while the closely-allied *A. sancti-vincenti* Fennah, which lives in the mountain forest, is in evidence throughout the day and is relatively agile and wary. [The most striking differences in habits between species are perhaps to be found in the Hymenoptera, notably in the genus *Trypoxylon* Latreille, but such examples do not fall within the range of Lesser Antillean endemic species as far as the author is at present aware.]

Differences occur in the pigmentation of the nymphs of some Hemiptera: these are of no great magnitude or reliability, and otherwise the nymphs remain very uniform in gross structure. In holometabolous groups larval distinctions are often found possible though on characters both slight and few. Rather unexpectedly a series of pronounced and bizarre morphological differences have been found to occur in the egg stage between species of the genera *Dioxyomus* Fennah and *Neotangia* Melichar in the Tropiduchid Fulgoroidea. Such differences, which involve the operculum and its process, are apparently not widespread in the Fulgoroidea or elsewhere, though the subject requires study.

Between endemic genera the differences are so pronounced and so divergent in kind in different families or orders as to offer little clue to their relationship through common ancestry. All the characters which have been listed before are included in these differences—pigmentation, size, shape of vertex, fore-wings and genitalia, and habits—and are reinforced with further differences, such as occur in general bodily proportions, fore- and hind-wing venation. Moreover at this stage differences may develop in internal structure; for example, in the New World subgenus *Melanoliarus* Fennah of *Oliarus* Stål in the Cixiidae the number of follicles in each testis is six in all species so far examined: in the superficially very closely allied genus *Vincentia* Uhler, on the other hand, there are eighteen to twenty follicles in each testis. It is at the generic level that sexual dimorphism begins to appear in some groups, such as the Cenchreine Derbidae, where genera such as *Patara* Westwood show sexual dimorphism while others do not. Differences in habit are found between genera: in the family Kinnaridae (Fulgoroidea) members of the genus *Prosotropis* Uhler almost invariably feed and rest with the wings held upward and diverging, but species of its nearest ally, *Quilessa* Fennah, continually carry the wings folded against the abdomen.

Nymphal differences between genera become fairly well marked in hemimetabolous insects, while in holometabola larval differences often are very pronounced, especially in some groups of widespread Lepidoptera, such as the SPHINGIDAE.

What is believed to be an example of the recent formation of genera is provided by the Tropiduchid genera *Cyphoceratops* Uhler, *Parahydriena* Muir and *Chasmacephala* Fennah. These are all isolated from other genera of the family by the compressed form of the pronotum, and from each other by bizarre differences in the shape of the vertex. The genus *Chasmacephala* contains species distributed throughout the Windward Islands, and well separated by conventional differences in the male genitalia; *Cyphoceratops* occurs in Cuba and Haiti, and *Parahydriena* in Santo Domingo and Puerto Rico. The number of characters which these have in common would seem to indicate that in spite of their different head-formation they have diverged at no distant period from an isolated ancestral form, and have scarcely passed the stage of being subgenera.

Such are the differences at various group-levels in the Lesser Antillean insect fauna. Now let us consider the way in which they may have arisen.

Three sets of factors appear to be involved in the evolution of an endemic species: factors stimulating variation, factors governing the direction of variation and lastly factors controlling the fixation of the variants.

The nature of the factors which stimulate the organism to vary is a matter of speculation. The author suggests that fundamentally only one is operative and this is simple irritation of protoplasm, brought about, perhaps, by fluctuations in the micro-environment affecting the metabolism of the individual throughout its development. Heat, cold, low or high humidity, varying diet and the need for movement all affect the glandular and muscular activity of the insect. Muscular activity, coupled with activity of the spiracles, will influence the degree of oxygenation of the tissues. It would seem by no means impossible that fluctuation in the oxygen content of the tracheolar fluid which bathes and supplies the germ plasm throughout its differentiation has a sufficiently irritating effect to cause occasional abnormality at the reduction division of the ovogenic and spermatogenic cells.

If this possibility be admitted for the fluctuations of gases dissolved in the body fluid it must also be admitted for fluctuations, both quantitative and qualitative, of compounds in solution—compounds resulting from the metabolism of different kinds of plant or animal food.

The effect of variation in food on the development of certain phytophagous insects is known to be considerable, though evidence of any effect on the germinal tissues is wanting. The presence of metallic salts in the larval food leads to the appearance of melanic forms of the adult in some Macrolepidoptera. Moreover, the author has obtained a black form of the Green Stink-bug, *Nezara viridula* L., by rearing a brood on diet similarly treated. It may be added that a black form of this bug has been recorded in the field in Florida, and it would seem not unreasonable to ascribe its appearance to a nutritional cause.

(If it is permissible to digress for a moment, the author would like to emphasise that the food of many insects, especially in the Hemiptera and Thysanoptera, should be defined not in conventional terms of host *plants* but of host *cell-solutes*. Many Homoptera feed on a variety of plants, often botanically unrelated, but only thrive vigorously when their hosts are in a certain physiological state (usually with a high C/N ratio). The mealy-bug *Puto barberi* Cockerell, which attacks citrus in the West Indies, cannot be reared or even kept alive on young, fresh foliage or twigs, but grows and multiplies readily when provided with twigs that are in an unthrifty condition, notwithstanding the fact that both sets of twigs may be growing on the same individual plant. Furthermore, it has been shown by Squire that the long diapause of the Pink Boll-worm of cotton in the West Indies (*Pectinophora gossypiella* Saunders) occurs only after the larva has fed exclusively on dry food. When it feeds on normally moist food it pupates after a very transient diapause.)

As to the factors which govern the direction of variation, it can only be stated that in each group of insects there seems to be a more or less definite order of instability in the arrangement of the genes and that displacements of groups of genes tend to occur in a parallel manner in allied species, producing the parallel variation which is so common. The order of instability may be determined by the arrangement of the genes on the chromosome: certain groups of genes, occupying the same relative position on a similar chromosome in allied insects, may be exposed, by the accident of their position, to a greater hazard of displacement during an abnormal mitosis than other groups. While parallel variation is usual (as, for instance, in the subequal changes in genitalia in each of a compact group of species), occasionally a character is observed to vary at a genealogically earlier stage in one species than in others, as if the genic displacements and rearrangements had not conformed to the standard sequence. The result, in a well-known genus, is a perfectly recognisable *species* set apart by reason of variation in what is regarded by the taxonomist as a single *generic* character. In the Cixiid Fulgoroidea *Pintalia discrepans* Muir is perhaps an example of this kind of genetically precocious change.

Fixation of variations when they have occurred is, on present evidence, overwhelmingly a function of isolation of the variants. Topographical isolation at once suggests itself—oceanic islands, plant associations and the like, because the distribution of the variants is coextensive with the area which they occupy. But the author would suggest that isolation of variants begins at a much lower level than that of the district community, and that possibly the earliest type of isolation is physiological, and originating in a preference which becomes habitual, and that the fixation of the habit leads to reproductive isolation. In an examination of the male genitalia of comparatively long series of specimens of endemic species each confined to a single island, the author has repeatedly been impressed by the homogeneity of the sample as far as the organs under scrutiny were concerned. In each endemic species of Fulgoroidea nothing indicative of a range of subliminal morphological variations has yet been noted, nor has any abnormal, freak or mutant specimen been discovered. Yet if the island, or plant association, is the initially operative isolating agent, as it might appear to be from the distribution of each endemic species, more variation within the population inhabiting such areas is to be expected than has been found. It must be borne in mind that, in some groups of insects at least, morphological change leading to species-formation begins in organs which from their position are not subject to any test of efficiency in a hostile external environment. As far as the Fulgoroidea are concerned, the author is forced by the weight of evidence to believe that the variations in phallic and periphallic armature found in Lesser Antillean endemic species raise no mechanical barrier to copulation between the male of any one species and the female of an allied species; furthermore in view of the almost unchanging nature of the female organs in some of these species it is difficult to imagine how any slight modification in the male armature can be of immediate advantage to its possessor, as the modified element has no critical function to discharge.

It was found that when specimens of both sexes of the two endemic species *Antillormenis contaminata* Uhler and *A. sancti-vincenti* Fennah, which inhabit respectively the coast scrub and the mountain forest in St. Vincent, were placed together in a cage after being reared from the last instar the male of one species ignored the female of the other but mated with the female of his own species. This finding has not yet been confirmed by repetitions of the test, so that no final conclusions can be drawn, but the first result does legitimately suggest the possibility that reproductive isolation may be brought about at an early stage in variation by sexual selection on the basis of an imponderable factor of a physiological nature.

The outstanding problem, at least in the study of endemic Fulgoroidea, is to account for the lack of subliminal or minor variation within the isolated species in morphological characters which are strikingly different between species. The above hypothesis carries with it the implication that the imponderable factor which limits the extent of mating or otherwise governs selection is linked or highly associated with a capacity to influence the morphological development of the offspring of the opposite sex in a definite and precise direction, as it is evident from observation that in some families both sexes vary together from their counterparts in other islands, and in both sexes the morphological changes are equally uniform in samples of any one population. This generalisation may be best understood from a hypothetical example. Let it be supposed that a female variant with the biological habits of a Fulgoroid becomes sexually mature after reaching the adult form more rapidly than the remainder of the population. She lays eggs sooner and accordingly spends less time exposed to predators before oviposition than do her companions. Moreover, in a seasonal rise in population the early-laid eggs are less liable to destruction by egg-parasites, as the parasite population has not built itself up. If the character is inheritable, and the males prefer the females of their own strain, a quick-maturing form will replace the normal form in relatively few generations (and incidentally set in motion the natural selection of a more early-attacking strain of parasite). If it be further assumed that the physiological or genetical change which expressed itself in early maturity of the original female also incidentally affected the mechanism governing the reduction division of the egg so that in the males of the offspring, when they reached the last instar, " growth organisers " at certain unstable growth centres were more than usually stimulated, then elongation (by more prolonged cell division) and stronger curvature (by prolonged cell division and growth on one side more than another) of processes on the male genitalia could be produced almost in one step. In this hypothetical case the processes on the male genitalia could all be changed in shape in the same way in each individual (giving the uniformity actually found in the field) and yet their shape would be merely the incidental by-product of competitive evolution in the female of the species, and of no immediate biological significance (as seems actually to be so in many male Fulgoroidea).

The only alternatives to such a view seem to be either that these uniform populations diverge at an equal rate from their common ancestor through some orthogenetic influence, or, what is even less acceptable, that all the present island species, normally exhibiting a wide range of variation between individuals, happen to have reached a temporary (and simultaneous) stability, with the most successful strain in complete possession of the habitat. Compared with the last two, the first hypothesis imposes the least strain on the investigator's credulity.

References.

Barber, H. G., and Bruner, S. C., 1932, The Cydnidae and Pentatomidae of Cuba. *J. Dep. Agric. P.R.* **16** : 245 (figures of *Augocoris illustris* (Fabricius)).

Fennah, R. G., 1942, The Citrus Pests Investigation in the Windward and Leeward Islands, B.W.I., 1937–1942. *Imp. Coll. Trop. Agriculture*, Trinidad (figures of *Diaprepes abbreviatus* L.).

——, 1945, The Tropiduchidae of the Lesser Antilles (Homoptera : Fulgoroidea). *Proc. ent. Soc. Wash.* **47** : pl. 16 (figure of *Chasmacephala*), pl. 17 (some opercular structures).

Imms, A. D., 1937, *Recent Advances in Entomology*, 2nd edn. London : 198 (Melanism), 286 (Host Selection).

Metcalf, Z. P., and Bruner, S. C., 1930, Cuban Fulgorina. I. The families Tropiduchidae and Acanaloniidae. *Psyche* **37** : 421, pl. 22 (figures of *Cyphoceratops* Uhler).

Muir, F. A. G., 1924, New and Little-known Fulgorids from the West Indies. *Proc. Hawaii ent. Soc.* **5** : 471, pl. 1 figs. 3, 3a, 3b (figures of *Parahydriena* Muir).