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ENTOMOLOGY.—*Insect taxonomy and principles of speciation.*[1] J. Manson Valentine, Bureau of Entomology and Plant Quarantine.

Probably no taxonomic science has been built upon so many conflicting systems and standards as has entomology. There are three apparent reasons for this heterogeneity—the tremendous scope of the science, its long history, and the diversity of approach of its many contributors. Furthermore, during the past few decades it seems to have suffered an era of isolation during which it attained a high degree of specialization and artificiality. The effort to standardize in terms of simple "generic" and "specific" characters, usable in keys, has resulted in great confusion and has considerably obscured the evolutionary picture. Nature, deeply subtle, can not reveal itself fully when examined piecemeal, each part dissected from the whole; and a collection of organisms so classified is therefore apt to reflect merely an arbitrary system in the mind of the worker, and to contribute little toward a comprehension of evolutionary phenomena.

Some of the early naturalists, such as Thomas Say and John L. LeConte, unhampered by conventionalities that have arisen since their time, seem to have had almost an intuitive approach to problems of speciation. Knowingly or not, they worked as if impressed by the more or less qualitative characteristics distinguishing reproductively insulated populations—the true test of specific integrity. They used their judgment and rarely did they commit a serious error. Contrast their relatively sound work with that of turn-of-the-century nomenclators, whose deductive, conventional taxonomy often led to such extremes as the attachment of multitudes of specific names to individual variations and anomalies, worn and bleached specimens, vague geographic races, stages of maturity, and, not infrequently, to the sexes of the same species.

Of recent years, systematic workers have begun to treat insects more as complex, living organisms. They have found it better science to study a relatively few species exhaustively than a large number of miscellaneous species superficially. There has thus accumulated enough evidence in entomology alone to place the species principle on a firm basis of fact, and some hope now dawns that the naming and arranging of insects will reflect the biological forces under which they have evolved. This practice, continued, will tend to produce a simple, flexible taxonomy—one that may eventually bring a gratifying degree of order to a subject now in considerable chaos.

In simplest terms, the species may be defined as a unit population of genetically similar though sometimes outwardly variable organisms that will interbreed freely in their natural habitat. No barrier due to internal factors operates to prevent normal individuals from reproducing. In other words, the species is a clan whose members are compatible psychologically, physiologically, and morphologically. When closely related species of this ideal type are not isolated by spatial or temporal limitations, they are *insulated* from one another as a result of the operation of internal specific systems ("mechanisms"), which may be classified as follows:

1. *Anatomical insulation.* The lock-and-key-like, sclerotized genitalic structures of both sexes, often extremely complex and usually characteristic of the species, tend to restrict successful insemination to within the species.

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2. *Physiological insulation.* Egg-sperm specificity, i.e., incompatibility between the sexual products of two species as exhibited in resistance to cross fertilization, in abnormality of development, in disturbances of fertility of offspring, etc.

3. *Ethological* (*behavioristic*) *insulation.* Specific selectivity, i.e., reluctance under natural conditions to engage in interspecific mating. This may be extended to include ostracism and isolationism of hybrids and anomalies.

The first is hypothetical but doubtless operates to a greater or lesser extent in insects; the second is a possibility that lacks experimental proof in insects; the third, however, is a demonstrable fact not only in insects but in other groups of animals as well. Related species of migratory ducks, for example, traveling in mixed company during the mating period, preserve perfectly their specific integrity in spite of occasional crossing, whereas the same species will hybridize much more freely in confinement. A similar phenomenon occurs in ungulate, carnivorous, and primate mammals. Indeed, it may be said of all closely related and associated species that a most important segregating factor, and perhaps often the *chief* one, is preferential selectivity. This amounts to habitual or instinctive reluctance on the part of an individual to accept for a mate any other individual, presumably of another species, presenting sexual stimuli other than those to which the first has been conditioned. That this specific conditioning can be artificially overcome, at least in the higher vertebrates, has been adequately demonstrated, and there is little reason to doubt that, in like manner, ethological (social) interspecific avoidances between related and associated species of insects will also tend to dissolve as a result of selective confinement under laboratory conditions.

From a general survey over the whole compass of speciation, beginning with minor, local variants and culminating with very distinctive aberrant species (many monobasic genera), it is at once obvious that the gradient is not a simple, gradual one but is beset with numerous plateaus and peaks that represent categories into which various kinds of "species" may be roughly classified. Further analysis reveals a rather distinct split of the entire picture into two curves, which are more or less superimposed at their bases. The object of the present paper is to compare these two major categories in their purest form in an effort to detect a possible fundamental, causal difference that might justify a clear-cut taxonomic interpretation.

In groups of plastic organisms exhibiting an abundance of valid species, it is a common phenomenon to find the most similar forms (perhaps those of most recent origin) living in closest ecological proximity. This is well illustrated in the Coleoptera, where species closest of kin very often live in intimate association, providing evidence that environmental segregation in these cases may be virtually ruled out as a functional isolating mechanism. Very similar and apparently congenetic species of Carabidae, for example, commonly share the same micro-habitats, nor is there any reason to believe that in most instances their respective breeding seasons do not at least overlap. Two and even three species of cave beetles (*Pseudanophthalmus*), showing extremely close affinity yet representing unquestionably distinct forms, repeatedly have been taken running together in the same cave or cave system in which they are localized. To cite another example, out of an almost inexhaustible field, certain species of archaic, flightless weevils (*Proterhinus*) in the Hawaiian Islands are proximate not only in kinship but in habits as well, being found together on identical host plants. Very closely related but discrete species not infrequently occur in pairs and occupy the same macro- and micro-ranges. Familiar examples among the carabids are *Calosoma scrutator* (F.) and *C. willcoxi* LeC., *Scarites subterraneus* F. and *S. substriatus* Hald., and *Galerita janus* F. and *G. bicolor* Drury.

Such species automatically receive the acid test of integrity since, in the natural state, they habitually refuse to cross with their related associates although there is no apparent lack of opportunity. The separating factor appears to be essentially an internal one—a specific "awareness" or recognition of kind. Furthermore, the phenomenon is suggestive of an intrapopulational origin of an important class of species which may owe their existence, in large measure, to self-restricting conditionings, sexual and social, within the morphological (mutational?) range of the population. Indeed, it can be maintained that speciation of this type is fundamentally psychophysiological. At least, when once it is started there is no reason to suppose that it can not be sustained by autoselectivity over and above any help from anatomical incompatibilities that may have arisen during the course of speciation. Although the first-stage products are not always easy to distinguish taxonomically, careful study usually reveals separating characters that are multiple and localized rather than generalized, constant rather than fluctuating, and qualitative rather than quantitative. Oftener than not, drastic changes in male genitalia, of a higher order than the usual variations in this plastic structure, give the clue to such specific dichotomy.

Unfortunately, there is a current tendency on the part of biologists to treat genitalic barriers merely as another "isolating mechanism" on a par with environmental segregation. Perhaps it would be well to bear in mind that these distinctive anatomic features are, after all, part of the speciation phenomenon itself. It is confusing, if not illogical, to accept the results of a biological process as their own initial cause. To clarify the problem one must proceed further with the analysis. Although the genitalic dissimilarities that tend to insulate related forms may contribute to the "purification" of a species, they should, in the writer's opinion, be viewed also as part of the consequences of a far more intrinsic and complex biogenic process with roots deep in the behavioristic psychology and sexual interactions of organisms. Perhaps it is not too extreme a view to hold that true speciation, a phenomenon not encountered in the intricate divergences of parthenogenetic forms, or in the plastic instability of asexually reproducing lower organisms, is essentially correlated with sex. More completely, it is the liberation of discrete morphological momenta, which are to some extent sustained and directed by the attractions, aversions, and compatibilities of organisms, but on which these psychophysiological momenta or conditionings are to the same degree dependent.

In antithetic contrast to associative speciation is dissociative raciation, the products of which are customarily (but very possibly inaccurately) termed "subspecies." Typical raciation, as has often been pointed out, is the effect on a species of an external factor—environmental segregation. This operates principally to circumscribe specialized adaptive salients and to establish genetic strains much as would selection. The segregating agency, always circumstantial, is usually secular (geographical, ecological, or temporal), though occasionally it is biological, as in the case of parthenogenetic forms whose various lines become isolated by virtue of their inability to cross. The ideal picture of raciation is one in which autoselectivity is notably absent, the local populations, or races, hybridizing freely where ranges overlap. They differ from true species in that they tend to exhibit distinguishing characters that are relatively superficial, generalized, quantitative and fluctuating. Even when, in extreme raciation, the changes taking place may pervade the entire facies to such an extent as to appear of qualitative value, they may usually be interpreted as alterations in degree rather than in kind, since no new character is ordinarily involved. Assuming, as seems permissible from the available evidence in Coleoptera, that totally different factors enter into the origin of associative species and dissociative races, it is not unreasonable to suppose that the observable differences between the two categories reflect on the one hand the relatively internal nature of the speciating "drives" in contrast to the relatively external mechanism of raciation on the other.

The two processes, though dissimilar in principle, are not, however, mutually exclusive, and long-continued isolation of sister colonies might conceivably result in potential speciocentrism demonstrable as refusal to cross when the opportunity arrives. It is true that in cases of discontinuous geographical raciation, and of raciation due to abrupt adaptation to environmental differences, populations sometimes exhibit such conspicuous departure from ancestral type as to render their specific or racial status a matter of considerable question. The taxonomic problems that thus arise are admittedly often very difficult; but in the writer's experience indecision is due oftener to an inadequate knowledge of the species in its entirety than to the unavailability of valid evidence.

In the Caraboidea, geographically discontinuous or "spotty" distribution of a species is the exception rather than the rule, discounting, of course, the clearly obligatory type of segregation such as that imposed by insular, mountain-top, and cave life. Nor does the condition involving obligatory segregation necessarily correlate with increased taxonomic confusion. In cavernicolous faunas, for instance, it is surprising how trivial are the observable differences between colonies of widely ranging species of cave beetles (*Pseudanophthalmus*) isolated in individual caves over a subterranean system scores or even hundreds of miles in extent—a phenomenon in distinct contrast to the unmistakable, nonoverlapping distinctions between related species in the same cave. It is more than likely that most of these populations have had an extremely long history of isolation; yet a recent survey of the genus has shown that there are remarkably few forms that can not immediately be assigned either specific or racial rank.

Products of mountain-top isolation often exhibit similar conservatism. The following is a typical example: *Steniridia aeneicollis* (Beutenmüller) and *S. tricarinata* Casey are very closely related "species" of an ancient stock of cychrine carabids endemic to the Appalachian region south of glaciation. These two forms are at present restricted to the forests above an altitude of about 4,000 feet, respectively, in the Black and Pisgah-Balsam-Smoky Mountain Ranges of North Carolina and Tennessee. In their consistent and distinct differences, and in their inability or unwillingness to traverse the extensive surrounding valleys, they stand out as conspicuous isolation products in an otherwise itinerant group containing five clear-cut species whose comparatively wide ranges broadly overlap. At least two of these species ascend the mountains sufficiently high to live in association with the two summit-dwelling relicts. If we consider the latter as a single species, the characters that separate all six are trenchant and multiple, involving drastic genitalic and tarsal modifications; whereas the relicts differ one from the other only quantitatively, in minor changes of contour, development of the interstrial costae, and suppression of sclerotization in the transfer apparatus of the male copulatory organ. They represent a distinctly lower order of mutual divergence than do their associated relatives of higher rank, despite the probability that these extreme orophilic forms have had the long-time "advantage" of complete isolation from each other.

Insular races often seem to be stabilized by a similar evolutionary inertia. An experiment performed by the writer illustrates this rather clearly. A tiger beetle, *Cicindela vitiensis* Blanchard, inhabiting the larger Fiji Islands, is both abundant and ubiquitous throughout its range. Each large island and each of a variety of overlapping ecological frames furnishes its distinctive race or subrace. For many years *vitiensis* has been considered the only tiger beetle in Fiji. Not long ago, however, the writer discovered a local, mountain-dwelling colony of another cicindelid living in intimate association with *vitiensis* but apparently not hybridizing with it. The new form exhibits qualitative specializations of characters present in *vitiensis* that establish without doubt its status as a distinct species as well as its probable origin from *vitiensis*. Interspecific copulation tests under laboratory conditions gave the following results: With equal numbers of each sex of both species present, out of 38 matings observed, only 3 were interspecific. The latter were abortive, recognition apparently causing premature separation. Psychological insulation of this order coupled with probable physiological and morphological barriers could easily account for the genetic preservation of the species, while the fact that specific selectivity in mating was not found to be absolute merely confirms the closeness of the relationship. These data contrast strikingly with those resulting from a similar experiment in which two geographic races of *vitiensis*, differing quantitatively chiefly in respect to color pattern, were brought together—the Vitilevu race (*vitiensis* s. str.) used in the above tests, and another (*v. imperfecta* Horn) inhabiting the island of Taveuni 100 miles distant. Out of 121 matings observed in cages containing equal numbers of both sexes of the two races, 59, or almost exactly half, were interracial.

It may well be that raciation under certain circumstances, such as at the extremes of extensive, divergent clines, can proceed to the point of potential insulation tantamount to speciation. Indeed, there is some evidence to this effect; yet the basic concept of speciation through biogenic discontinuity is not invalidated thereby. Fulfillment of the species standard would still depend, in the last analysis, upon the natural association of diverging groups and the spontaneous building up of an internal block between them. All the indications are that, if there is a potential split, interracial aversions must actuate the final disunity and determine its permanence. One would therefore expect speciation by raciation to be, at most, atypical, since isolation, the one factor most responsible for raciation, precludes association, the one condition essential to a true test of speciation. For example, the most distinctive races of caraboids, and consequently those most likely to establish species, occupy relatively restricted ranges, to which they are often secured by adaptive and sedentary instinct, or confined by actual physical barriers. Although negative, evidence arising from this relationship militates strongly against a total explanation of speciation in terms of raciation. On the other hand, gradual eradication of ecological and geographic obstacles over considerable geologic time, followed by colonization of available areas, could and probably has played an important part in the union of isolated races; but there seems to be no more evidence that races thus thrown together will take a specific stand than there is that they will cross. Field data from various sources, including vertebrate as well as invertebrate groups, have shown both to be possibilities. Probably significant, however, is the relative scarcity of observed instances of insulation between merging races in contrast to the abundance of cases illustrative of closely related and associated species exhibiting little or no indication of raciation, past or present. It is therefore difficult to escape the conclusion that intolerance of the unfamiliar, regardless of mode of origin or apparent tangibility of the departure, is a more fundamental factor in true speciation than isolation, which does not necessarily contribute to the establishment of distinctions appreciable to the organism.

Radical speciation apparently resulting from ancient and complete isolation may, in some cases, be interpreted as the survival of the more specialized of two or more congenetic and possibly competing species. It does not seem necessary, however, to assume extinction of the more conservative, ancestral forms to account for drastically distinct endemics, since it is well known that species confined to small areas, particularly to small islands, often fail to meet the usual specific standards of consistency established by free-ranging continental forms. Their variability, or "fluidity," may be a direct result of a sedentary life, or it may be due to the entrapment of genetic strains, or to both, but whatever the origin such a plastic potential must function as the ideal set-up for divergent speciation of the true associative type involving not only the new products but the more conservative progenitors as well. In the Carabidae, at least, endemic faunas of circumscribed ranges are largely made up either of obvious races or of compact groups of many species. The much rarer instances of single species occupying isolated ranges usually fall into the category of geologically antique, aberrant residua of one-time flourishing evolutionary tangents.

In summary, the results of an analysis of the species problem as presented by studies in various groups of the Caraboidea indicate that speciation may be defined as relatively complete morphogenic (mutational?) departure sanctioned and channelized by psychophysiological conditioning; and that raciation, a process involving environmental closeting, is the establishment of genetic lines, adaptive or fortuitous, that are essentially superficial and devoid of internal, insulating organization. The two do not appear mutually dependent, nor are they mutually exclusive. Whether raciation attains the species level depends upon the synchronous introduction of antipathetic responses between two or more merging races formerly spatially remote, an event that certainly is possible but, supported as it is by very few factual data, is probably atypical. Whether or not the species level is maintained depends largely upon the degree of fixation of an internal "awareness" whose sporadic involution in related associates may cause occasional anastomoses in the dichotomous tree of normally repellent, discrete evolution. Endless shifting circumstances, such as bring about sequestration, changing habits and locale, introduction of new faunistic elements, adoption of the parthenogenetic method of reproduction, etc., may mask the history of a species, its origin, deployment, and restriction, but so indelible is the nucleus of specific character that the relatively minor alterations due to change of life seldom, if ever, succeed in eradicating the stamp beyond recognition. All things considered, it is probably not too extreme a view to hold that sexual reproduction, together with at least initial association of divergent elements, is a *sine qua non* of the actual process of true speciation.

From the foregoing, two fundamental evolutionary principles suggest themselves: (1) True species may not be essentially dependent upon isolation for their origin; (2) secular isolation, though correlated with differentiation, may not by itself be a primary speciating factor. Speciation often appears to be the spontaneous introduction of new, self-insulating units within a parent-species population; it is the end product of self-augmenting, biogenic momenta involving the organism in its entirety. Typical raciation, on the other hand, is the effect on the species of group segregation, a factor imposed from without and operating disinterestedly in much the same manner as natural selection. To evaluate the mixed products of these two processes is the chief concern of taxonomy, a science whose complexity increases with the plasticity, youth, and colonizing drive of the group under consideration.

The scope of entomological taxonomy is so vast that the experimental approach to all its problems is out of the question. However, if good judgment based on carefully studied models takes the place of indiscriminate key-character hunting, great strides can be expected toward a system that will reflect evolution. A supposed new species should in every instance be subjected to a critical analysis, both as to the nature of its distinctions and as to the spatial relationships existing between it and its nearest allies. If these criteria were universally applied, systematics would gain immeasurably in significance, for it would then portray evolution in such a manner as to bring out not merely degrees of differences but *kinds* of differences as well.

GEOLOGY.—*The paleontology and stratigraphy of the upper Martinsburg formation of Massanutten Mountain, Virginia.*[1]

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During the course of field work on Silurian stratigraphy, Dr. Charles K. Swartz found what at first was thought to be a new species of the gastropod *Lophospira* in the upper part of the Ordovician Martinsburg formation in the Massanutten Mountain region of Virginia. In order to determine the significance of this fossil, Dr. Swartz approached the senior author, who has been engaged for some years in a study of the general problems concerning the stratigraphy and fauna of the Martinsburg, assisted, since the summer of 1941, by the junior author. As a result of this inquiry, a study was made not only of the section in which Dr. Swartz found the gastropod in question but also of another section somewhat farther south. The material collected has yielded ten new species of gastropods, pelecypods, and brachiopods. It has become evident that both the fauna and the lithology of the upper Martinsburg in these eastern sections indicate conditions different from those represented by the upper Martinsburg farther to the west and south.

[1] Received July 12, 1943.