The Species Problem and Evolution.

By O. W. RICHARDS and G. C. ROBSON.

I.

THE object of these articles is to describe and discuss some of the chief attributes of closely allied species in so far as they may cast some light on the process of evolution. The method by which the latter has been brought about is still a matter for discussion, and one of the chief lines of inquiry to which great importance is attached to-day is the intensive study of the early stages of specific divergence. Darwin and the biologists of last century did not, of course, neglect this question; but within the last twenty-five years much has been discovered concerning animal ecology, genetics, and the intensive study of distribution, so that a review of the evolutionary position from these points of view may be of service. The problem will be here discussed principally from the zoological point of view; but some attempt will be made to indicate to what extent the method of evolution in plants is likely to differ from that in animals.

In the course of this discussion it will be seen that no absolute criterion of species can be given. Such distinctions have been sought in structural differences or in some special type of sterility. With regard to the latter criterion, sterility between many forms is well known, but it is uncertain whether there is a special type which can be called specific. Structural discontinuity has been supposed to be a good criterion of species; but the number of characters in which such discontinuity may occur and the degree of discontinuity itself are variable.

In any genus, when the taxonomically described species are compared one with another, it is found that the latter differ in a variable number of structural characters and that no fixed amount can be proposed by which they must differ in order to be called species rather than varieties. Structural discontinuity between such species is sometimes very evident within the limits of a single area; but it frequently becomes much less marked when a complete range of such forms is investigated. In the majority of cases specific distinction is based on the examination of a few characters only which are selected for convenience, and, as a result, the actual amount of difference between species is often doubtful in a particular case. However, in spite of the lack of an absolute criterion, the majority of forms recognised as species by taxonomists represent within broad limits a certain grade of divergence in structure and habit, and are frequently sterile, when crossed.

Some palæontologists have shown that certain forms occurring in successive strata are continuously connected by 'intermediates,' and have thought that the species concept, as it is employed by zoologists, is inapplicable to series of forms in which only the lineage of single characters can be traced. In the first case our knowledge of the relationship of different specimens must be confused by the effects of the environmental conditions which they have experienced; while the second phenomenon has not been shown to be widely spread, and in many groups species may remain well defined over long periods of time.

SPECIFIC CHARACTERS.

Specific differentiation may show itself in several ways, namely, in (1) structure, (2) physiological activities, (3) reproduction, (4) habitat-preference, (5) food, (6) special types of behaviour. When species differ in habits or structure it is probable that they differ physiologically as well, though it is difficult to show a correlation between such differences and any particular physiological process. The result is, therefore, that in practice species are distinguished by differences in their habits and structure because it is not yet possible to do so by reference to their more fundamental properties. The term physiological difference is here used in the narrow sense of difference in metabolism.

1. STRUCTURE. — Constant structural differences between species occur in all organisms from the simplest to the most complex with the exception of the Bacteria, in which, according to the present view, the physiological differences are those which can be best employed for the recognition of species. In the Spirochaeta structural and physiological characters seem to be of equal importance. A comparison between the species or races of Bacteria and those of higher organisms is of doubtful value because of the more rapid multiplication of the former. In the higher plants, structural characters may show a remarkable amount of plasticity; among animals, some, such as the corals and particular genera of other groups, are equally plastic. Not enough is yet known to enable us to say whether the degree of plasticity is a real difference between animals and plants. If such a difference exists it is more likely to occur between motile and sessile organisms.

When closely allied species in various phyla are examined, it seems to result on the whole that no particular organ or system is especially differentiated. The differences that occur usually consist of slight divergencies in size, proportion, and colour and in the number of individual parts, such as the cusps of teeth or 'ornamental' bosses and lines on shells. On the other hand, in certain groups there is no doubt that secondary sexual characters stand out as being affected; though in some these are scarcely differentiated at all, for example in the Polychaeta, the Lamellibranchia, and some Prosobranchiate gastropods.

Of those forms which show such differences, some exhibit them in the organs connected with copulation, for example many of the Platyhelmia, a large proportion of the Arthropoda, Pulmonate gastropods, and many groups of mammals; while in birds other secondary sexual characters are affected. No other generalisation as to the structural characters which distinguish closely allied forms can be made; but the following points are worthy of attention. Species often differ in the frequency with which certain characters occur together; thus the common limpet (*Patella vulgata*) differs from the "flither" or low-water limpet (*Patella athletica*), with which it has many features in common, in that it possesses more frequently a broad shell and a grey foot, while the flither usually has a narrow shell and an orange-yellow foot. Many allied

forms differ in total body size, though if their sizes were plotted graphically the frequency curves would overlap considerably.

It has been pointed out frequently that allied species tend to throw parallel variations; but it is equally true that one of two closely allied forms may be distinguished by its ability to throw some particular variant, for example, the fly *Dorniphora abdominalis* always has two antero-dorsal bristles on the hind tibia, while *D. florea* may have two or three (Lundbeck, 1922). Furthermore, species may be polymorphic in one part of their range and not in another, so that their races may differ in the ability to produce certain variants.

Colour differences between species are often held to be of great importance, but many cases are known in which such differences do not obtain, and it is uncertain whether colour is markedly affected at the onset of divergence. Some colour differences, for example melanism, constitute special problems which cannot readily be explained.

2. PHYSIOLOGICAL DIFFERENCES.—Differences between species of the same genus have been reported in many activities and properties which we define as physiological and biochemical; for example, in actual metabolic processes and their products (including special secretions such as venoms), in the fertilisation reaction, and in the behaviour of grafts. In a wide sense physiological distinction is ultimately implied in all differences of structure and habit. If we consider measurable differences in metabolism only, it is very difficult to say whether a physiological differentiation parallel to that of structure is at all universal. The study of such processes is usually limited to different genera, and the differences between species are not often considered. Furthermore, when species of the same genus are examined, no allowance is made for individual idiosyncrasy, sexual and seasonal difference, and other factors important from the taxonomic point of view. There remains, however, some evidence which suggests that taxonomic species may be as clearly differentiated in their metabolic activities and products as in their structure; for example, in carbon dioxide output, certain properties of hæmoglobin, amount of blood-sugar, starches of plants, and the precipitin reaction of vertebrate blood. The data on most of these points, however, require investigation from the taxonomic point of view, and there is furthermore a real need for the study of the physiological differentia of closely allied species.

3. REPRODUCTION.—The phenomena to be considered here include (*a*) breeding season, (*b*) mating habits, (*c*) coitus, (*d*) sterility, and may be considered in two ways, first as criteria of species and secondly as means of isolation. The latter will be more fully considered in a later section.

(*a*) *Breeding Season.*—In those parts of the world where there is marked seasonal change in physical conditions, the breeding period of animals and plants is more or less determined by such change, but within the somewhat wide limits of the general breeding period allied species may breed at different times. These differences may be absolute so that such forms cannot interbreed, or the two breeding seasons may have a larger or smaller amount of overlap. Some species, however, breed throughout the year even in temperate regions, while some allied forms breed at the same time of the year. We do not think there is at present enough evidence to determine whether differences in the breeding season are frequent in closely allied species.

(*b*) *Mating Habits.*—There are two main divisions of this subject—differences in mating-place and differences in mating-behaviour. Neither of these exist in many animals (*e.g.* sessile forms), and in others there is no definite mating-place as distinct from the general habitat.

Mating-Place.—In many cases physical conditions, such as light and temperature, control mating to a considerable extent, and it is quite possible that allied species may be isolated by definite requirements. Very little exact evidence, however, is available on this point. Many species choose particular mating-places which may or may not coincide with the nesting site. Thus Kemp (1915) records that while in *Palæmon malcolmsi* the male probably fertilises the female in fresh water outside the Chilka lake, in *P. rudis* the male accompanies the female into the lake. Both these species perform their migration when the lake is full of fresh water, while a third species, *P. lamarrei*, migrates into it in the brackish season. Comparable cases occur in fishes and birds. When the choice of mating-place involves migration the latter may take place from one particular area to another, so that allied forms are separated throughout the year; or it may take place from an area in which many species live together to a special area. In particular cases this choice of breeding-area may lead to isolation; though how often this results is uncertain.

Mating-Behaviour.—The complex behaviour that often occurs in this connexion may be divided into (1) expressions of excitement, (2) incitement and suggestion, and (3) various types of preliminary manipulation of the female. The second may include either specially developed ceremonies, for example the display by spiders of a special coloured patch, or the abortive use of behaviour included in (3); for example, in many insects the male will jump on the female's back long before coitus. Instances of specific differentiation may be found in all these types, but it is possible that it may be more marked in the second. When differences occur they are often as diagnostic as structural characters.

(*c*) *Copulation.*—The mechanics of coitus involve a complicated adjustment of the musculature and skeletal parts. Differentiation of the latter may be very frequent in intromittent and receptor organs and in parts developed for clasping. Connected perhaps with structural differences are differences in posture and the duration of coitus.

(*d*) *Sterility.*—The sterility which occurs when two species are crossed has often been supposed to be a special characteristic of such crosses. The incidence of sterility is, however, capricious, and no absolute correlation between it and structural divergence can be shown. There is, therefore, a danger of arguing in a circle as to the relationship of species, according as one or the other criterion is used. At present it is only the structural criterion which can be employed satisfactorily; for by this method the degree of sterility and other phenomena difficult of interpretation can be referred to a standard more easily fixed.

The capricious incidence of sterility was known to such an early worker as Kölreuter, and was further

emphasised by Darwin and later workers. While sterility is well substantiated among species-crosses in general, the evidence is at present insufficient to decide whether *closely allied* forms are usually sterile. Various forms (for example, species of Drosophila and Poecilopsis), which must be regarded as very closely allied, show a high degree of sterility when crossed. On the other hand, fertility of varying degree may occur between structurally distinct forms which have even been placed in different genera, *e.g.* the mallard and pintail (Philipps 1915); *Xiphophorus strigatus* and *Platypoecilius maculatus* (Gerscheler 1914). In the Teleost crosses made by Newman (1916) one effected between different orders was as successful as that between species of the same genus. Thus it is evident that sterility does not necessarily precede structural divergence and is probably produced in many cases as the sequel to a certain degree of general differentiation. This view is substantiated by the occurrence of many degrees of sterility, of which the following are some examples :—

1. Absolute sterility. (*Poecilopsis isabellæ* and *lapponaria*, Harrison.)
2. F^1 produced but with disturbed sex ratio, low vitality, or other abnormality. (Lymantria, Goldschmidt; certain Bistoninæ, Harrison.)
3. F^1 normal but sterile. (Mule.)
4. F^2 produced but weak. (*Drepana curvatula* and *falcataria*, Standfuss.)
5. F^2 healthy. (Antirrhinum, Baur; Bistoninæ, Harrison.)

Between most of the categories no definite distinction can be drawn; as, for example, two forms can only logically be called absolutely sterile if the sperm is unable to enter the egg, yet in practice they will be called sterile if the embryos are produced but die in early stages. If the embryos live a little longer they will be regarded as a sickly F^1. In addition to the categories listed above, it is sometimes found that the result of a cross between species depends on which of them provides the male and which the female.

In discussing sterility there is a danger of identifying phenomena which are only apparently similar (cf. Bateson 1912) and also of confusing sterility produced by unnatural condition with that due to genetic incompatibility. It is sometimes found that crosses at first unsuccessful are, under different conditions, quite fertile.

4. HABITAT-PREFERENCE.—In plants the habitat depends mainly on the physical and chemical factors of the environment, but in many animals an active search for more or less diverse foods determines the exact habitat almost as much as the other factors. Thus two species occurring in one plant habitat, but seeking diverse foods, may be exposed to very different conditions of competition and experience a certain measure of isolation.

Closely allied species of animals and plants may be found in different geographical areas or in habitats differentiated within the same area, and, so far as animals at least are concerned, our knowledge of their distribution is largely founded on the former. The importance of such geographical isolation is, however, uncertain unless at the same time the actual habits and mode of life are known. No two habitats in different countries perhaps can be identical, at any rate in the conditions of competition; yet conditions may be sufficiently similar for the amount of divergence attributable to them to be unimportant.

The occurrence amongst the majority of animals of specific differences in habitat between close allies is not easy to show at present. The geographical range of species may be known, but even in the commonest forms the number of plant-habitats, for example, in which they occur may be very uncertain. Amongst the forms of which the distribution is satisfactorily known, some species occur in the same habitat as their close allies, and some occur in separate ones. The common view that allied species always occur in separate habitats is by no means true. In many mammals the separation seems to be fairly complete; but this is not the case in some insects and Mollusca. When a species occurs in a particular habitat, it is often not restricted to it by a general adaptation but by a reaction to a particular factor. A habitat is usually defined by many factors, and the occurrence of a species in a particular habitat may be determined by different factors in different parts of its range. Structural modifications shown to be adapted to particular habitats or modes of life seem to be more characteristic of genera or groups of higher rank than of species. Thus, when allied species do occur in different habitats, it may not be because of any simple difference in them which could be the result of a single variation.

5. DIFFERENCES IN FOOD.—When animals live on organic débris or on food in solution, it is obviously impossible to say whether there is any difference of diet between species. When the feeding habits are more specialised, the food eaten by any species may consist of the members of a single species or genus, or of a larger range of forms. Differences in diet are not easily detected unless the range of foods is small; for when the diet is more varied a difference between allied species may relate only to a few components of the diet. In the latter case, the food-habits are rarely known well enough to differentiate species. Among insects there are many closely allied vegetarian forms which can be distinguished by the food-plant, though it is probable that such cases are not frequent in the rest of the animal kingdom. With a few exceptions, there is very little satisfactory evidence as to differences between closely allied species in this respect. When parasites are limited to specific hosts their distribution is probably determined by many factors besides food.

6. MISCELLANEOUS DIFFERENCES.—Many differences in habit between species will be recalled which are not considered in the previous discussion. The following are a few well-authenticated examples in closely allied forms. In the moths of the genus Nepticula, the larvæ of which are leaf-miners, the species are sometimes distinguished by the shape of the mine and sometimes by the way in which the larvæ dispose of their dung (Tutt 1899). G. T. Lyle (1925) records differences in closely allied species of Apanteles in the method of making cocoons. Closely allied forms of birds may differ in the degree of their timidity towards man (for example, the British and Continental robins) and in their alarm notes (meadow and tree pipits). Such cases show that habits just as structure are liable to differ specifically.

(*To be continued.*)