

Organic Evolution.<sup>1</sup>

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FOR any profitable discussion of the origin of species it is essential to know what we mean when we use the word "species." In Nature we find that a number of similar individuals, with similar habits, live in a certain area; such an aggregation of individuals may be termed a community. It is unfortunate that this word has sometimes been used for dissimilar and unrelated organisms that occur together—for example, the animals found on a muddy bottom in the North Sea, or the plants of a range of chalk hills—but I am satisfied that the word "association" is more appropriate to these, and that "community" is the right name for a number of similar individuals that live together and breed together. All this is preliminary to my definition of a species. A species is a community, or a number of related communities, the distinctive morphological characters of which are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name. Groups of higher or lower rank than species can be defined in a similar way. Thus a sub-species is a community, or a number of related communities, the distinctive morphological characters of which are not, in the systematist's opinion, sufficiently definite to merit a specific name, but are sufficient to demand a sub-specific name. Similarly a genus is a species, or a number of related species, the distinctive morphological characters of which entitle it, or them, to generic rank.

There are, of course, many species so distinct from all others and so uniform throughout their range that every one is agreed about them; but frequently the limits and contents of a species, as of a genus, are a matter of opinion. No systematist has, or should have, any rule as to the amount of difference required for the recognition of a species or a sub-species; he is guided by convenience. In practice it often happens that geographical forms, representing each other in different areas, are given only sub-specific rank, even when they are well defined, and that closely related forms, not easily distinguished, are given specific rank when they inhabit the same area but keep apart.

I have seen a species defined as a stable complex of genes—or words to that effect—and Bateson, without exactly defining a species, has insisted that those systematists who distinguish between good and bad species are right, and that the distinction between the two is not simply a question of degree or a matter of opinion. There is some truth in this; in the absence of exact knowledge, seasonal or sexual differences have been regarded as specific, and hybrids, as well as varieties that differ from the normal in some well-marked character, have been given specific names: these are certainly bad species. There is truth also in Bateson's contention that species are qualitatively different from varieties, if we restrict this word to the kind of varieties he has specially studied and do not use it for communities that differ from each other in morphological characters.

According to Bateson the principal qualities of species are morphological discontinuity and interspecific

sterility; but to the implication that these have been suddenly acquired, I would reply that in Nature there is every gradation from communities that are morphologically indistinguishable to others that are so different that every one is agreed that they are well-marked species; and it is not surprising that when morphological differentiation has proceeded to this extent it should generally, but not always, be accompanied by mutual infertility. That morphological discontinuity in a continuous environment which appears to Bateson to support the theory of the discontinuous origin of specific characters is seen to be the final term of a habitual discontinuity that began with the formation of communities that were at first morphologically identical. Bateson's argument that the Natural Selection theory, or any theory of gradual transformation, demands that the ancestral form from which two species have diverged should persist as an intermediate is seen to be quite fallacious if we get a firm grip of the idea of the division of a species into communities, followed by the evolution of each community as a separate entity.

A great deal of work has been done, especially on our more important food-fishes, in making biometrical analyses and investigating the life-histories of the different communities.

I have studied with particular attention the fishes known as char, or salmonoid fishes of the genus *Salvelinus*. Char are very like trout in appearance, but have orange or scarlet spots instead of black ones; they inhabit the Arctic Ocean and in the autumn run up the rivers to breed in fresh water, often forming permanent freshwater colonies in lakes. There are many such colonies in the lakes of Scandinavia, of Switzerland, and of Scotland, Ireland, and the Lake District of England; the formation of these colonies must date back to glacial times, when these Arctic fishes occurred on our coasts and entered our rivers to breed. These lacustrine communities show considerable diversity in habits and also in structure; for example, the char of Lough Melvin in Ireland are quite unlike those of Loch Killin in Inverness in form, in coloration, in the shape of the mouth, and in the size of the scales; these differences are sufficient to entitle them to be regarded as different species, and I have so regarded them; but now I doubt whether it is not better to look upon all these lacustrine char, however well characterised, as belonging to the same species as the migratory char of the Arctic Ocean, for once you begin giving specific names to lacustrine forms of char you never know where to stop. But if we were to exterminate the char in the British Isles and on the Continent, except in a dozen selected lakes, we should have left a dozen well-marked forms which it would be convenient to recognise as species. A somewhat similar problem arises in the classification of man; it is convenient to place all the living races in one species. But if there were only Englishmen and Hottentots we should probably regard them as specifically distinct.

In our British char, habitual segregation—the formation of communities in lakes—has been followed by a geographical isolation which commenced at the

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end of the glacial period, when the migratory char retreated northwards. The char of each lake have evolved separately, and one can see clearly how many of the differences between them are related to the conditions of life; for example, the large eyes of the Loch Rannoch char, which lives in a very deep lake, and the blunt snout and rounded subterminal mouth of several kinds which always feed at the bottom. I confess that I do not understand why the scales are much smaller and more numerous in the char of some lakes than in those of others, but I suspect that these differences in scaling are the expression of physiological differences, and are the result of differences in the environment or in the activities of the fish.

The genus *Salmo* comprises about ten species from the North Atlantic and the North Pacific, and I have shown that the salmon and trout of the Atlantic form one natural group and those of the Pacific another. Our own salmon and trout are two closely related species; both of them range in the sea from Iceland and northern Norway to the Bay of Biscay, both enter rivers to breed, and in both the young fish, known as parr, remain in fresh water until they are about two years old and six inches long, and then go to the sea. From Mr. F. G. Richmond, a well-known pisciculturist, I have the information that although at certain seasons the parr of both salmon and trout may eat the same kind of food—for example, both take flies at the surface—yet on the whole their food and feeding habits appear to be different. Salmon parr seek their food, such as insect larvæ, small molluscs and crustaceans, on the bottom, whereas young trout tend to keep in mid-water and to subsist more on water-borne food; thus the salmon parr may be hunting for food in a stretch of shallow rapid water, while the young trout wait for it in the quieter water just below. When they are about six inches long the parr of both species become silvery and are termed smolts; the trout smolts go to the sea in a leisurely manner, hanging about the estuaries, and the older fish frequent the coastal waters; but the salmon smolts make straight for the open sea and there grow much faster than the trout, attaining a weight of several pounds in a year.

I have gone into these details because I think it is important to establish that two closely related species in the same area have different habits, and to a large extent avoid competing with each other.

The morphological differences between salmon and trout are slight. The salmon, more active and a stronger swimmer, is more regularly fusiform in shape and has a more slender tail and a more spreading and more deeply emarginate caudal fin, differences of the same kind but not of the same extent as between a perch and a mackerel. The rows of scales between the adipose fin and the lateral line are usually fewer (10 to 13) in the salmon than in the trout (12 to 16); but this may be directly related to the fact that the tail is more slender. On an average the salmon has one ray more in the dorsal fin than the trout, and I am tempted to regard this as a step towards that increased number and concentration of the dorsal rays which is so characteristic of swift-swimming pelagic fishes. The last difference between the two species—the smaller mouth of the salmon—may be related to the food and feeding habits of the parr. In structure as in habits the salmon

is more specialised than the trout, and may have evolved from it. The salmon is found on the Atlantic coast of North America, where there are no trout; but I think this is because its habit of going farther out to sea has given it a greater opportunity of extending its range. There can be little doubt that the differentiation of these species has been not geographical but habitudinal, comparable to the differentiation of the coastal and open-sea herrings.

In every river and lake that it enters, the trout forms freshwater colonies, and on the other side of the Atlantic the salmon does so fairly readily, although not nearly so generally as the trout does on this side. In Europe, trout being present, the salmon forms freshwater colonies only in exceptional circumstances. Thus Lake Wenern in Sweden, now cut off from the sea by inaccessible falls, has a stock of salmon; there can be no doubt that in former times salmon entered the lake and bred in its tributaries, and that some of the smolts, when they reached the lake on their seaward migration, considered this very large lake a sufficiently good substitute for the sea to stay there, and so founded a lacustrine race.

Freshwater colonies of trout are found in the Atlas Mountains and in the countries north of the Mediterranean eastwards to the Adriatic, proving that in glacial times the range of sea-trout extended southward to the Mediterranean. The rivers of Dalmatia and Albania are inhabited not only by trout but also by fish of another species, known as *Salmo obtusirostris*. This little fish, which never grows larger than fifteen inches long, has all the structural characters that distinguish salmon from trout, and, indeed, looks very like an overgrown salmon parr; but when compared with salmon of the same size it is seen to differ in having a considerably smaller mouth, weaker teeth, and more numerous gill-rakers (15 to 18 instead of 11 to 14 on the lower part of the first arch). In fishes generally the number and length of the gill-rakers—projections from the gill-arches that prevent food from entering the gill-chamber with the respiratory current—are related to the nature of the food; thus, in exclusively piscivorous fishes, such as the pike, they are represented by a few short knobs, and in feeders on minute plankton organisms they are very numerous, long, slender, and close-set. It has been recorded that *Salmo obtusirostris* subsists mainly on the larvæ of Ephemeroidea, which are very abundant in the rivers it inhabits, and there can be no doubt that the small size of the mouth, the feeble dentition, and the increased number of gill-rakers are related to this diet.

The presence of this fish in the rivers of the east side of the Adriatic seems to me to point to the probability that in glacial times salmon, as well as trout, occurred in the Mediterranean, and that in these rivers some of the salmon parr, tempted by the abundance of parr food, preferred to continue the parr life instead of going to the sea as smolts, thus forming a freshwater colony in quite a different way from the salmon of Lake Wenern. The question may be asked: If these fishes are derived from salmon and live in the same way as salmon parr, how can their differences from salmon be adaptive? The reply to this is that the size of the mouth in the salmon parr must have some relation to the fact that it is going to become a salmon, feeding on fishes in the sea,

and that, as *S. obtusirostris* grows to twice the length of a salmon parr, we should expect the number of gill-rakers to be increased, for it is not number but the size of the interspaces that is important in relation to food.

The work of Dr. Johannes Schmidt on the viviparous blenny (*Zoarces viviparus*) is of great interest. He found that samples of *Zoarces* from various parts of the Kattegat and Baltic differed slightly, but generally had an average of about 118 vertebræ, but that in the shallow Danish fiords the number was less, and decreased progressively the farther the distance from the sea. Conditions of temperature, salinity, etc., are very different in the different fiords, and I am inclined to think that the critical character common to all of them is that they give the *Zoarces* an opportunity of leading a quiet life amidst a plentiful supply of food; hence the fiord *Zoarces* can be distinguished at a glance from those outside by their shorter and deeper form. For example, in the Mariager Fiord, a narrow inlet about twenty miles long, the average number of vertebræ decreases from 115 at the mouth to 111 about seven miles inland and 110 about fifteen miles inland; two samples from the extreme end of the fiord and from a point four miles from the end both showed exactly the same average, 109.3.

There can be no doubt that the fiords were originally populated from the outside, and it seems likely that the decreased number of vertebræ in the fiords is related to the lesser activity of the fiord fish. Evolution has proceeded to such an extent that the *Zoarces* of the Roskilde Fiord differs from that of the Kattegat more than does the European eel from the American, and these are generally regarded as good species. But the repetition of the same phenomenon in different fiords, and the continuous gradation from one form to another, make it impossible to recognise species here. *Zoarces* are very stationary, but possibly the young are more migratory than the adults. If we suppose that these fishes move on an average a mile a year, or even less, and mate with the nearest fish of the opposite sex, we can understand how the tendency to form a pure fiord race is hampered by continuous interchange, and how the influence of the outside form gradually diminishes until in the innermost waters it is not felt at all and isolation is accomplished. In each fiord a series of intermediates, hybrids if we like so to term them, connect two well-differentiated communities, one in the sea, the other in the inner waters of the fiord.

These detailed examples are sufficient to illustrate my view that some form of isolation, either physical or produced by localisation or by habitual segregation, is a condition of the evolution of a new species. The effects of physical isolation, due to the formation of a barrier, are well seen in comparing the fishes of the Atlantic and Pacific coasts of Central America, most of which can be paired, one species being found on the Atlantic side and its nearest ally on the Pacific side. The effects of habitual segregation are, as it seems to me, seen in the cichlid fishes of Lake Tanganyika, where there are ninety species that appear to have evolved in the lake from two ancestral forms; the differences between these species in the form and size of the mouth, and in the dentition, are an indication that their diversity is related to specialisation for different kinds of food.

The whole of my work leads to the conclusion that the first step in the origin of a new species is not a change of structure, but the formation of a community either with new habits or in a new or a restricted environment. For some species we know fairly certainly what has happened, and where, when, and why: Shall we ever know how? Experimental attempts to repeat the operations of Nature might perhaps give us a clue, but I do not expect one from experiments of the kind that are so fashionable nowadays.

For example, if *Salmo salar* and *Salmo obtusirostris* could be bred together, it would not matter much whether the hybrids were sterile or fertile; and if they were fertile it would not interest me to know that the variation in their offspring could be squared with the factorial hypothesis by the ingenious assumption that there were several factors for both larger mouth and smaller mouth and for fewer gill-rakers and more gill-rakers. Even if the number of gill-rakers in either species could be increased or decreased by thyroid extract, I should still be unconvinced that we had got much nearer to the root of the matter. . . .

Throughout, the evolution of fishes illustrates the same principles. Changes of structure have been intimately related to, and may even be said to have been determined by, changes of habits, and especially changes of food and of feeding habits. Evolution has been adaptive, but modifications of structure that were originally adaptive persist when they are so no longer; they become historical and the basis for further adaptive modifications. I am satisfied that these principles, which I have illustrated by examples from the group I have specially studied, have a general application.

Darwin's theory of evolution was that it had been accomplished mainly by natural selection, aided by the inherited effects of use and disuse. Whether that theory be permanent or not, it was put forward by a man pre-eminent for his wide knowledge and his great reasoning powers, who knew the facts that had to be explained and gave us a theory that explained them. The "Origin of Species" still remains the one book essential for the student of evolution.

Darwin has been criticised because, we are told, he did not know that there were two sorts of variations—mutations, which are inherited, and fluctuations, which vary about a mean and are not inherited. But when you point out to a mutationist that the heredity of many fluctuating variations has been proved—parents above the mean, for example, giving offspring above the mean—he tells you that that shows that the variation is not really fluctuating, but only apparently so, and that a large number of "factors" must be involved. This is in effect a complete withdrawal, for it amounts to an admission that Darwin was right if he considered that these types of variation differed only in size and frequency.

There are other critics, however, who admit that at any rate some fluctuations are inherited but say that the effect produced on a population by selection is limited; elimination of certain types will change the average, but will produce nothing new. This criticism has also, as it seems to me, been disproved experimentally; for example, by De Vries, who from two plants of clover in which a few leaves were four-lobed produced by selection a variety in which the number of

lobes of the leaves varied from three to seven, fluctuating about a mean of five. Incidentally this experiment shows the relation between mutations and fluctuations.

The criticism that many specific characters are non-adaptive merely amounts to this, that we do not know the meaning of many specific characters. Moreover, we are not likely to for a long time, for a prolonged study would be necessary to understand fully the meaning of the differences between any two species, to determine which characters were adaptive, which historical, which due to the environment, and which the expression of metabolic differences.

If these criticisms of the natural selection theory can be met, it does not follow that it is a complete theory. It may be a sufficient explanation of certain types of evolution, and one cannot wonder that those who have studied mimicry in insects are firmly convinced of its truth; but the evolution of the dodo, and of the blind fishes of subterranean waters, put rather a strain on the theory and almost demand the recognition of the inheritance of the effects of use and disuse.

If this be admitted, if the adaptive responses of an organism to changed habits and changed conditions make it possible for subsequent generations to respond with greater effect, then the part played by natural selection in evolution of this kind would be subsidiary, the selection of those individuals who responded earlier or better than their fellows. How well this idea fits in with that fundamental generalisation, the law of recapitulation, which states that ontogeny tends to repeat phylogeny, and that the more remote the ancestor the earlier it will be represented in the developmental history! This generalisation, based on embryological data, has since received strong support from paleontological evidence.

Most people are aware that a flat-fish when first hatched is symmetrical and swims vertically, but that at an early age one eye migrates round the top of the head to the other side, and the little fish sinks to the bottom and henceforth lives with the eyed side uppermost. But perhaps it is not so well known that it has been shown that almost as soon as the fish is hatched the cartilaginous supraorbital bar above the eye that is going to migrate begins to be absorbed, and is eventually represented only by short processes of the otic and ethmoid cartilages, with a wide gap between them. Through this gap the eye migrates, with the result that, when ossification begins, the main part of one frontal bone is on the wrong side of its eye. The flat-fishes are an offshoot of the perch group, and it is known that some of these have a habit of resting on one side. If such a fish found it profitable to lie in wait for its prey in this position, it would naturally try to make some use of the eye of the under side, pressing it upwards against the edge of the frontal bone. In the flat-fishes the migration of the eye into and across the territory of the frontal bone, prepared for by the absorption of the cartilaginous precursor of the frontal bone before the eye shows any sign of migration, may well be interpreted as the final stage of a process thus initiated.

You will have seen, then, that I am inclined to accept Darwin's theory as a whole, including both natural selection and the inherited effects of use and disuse, at any rate until some better explanation of the facts is forthcoming. But still there are difficulties,

and to illustrate them I must give one more example from the fishes.

The most primitive spiny-rayed fishes are the Berycoids, which flourished in Cretaceous times; in some of these the vertebræ number 24—10 præcaudal and 14 caudal. In many families of Percoids, not at all closely related to each other, we find this number of vertebræ is a constant family character; for example, all the genera and species of sea-brems (Sparidæ), red mullets (Mullidæ), chaetodonts (Chaetodontidæ), grey mullets (Mugilidæ), and barracudas (Sphyrænidæ) have 24 (10+14) vertebræ. The conclusion is inevitable that this is a primitive percoid character derived from a berycoid ancestor. Yet we have clear evidence that whenever the circumstances demanded it this number could be decreased or increased. There is no variation and therefore no material for selection; also the number of vertebræ is settled at a very early stage, and no fish can increase or diminish that number in its lifetime. Psettodes, the most primitive living flat-fish, has 24 (10+14) vertebræ; it is simply an asymmetrical perch. It has a large mouth and strong, sharp teeth, and its principal movements are probably short dashes after fishes that come near enough to be caught. But in other flat-fishes the number of vertebræ is greater: in the sole, which feeds on small invertebrates that it finds in the sands, and swims along with undulating movements of the whole body, the number is about fifty, and in the tongue-soles (Cynoglossus) there may be so many as seventy vertebræ.

We are almost compelled to believe that muscular movements, the efforts of a fish to swim in a certain way, may lead to an alteration in the number of muscle segments of its descendants; the number of vertebræ is, of course, determined by the number of muscle segments. This is an extension of the Lamarckian theory, and some may regard it as a teleological speculation unworthy of serious consideration; some may even think that, as my suggested explanation is incredible, we have here another example of the truth of the mutation theory, which in effect states that it is only by accident that a structure has a function.

Many biologists have adopted Weismann's germ-plasm hypothesis so whole-heartedly that they seem to regard it as a final disproof of Lamarck's theory. But when we consider that in progressive evolution, as in the development of the individual, increasing complexity of structure and localisation of functions is accompanied by co-ordination of the activities of all the parts, that differentiation and integration go together and the organism remains a unit, the so-called "inheritance of acquired characters" seems no more unlikely in the most advanced Metazoa than in the simplest unicellular organisms; and in some of these it has been proved.

When I read Huxley's essays as an undergraduate I was greatly impressed with his remark that "Suffer fools gladly" was very good advice. If a man does not agree with you, try to find out why he thinks as he does; you may discover the weakness of your own position. We should not adopt theories as creeds and denounce other theories as heresies. We are more likely to make progress towards the solution of the problem of evolution if we keep open minds and take broad views.