Definition of the Theory of Natural Selection.

IN his Presidential address before Section D of the British Association, Mr. Dyer is reported to have said, while alluding to myself:—"He has startled us with the paradox that Mr. Darwin did not, after all, put forth, as I conceive it was his own impression that he did, a theory of the origin of species, but only of adaptations. And inasmuch as Mr. Romanes is of opinion that specific differences are not adaptive, while those of genera are, it follows that Mr. Darwin only really accounted for the origin of the latter, while for an explanation of the former we must look to Mr. Romanes himself" (NATURE, September 13, p. 476).

It is here stated: (1) that in my opinion specific differences are not adaptive; (2) that I regard Mr. Darwin's theory as explaining the origin of genera, but not the origin of species; and (3) that, consequently, biologists are virtually invited by me to accept the theory of physiological selection as a substitute for Mr. Darwin's theory of natural selection, in so far, at all events, as the origin of species is concerned.

In direct contradiction to all these statements I will now quote passages from the paper with reference to which they are made. It would be easy for me to add further quotations to the same effect under each of the three heads, but the following will be sufficient to serve the double purpose which I have in view—namely, first to correct misrepresentations, and next to furnish a basis for further remarks upon the subject. The italics have reference only to the former purpose.

(1) and (2).—"It [the theory of natural selection] is not, strictly speaking, a theory of the origin of *species*: it is a theory of the origin—or, rather, of the cumulative development—of *adaptations*, whether these be morphological, physiological, or psychological, and whether they occur in species only, or likewise in genera, families, orders, and classes.

"These two things are very far from being the same; for, on the one hand, in an enormously preponderating number of instances, adaptive structures are common to numerous species; while, on the other hand, the features which serve to distinguish species from species are, as we have just seen, by no means *invariably*—or even *generally*—of any adaptive character. Of course, if this were not so, or if species *always* and *only* differed from one another in respect of features presenting some utility, then any theory of the origin of such adaptive features would also become a theory of the origin of the species which presented them. As the case actually stands, however, not only are specific distinctions *very often* of no utilitarian meaning; but, as already pointed out, the most constant of all such distinctions is that of sterility, and this the theory of natural selection is confessedly unable to explain. . . . *In so far as natural selection has had anything to do with the genesis of species, its operation has been, so to speak, incidental: it has only helped in the work of originating species in so far as some among the adaptive variations which it has preserved happen to have constituted differences of only specific value.* But there is an innumerable multitude of other such differences with which natural selection can have had nothing to do—particularly the most general of all such differences, or that of mutual sterility; while, on the other hand, by far the larger number of adaptations which it has preserved are now the common property of numberless species. *But let me not be misunderstood. In saying that the theory of natural selection is not, properly speaking, a theory of the origin of species, I do not mean to say that the theory has no part at all in explaining such origin. Any such statement would be in the last degree absurd.* What I mean to say is that the theory is one which explains the origin or the conservation of adaptations, whether structural or instinctive, and *whether these occur in species, genera, families, orders, or classes.* *In so far, therefore, as useful structures are likewise species-distinguishing structures, so far is the theory of their origin also a theory of the origin of the species which present them.*"

(3) "Let it, therefore, be clearly understood that it is the office of natural selection to evolve adaptations—not therefore or necessarily to evolve species. *Let it also be clearly understood that in thus seeking to place the theory of natural selection on its true logical footing, I am in no wise detracting from the importance of that theory.* On the contrary, I am but seeking to release it from the difficulties with which it has been hitherto illegitimately surrounded. . . . I cannot feel that I am turning traitor to the cause of Darwinism. On the contrary, I hope thus to remove certain difficulties in the way of Darwinian teaching;

and I well know that Mr. Darwin himself would have been the first to welcome my attempt at suggesting *another factor in the formation of species, which, although quite independent of natural selection, is in no way opposed to natural selection, and may therefore be regarded as a factor supplementary to natural selection.* . . . And here, as elsewhere, I believe that the co-operation enables the two principles to effect very much more in the way of species-making than either of them could effect if working separately. On the one hand, without the assistance of physiological selection, natural selection would, I believe, be all but overcome by the adverse influences of free intercrossing—influences all the more potent under the very conditions which are required for the multiplication of species by divergence of character. On the other hand, *without natural selection, physiological selection would be powerless to create any differences of specific type, other than those of mutual sterility and trivial details of structure, form, and colour—differences wholly without meaning from a utilitarian point of view.* But in their *combination* these two principles appear to me able to accomplish what neither can accomplish alone—namely, a full and satisfactory explanation of the origin of species."

These quotations appear to me sufficient to prove the inaccuracy of Mr. Dyer's remarks. But I should not have taken the trouble to notice misinterpretations of so absurd a kind, were it not that I have something more to say on the subject of which they treat. For Mr. Dyer, in his address, alludes to a recent criticism by Mr. Huxley, which also deals with my "paradox," but does so in a very different manner. That is to say, the passages which Mr. Huxley devotes to this subject exhibit a much more careful consideration of the points in it to which he alludes, as well as a manifest desire to state the issue fairly. I will therefore pass on to consider the criticism as it was originally presented by Mr. Huxley, leaving behind the teratological reproduction of it by Mr. Dyer as effectually disposed of by mere quotations from my paper itself.

The substance of Mr. Huxley's criticism, in so far as it apparently applies to me, is conveyed in the following words:—"Favourable variations' are those which are better adapted to surrounding conditions. It follows, therefore, that every variety which is selected into a species is so favoured and preserved in consequence of being, in some one or more respects, better adapted to its surroundings than its rivals. In other words, every species which exists, exists in virtue of adaptation, and whatever accounts for that adaptation accounts for the existence of the species. To say that Darwin has put forward a theory of the adaptation of species, but not of their origin, is therefore to misunderstand the first principles of the theory. For, as has been pointed out, it is a necessary consequence of the theory of selection that every species must have some one or more structural or functional peculiarities, in virtue of the advantage conferred by which, it has fought through the crowd of its competitors, and achieved a certain duration. In this sense, it is true that every species has been 'originated' by selection" (*Proc. Roy. Soc.*, vol. xlv. No. 269, p. xviii.).

Now, in the first place, I have nowhere said that "Darwin has put forward a theory of the adaptation of species, but not of their origin." I said, and continue to say, that he has put forward a theory of *adaptations in general*, and that where such adaptations appertain to species only (*i.e.* are peculiar to particular species), the theory becomes *also* a theory of the origin of the species which present them." The only possible misunderstanding, therefore, which can here be alleged against me is, that I fail to perceive it as a "necessary consequence of the theory of selection that every species must have some one or more structural or functional peculiarities" of an adaptive or utilitarian kind. Now, if this is a misunderstanding, I must confess to not having had it removed by Mr. Huxley's exposition.

The whole criticism is tersely conveyed in the form of two sequent propositions—namely, "Every species which exists, exists in virtue of adaptation; and whatever accounts for that adaptation accounts for the existence of the species." My answer is likewise two-fold. First, I do not accept the premiss; and next, even if I did, I can show that the resulting conclusion would not overturn my definition. Let us consider these two points separately, beginning with the latter, as the one which may be most briefly disposed of.

I. Provisionally conceding that "every species which exists, exists in virtue of adaptation," I maintain that my definition of the theory of natural selection still holds good. For even on the

basis of this concession, or on the ground of this assumption, the theory of natural selection is not shown to be *primarily* a theory of the origin of species. It follows, indeed, from the assumption—is, in fact, part and parcel of the assumption—that all species have been originated by natural selection; but why? *Only because natural selection has originated those particular adaptive features in virtue of which species exist as species.* It is only in virtue of having created these features that natural selection has created the species presenting them—just as it has created genera, families, orders, &c., in virtue of *other* adaptive features extending through progressively wider areas of taxonomic division. Everywhere and equally this principle has been primarily engaged in the evolution of adaptations, and if one result of its work has been that of enabling the systematist to trace lines of genetic descent under his divisions of species, genera, and the rest, such a result is but secondary or incidental. A wing, for example, is an adaptive structure which is formed on at least four completely different plans in different classes of the animal kingdom; and it is the function of natural selection as a theory to explain all this variety of adaptive structure, with its infinite number of subordinate variations through the different forms in each class, whether “species” or otherwise. Now, I say that such a theory is first of all a theory of the evolution of adaptations, even though it be conceded that all species exist in virtue of differing from one another in respect of adaptations, and hence that the theory becomes *also* a theory of the evolution of species, as it is *also* a theory of the evolution of genera, families, &c. Take a parallel instance. If a man were to define the nebular theory as a theory of the origin of Saturn’s rings, an astronomer would tell him that his definition is much too limited. The theory is, indeed, a theory of the origin of Saturn’s rings; but it is so because it is a theory of the origin of the entire solar system, of which Saturn’s rings constitute a part. Similarly, the theory of natural selection is a theory of the entire system of organic Nature in respect of adaptations, whether these are distinctive of particular species only, or likewise common to any number of species. In short, it is “*primarily*” a theory of adaptations *wherever these occur*, and only becomes “*also*” or “*incidentally*” a theory of species in cases where adaptations happen to be restricted in their occurrence to organic types of a certain order of taxonomic division.

This, I think, is enough to justify my definition in a formal or logical sense. But as Mr. Huxley’s criticism involves certain questions of a material or biological kind, I should like to take this opportunity of considering what he has said upon them. Therefore I will now pass on to the second head of my answer.

II. Hitherto, for the sake of argument, I have conceded that, in the words of my critic, “it is a necessary consequence of the theory of selection that every species must have some one or more structural or functional peculiarities” of an adaptive kind. But now I will endeavour to show that this statement does not “follow as a necessary consequence” from “the theory of selection.”

Be it observed, the question which I am about to consider is not whether “every species which exists, exists in virtue of adaptation” common to its genus, family, order, class, or sub-kingdom. The question is whether every species which exists, exists in virtue of some advantageous “*peculiarity*” or adaptive advantage *not shared by its nearest allies*. In other words, we are not disputing whether it is a necessary consequence of Mr. Darwin’s theory that all “species” must present “adaptations.” This, of course, I fully admit. But what we are disputing is, whether it is a necessary consequence of Mr. Darwin’s theory that every species must present at least one adaptive character (or combination of adaptive characters) *peculiar to itself alone*. Now, such being the question, let us consider Mr. Huxley’s treatment of it.

Most obviously “it follows” from the theory of selection that “every variety which is selected into a species is favoured and preserved in consequence of being, in some one or more respects, better adapted to its surroundings than its rivals.” This, in fact, is no more than a re-statement of the theory itself. But it does not follow that “every species which exists, exists in virtue of adaptation” peculiar to that species; *i.e.* that every species which exists, exists *in virtue of having been “selected.”* This may or may not be true as a matter of fact: as a matter of logic, the inference is not deducible from the selection theory. Every variety which is *selected into* a species must, indeed, present some such peculiar advantage; but this is by no means

equivalent to saying, “in other words,” that every variety which *becomes* a species must do so. For the latter statement imports a completely new assumption—namely, that every variety which becomes a species must do so because it has been selected into a species. In short, what we are here told is, that if we believe the selection principle to have given origin to *some* species, we must further believe, “*as a necessary consequence,*” that it has given origin to *all* species.

Not to perceive a consequence so necessary is said to betray a fundamental misunderstanding of the first principles of Mr. Darwin’s theory. Perhaps, therefore, it is worth while to consider the matter from another and less formal point of view.

It surely is no essential part of Mr. Darwin’s theory to deny that isolation (in all its kinds) may lead to the survival of new varieties, and so, in some cases, to the origin of new species, which need not necessarily present any change in the adaptive characters respectively inherited from their parent stocks. Under isolation, and the consequent absence of what Prof. Weismann has called panmixia, there is much reason to believe that new “structural or functional peculiarities” may arise (whether by direct action of changed conditions, by independent variation in the absence of panmixia, or by both these principles combined) which are without any adaptive significance; and I cannot see why it should be held to constitute any essential part of Mr. Darwin’s theory to deny that such is the case. No one, I suppose, will venture to express a doubt that there are named species, both of plants and animals, which have been formed under isolation, and which experiments—such as those recently made with our severally-isolated forms of British trout—would prove to be but “local varieties,” capable of being changed one into another by mere change of habitat, without any question of “selection” being so much as possible. Here it is the direct action of changed conditions which induces modifications of type sufficiently pronounced to take rank as distinct species in the eyes of a systematist; and the only difference between such a case and one where the modifications are due to independent variation is that in the former case their non-adaptive character admits of being proved by experiment. According to the general theory of evolution, there is no distinction to be drawn between a local variety and a new species, save as regards the extent to which modification may have proceeded. If, therefore, as in the case of the trout, mere change of habitat from one district of Great Britain to another (apart from any “selection”) is able to induce modifications sufficient in amount to have been ranked as species by expert ichthyologists, much more may this frequently be the case under geographical isolation in larger areas, with exposure to different climates, and subject to the superadded influence of independent variation.

I have good reason to be well aware that great differences of opinion are entertained by different naturalists touching the degree of importance which should be assigned to isolation as a factor of organic evolution; and in one of the very last issues of NATURE, Mr. Wallace presents with great lucidity the view that isolation alone can never originate a new species by independent variation without the unavoidable intervention of natural selection, seeing that “at each step of the divergence” there must be “necessarily selection of the fit” from the less fit (September 20, p. 491). I will not wait to show that, if in an isolated section of a species no new peculiarities should be required to render its constituent individuals more “fit,” selection need not necessarily effect any change with regard to adaptive characters; nor need I remark that even when selection is enabled to effect such a change under such circumstances, it does so *because it is assisted by isolation*, thus becoming, not the cause, but a *con-cause* of “the origin of species.” A great deal could be said on both these points; but, for the sake of brevity, I will take my stand on the bare fact that, according to the general theory of evolution, a local variety is what Mr. Darwin calls “an incipient species”; and, on the ground of this fact, I ask where the line is to be drawn between varieties and species in respect of adaptive characters? If no answer can be given, we must take it from Mr. Huxley, as “a necessary consequence of the theory of selection,” that every *variety* “which exists, exists in virtue of adaptation.” Thus, to take but two illustrations from among several that might be drawn from the trout just alluded to, when two lots of “Lochlevens” were placed in two separate ponds within a very short distance of each other, and exposed, as far as could be ascertained, to parallel conditions of life, remarkable—but in no conceivable respect adaptive—differences in coloration were developed be-

tween the trout which respectively inhabited the two ponds ("British and Irish Salmonidæ," pp. 226-27, 1837). Will anyone undertake to affirm, after looking at the coloured plates, that these changes must necessarily have been due to selection? Again, in a recent communication to the *Field* (July 7), Mr. Day gives an engraving of a remarkable variation which is taking place in the gill-covers of trout which have been transported to New Zealand, and there "turned down" under nature. Premising only that, although this is a change of structure, there is no more adaptive meaning to be found in it than in those changes of colour above mentioned,¹ I will quote Mr. Day's remarks upon the subject: "It will be interesting to watch the changes occurring among these trout in their new home, and to observe whether these serrations are continued or merely temporary; for if they should become developed with time there would be still more reason for constituting them a new species than now exists among the various European races; while, should trout with serrated preopercles and interopercles be admitted as constituting a new species, we could now trace the process of development from its commencement, and show how such has been occasioned by transplanting our European trout to the warmer waters of the Antipodes."

Should it be objected that, as a matter of fact, the state of matters anticipated by Mr. Day has not yet arrived, my answer would be obvious—namely, *supposing that such a state of matters had arrived*, could the fact be reasonably held to annihilate the whole theory of natural selection? Yet this is what such a fact would necessarily do, if we hold it to be "a necessary consequence of the theory" that every species which exists, exists in virtue of having been "selected." If we have not here a *reductio ad absurdum*, I do not know how one can ever hope to apply that method.

Of course I am not disputing that in general there is a very great distinction between local varieties and good species in respect of peculiar adaptive characters. In other words, I have no doubt at all that probably the great majority of species have been originated by natural selection, either as the sole cause or in association with other causes. But the allegation which I am resisting is, that it follows as a necessary consequence from the theory of selection itself that every species must owe its origin to selection. And I have endeavoured to show that this allegation admits of being reduced to an absurdity. When Mr. Wallace, in the letter above referred to, expresses dissent from Mr. Gulick's view that species are frequently originated by the influence of isolation alone, he adds: "If this is a fact, it is a most important and fundamental fact, equal in its far-reaching significance to natural selection itself; I accordingly read the paper with continual expectation of finding some evidence of this momentous principle, but in vain." Now, supposing that Mr. Wallace had found the evidence which would have fully satisfied him, would he therefore have been logically required to abandon his own great generalization? Would he have been required to acknowledge, not only, as he says, a principle "equal in its far-reaching significance to natural selection itself," but a principle which altogether superseded that of natural selection? I say it is absurd to suppose that such would have been the case, and yet it must necessarily have been the case if it be "a necessary consequence" of his theory that all (if any) species are originated by selection.

It will be remembered that I am not arguing the biological question whether, or how far, species exist which do not owe their existence to selection; I am arguing only the logical question whether it is "a necessary consequence of the theory of selection" that they cannot. And I now submit that it no more follows from the selection theory alone, that "every variety" which becomes "a species" does so "in consequence of being in some one or more respects better adapted to its surroundings than" its existing contemporaries, than it does that every variety which becomes a variety does so for the same reason. If the former statement is a statement of biological fact (which, for my own part, I do not believe), the fact is one that would stand to be proved inductively as a fact: it cannot be made good by way of logical deduction "from the theory of selection."

¹ In this connection, also, it is of great importance to remember that it is only twenty years ago since the trout in question were sent to New Zealand, and their fry liberated in the waters there: for the most ardent upholder of the theory of natural selection as the sole cause of specific transmutation will scarcely maintain that twenty years is long enough for survival of the fittest to effect a structural change of an "unknown" adaptive character in a long-lived animal with all the waters of New Zealand to spread over.

I have thus dealt with Mr. Huxley's criticism at some length, because, although it has reference mainly to a matter of logical definition, and in no way touches my own theory of "physiological selection," it appears to me a matter of interest from a dialectical point of view, and also because it does involve certain questions of considerable importance from a biological point of view. Moreover, I object to being accused of misunderstanding the theory of natural selection, merely because some of my critics have not sufficiently considered what appears to them a "paradoxical" way of regarding it.

GEORGE J. ROMANES.

How Sea-Birds Dine.

As I have ascertained that the following fact is not well known, I send you this account in the hope that it may be of interest to naturalists and to the general public. Anyone who lives in the Western Hebrides will have often watched on a calm day the sea-birds feeding with noisy clamour in the sea-lochs and about the numerous islands. This is especially the case in August, when the shoals of small herring are very plentiful. Some years ago, when in a sailing-boat off the west coast of Mull, I caught with a hand-net a dishful of these small fry as they swam along the surface of the water. Last year, noticing from a steam-launch the birds congregated in great numbers at one spot, the idea struck me to steam to the place and try to get a share of the birds' repast. The idea was at once carried out. I stood on the prow with landing-net in hand, and the launch was steered towards the birds. As we drew near, the banqueters flew away with evident dissatisfaction at the interruption, a few of the more greedy making their last hasty dives. In another moment we were at the spot, and I saw, to my intense surprise, about 2 feet under the surface, a large reddish-brown ball, 2 to 3 feet in length and 2 feet in depth. I made a frantic swoop with the net into the ball, and brought on deck half a painfull of the sea-birds' dinner. Even as we passed we could see the great living ball sinking and breaking into pieces. This year I and others have tried the same spot with great success. Sometimes the ball has sunk too deep to be reached; sometimes there was no ball to be seen; but on the most successful day I filled a painfull in three hauls. In September we saw no ball, because, perhaps, the fish had grown too large for the birds to manage. As far as I can judge, the *modus operandi* is carried out by the divers, who surround a shoal and hem them in on all sides, so that the terrified fish huddle together in a vain effort to escape inevitable destruction. The divers work from below and other sea-birds feed from above; and, as in some cases after the birds had been at work for some time I saw no ball, I suppose not one fish is left to tell the tale. I must leave to naturalists the real explanation of the matter; but I may mention that, when disturbed by the boat, the divers seem to come to the surface in a great ring round the scene of their feast. I may also mention that once, when the boat was still 300 or 400 yards away, the birds suddenly rose and whirled about with frightened screams. I wondered what could be the cause, until I saw the round back of a porpoise rolling lazily round at the exact spot, and then rolling back again. When we steamed past there was no sign of a ball. What two delicious mouthfuls for the porpoise!

COMPTON.

Loch Luichart, Ross-shire, N.B.

The Zodiacal Light.

MR. O. T. SHERMAN gives an interesting communication on the zodiacal light in *NATURE* of October 18 (p. 594), and asks for reference to any observations. He alludes to Cassini. The following extract from a letter by Cassini may not have come under his notice: "It is a remarkable circumstance that since the end of the year 1688, when this light began to grow fainter, spots should have no longer appeared on the sun, while in the preceding years they were very frequent, which seems to support, in a manner, the conjecture that the light may arise from the same emanations as the spots and faculæ of the sun." This does not quite tally with Mr. Sherman's notion that the maxima of the zodiacal light coincide with the minima of sun-spots. May it not rather be that, supposing sun-spots to be largely occasioned by increased influx of meteoric matter falling into the sun, which matter gets sublimed and repulsed to augment the materials forming the zodiacal light, therefore the maxima of the latter may then lag behind the maxima of the sun-spots.

HENRY MUIRHEAD.

Cambuslang, October 20.