"WHAT IS A SPECIES?"

The late Professor Max Müller, in an eloquent speech delivered at Reading in 1891, spoke of the necessity of examining, and, as time passes by, re-examining the meaning of words. He referred as an illustration to the man at the railway station who taps the wheels with his hammer, testing whether each still rings true or has undergone some change that may mean disaster. In almost the same way, the speaker maintained, a word may slowly and unobtrusively change its meaning, becoming, unless critically tested to ascertain whether it still rings true, a danger instead of an aid to clear thinking, a pitfall on the field of controversy. He then went on to say, that Darwin had written a great work upon the Origin of Species, and had never once explained what he meant by the word Species. So decided an utterance—the statement was made emphatically—ought to have involved a careful and critical search through the pages of the work that was attacked. However this may be, it is quite certain that the search was unsuccessful; and yet a few minutes' investigation brought me to a passage in which the meaning attached by the author to the term Species is set down in the clear, calm, and simple language which did so much to convince an unwilling world.

Darwin is speaking of the revolution which the acceptance of his views will bring about. "Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. This, I feel sure, and I speak after experience, will be no slight relief. The endless disputes whether or not some fifty species of British brambles are true species will cease. *Systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms to be capable of definition, and if definable, whether the differences be sufficiently important to deserve a specific name.* This latter point will become a far more essential consideration than it is at present; for differences, however slight, between any two forms, if not blended by intermediate gradations, are looked at by most naturalists as sufficient to raise both forms to the rank of species. *Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected.* Hence, without quite rejecting the consideration of the present existence of intermediate gradations between any two forms, we shall be led to weigh more carefully, and to value higher, the actual amount of difference between them. It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names, as with the primrose and cowslip; and in this case scientific and common language will come into accordance. In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect, but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species." I have quoted from pages 484, 485 of the original edition (1859), and have italicised the sentences in which Darwin defines a species and distinguishes it from a variety.

Max Müller's special criticism falls to the ground, but his general exhortation remains, and I think we shall do well to be guided by it, and attempt to apply it to this difficult and elusive word SPECIES.

The passage I have quoted was Darwin's prediction of the meaning which would be attached to the word "species" by the naturalist of the future. Nearly half-a-century has passed since those words were written. For more than a generation the central ideas of the "Origin" have been an essential part of the intellectual equipment, not only of every naturalist, but of every moderately intelligent man. What then is the meaning of the word "species" to-day, and how does it differ from that of the years before July 1, 1858, when the Darwin-Wallace conception of natural selection was first launched upon the world?

The present occasion is especially favourable for this inquiry, because we have just been given two additional volumes of the letters of Charles Darwin. After the three volumes published in 1887, naturalists were certainly unprepared for the welcome revelation of such a mine of wealth. The work is all the more valuable because it contains many letters from Alfred Russel Wallace and Sir Joseph Hooker, thus giving both sides of a part of their correspondence with Darwin. Then in 1900 the "Life and Letters of Thomas Henry Huxley" appeared, so that we are now admitted "behind the veil," and can read, as never before, the central thoughts of the great makers of biological history. On the publication of the last-named work, I took occasion to combat the view that the thousand closely-printed pages might have been reduced by omitting and condensing many of the letters. The serious student of those stirring years requires the opportunity of thinking over and comparing all the available thoughts and opinions of the chief actors in the memorable scene; and the very repetition of certain ideas, which proves their persistence and dominance in the writer's mind, is a matter of deep importance and interest. However it may be to the general reader, the student would deprecate the omission or condensation of any of the writings of Darwin or Huxley. The special interest and value in the letters of these men depend on the fact that their inmost convictions on matters of the deepest scientific importance are to be read, often in the compass of a brief sentence. There we find, as we cannot find in any other way, the real core of the matter, with all accessory and surrounding considerations stripped away from it.* A careful study of the two recent volumes of Darwin's letters, and a re-study of the three earlier volumes, with a view to this Address, have shown how Darwin's thoughts were again and again occupied upon subjects bound up with the problem I have ventured to bring before you this evening. The interest reaches its height when we find that strongly-marked differences of opinion on fundamental questions are threshed out in the correspondence, when we see, as I shall have occasion to point out in greater detail in the later pages of this Address, Darwin differing sharply from Huxley on the one hand, and with Wallace on the other, as to the significance and history of sterility between species.

In such episodes we are permitted to become the witnesses of a supremely interesting struggle, where the central figure of modern biological inquiry is contending with his chief comrades in the great fight,—with the co-discoverer of natural selection, with the warrior hero who stood in the forefront of the battle.

The correspondence of Charles Darwin has a further deep interest for us. We see the means by which a gentle, sympathetic, intensely human nature overpassed the stern limits imposed by health, and was able to impart and to receive fresh ideas, and a stimulus ever renewed—the impulse to varied and unceasing research. I have lately been studying with keen interest the life of another great Englishman, William John Burchell,† than whom no better equipped or more learned traveller ever explored large areas in two continents. When I state that searching inquiry has only brought to light a dozen of his letters, and that he was known to hardly any of the great naturalists of his day, we see the reason for the sad, unproductive, brooding close of a career which opened with almost unexampled brilliancy and

* "Quarterly Review," January 1901, p. 258.
† "Ann. and Mag. Nat. Hist.," January 1904, p. 45.

promise. The time which we give to Societies such as this—time we are sometimes apt to grudge—is well spent. Here, and in kindred communities, a "man sharpeneth the countenance of his friend," and there is born of the influence of mind upon mind thought which is not a mere resultant of diverse forces, but a new creation.

The scientific man who shuts himself away from his fellow-men, in the belief that he is thereby obtaining conditions the most favourable for research, is grievously mistaken. Man, scientific man perhaps more inevitably than others, is a social animal, and the contrast between the lives of Darwin and Burchell shows us that friendly sympathy with our brother naturalists is an essential element in successful and continued investigation.

I do not suppose that it is necessary to justify a discussion of the term "species" as the subject of the Anniversary Address to the Entomological Society of London. The students of insect form and function hold an exalted place among naturalists. The material of their researches enables them, almost compels them, to take the keenest and most active interest in broad questions affecting the history and course of life on our planet. Naturalists engaged upon other groups may reasonably inquire why *insects*, above all other animals, should be so especially valuable for the elucidation of the larger problems which deal, not only with the species of a single group, but with every one of the innumerable and infinitely varied forms, vegetable no less than animal, in which life manifests itself. The answer is to be found in the large number of offspring produced by each pair of insects, and the rapidity with which the generations succeed each other, many cycles being completed in a single year in warm countries; in the severity of the struggle for life which prevents this remarkable rate of multiplication from becoming the cause of any progressive increase in the number of individuals; and finally, in the character of the struggle itself, which is precisely of that highly specialised kind between the keen senses and activities of enemies, and the means of concealment or other modes of defence of their insect prey, which leads, by action and answering reaction, to a progressive raising of the standard in both pursuer and pursued. This is why it is that insects mean so much to the naturalist or to the philosopher who desires to look beneath the surface for the forces which have moulded existing forms of life out of earlier and very different forms. The wings of butterflies, it has been said, serve as a tablet on which Nature writes the story of the modification of species.* But the careful study of insects tells us even more than this; for it gives us the clearest insight we as yet possess into the forces by which these changes have been brought about. Light is thrown upon the causes to which organic evolution is due no less than upon the course which organic evolution has pursued.†

And I think we shall find that a consideration of the numerous distinct categories of forms presented by the insect world is especially advantageous in an attack upon the difficult question—"What is a species?", while properly-directed observation of insects, and experiments upon insects afford the most hopeful prospect of a final answer.

And here I am compelled to say a word in defence of the Lepidoptera from this point of view. Undoubtedly it is most unfortunate that the obvious attractions of the group have led entomologists to neglect other Orders; for this can be the only explanation why naturalists have so often preferred to do over again what others have done already, apparently oblivious of fields comparatively empty and unexplored. It must further be admitted, that the greater visibility of structure, and the more urgent necessity for the study of structure in other groups, render them better instruments of zoological education. But although the Lepidoptera are inferior in this respect, although they lack the unique interest of the Hymenoptera and the social Neuroptera, and cannot claim any of the respect due to venerable age like the Aptera, Orthoptera and Neuroptera—in spite of their many demerits they stand at the head, not only of all insects, but

* H. W. Bates, quoted by A. R. Wallace in "Natural Selection," London, 1875, p. 132. The original passage may be found in "The Naturalist on the Amazons" (London, pp. 347, 348 of the 1879 edition).

† This justification for the study of insects was urged by the present writer in the Hope Reports, vol. iii, 1903, preface, pp. 4, 5.

of the whole organic world, as the registers of subtle and elusive change—ever going on, yet never seen,—by means of which forms are slowly becoming different from what they have been in the past. It is the existence of a complex pattern composed of several colours, which renders butterflies and to a less extent moths such a remarkably delicate record of change. As we trace the representative individuals of a community of butterflies over any wide range, the trained eye, and often the inexperienced eye, can detect differences which are not seen to anything like the same extent in the individuals of other Orders with corresponding ranges. If the wings of Hymenoptera, Diptera, or Orthoptera possessed the same elaborate patterns as the Lepidoptera, we cannot doubt that they too would exhibit the same differences in various parts of their areas. These continual changes which we find as we study the distribution of Lepidopterous forms in space, is undoubtedly a measure of the speed with which they have occurred in time. Rapidity of change is essential if it is to keep its adjustment with nicety to the fleeting details of distribution.* Hence we may confidently believe, that if we

* It is to be observed that I speak of the *details* as fleeting. The *general* area of distribution is doubtless extremely ancient in most cases. Thus, although a species of *Heliconius*, etc., may have originated within the South American tropics, and never have wandered beyond them, the complex shape of its actual area of distribution at any one time cannot be regarded as fixed or ancient. Yet in many a species the variation of the constituent individuals is adjusted with precision to the geographical details of the existing range.

Mr. Roland Trimen, on reading the above footnote, writes to me January 24, 1904:—"Your note reminds me of the recent appearance on the Natal coast of several conspicuous East-African butterflies, *vid.: Pieris spilleri*, *Crenis rosa*, and *Godartia wakefieldii*, all of which are shown to have not only extended their range to a point where they were previously quite unknown, but to have also *established* themselves in the fresh area. This is a good case, as Durban has had, for the last twenty-five years at least, a number of keen collectors of Lepidoptera, whom such conspicuous forms could not possibly have escaped had they inhabited the neighbourhood. Besides these species, the last butterfly that my friend and collaborator, the late Colonel Bowker, sent to me (1898) was the large and extremely conspicuous black-and-white *Acræa satis*, which he took at Malvern, near Durban. This is the only example known to me to have occurred in Natal; but Bowker, who noted the resemblance on the wing to *Papilio morania*, wrote that he had seen one other for certain, and thought that he might very possibly have passed over more examples for the common *Papilio* named. This last case is of special interest (should it prove one of extended range like the three mentioned), because the *Acrææ* are so exceptionally slow-flying and gregarious, that they must spread *very* slowly indeed into fresh areas."

could wake up in say a thousand years, we should be able to detect changes in the patterns of some butterflies. Although I am afraid the advance of science is not likely to be sufficiently rapid in our time for me to hold out any prospect of such an experience for any of you, there is every reason why we should afford this opportunity to posterity. A critical examination of the fragments of many species of butterflies captured ninety years ago by Burchell in S. Africa, and gnawed to pieces during his Brazilian travels from 1825 to 1830, renders it probable, nay, almost certain, that with moderate care, insect pigments will endure for an indefinite period in our museums. One important justification for the great and permanent outlay required to bring together and maintain large collections of insects is, that we are allowing our successors the chance of detecting and measuring the rate of specific change.* And, as I have already said, for this purpose the Lepidoptera stand pre-eminent.

For the purpose of the inquiry this evening, our instances will be drawn from the Lepidoptera rather than other Orders of insects, because of the numberless examples of subtle distinction between forms which but yesterday, so to speak, became separate; because of our knowledge, insufficient but considerable, of their geographical ranges; because of our experience, excessively imperfect and scanty, but still much larger than in other Orders, of inter-breeding and of descent from parent to offspring.

First among the attempts to define species must be placed that which we rightly associate with the name of Linnæus.

It has been admirably pointed out by the late Rev. Aubrey L. Moore,† that the dogma of the fixity of species is entitled to none of the respect which is due to age. "It is hardly credible to us," he wrote, "that Lord Bacon, 'the father of

* Karl Jordan argues with great force in favour of specialisation in this direction by our museums. (See "Novitates Zoologicæ," vol. iii, December 1896, pp. 431–433.) The Burchell collection from Brazil is only seventy-four to seventy-nine years old, but the species are numerous, and often represented by long series. An account of the butterflies by Miss Cora B. Sanders will shortly appear in the "Annals and Magazine of Natural History"; and it will then be seen that the evidence of change in certain forms is by no means wanting.

† "Science and the Faith," London, 1889, pp. 174 *et seq.*

modern science' as he is called, though he was only a schoolman touched with empiricism, believed not only that one species might pass into another, but that it was a matter of chance what the transmutation would be. Sometimes the mediæval notion of vivification from putrefaction is appealed to, as where he explains the reason why oak boughs put into the earth send forth wild vines, 'which, if it be true (no doubt),' he says,* 'it is not the oak that turneth into a vine, but the oak bough, putrefying, qualifieth the earth to put forth a vine of itself.' Sometimes he suggests a reason which implies a kind of law, as when he thinks that the stump of a beech tree when cut down will 'put forth birch,' because it is a 'tree of a smaller kind which needeth less nourishment.'† Elsewhere he suggests the experiment of polling a willow to see what it will turn into, he himself having seen one which had a bracken fern growing out of it! ‡ And he takes it as probable, though it is *inter magnalia naturæ*, that 'whatever creature having life is generated without seed, that creature will change out of one species into another.' Bacon looks upon the seed as a restraining power, limiting a variation which, in spontaneous generations, is practically infinite, 'for it is the seed, and the nature of it, which locketh and boundeth in the creature that it doth not expatiate.'" And the author also shows that much earlier than the date at which Bacon wrote, theologians were by no means unanimous in accepting "special creation"; that St. Augustine even distinctly rejected it, and propounded an idea which was evidently considered tenable by the greatest of the schoolmen, St. Thomas Aquinas. St. Thomas' words, quoted by Mr. Aubrey Moore, are as follows:—"As to the production of plants, Augustine holds a different view. For some expositors say that, on this third day (of creation), plants were actually produced each in his kind—a view which is favoured by a superficial reading of the letter of Scripture. But Augustine says that the earth is then said to have brought forth grass and trees *causaliter*—*i. e.* it then received the power to produce them." §

* "Nat. Hist." *Cent.* vi, 522, fol. ed.

† *l. c.* p. 523.

‡ *l. c.* p. 112.

§ St. Thomas Aquinas, "Summa Theol." Prima Pars. Quaest., lxix, Art. 2.

How then did the fixity of species become an article of belief in later years? Aubrey Moore traces it to the influence of Milton's account of creation in the seventh book of "Paradise Lost" (l. 414, *et seq.*), and Professor Huxley had still earlier suggested the same cause in his "American Addresses." I cannot help thinking that the belief had even more to do with the spirit of the age which spoke, and spoke for all time, with Milton for its interpreter,—the spirit of the Puritan movement, with its insistence on literal interpretation and verbal inspiration.

John Ray was Milton's younger contemporary, and many writers, including Aubrey Moore, have thought that with him began the idea of the fixity of species. Sir William Thiselton Dyer has, however, recently pointed out, that a conception similar to Ray's may be traced to Kaspar Bauhin (1550–1624) and to Jung (1587–1657).*

From Ray we pass to Linnæus with his often-quoted definition, "Species tot sunt, quot diversas formas ab initio produxit Infinitum Ens, quae formae, secundum generationis inditas leges produxere plures, at sibi semper similes." Of the Ray-Linnæus-Cuvier conception of species, which found its most precise and authoritative expression in the above-quoted latin sentence, Dr. F. A. Dixey has well said that it "left order where it found confusion, but in substituting exactness of definition for the vague conceptions of a former age, it did much to obscure the rudimentary notions of organic evolution which had influenced naturalists and philosophers from Aristotle downwards." † At the same time it is by no means improbable, as Dixey has suggested, that the Linnean conception "of the reality and fixity of species perhaps marks a necessary stage in the progress of scientific enquiry." ‡

The Linnean idea of special creation has no place in the realm of science; it is a theological dogma. The formation of species, said Darwin in a letter to Lyell, "has hitherto been viewed as beyond law; in fact, this branch of science

* "The Edinburgh Review," Oct. 1902, p. 370.

† "Nature," June 19, 1902, p. 169. For the history of these early ideas upon evolution see "From the Greeks to Darwin," by H. F. Osborn, New York, 1894.

‡ "Church Quarterly Review," Oct. 1902, Art. II, p. 28.

is still with most people under its theological phase of development."* And this explains the intense opposition at first encountered by the principles of the "Origin." The naturalist whose genius sympathised most fully with the Linnean conception would feel that he was admitted, like a seer of old, into the presence of the Maker of the Universe. His convictions as to species were to him more than the conclusions of the naturalist; they were a revelation, stirring him to "break forth and prophesy." Do we not sometimes recognise a lingering trace of this phase of thought in the serious shake of the head and tone of profound inner conviction with which we are sometimes told that the speaker is decidedly of the opinion that so-and-so is a perfectly good species?

We recognise the same sharp antagonism between two irreconcilable sets of ideas when the late W. C. Hewitson expressed such horror at Roland Trimen's remarkable discovery of the polymorphic mimetic females of the *Papilio merope* group. The wonderfully acute detection of minute but significant resemblance hidden under the widest possible superficial difference, which enabled the great South African naturalist to unravel the tangled relationships, was to Hewitson but one of "the childish guesses of the . . . Darwinian School." To meet the carefully-thought-out argument, the only objections that could be urged were that the conclusion stretched too severely the imagination of the writer, and that it shocked his notion of propriety! †

* Letter 132 to C. Lyell, Aug. 21, 1861. "More Letters of Charles Darwin," London, 1903, i, p. 194.

† See an account of the controversy in Trans. Ent. Soc. Lond., 1874, p. 137. The passages I have alluded to are as follows:—"*P. merope*, of Madagascar, has a female the exact image of itself; and it would require a stretch of the imagination, of which I am incapable, to believe that the *P. merope* of the mainland, having no specific difference, indulges in a whole harem of females, differing as widely from it as any species in the genus. . . . In the two species of *Papilio* which have lately been united, *Torquatus* and *Candius*, and *Argentus* and *Torquatinus*, though much unlike each other, there is quite sufficient resemblance not to shock one's notions of propriety." A little later Mr. Hewitson himself received evidence of the truth of the conclusion he so disliked; for he told how his collector Rogers had sent "*Papilio merope* and *P. hippocoon*, taken by him in copulation, another illustration of the saying that 'truth is stranger than fiction.' I find it very difficult (even with this evidence) to believe that a butterfly, which, when a resident in Madagascar, has a female the image of itself, should, in West Africa, have one without any resemblance to it at all" ("Entomologist's Monthly Magazine," Oct. 1874, p. 113).

In leaving the dogma of "special creation," and the assumption of "fixity of species" with which it is bound up, it is only right to point out how completely the logical foundations of both were undermined by the great thinker who has just passed away. Years before the appearance of the Darwin-Wallace essay, and of the "Origin," Herbert Spencer wrote on "The Development Hypothesis." * Although of course wanting the great motive power to evolution supplied by natural selection, this essay is a powerful and convincing argument for evolution as against special creation. It is astonishing that it did not produce more effect. I may appropriately conclude this section of the Address by quoting the results of Herbert Spencer's critical examination, from every point of view, of the Linnean conception of species. "Thus, however regarded, the hypothesis of special creations turns out to be worthless—worthless by its derivation; worthless in its intrinsic incoherence; worthless as absolutely without evidence; worthless as not supplying an intellectual need; worthless as not satisfying a moral want." †

If then the Linnean conception of species—separately created and fixed for all time at their creation—has been abandoned, what have we to put in its place? In a letter to Hooker, Dec. 24, 1856, Darwin gave a list of the various definitions he had met with. "I have just been comparing definitions of species, and stating briefly how systematic naturalists work out their subjects. . . . It is really laughable to see what different ideas are prominent in various naturalists' minds when they speak of 'species'; in some, resemblance is everything, and descent of little weight—in some, resemblance seems to go for nothing, and creation the reigning idea—in some, descent is the key—in some, sterility an unfailing test, with others it is not worth a farthing. It all comes, I believe, from trying to define the indefinable." ‡

As regards the work done by the systematist, we find that Darwin did not agree with those of his friends who thought

* In the *Leader*, between January 1852 and May 1854, reprinted in "Essays Scientific, Political, and Speculative." London, 1868, vol. i, p. 377.

† "The Principles of Biology." London, 1864, vol. i, p. 345.

‡ "Life and Letters of Charles Darwin" London, 1887, vol. ii, p. 88.

that a belief in evolution would entirely alter its character. Thus he wrote to Hooker, Sept. 25, 1853 :—"In my own work I have not felt conscious that disbelieving in the mere *permanence* of species has made much difference one way or the other; in some few cases (if publishing avowedly on the doctrine of non-permanence) I should *not* have affixed names, and in some few cases should have affixed names to remarkable varieties. Certainly I have felt it humiliating, discussing and doubting, and examining over and over again, when in my own mind the only doubt has been whether the form varied *to-day or yesterday* (not to put too fine a point on it, as Snagsby would say). After describing a set of forms as distinct species, tearing up my MS., and making them one species, tearing that up and making them separate, and then making them one again (which has happened to me), I have gnashed my teeth, cursed species, and asked what sin I had committed to be so punished. But I must confess that perhaps nearly the same thing would have happened to me on any scheme of work." *

The essentially subjective character of the results reached by the systematist stands out with remarkable force in this as in other passages of Darwin's letters.

A few years later, on July 30, 1856, he wrote to the same friend :—"I differ from him [Lyell] greatly in thinking that those who believe that species are *not* fixed will multiply specific names: I know in my own case my most frequent source of doubt was whether others would not think this or that was a God-created Barnacle, and surely deserved a name. Otherwise I should only have thought whether the amount of difference and permanence was sufficient to justify a name." †

Disregarding for the moment the term species, it is convenient to consider the various groupings of individual animals and plants.

1. Forms having certain structural characters in common distinguishing them from the forms of other groups. Groups thus defined by *Diagnosis* may be conveniently called *Syndiagnostic* (σύν, together; διάγνωσις, distinction).

* "Life and Letters," vol. ii, p. 40.
† *Ibid.* vol. ii, p. 81.

2. Forms found together in certain geographical areas and not in other areas. Such groups may be called *Sympatric* (σύν, together; πάτρα, native country). The occurrence of forms together may be termed *Sympatry*, and the discontinuous distribution of similar forms *Asympatry*.

3. Forms which freely inter-breed together. These may be conveniently called *Syngamic*. (σύν, together; γάμος, marriage). Free inter-breeding under natural conditions may be termed *Syngamy*; its cessation or absence, *Asyngamy* (equivalent to the *Amixia* of Weismann).

4. Forms which have been shown by human observation to be descended from common ancestors. Such groups may be called *Synepigonic* (σύν, together; ἐπίγονος, descendant). Breeding from common parents may be spoken of as *Epigony* or the production of *Epigonic* evidence.*

My friend, Professor E. Ray Lankester, to whom I owe so much, in this as in many other subjects, is inclined to think that we should discard the word species not merely momentarily but altogether. Modern zoology having abandoned Linnæus' conception of "species" should, he considers, abandon the use of the word. In his opinion the "origin" of species was really the abolition of species, and zoologists should now be content to describe, name, draw, and catalogue *forms*. Furthermore, the various groups of forms briefly defined above should be separately and distinctly treated by the zoologist, without confusion or inference from one to the other. The systematist should say, "I describe and name certain forms *a*, *b*, etc."; and then he or another may write a separate chapter, as it were:—"I now show that the forms *ab*, *ac*, *ad* (form names) are syngamic:" at another time he may give reason for regarding any of them as related by epigony.

I fear that this suggestion is a "counsel of perfection," impossible of attainment, although there would be many

* My friend Mr. Arthur Sidgwick has kindly helped me by suggesting the appropriate Greek words. The use of ἐπίγονος I owe to my friends Mr. Arthur Evans and Mr. R. W. Macan. The adjectival termination is made *-ic* throughout for the sake of convenience, although *Sympatriote* or *Sympatrid* would have been more correct.

and great advantages in thus making a fresh start and in the abandonment of "species," or the restriction of the word to the only meaning it originally possessed before it was borrowed from logic to become a technical term in zoology.*

Professor Lankester in former years published (I cannot at this moment lay my hands upon the communication) the suggestion that the term species should be limited to a group which includes all the forms derived from common ancestors within human experience, or inferred to be so derived within the possible period of human observation. Thus if the common ancestry of two forms has to be traced back to a period beyond the late pre-historic times (or beyond any other arbitrary line which is agreed upon), then they are not members of the same species. Professor Lankester is the first to admit that the practical application of this as of every other conception of species would very often mean a great deal more than we can prove, in fact, hypothesis.

It is evident too that Darwin regarded persistence of form as an important criterion of a species. We recognise this in the definition I have quoted from the "Origin" (see p. lxxviii), and it is stated with even greater force in the following passage, where persistence is placed beside other distinguishing marks of a species and given the pre-eminence. In a letter to Hooker (October 22, 1864) Darwin says:—"I will fight to the death that as primrose and cowslip are different in appearance (not to mention odour, habitat, and range), and as I can now show that, when they cross, the intermediate offspring are sterile like ordinary hybrids, they must be called as good species as a man and a gorilla. The power of remaining for a good long period constant I look at as the essence of a species, combined with an appreciable amount of difference." †

It is now necessary to examine in some detail the most usual conception of a species, a conception based upon distinguishing structural characters, or diagnosis.

This idea of a species is clearly expressed by Sir William Thiselton Dyer, when he speaks of the older writers who

* See F. A. Dixey in "Nature," June 19, 1902, p. 169.
† "More Letters," vol. i, p. 252, Letter 179.

employed "the word species as a designation for the totality of individuals differing from all others by marks or characters which experience showed to be reasonably constant and trustworthy, as is the practice of modern naturalists." *

This conception of a species is founded upon transition. Whenever a set of individuals can be arranged, according to the characters fixed upon by the systematist, in a series without marked breaks, that set is regarded as a species. The two ends of the series may differ immensely, may diverge far more widely than the series itself does from other series; but the gradual transition proclaims it a single species. If transitions were all equally perfect of course there would be no difficulty. But transitions are infinite in their variety; while the subjective element is obviously dominant in the selection of gaps just wide enough to constitute interspecific breaks, just narrow enough to fuse the species separated by some other writer,—dominant also in the choice of the specific characters themselves.† Looking back upon the interval between Linnæus and Darwin, it seems remarkable that the mutability of species was not forced upon systematists as the result of their own labours. It is astonishing that many a naturalist was not driven by his descriptive work to the conclusion which Darwin stated to Asa Gray on July 20, 1856: "— as an honest man, I must tell you that I have come to the heterodox conclusion, that there are no such things as independently created species—that species are only strongly defined varieties." ‡

For, as I have said above, every describer of species made continuity and transition in characters the test of a variety, discontinuity the test of a separate species. And in difficult cases no two of them agreed in their conclusions. Many passages in Darwin's correspondence convincingly prove how essential an element is this continuity, and how inevitable

* *l. c.* p. 370.

† How important this choice may be is well shown by Karl Jordan in "Novitates Zoologicæ," vol. iii, Dec. 1896, pp. 428–430. Characters are subject to *independent variation* as well as *correlated variation.* Hence there may be the widest discrepancy between the transitions constructed by naturalists making use of different characters.

‡ "Life and Letters," vol. ii, p. 79.

is the dominance of the subjective element. Thus he writes about his descriptive work on Cirrhipedes to Hooker, October 12, 1849 :—"I have of late been at work at mere species describing, which is much more difficult than I expected, and has much the same sort of interest as a puzzle has; but I confess I often feel wearied with the work, and cannot help sometimes asking myself what is the good of spending a week or fortnight in ascertaining that certain just perceptible differences blend together, and constitute varieties and not species. As long as I am on anatomy I never feel myself in that disgusting, horrid, *cui bono*, inquiring humour." *

On another occasion, when Darwin was anxious to ascertain the "close species" in the North American Flora, and wrote for information to Asa Gray, he frankly adopted the subjective criterion in order to explain exactly what he meant. He wrote, June 8, [1855]:—"The definition I should give of a '*close species*' was one that *you* thought specifically distinct, but which you could conceive some other *good* botanist might think only a race or variety; or, again, a species that you had trouble, though having opportunities of knowing it well, in discriminating from some other species." †

Asa Gray's reply is also very interesting from the same point of view. He wrote, June 30, 1855 :—"Those thus connected" [he had bracketed the "close species" in a list of the Flora], "some of them, I should in revision unite under one, many more Dr. Hooker would unite, and for the rest it would not be extraordinary if, in any case, the discovery of intermediate forms compelled their union." ‡

Darwin was evidently in high spirits when he wrote the following passage which bears on the same subject. The "Origin" had been published on November 24, 1859, and the whole edition of 1250 copies sold on the day of issue. On November 29 he wrote to Asa Gray :—"You speak of species not having any material base to rest on, but is this any greater hardship than deciding what deserves to be called a variety, and be designated by a Greek letter? When I

* "Life and Letters," vol. i, p. 379.
† *Ibid.*, vol. ii, p. 64.
‡ "More Letters," vol. i, p. 421, Letter 324.

was at systematic work I know I longed to have no other difficulty (great enough) than deciding whether the form was distinct enough to deserve a name, and not to be haunted with undefined and unanswerable questions whether it was a true species. What a jump it is from a well-marked variety, produced by natural cause, to a species produced by the separate act of the hand of God! But I am running on foolishly. By the way, I met the other day Phillips, the palæontologist, and he asked me, 'How do you define a species?' I answered, 'I cannot.' Whereupon he said, 'At last I have found out the only true definition—any form which has ever had a specific name!'" *

The idea of a species as an inter-breeding community, as syngamic, is, I believe, the more or less acknowledged foundation of the importance given to transition. This will become clearer from the consideration of a concrete example. The common black-and-white Danaine butterfly, *Amauris niavius* of West Africa, is represented on the East and South-East Coasts by a very similar butterfly, distinguished by the greater size of the largest white patch, and of the white spot in the cell of the fore-wing. Both forms are very constant in the areas over which they were known, and on these constant easily recognisable characters the eastern butterfly was described as a distinct species under the name of *A. dominicanus*. Aurivillius, however, in his valuable Catalogue refuses to recognise this latter as a distinct species, and considers it as the *dominicanus* variety of *niavius*. Through the kindness of Mr. C. A. Wiggins and Mr. A. H. Harrison, the Hope Department has recently been presented with an exceedingly fine series of butterflies from both east and west of the northern shores of Lake Victoria Nyanza. These have been carefully studied by Mr. S. A. Neave, B.A., of Magdalen College, Oxford, who finds that the typical *niavius* occurs in great abundance to the west of the lake, while on the east he meets, in both collections, with varieties beautifully intermediate between it and *dominicanus*. These varieties, occurring precisely in the zone where the eastern form meets the western, complete for the systematist the transition which

* "More Letters," vol. i, p. 127, Letter 79.

renders *dominicanus* a variety of *niavius* and not a distinct species. But it is clear that they do more than this; they make it almost certain that the two forms freely interbreed, and constitute but a single syngamic community.

This is one of the remarkably clear examples. In many cases we know the transition, but the extremes are not sorted out in different parts of the total area of distribution. Nevertheless if complete enough the transition of forms on the same area always raises the strong presumption that we are dealing with a syngamic community.

Probably the most remarkable series of transitional varieties ever depicted is that shown in the eleven quarto plates of the last part of Monsieur Charles Oberthür's great "Études d'Entomologie," entitled "Variation des *Heliconia thelxiope* et *vesta*" (Rennes, February, 1902).

The method of diagnosis, at its clearest and simplest, is always consistent with, and often strongly suggests, an underlying syngamy. There are, however, numberless examples belonging to various categories in which a rigid adherence to diagnosis cannot avail. In these cases the systematist frankly appeals to syngamy or synepigony as decisive; and if he has not direct proof of the existence of either of these, indirect evidence is, at any rate provisionally, regarded as sufficient.

I. *Dimorphism, Polymorphism*:—In an ever-increasing number of examples an assemblage of individuals is regarded as a single species, although split up into two or more widely different and sharply separated groups, between which transitional varieties are excessively rare or even unknown. For instance, the extremely abundant, widely distributed butterfly *Limnas chrysippus* includes among other forms one in which the black-and-white tip is wanting from the fore-wing, the *dorippus* (= *klugii*) form. This variety is sharply cut off from the type form. Although faint traces of a former white bar can be made out in *dorippus*, I have never seen, among thousands of individuals, the material out of which a good transitional series between it and *chrysippus* could be constructed. In this case the evidence of syngamy is strong and complete; for Col. Yerbury has recorded the fact that the two forms certainly occur *in copulâ*.* But if this evidence were wanting there would still be strong presumptive evidence that the forms are associated by syngamy and synepigony. Thus, so far as our knowledge extends, *dorippus* occurs as the only form in certain parts of N.E. Africa alone. From this, its metropolis, *dorippus* spreads on all sides, its individuals existing intermingled with those of *chrysippus*, becoming less and less numerous until they finally die out. Thus if we trace the two forms eastward we find them both abundant at Aden; further east, at Karachi, *dorippus* is well known, but very scarce as compared with *chrysippus*; in Southern India it is a great rarity, if indeed it is known at all on the mainland; in Ceylon a single specimen was captured by Col. Yerbury in 1891, and since then others have been taken.† Further east I have never heard of a specimen. Similarly when it is traced southward in Africa, *dorippus* is dominant in the coast strip of British East Africa, where it constitutes about three-quarters of the total number of individuals. Further to the south it becomes rarer and rarer, until in Natal and the Cape, if it occurs at all, it is even rarer than in Ceylon.‡ Such a distribution is consistent with the interpretation that *dorippus* and *chrysippus* are two forms in one syngamic community. It is difficult on any other hypothesis to account for the facts which we observe on the outskirts of

* Speaking of his experience at Aden, Col. Yerbury says: "I have taken them [the forms of *chrysippus*] *in coitu* in every possible combination." (Journ. Bomb. Nat. Hist. Soc., vii (1892), p. 209.)

† See Major N. Manders, F.Z.S., in Journ. Bomb. Nat. Hist. Soc., xiv (1902), p. 716:—

"The first specimen of this insect [*dorippus*=*klugii*] in Ceylon was captured by Lieut.-Colonel Yerbury at Trincomalie, April 15th, 1891 . . ." Of five or six more recent examples Major Manders writes, "These specimens were captured by Mr. Pole at Puttalam on the east coast and Hambantotte on the south coast in the dryest and perhaps most arid portion of the island. It is evidently widely distributed in the desert portion of the island and is possibly not uncommon."

"The distribution of this insect in India cannot yet be fully known; it is rare in Canara, but is not yet reported from the plains of the Deccan, or Southern India, so far as I am aware, though it probably exists." The occurrence of *dorippus* at Bombay, Kutch, and Sind had been previously published by Major Manders and the late Mr. de Nicéville in Journ. As. Soc. Bengal, vol. lxviii, Pt. ii, No. 3, 1899, p. 170.

‡ Mr. Roland Trimen tells me that he knows of only three South-African *dorippus*:—two from Durban and one from Pretoria. The latter and one of the former were taken by Mr. W. L. Distant (Ann. Mag. Nat. Hist. (7), vol. i, 1898, pp. 48, 49).

the range of *dorippus*—the occasional appearance of single individuals in the swarms of the type form. And if the two are syngamic on the outskirts, the gradual transition in proportions towards the metropolis of *dorippus* suggests that they are syngamic throughout. Common as the species is—probably the commonest butterfly in the world,—the evidence from epigony has never been obtained, although from the point of view of heredity the investigation promises to be of the deepest interest.

The remarkable forms of the females of the *Papilio merope* group already alluded to afford another excellent example, although in this case good transitional series can be constructed. The evidence of syngamy was first obtained by Hewitson (see p. lxxxvii), but is now well known. The evidence of epigony has fortunately been obtained in 1902 and again within the last few weeks by one of our Fellows at Durban, Mr. G. F. Leigh. Eggs from a female of the commonest *cenea* form yielded a synepigonic group, including a large majority of forms like the parent, but also examples of the very different *hippocoon* form. Still more recently seven eggs from the rarest of the forms, *trophonius*, produced, in addition to males, two females of the *cenea* variety, and not one resembling the parent.

These differences, although only of colour and pattern, greatly exceed those between ordinary close species. When we deal with other kinds of dimorphism or polymorphism involving important structural differences, such as those of the social Hymenoptera and Neuroptera, the discriminating characters between nearly related genera are commonly equalled or exceeded.

II. *Seasonal Dimorphism* :—In certain exceedingly interesting examples of dimorphism the relation between the forms is epigonic and not syngamic; for rare and occasional inter-breeding is not syngamy. I refer to the most strongly-marked cases of seasonal dimorphism in butterflies, especially the wonderful examples proved to be epigonic by Guy A. K. Marshall. In some of the forms the two seasonal phases were not even regarded as closely related species. In these extraordinary cases, where the widest difference in colour and pattern exists, in combination with others which are far more deep-seated, I urged upon Mr. Marshall that the few recorded examples of capture or observation *in coitu* were insufficient evidence of specific identity, and that nothing short of epigony would suffice.

In seasonal dimorphism, in the dimorphism of social insects, and doubtless in a large proportion of other examples, it is probable, indeed often certain, that the different forms are produced in response to some stimulus which acts at a specially susceptible period of the life-history; but from the point of view of the systematist the mature individuals can only be known as forms which, structurally widely different, must nevertheless be placed within the limits of a single species. The investigation of the probable physiological causes of difference is, however, of the utmost importance from other points of view. Altogether apart from its bearing upon dimorphism, the effect of individual susceptibility to stimulus requires treatment in a separate category.

III. *Individual Modification:* *—One of the most striking developments of recent years has been the growth in the number of these very cases in which an individual animal or plant has been rendered by natural selection susceptible to some stimulus associated with each one of its possible normal environments. Every individual of such species comes into the world with two or more very distinct and very different possibilities before it, each of which will be realised only in the appropriate environment—realised as the response to some stimulus provided by the environment itself. We can see clearly that this idea was in Darwin's mind, although there were then but few facts which pointed in its direction. Thus in Schmankewitsch's experiments Crustacea of the species *Artemia salina* were described as gradually changing in the course of generations, as the result of a progressive freshening of the water in which they were kept, until they took on the characters of the genus *Branchipus.* On this subject Darwin wrote to Karl Semper, February 6, 1881:—"When I read imperfectly some years

* "A structural change wrought during the individual's lifetime (or acquired), in contradistinction from variation, which is of germinal origin (or congenital)." Dict. of Phil. and Psych., ed. by J. Mark Baldwin, New York and London, vol. ii, 1902, p. 94.

ago the original paper, I could not avoid thinking that some special explanation would hereafter be found for so curious a case. I speculated whether a species very liable to repeated and great changes of conditions might not assume a fluctuating condition ready to be adapted to either conditions." *

I venture to express the prediction that this class of cases, already very numerous, will hereafter be immensely enlarged, and will become especially important in the vegetable kingdom.† Although Hooker at one time took the opposite side, and thought that plants were never "changed materially by external conditions—except in such a coarse way as stunting or enlarging," ‡ Darwin considered that "physical conditions have a more direct effect on plants than on animals." § Undoubtedly the view at the time was that of Buffon, the idea of an operation of the environing forces almost as direct as those which produce the weathering of rocks or the whitening of an exposed flint. But it is probable that the more intimately we know of the conditions of plant-life, the more fully it will be recognised that all such changes are adaptive.

* "More Letters," vol. i, p. 391, Letter 303.

† See "Stimulus and Mechanism as Factors in Organisation" by J. Bretland Farmer, F.R.S. (the New Phytologist, vol. ii, Nos. 9 and 10, Nov. and Dec. 1903). Professor Farmer speaks of the probable prevalence in the plant-world of "a constant specific mechanism that is able to be actuated in different ways by different kinds of stimuli." Although for the purpose of his paper Professor Farmer is concerned with the train of physico-chemical sequences which is set going, utility or no utility, whenever the mechanism of an individual is stimulated, he fully admits that the mechanism itself has come to be a character of the species by the operation of natural selection. "Naturally," he says, "only those species whose inner character expressed itself in making these 'suitable' adjustments to the environment were able to survive."

Toward the close of his paper Professor Farmer seems to bring the considerations that have regard to the species into somewhat unnecessary conflict with those that have regard to the individual. Thus he says that "current literature still teems with teleological explanations that really explain nothing, but rather bar the way of scientific enquiry."

A properly loaded, well-constructed modern gun goes off, for disadvantage no less than for advantage, when its trigger is pulled ; but the very existence of the gun depends upon a long succession of past stages, each of which was more advantageous than its predecessor. The recognition of this history does not bar the way of enquiry, but rather stimulates and suggests a searching and intelligent study of the latest mechanism with all its intricacy.

‡ See the letter from Hooker to Darwin, March 17, 1862, in "More Letters," vol. i, p. 197.

§ See the letter from Darwin to Lyell [June 14, 1860], "Life and Letters," vol. ii, p. 319.

I will mention merely by way of illustration, that my attention has been called in recent years to the dwarfing effect of the prevalent south-western winds on the vegetation of the exposed chalk downs of the Isle of Wight. It has occurred to me as a mere suggestion, but one worth investigating, that the effect of wind upon a tall flower-head might be such as to render less easy and less frequent the visits of insects. If this were so, it would perhaps explain why certain species of entomophilous plants liable to grow in such situations have gained a special susceptibility to the stimulus provided by constant winds during some particular period of growth. The absence of this stimulus would also correspond to a condition in which the plants would gain in the conspicuousness brought about by increased height.

The further growth of a class already proved to be large, would play havoc with a definition of species rigidly based upon discriminating structural characters alone.

IV. *Geographical Races or Sub-Species* :—If we depend upon unaided diagnosis there is no means of discriminating between species and those sub-species of which the whole mass of individuals are distinguished by recognisable characters. Here again the mere beginning of the difficulty is in sight; for as museums recognise more and more the necessity for long series of specimens with exact geographical data, so will the comparatively simple conception of the single species be replaced again and again by the far more complex but much truer idea of sub-specific groups still fused by syngamy into a single species, but as it were trembling on the edge of disruption, ever ready, by the development of pronounced preferential mating or by the accumulated incidental effects of isolation prolonged beyond a certain point, to break up into distinct and separate species.

V. *Results of Artificial Selection* :—These obvious difficulties encountered by a mechanical adherence to definition by diagnosis naturally lead to the consideration of the further difficulties presented by domestic races of animals and plants. The wide structural differences between the forms accumulated by human selection greatly impressed Darwin. Thus he wrote to Hooker, September 8, [1856]:—"By the way, I have been astonished at the differences in the skeletons of domestic rabbits. I showed some of the points to Waterhouse, and asked him whether he could pretend that they were not as great as between species, and he answered, 'They are a great deal more.' How very odd that no zoologist should ever have thought it worth while to look to the real structure of varieties. . . ." * Then again, the differences between many of our domestic breeds, and between them and the nearest wild species, are, as is well known, generic rather than specific. Why do we not consider such races to be of different species and genera? Because of the criterion suggested by Lankester; because we have reason to believe in their descent from common parents within the historic period; because, in spite of their wide differences, they are still syngamic.

What is the practical bearing of these criticisms upon the definition of species by diagnosis and diagnosis alone? The systematist, confronted by his series of specimens in a museum cannot do otherwise than arrange them in groups which he will describe and name as species. But much would be gained if he admitted at the outset that his conclusions are provisional, if he said with Dr. Karl Jordan, "The actual proof of specific distinctness the systematist as such cannot bring; . . . we work, or we ought to work, with the mental reservation that the specific distinctness of our *species novæ* deduced from morphological differences will be corroborated by biology." †

The advantage of this attitude is obvious. Work would go on as at present. Powers of acute observation and good judgment would still furnish descriptions of species to be hereafter confirmed, or confirmed at the time by observation and experiment upon the living material. But the systematist would not only receive our gratitude for the performance of these important and necessary duties: he would also be seeking in every direction for the evidence of syngamy and of epigony. The museum would become a centre for the inspiration of researches of the highest interest to the investigator himself, of the greatest importance to the whole body of naturalists.

* "More Letters," vol. ii, p. 210, Letter 543.

† "Novitates Zoologicæ," vol. iii, Dec. 1896, pp. 450, 451. I here desire to express my indebtedness to the author of this learned and valuable paper.

We now turn to the consideration of interspecific sterility, which many have supposed to be an infallible criterion. Huxley himself felt this so strongly that he was, in consequence, never able to give his full assent to natural selection. The grounds of his objection were the subject of prolonged correspondence with Darwin. In order to prove that natural selection has produced natural species separated rigidly, as he believed, by the barrier of sterility, Huxley maintained that we ought to be able to produce the same sterility between our artificially selected breeds; and until this had been done he could not thoroughly accept the theory of natural selection. This objection he expressed, or implied, in many speeches and writings up to within a few months of his death. One of the simplest statements is contained in a letter to the late Charles Kingsley. Huxley wrote, April 30, 1863, "Their produce [viz. that of Horse and Ass] is usually a sterile hybrid.

"So if Carrier and Tumbler, *e. g.*, were physiological species equivalent to Horse and Ass, their progeny ought to be sterile or semi-sterile. So far as experience has gone, on the contrary, it is perfectly fertile—as fertile as the progeny of Carrier and Carrier or Tumbler and Tumbler.

"From the first time that I wrote about Darwin's book in the *Times*, and in the *Westminster*, until now, it has been obvious to me that this is the weak point of Darwin's doctrine. He *has* shown that selective breeding is a *vera causa* for morphological species; he has not yet shown it a *vera causa* for physiological species.

"But I entertain little doubt that a carefully devised system of experimentation would produce physiological species by selection—only the feat has not been performed yet."*

It was against this same view, as expressed in Huxley's "Lectures to Working Men" in 1863, that Darwin argued with convincing force in many letters. The main facts with which he confronted Huxley again and again were the artificially selected races of certain plants which are sterile *inter se*. The position is clearly expressed in the following amusing, vehement passages from two letters:—

* "Life and Letters of Thomas Henry Huxley," vol. i, p. 239.

"*Dec.* 18, [1862.]

"Do you mean to say that Gärtner lied, after experiments by the hundred (and he a hostile witness), when he showed that this was the case with *Verbascum* and with maize (and here you have selected races): does Kolreuter lie when he speaks about the varieties of tobacco? My God, is not the case difficult enough, without its being, as I must think, falsely made more difficult? I believe it is my own fault—my d——d candour: I ought to have made ten times more fuss about these most careful experiments." *

"[*Jan.*] 10, [1863.]

"In plants the test of first cross seems as fair as test of sterility of hybrids, and this latter test applies, I will maintain to the death, to the crossing of varieties of *Verbascum*, and varieties, selected varieties, of *Zea*. You will say, Go to the Devil and hold your tongue. No, I will not hold my tongue; for I must add that after going, for my present book [Variation under Domestication], all through domestic animals, I have come to the conclusion that there are almost certainly several cases of two or three or more species blended together and now perfectly fertile together. Hence I conclude that there must be something in domestication,—perhaps the less stable conditions, the very cause which induces so much variability,—which eliminates the natural sterility of species when crossed. If so, we can see how unlikely that sterility should arise between domestic races. Now I will hold my tongue." †

Darwin made attempts to "produce physiological species by selection," and thus meet his friend's criticism. He thought out and suggested a plan of experiment to W. B. Tegetmeier,‡ and gave a brief account of the scheme to Huxley, December 28, [1862]:—"I have —— given him [Tegetmeier] the result of my crosses of the birds which he proposes to try, and have told him how alone I think the experiment could be tried with the faintest hope of success—namely, to get, if possible, a case of two birds which when

* "More Letters," vol. i, p. 230, Letter 156.
† *Ibid.* vol. i, pp. 231, 232, Letter 157.
‡ *Ibid.* vol. i, pp. 223, 224, Letter 153, [1862, Dec.] 27.

paired were unproductive, yet neither impotent. For instance, I had this morning a letter with a case of a Hereford heifer, which seemed to be, after repeated trials, sterile with one particular and far from impotent bull, but not with another bull. But it is too long a story—it is to attempt to make two strains, both fertile, and yet sterile when one of one strain is crossed with one of the other strain. But the difficulty . . . would be beyond calculation." *

The experiment was evidently unsuccessful,—perhaps was never seriously undertaken,—and a few years later Darwin added the following postscript to a letter to Huxley, January 7 [1867].

"P.S.—Nature never made species mutually sterile by selection, nor will men." †

This was probably only an offhand expression of opinion, not intended to be taken seriously. An altogether hopeless attitude would not be reasonable until the suggested scheme had been applied many times, and in several parts of the animal and vegetable kingdoms.

But the positive results demanded by Huxley, even if obtained, would by no means justify his far-reaching conclusions. If the barrier of sterility were thus artificially produced, we should be very far from the proof that its existence in nature is due to the same kind of cause, viz. selection. If Darwin was right in his controversy with Wallace, if "Nature never made species mutually sterile by selection," the suggested experiment would merely do by artificial selection what is not done by natural selection.

It is by no means difficult to understand the mutual sterility which is usual between natural species as an incidental result of their separation by asyngamy for a long period of time. In the process of fertilisation a portion of a single cell nucleus from one individual fuses with a portion from another individual, the two combining to form the complete nucleus of the first cell of the offspring, from which all the countless cells of the future individual will arise by division. Each part-nucleus contains the whole of the hereditary qualities

* "More Letters," vol. i, pp. 225, 226, Letter 154.
† *Ibid.* vol. i, p. 277, Letter 197.

received from and through its respective parent, and must therefore be of inconceivable complexity. We can only speak in generalities about processes of which so little is known, but we cannot be wrong in assuming that sterility is sometimes due to the fact that the complex architecture of one part-nucleus fails in some way to suit the equally complex structure of the other. The individuals of an inter-breeding community form a biological whole, in which selection inevitably keeps up a high standard of mutual compatibility between the sexual nuclei. Individuals whose sexual nuclei possess a structure which leads to sterile combinations with those of other individuals are excluded from contributing to the generations of the future. As soon, however, as a group of individuals ceases, from any reason, to breed with the rest of the species, there is no reason why the compatibility of the sexual nuclei of the two sets should be retained. Within each set, selection would work as before and keep up a high standard of compatibility; between the sets, compatibility would only persist as a heritage of past selection, gradually diminishing as slight changes of structure in either or both of the sets rendered them less and less fitted to produce fertile combinations.*

It is probable that of all the nice adjustments required in the living organism, the mutual adjustment of these inconceivably complex part-nuclei is the most delicate and precise. Now, delicately adjusted organs, such as those of sight, rapidly become incapable of performing their functions when in any species they have been withdrawn from the operation of natural selection; similarly it is suggested, that the adjustment of sexual nuclei to each other would sooner or later give way

* I must guard against the inference that the only explanation of sterility is here set forth. It is indeed maintained that incompatibility of the sexual part-nuclei is the inevitable outcome of enduring asyngamy, and is the almost certain cause of the sterility of hybrids. And it may be suggested that sterility is a result of the combination of two incompatible germ-plasms in the sexual cells of the hybrid. When the incompatibility is not strongly marked we can understand how such sexual cells may be capable of fertile fusion with the cells of either parent, but not with those of another hybrid.

But short of these ultimate effects it must not be forgotten that there are many obscure factors of asyngamy—causes of various kinds which interfere with the fusion under normal conditions or entirely prevent the meeting of the sexual cells.

when no longer sustained by selection. If, then, mutual fertility be the result of unceasing selection, and mutual sterility the inevitable, even if long-postponed, consequence of its cessation, it is obvious that Huxley's difficulty is solved, while his suggested experimental creation of sterility by selection would not reproduce any natural operation: it would afford a picture of a natural result but would be produced in an unnatural way. This criticism of Huxley's contention was advanced by the present writer three years ago,* the final conclusion being stated in the paragraph printed below:—

"If, then, we cannot as yet reproduce by artificial selection all the characteristics of natural species-formation, but can only imitate natural race-formation, we can nevertheless appreciate the reasons for this want of success, and are no more compelled to relinquish our full confidence in natural selection than we are compelled to adopt a guarded attitude towards evolution because our historical records are not long enough to register the change of one species into another."†

It was therefore with intense interest and pleasure that I read the following sentences in a letter written by Darwin to Huxley, Dec. 28, [1862]—sentences which show that criticism practically identical had been made by the illustrious naturalist nearly forty years earlier.

"We differ so much that it is no use arguing. To get the degree of sterility you expect in recently formed varieties seems to me simply hopeless. It seems to me almost like those naturalists who declare they will never believe that one species turns into another till they see every stage in progress." ‡

After reading, in the first volume of "More Letters," the often-repeated refutation of Huxley's objection so clearly and strongly expressed in letters received by the objector himself, it is surprising that no effect was produced, and that reference should have been nearly always made to this supposed flaw in the theory of natural selection, whenever the great compara-

* "The Quarterly Review," No. 385, January 1901, pp. 368–371.
† *l. c.* p. 371.
‡ "More Letters," vol. i, p. 225, Letter 154.

tive anatomist had occasion to speak or write on the broader aspects of biological inquiry.*

Darwin also considered that there was something in the very conditions of domestication which tended to promote fertility between races and even between distinct species. Thus he followed Pallas in believing that the domestic dog has been derived from more than one wild species, although he did not trace existing differences to this cause but to artificial selection.† However, as regards the origin of the dog, "the evidence is, and must be, very doubtful," as he wrote to Lyell, August 11, [1860]. The fact which Darwin "considered the most remarkable as yet recorded with respect to the fertility of hybrids," was the fertility of the offspring of the Common and Chinese Goose, originally described by Eyton, and confirmed by Goodacre and by Darwin himself. "The two species of goose now shown to be fertile *inter se* are so distinct that they have been placed by some authorities in distinct genera or sub-genera." ‡

Another interesting and exceedingly difficult experiment in hybridisation has been carried through by the Rev. P. St. M. Podmore, F.Z.S., who in Sept. 1899, after numerous failures, succeeded in rearing a healthy male hybrid between the Ring Dove (*Columba palumbus*) and the domestic pigeon. On May 27, 1903, this male was mated with a Blue Homer hen, which produced healthy offspring. §

* For several instances see Poulton's "Charles Darwin and the Theory of Natural Selection," Lond. 1896, pp. 124–141.

† "Though I believe that our domestic dogs have descended from several wild forms, and though I must think that the sterility, which they would probably have evinced, if crossed before being domesticated, has been eliminated, yet I go but a very little way with Pallas & Co. in their belief in the importance of the crossing and blending of the aboriginal stocks.

* * * * * * *

"Although the hound, greyhound, and bull-dog may possibly have descended from three distinct stocks, I am convinced that their present great amount of difference is mainly due to the same causes [artificial selection] which have made the breeds of pigeons so different from each other, though these breeds of pigeons have all descended from one wild stock; so that the Pallasian doctrine I look at as but of quite secondary importance."

"More Letters," vol. i, pp. 127, 128, Letter 80, to Lyell, Oct. 31, [1859].

‡ "Life and Letters," vol. iii, p. 240.

§ "The Zoologist," Nov. 1903, p. 401.

A comparison between the difficulty of producing such a cross and that of obtaining hybrids between the Ring Dove and the Rock Pigeon, the ancestor of the domestic breeds, would probably throw much light on the Pallasian hypothesis.

If the view here proposed be sound—that syngamy lies behind, and is at least provisionally implied in the transition which means so much to the systematist, and is his only real evidence when the structural test breaks down, the conclusion is suggested that the real interspecific barrier is not sterility but asyngamy. Nevertheless, as argued on pages civ–cvi, asyngamy will infallibly lead to sterility, although the result may be long delayed. This latter view, which was that of Darwin, is the exact opposite of the "physiological selection" of Romanes, in which sterility is supposed to arise spontaneously, asyngamy being not the cause, but the consequence.

Asyngamy may be brought about in various ways, of which the most obvious is geographical separation. But asyngamy is by no means the necessary result of geographical discontinuity or asympatry. Thus Darwin considered that there is regular inter-breeding between Madeiran and continental birds of the same species. He wrote to Hooker, August 8 [1860]: "I do not think it a mystery that birds have not been modified in Madeira. Pray look at p. 422 of *Origin* [ed. iii]. You would not think it a mystery if you had seen the long lists which I have (somewhere) of the birds annually blown, even in flocks, to Madeira. The crossed stock would be the more vigorous." * An even more striking case is that of *Pyrameis cardui*, which ranges over nearly the whole world. The singular absence of local geographical races in this abundant butterfly is almost certainly due to the astonishing powers of dispersal which enable intermittent syngamy to prevail over the whole vast area of its distribution.

An interesting and curious cause of persistent asyngamy is the "Mechanical Selection" so thoroughly explained and abundantly illustrated by Karl Jordan.† The complex genital armature of Lepidoptera is during syngamy kept constant by

* "More Letters," vol. i, pp. 487, 488, Letter 370.
† *l. c.* p. 518–522.

unceasing selection. Comparatively brief isolation of a group of individuals may lead to a departure from the specific type of apparatus prevalent in other areas, and may thus mechanically prevent syngamy if from any cause members of the group became again sympatric with those of the parent species.

A very different but exceedingly interesting origin of asyngamy is suggested by observations which support the conclusion that varietal forms may show a tendency towards preferential inter-breeding.

H. W. Bates believed that he had strong evidence for the existence of this tendency in the races of certain tropical American butterflies. He stated this in his epoch-making paper on the butterflies of the Amazon valley,* and it is interesting to observe in the published letters how Darwin instantly fixed upon the point and tried to elicit the data upon which the conclusion was formed. Thus he wrote to Bates, Nov. 20 [1862]:—"No doubt with most people this [viz. the interpretation of Mimicry] will be the cream of the paper; but I am not sure that all your facts and reasonings on variation, and on the segregation of complete and semi-complete species, is not really more, or at least as valuable, a part. I never conceived the process nearly so clearly before; one feels present at the creation of new forms. I wish, however, you had enlarged a little more on the pairing of similar varieties; a rather more numerous body of facts seems here wanted." †

Then a few days later we find Darwin still thinking of the subject, and writing to Hooker [1862, Nov.] 24:—"I have now finished his [Bates'] paper . . .; it seems to me admirable. To my mind the act of segregation of varieties into species was never so plainly brought forward, and there are heaps of capital miscellaneous observations." ‡

He also again wrote to Bates, probably on the following day, Nov. 25 [1862?], asking for the solid facts which are so greatly wanted:—

"Could you find me some place, even a footnote (though

* Trans. Linn. Soc., vol. xxiii (1862), p. 495.
† "Life and Letters," vol. ii, p. 392.
‡ "More Letters," vol. i, p. 214, Letter 147.

these are in nine cases out of ten objectionable), where you could state, as fully as your materials permit, all the facts about similar varieties pairing—at a guess how many you caught, and how many now in your collection? I look at this fact as very important; if not in your book, put it somewhere else, or let me have cases." *

Remembering that Mr. Roland Trimen, F.R.S., had expressed the same opinion as the result of his wide and long experience of South African butterflies, I asked him if he would kindly furnish me with a statement. His reply, dated Dec. 28, 1903, is as follows:—

"*Dec.* 28, 1903.

"I have noticed the tendency of the sexes of a variety to pair together rather than with other varieties in the numerous cases of captured pairs sent to me by correspondents in South Africa, and sometimes in cases of the same kind which occurred to myself when collecting. The species which particularly attracted my notice in this way during my visit to Natal was *Hypanis acheloia* (= *Götzius*, Herbst, part), which is curiously variable on the underside, from pale creamy to deep chocolate. I did not know of its *seasonal* variation at the time, but I was in Natal just at the change of season from wet to dry, when the intermediate gradations were about, and I was struck with the close resemblance of the sexes in pairs that I caught. I am sorry to have nothing more definite to give on this head; it is a point much requiring exact and prolonged observation."

Mr. Trimen furthermore entertains no doubt that much, if not all, of the material upon which he based the conclusion that the individuals of the same race tend to interbreed, exists, distinctively labelled, in the South African Museum, at Cape Town. It is greatly to be hoped that collectors will in future carefully label all specimens captured *in coitu*, and that the fact will be recorded on the labels in museums and in private collections. It is tantalising to reflect upon the number of interesting and important questions which could be now decided if this practice had prevailed during the past fifty years. The question of the possible origin of species

* "More Letters," vol. i, p. 215, Letter 148.

from races by preferential syngamy is of such high importance that we may confidently hope that the attention here directed to the question, and especially the quotation of Darwin's letters to Bates, may lead to that "exact and prolonged observation," accompanied by careful records, without which a safe decision cannot be reached. In the meantime the decided impressions of two such naturalists as H. W. Bates in South America and Roland Trimen in South Africa render it in every way probable that the conclusion will be established on a firm foundation.*

It is also possible that asyngamy may be brought about by the breaking of what we may call "a syngamic chain." In the case of large and widely-distributed interbreeding communities, it is an open question whether syngamy would freely take place between the most distant of the outlying sections if directly brought into contact, and whether, even if syngamy prevailed, there would be any diminution in fertility.

Limnas chrysippus, perhaps the commonest butterfly in the world, forms a probably continuous syngamic chain stretching from the Cape of Good Hope at least as far as Southern China. It is even reported from Japan. The far Eastern forms are readily distinguishable by the greater size of a single white spot, giving quite a different appearance to the fore-wing. If pupæ or eggs were transferred from Hong-Kong or Macao to South Africa, would the perfect butterflies freely interbreed

* Dr. T. A. Chapman sends me the following interesting and suggestive note:—

"I met lately with a curious instance that deserves following up, of some bearing on the question of selective mating of varieties.

"I saw some broods of *P. phlæas* lately that differed from each other, but each brood was remarkably uniform. There were three broods, all bred in the same conditions, in a greenhouse (by Mr. Carpenter of Leatherhead). It seems difficult to explain this, unless *both* parents of each brood were very nearly identical.

"Mr. Frohawk, who has bred the species largely, tells me he has noticed similar facts.

"When I bred *Acronycta tridens* and *psi* largely, some fifteen or more years ago, I noticed that each brood had its own pairs, and suggested that *tridens* was now trying to break up into separate species just as some ancestor split into *psi*, *tridens* and *cuspis*.

"Another fact I observed in *Acronycta* rather bears on the other side of the question. Of *A. strigosa* I reared a large brood, which paired readily and frequently together, but no eggs were laid. I then got some captured males, which paired with equal readiness with the bred females, and as a result obtained plenty of fertile eggs."

with the indigenous forms of *chrysippus?* We do not know; but it is an experiment well worth trying, and one which would yield results valuable in many ways. If inter-breeding did not take place, or if the unions were sterile, then we should have the interesting case of a single species which would instantly become two if through any circumstance a central link dropped out of the chain. Even if *chrysippus* yielded negative evidence in this respect, it is highly probable that other widely-distributed species would, under these circumstances, fall into two or more groups, each held together by inter-breeding, and divided from others by asyngamy.

Sterility, if present in any degree, would have been brought about quite independently of selection; for in such cases each link of the chain would be freely syngamic with the links on either side, and asyngamy or sterility would only be revealed by artificially bringing together the widely-separated ends of the chain.

I cannot but think, therefore, that such experiments made upon many carefully-selected species would probably bring important additional evidence to bear upon the controversy as to whether sterility between species is, as Wallace believes, a selected quality, or, as Darwin held, an incidental one. The deep interest of this question is realised when we thus remember that the two discoverers of natural selection held widely different opinions about it. We cannot read the letters on both sides, printed in the first volume of "More Letters," without realising how deeply this divergence—one of the principal differences between them—was felt by the two great naturalists.

This is one of the many reasons for which I plead with Mr. Roland Trimen for the establishment of tropical biological stations where work of the kind could be carried on. Such establishments should be associated with and be under the control of museums at home, where the experiments could be directed and the results studied and made available for all time for the researches of the naturalist. Just as Harvard has her main Observatory at the University, but also maintains an outlying institution in the Peruvian Andes, where certain kinds of research, unsuited to New England, can be carried on under the most favourable conditions, so our chief museums should be provided with the means of establishing temporary stations in the most favourable parts of the tropics. When I say temporary, I do not refer to the means, but to the position of the station, which should be freely movable in response to the call of important problems as they present themselves for solution in other localities.

Another urgent reason for the establishment of biological stations is forced upon us by the inadequacy of diagnosis for the separation of very variable species, such as many of the African *Acræinæ.* I cordially agree with the view often expressed to me by my friend Mr. F. A. Heron, that we shall never reach a secure foundation until synepigonic series have been obtained on a large scale. To achieve this end a temporary station would be required. In this way our museums could receive, and should keep for permanent study, the *whole* of the offspring reared from the eggs of a single parent. If several species were thus represented by one or more large synepigonic series, we should know what to expect and what to allow for; and diagnosis in general would gain the most helpful guidance.

Asyngamy, as regards particular lines of union, has also been incidentally brought about by certain adaptations for cross-fertilisation in plants, and such asyngamy has in some cases persisted long enough to have led to sterility in greater or less degree. Of all Darwin's work, that upon the fertilisation of heterostyled plants threw most light, he considered, upon sterility between species. As Francis Darwin has stated, "He found that a wonderfully close parallelism exists between hybridisation and certain forms of fertilisation among heterostyled plants. So that it is hardly an exaggeration to say that the 'illegitimately' reared seedlings are hybrids, although both their parents belong to identically the same species. In a letter to Professor Huxley, given in the second volume [of 'Life and Letters'], p. 384, my father writes as if his researches on heterostyled plants tended to make him believe that sterility is a selected or acquired quality. But in his later publications, *e. g.* in the sixth edition of the 'Origin,' he adheres to the belief that sterility is an incidental rather than a selected quality. The result of his work on heterostyled plants is of importance as showing that sterility is no test of specific distinctness, and that it depends on differentiation of the sexual elements which is independent of any racial difference." *

The different forms of a heterostyled plant are adapted for cross-fertilisation by insects, and each individual of each form is by the same means excluded more or less completely from fertilisation by another of the same form. In the former case the sexual cells and the accessory apparatus have been kept by selection during long generations of syngamy in a high state of mutual compatibility; in the latter asyngamy, partial or complete, has produced a large measure of the sterility which is its inevitable even if long-delayed result.

This argument has, I admit, carried me much further than I originally intended, and it will be a pleasure to me if the following criticism can be overthrown.

If the special adaptation of heterostyled plants for particular lines of syngamy has incidentally resulted in lessened fertility, when the unions discouraged by these adaptations are artificially secured, and in this case without appeal to the physiologically injurious effects of self-fertilisation, why should we not similarly explain these effects whenever manifest in the self-bred † offspring of any plant especially adapted for cross-fertilisation?

Darwin tells us in the Autobiography that as soon as his "attention was thoroughly aroused to the remarkable fact that seedlings of self-fertilised parentage are inferior, even in the first generation, in height and vigour to seedlings of cross-fertilised parentage," ‡ he entered upon a series of experiments which lasted eleven years, appearing in 1876 as "Effects of Cross and Self-Fertilisation in the Vegetable Kingdom." Of this work he wrote in 1881, "the results there arrived at explain, as I believe, the endless and wonderful contrivances for the transportal of pollen from one plant to another of the same species." § It is here suggested that

* "Life and Letters," vol. iii, p. 296.

† See Francis Darwin on "The Knight Darwin Law," Nature, October 27, 1898, p. 630.

‡ "Life and Letters," vol. i, p. 96. § *Ibid.*, vol. i, p. 97.

these injurious results have been not the cause but the consequence of specialisation for cross-fertilisation. In such plants fertilisation is mainly brought about along the line for which special adaptation is made: self-fertilisation is relatively infrequent, often very rare, sometimes perhaps absent altogether. May not the less successful results have followed from a condition in which self-fertilisation is but little tried by the fires of selection?* It would be of much interest to compare a long series of experiments on the cross-fertilisation of plants which are habitually self-fertilised, and on the self-fertilisation of plants in which the adaptations for cross-fertilisation are made use of in widely different degrees.

This criticism, should it be sustained, would of course throw much light upon the case of the Bee Orchis and the numbers of tropical Orchidaceæ, etc., which are now known to be regularly self-fertilising without apparent physiological injury. It might also have a bearing upon an intrusive set of facts which must often have weighed upon the minds of naturalists, as they reflected upon the commonly received hypothesis that assumes the dangers of continued breeding between near of kin. A. R. Wallace speaks of these facts in "Darwinism,"† and I have drawn attention to them in discussing the meaning of insect migration, although, as will be seen in the following passage, without any serious doubt as to the physiological significance of cross-fertilisation.‡

"We may well inquire why it should be necessary for such emigration, with a possible successful issue in colonisation, to require the services of countless individuals when the importation of half-a-dozen rabbits or a few specimens of *Pieris rapæ* will, for the naturalist, change the face of a continent. The results of these unintentional, or intentional but ill-considered, experiments do indeed shake the belief in the paramount necessity for crosses and the dangers of in-and-in breeding; but the end is not yet, and the teeming colonies which have arisen from such small beginnings may in time vanish from the operation of deep-seated causes. The varied adaptations for cross-fertilisation and the prevention of in-and-in breeding

* See also A. R. Wallace in "Darwinism," London, 1889, pp. 321–326.
† p. 326. ‡ Trans. Ent. Soc. Lond., 1902, pp. 460–465.

are so evident in nature, that we are compelled to believe that they meet and counteract serious dangers which sooner or later would menace the very existence of the species. And among other adaptations it is significant that the instinct under discussion should lead to the streaming of large populations, and not of small batches of individuals, from an area of high-pressure." *

It is impossible to consider the advantages which may have favoured cross-fertilisation, if hereafter the generally accepted physiological necessity turn out to be a delusion. Brief reference may, however, be made to the special advantages of community which are possible through syngamy alone. By inter-breeding the favourable variations arising in one direction are combined with others arising in different directions; by the kaleidoscopic changes produced by inter-breeding more varied results are presented for selection, and the beneficial qualities arising in one part of the mass may quickly become the heritage of the whole; by inter-breeding excessive spontaneous variation is checked, and the whole community of the species advances surely and with stability into adjustment with the progressive changes of the environment.

We all remember Darwin's beautifully elaborated metaphor † by which the past history of evolution is shown forth in the form and branching of a great tree. Darwin represented species by the "green and budding twigs," and we may suppose that the leaves stand for individuals, and that syngamy is represented by the contact of leaf with leaf when the branches sway in the wind. And just as contact may run through large and small, irregular and compact masses of leaves, so syngamy binds together groups of varying size and distribution. So too a mass of foliage breached by a sudden storm pictures for us the splitting of a syngamic chain into two species by the disappearance of an intermediate link.

It has been a pleasure to me that the central idea which I have endeavoured to bring before you should be represented, I trust without violence to the imagery, by means of "the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever-branching and beautiful ramifications." ‡

* *l. c.* p. 464. † "Origin of Species," 1859, p. 129. ‡ *l. c.* p. 130.