

and are regarded as outwash deposits incident to the earlier glaciation. Between these highest gravels and the valley train of the last stage of glaciation several intermediate gravel-covered terraces occur that are believed to have been developed during the period of interglacial erosion which accomplished the dissection of the old surfaces upon which the early drift was deposited.

ARTHUR C. SPENCER,
Secretary.

THE TORREY BOTANICAL CLUB.

A MEETING of the club was held on January 9, at the American Museum of Natural History, with President Rusby in the chair. Sixteen persons were present.

The annual reports of the treasurer, secretary, corresponding secretary, editor and the editor of *Torreyia* were then read and placed on file. The committee on phanerogams, and the committee on cryptogams reported progress.

The following officers were elected for the ensuing year:

President—Dr. H. H. Rusby.

Vice-Presidents—Dr. Edward S. Burgess, Professor L. M. Underwood.

Recording Secretary—Dr. C. Stuart Gager.

Corresponding Secretary—Dr. John K. Small.

Editor—Dr. John Hendley Barnhart.

Treasurer—Dr. Carlton C. Curtis.

Associate Editors—Dr. Alex. W. Evans, Dr. Tracey E. Hazen, Dr. Marshall A. Howe, Dr. D. T. MacDougal, Dr. W. A. Murrill, Dr. Herbert M. Richards, Anna Murray Vail.

A request from Mrs. E. G. Britton for a grant of \$100 from the Herrman fund to be used in illustrating new species of mosses from the southern states and the West Indies was read and the application approved by the club.

C. STUART GAGER,
Secretary.

THE ELISHA MITCHELL SCIENTIFIC SOCIETY OF THE UNIVERSITY OF NORTH CAROLINA.

THE 162d meeting was held in the chemical lecture room, on Tuesday, January 23, 7:30 P.M. Under the topic 'Tropical Notes,' Pro-

fessor W. C. Coker described in a most interesting way a recent botanical trip to southern Florida and Cuba. Numerous specimens of plants were exhibited. The program was concluded by Professor Archibald Henderson, who discussed 'A Group of Cross Ratios.'

A. S. WHEELER,
Recording Secretary.

DISCUSSION AND CORRESPONDENCE.

ECOLOGICAL ADAPTATION AND ECOLOGICAL SELECTION.

It seems that in the recent discussion of evolution there is too much importance attached to variation. It is not so certain that variation itself, or the elucidation of the question how certain species came to have certain characters, is the most important question in the origin of species. The segregation of species may be only an ecological process in which the matter of structural variation is of secondary importance. In fact the Darwinian theory does not require the supposition that the origin of a new species begins with a change of structure, so that to insist upon the importance of ecological selection is only to emphasize a factor already recognized by Darwin. By limiting the development of species to the assumption of structural characters the theory of natural selection is made to appear at an unfair disadvantage. Species are characterized by non-competitive habits rather than by adaptive structures. Indeed, I hold that the origin of a new species begins with a change of place or habits and that the characters by which species are distinguished, as well as adaptive structures, follow as a consequence.

In the 'Origin of Species' there are several passages in which a change of habits is specified as a condition of selection. "For as all of the inhabitants of each country are struggling together with nicely balanced forces, extremely slight modifications in the *structure* or *habits* of one species would often give it an advantage over others" (p. 64). "The more diversified the descendants from any one species become in *structure, constitution and habits*, by so much the more will they be en-

abled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers" (p. 87). "The more diversified in *habits and structure* the descendants of our carnivorous animals become the more places they will be enabled to occupy" (p. 88). "I will now give two or three instances both of diversified and of changed *habits* in the individuals of the same species. In either case it would be easy for natural selection to adapt the *structure* of the animal to its changed *habits*, or exclusively to one of its changed *habits*. It is, however, difficult to decide, and immaterial for us, whether *habits* generally change first and *structure* afterwards" (p. 141). In view of the fact that in the ordinary cases the changes of structure are not adaptive, it seems to me quite material to recognize the change of habits as in itself adaptive and as an important condition of selection. "He who believes in the struggle for existence and in the principal of natural selection will acknowledge that every organic being is constantly endeavoring to increase in numbers; and that if any one being varies ever so little, in either *habits or structure*, and thus gains any advantage over some other inhabitant of the same country, it will seize on the place of that inhabitant, however different it may be from its own place. Hence it will cause him no surprise that there should be geese and frigate birds with webbed feet living on dry land and rarely alighting on the water; that there should be long-toed corncrakes living in meadows instead of in swamps; that there should be woodpeckers where hardly a tree grows; that there should be diving thrushes and diving Hymenoptera, and petrels with the habits of hawks" (p. 145). These quotations may give an idea of Darwinism quite different from that suggested by some current definitions which the authors have not felt obliged to connect with Darwin's writings.

By ecological adaptation is meant the kind of adaptation which occurs when a species occupies a favorable position without showing any obvious adaptive characters, except such as are common to other members of the same genus or larger group. By ecological selec-

tion is meant the kind of selection which is conditioned upon the species occupying a favorable position without developing any obvious adaptive characters.

No ecological position is favorable for an unlimited number of individuals. The multiplication of species results from the fact that the dominant species produce more individuals than can occupy the same position. Whenever the number exceeds the optimum, even when there is no kind of inferiority among the individuals, wholesale extermination must occur, or some of the individuals must avoid competition with the dominant form by a change of place or habits.

Change of place seems to be the easiest and most natural means of avoiding competition and one of the most obvious conditions of selection. I am inclined to regard this as the most important factor and the one which will explain the most cases. I think the students of geographical distribution can show a thousand incipient species where the mutationists can show a doubtful one. In a local fauna it is remarkable how few species belong to the same genus. It is almost certain that the nearest relatives of any form will be found outside the district. The homogeneous elements diverge from a given habitat and the heterogeneous elements converge there. What happens to the migrating form seems to me of less importance, if it can be shown that the migration was a condition of selection. This may be hard to show. It is obvious enough, if we contemplate the return of all of the forms to their original starting point. Modification of the geographical segregate by the intercrossing of its more or less isolated members, by the operation of the selective conditions of the new environment, or by the local influences which give an impress to large elements of the fauna, are all secondary to the selective conditions which induced the migration.

But a considerable proportion of species may have originated in the same place. In this case the condition of selection is the adoption of habits which relieve them from the pressure of competition with the dominant forms. If a form occupies a favorable posi-

tion, it will produce a great number of individuals forming what we call a common and polymorphic species, probably more or less variable in habits, or polytropic. When the number of individuals approaches the maximum, the pressure of competition increases until the position becomes unfavorable to a certain proportion of the individuals. The pressure is least on the set of individuals having the most divergent habits. There is a tendency for the polymorphous polytropic group to break up into a number of more uniform oligotropic groups. If the parent species is itself oligotropic, it may give rise to a form of quite different habits. The original form retains the original position and the derived form changes to a new position. Usually all that is required to place a form in an absolutely new ecological position and make it the progenitor of a varied line of descendants is a mere change in the kind of food. The assemblage of bees owes its existence to the fact that some aculeate hymenopteron abandoned the pursuit of other insects and provisioned its nests with honey and pollen.

Whenever competition becomes severe, natural selection may operate upon two sets of individuals, those which have the original habits and those which show a change of habits. In the first set it retains the most perfectly adapted individuals. This merely keeps the original species adjusted to the original habits. The second set becomes the new species and natural selection may further operate to fit it to the new habits. When an old organ is used for a new purpose, we can understand how, after competition has again become severe, individuals in which the organ is best fitted for the new use will have the advantage. The theory of natural selection itself as applied to adaptive structures implies that the development of a new organ is preceded by a change of habits, for how is natural selection to improve an organ for a certain purpose unless the organ is already being used for that purpose?

Those who attach so much importance to structural modifications as a condition of selection seem to me to overlook an important

element in the nature of adaptation. Adaptation is determined by the nature of the position as well as by the presence of structures fitting the organism for it. The bird which became the progenitor of the humming birds was better adapted to its new place than any of its more modified descendants, not because it was structurally better fitted to get nectar from flowers, but because it occupied a more favorable place. The favorable nature of this place is shown in the fact that it could produce 400 specific forms in a comparatively short time. The absence of adaptive structures does not show that a species is wanting in adaptive habits of the most distinct kind. It does not show that natural selection has been any less operative in producing segregation.

As an example of ecological adaptation I may mention several species of the bee genus *Colletes* which occur in my neighborhood. They are distinguished by structural differences of the labrum, antennæ, metathorax, by size and punctuation and by the color and arrangement of the hair. The proboscis and pollen-carrying apparatus are the same in all, and, as far as I can see, the species do not have any adaptive structural differences. The nine species so differ in habits and in seasonal distribution that only three are in competition. *C. inæqualis* is polytropic and flies from March 20 to May 31. *C. æstivalis* gets its pollen exclusively from *Heuchera hispida* and flies from May 8 to July 1. *C. brevicornis* is an oligotropic visitor of *Specularia perfoliata* and flies from May 29 to June 29. *C. willistonii* flies from May 28 to September 5, and *C. latitarsis* from June 13 to September 29. Both of these are competitors for the pollen of *Physalis*, but they are not closely related. *C. latitarsis* is more common and its flight begins and ends later. *C. eulophi* flies from May 28 to October 9. It is polytropic, but gets most of its pollen from Compositæ. It is a competitor of the following species only in 40 per cent. of its days and in 22 per cent. of its observed flower visits. Three species are autumnal and get their pollen exclusively from Compositæ: *C. armatus*, August 17 to October 7; *C. americanus*,

August 18 to October 23; *C. compactus*, August 26 to October 19. The times of flight of the three species nearly coincide and they are competitors in the order named by 80 per cent., 66 per cent. and 45 per cent. of their observed visits. According to the views expressed here, three closely related species having the same habits would not be expected to originate in the same neighborhood. A species having an abundant food supply will simply increase in the number of individuals. The three species above mentioned are not closely related. They have evidently become competitors by migrating from the outside.

In *Andrena* there are three species, each an oligotropic visitor of willows and each having a form, or closely related species, in which the female has the abdomen red. At least as far as these species go, it will refute my view if it can be shown that the red form indicates the development of a new species having the same habits and the same range. I regard the red form as a southern geographical race, or species, and hold that the forms in their distribution merely overlap here.

The views here stated may be expressed in the following propositions:

1. To occupy the same ecological position two species must have the same geographical and phenological range and the same food habits.

2. No ecological position is favorable for an unlimited number of individuals.

3. The origin of new species results from the fact that the dominant species produce more individuals than can occupy the same position.

4. Natural selection then operates in favor of any set of individuals which changes habitat or habits so as to avoid competition with the dominant form.

5. The dominant form retains the original position.

6. The new form becomes specialized in adjustment to the new position.

7. The least specialized members of a group occupy the original position. The specialized members of a group have not driven out the original forms from the original position, but have been driven out by them. The

highest specialized members are the ones which have most frequently been driven out of their positions by the competition of lower forms.

8. Specific characters usually are not adaptive.

9. Specific characters are the result of the intercrossing of the members of an ecological segregate and are the result rather than the cause of the segregation.

10. Adaptation to a position is determined by the nature of the position rather than by the characters fitting the organism for it. Usually it does not require the development of adaptive characters and usually is not associated with them.

11. Adaptive characters are the result of the operation of natural selection after the ecological segregation takes place and do not precede the occupation of the new position.

12. An ecological position is more favorable to a limited number of individuals with imperfect adaptive structures than to a great number of individuals having more perfect structures.

13. An ecological basis for morphology is found in the change of habits which requires an old organ to be used for a new purpose. An ecological basis for evolution is indicated by the endless taxonomic difficulties resulting from adaptation to function.

14. Species having the same habits are produced by geographical migration.

15. Species having different habits are produced by ecological selection.

CHARLES ROBERTSON.

'BARRIERS' AND 'BIONOMIC BARRIERS'; OR ISOLATION AND NON-ISOLATION AS BIONOMIC FACTORS.

DURING the last three months there have appeared in SCIENCE a most interesting series of communications, contributed by both zoologists and botanists, on the influence of isolation as a factor in the evolution of species and subspecies. While there has been some disagreement as to the facts in the case, especially from the side of the botanists, the zoologists appear to differ mainly in respect to the application of terms to phenomena about the existence and relations of which there is practically