SPECIATION WITHOUT ISOLATION

W. L. McATEE
3 Davie Circle, Chapel Hill, N. C.

Often we find in older discussions of evolutionary processes, statements possibly correct according to then existing information, but which subsequent accumulation of knowledge has rendered doubtful. In scarcely any instance has there been more frequent and rapid shifting of ground than in treatment of the general proposition of isolation.

Darwin recognized the importance of separation, both in artificial and natural selection, but he did not especially emphasize it. Moreover, he did not agree with Moritz Wagner "that migration and isolation are necessary elements for the formation of new species" (?1912, p. 90). In fact he could not well do so without depreciating just so much the force of the arguments for natural selection. The latter is in fact only a form of isolation (by allegedly restricting breeding to similar favorable variants) as recognized by Romanes, and every admission as to the importance in evolution of physical and other forms of isolation restricts the field of natural selection. It is not my intention to review the literature of isolation as a factor in evolution but rather to comment briefly on various phases in which the idea has been presented. Geographical isolation as a necessary factor to the formation of varieties and species of organisms was an early postulate. This crude generalization could not be approved for exceptions to it were part of the knowledge of every naturalist. It is well known both that isolation is not necessary to coexistence of related species, and that isolation does not necessarily result in differentiation. Then in turn ecological or seasonal separation were appealed to, and these not covering every case, finally physiological and morphological isolation were assumed as necessary to permit the development of specific differences among forms obviously not separated in any spatial sense.

It is unnecessary to cite cases typical of those that caused these changes of argument on the part of adherents to the hypothesis that some form of isolation is a necessity for speciation. It will serve to consider a few instances in which all of the suggested forms of isolation except the morphological or physiological are excluded. I may allude to the 8 species, more or less, of *Antennaria* that inhabit dry open places in the Northeastern States, to the same number of species of *Bidens*, all marsh plants of the same region. In Florida swamps there are 8 species of *Tillandsia* epiphytic on trees and 10 of *Utricularia* living in ponds and ditches. For a western example, there are 13 species, more or less, of *Eriogonum* in the Mojave Desert. Hodges (1936) has reported the identification of 32 species (besides several varieties) of *Fusarium* growing on sugar beets in storage at Syracuse, N. Y.

Woltereck (1933, p. 515) referred to "the fifty, about, endemic *Haplochromis* fishes living pell-mell in Lake Victoria, which, with one exception, are all unique, or the three hundred gammarids in the bottom mud of Lake Baikal, or the twelve to twenty species of cyprinid fishes in Lake Lanao; we cannot deny some internal causes of such differentiations or explosions, because they are not fifty or three hundred or twenty different localities (environments) within these lakes. And if we consider, for instance, the hundreds of very different Radiolaria or Tintinnidae or Coccolithophorides living pelagically under identical conditions in the same region and the depths of the Pacific Ocean, we face again the same necessity of admitting immanent capacity and trend to change."

Kofoid (1907, p. 503) stated that 50 species of *Coscinodiscus* occurred in Ant-

arctic plankton taken on one expedition between depths of 60 and 40 meters, and further, that in his own studies of the genus *Ceratium* of the dinoflagellates "in the plankton of the Pacific immediately at the surface, that is in the upper 2–3 meters, it is no unusual thing to take 25–30 species in a single 14-inch net."

It can hardly be argued, with reference to these cases, that there are niches in the necessarily very uniform environments named sufficient to accomodate such a multiplicity of species, but it can be postulated, although unreasonably so, that these species originated in spatially separated environments and congregated later. As a crucial case in which even such a far-fetched doubt cannot intrude, I would cite the tiny leafhoppers of the genus *Erythroneura* of which there are already known from the eastern United States about 50 species that live upon the leaves of grape. Several species so distinct that immature as well as mature examples can be recognized at a glance, as well as others more difficult of separation, can be simultaneously collected from a single plant, and individuals swarm.

Now in a case of this sort where isolation, if it exists at all, must be off a physiological (intersterility) or morphyological type (differentiation of the genitalia), it would seem that it is not isolation that permits the species to develop but rather that development of physiological or morphological differences have brought about whatever kind of degree of isolation that does exist. In other words, crowding in a uniform environment would provide such a free opportunity for interbreeding that speciation would be prevented except for intervention of some internally developed mechanism for preventing free crossing.

In such cases as that of the grape leafhoppers, and the example is merely extreme, not unique, it is clearly out of the question that specific characters could be developed by a process of selection of beneficial variations, for the organisms continuing to live together under identical conditions, there could be no advantage in merely being distinct. So far as advantage is concerned, such groups of species could just as well be one. If survival of the fittest ruled, there would be only one kind of grape leafhopper on the leaf at the same season, not several. Certainly in a stable environment an organism can be fittest only by being superlatively itself, not by diverging. Such examples are opposed to Darwin's postulate of divergence being promoted by natural selection as an advantage enabling occupation of new range, for in these instances divergence has clearly occupied without spread to new environment. The existing diverse species have manifestly developed together in identical environment. The picture presented is of organisms in the grip of an evolving power that brings about speciation without regard to environment.

The phenomenon probably may be taken as illustrative of what we shall find in many groups when their specific differentiation is worked out according to the most discriminative methods. Previously recognized specific groups will prove composite and we shall accordingly find numbers of species in environmental niches so uniform as to rule out the influence of external factors upon speciation.

Close analysis of groups has characterized modern work especially in insect taxonomy and the use of genitalic structures for separation of species has become increasingly prevalent. Peterson (1905, p. 224) has concluded from his work in this direction (upon butterflies) that "specific divergences have their origin in morphological differentiations in the sexual apparatus, which led to physiological isolation of groups of individuals and further that in the course of their isolation, indifferent and superficial characters by restricted breeding, become specific."

The tenor of the argument is that in cases really testing the validity of the isolation hypothesis, the origin and maintenance of characters preventing intercrossing has provided the degree of isolation necessary to the existence of closely related species in identical environment. Hence, speciation brought on isolation, not the reverse. The process is orthogenetic evolution and it undoubtedly prevails even in cases where isolation is more tangible, but has been neglected as an

explanation while other theories were having their day. Although endless discussion of external factors and their influence has served greatly to delay recognition of the fact, organic evolution clearly is in the main an innate process.

LITERATURE CITED

Darwin, C. 1912? The origin of species by means of natural selection. . . . Reprint, 6th ed., xix+501 pp. Hurst & Co., New York, N. Y.

Hodges, F. A. 1936. Fungi on sugar beets. Phytopathology, **26**: 550–563.

Kofoid, C. A. 1907. The limitations of isolation in the origin of species. Science, N.S., 25: 500–506.

Petersen, W. 1905. Urber die Bedeutung der Generationsorgane für Entstehung der Arten. 6th Congr. Internat. Zool., 213–224.

Woltereck, R. 1933. Endemism and the probable primary causes of organic evolution. Philippine Agriculturist, 21: 513–520.