

## The perfection of animals\*

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### INTRODUCTION

Listening to some physiologists, biochemists and karyologists, one might well get the impression that the phenotype is merely an inconveniently designed container for Krebs cycles and chromosomes. There are two complementary aspects of all organisms that everyone who wishes to be a zoologist (or botanist, or biologist) rather than a mere physiologist or geneticist (or taxonomist etc.) must know something about, namely (i) that of the production, maintenance and reproduction of the organism, and (ii) that of its adaptation to do particular things in particular places at particular times. The first related to development, general metabolism, regulation, coordination, the genetics of sex, biochemical genetics, etc. The second deals with evolution, ecology, population dynamics and genetics, and systematics in the modern sense explained by Huxley (1940) and more recently Simpson (1961); with, in short, *the origin, nature and evolutionary uses of diversity in organisms* instead of the main processes that must be exhibited by any organism to exist at all. At present in Britain and the U.S.A. this second aspect is being so successfully neglected, as Dobzhansky (1961) and Simpson (1962) have rightly complained, that there is grave danger of zoology, the study of *all* aspects of *all* animals, being seriously impoverished, to the detriment of the biological sciences generally.

Although a vast amount of work has been done on various aspects of the phenotype in particular forms or groups, it is no exaggeration to say that there is as yet no unified science of the phenotype, although some of the material for it does exist. The principle of adaptive radiation was recognized in the last century by Osborn but its universality of application has not been appreciated. The significance of the demonstration by mathematical geneticists, especially Fisher, Haldane and Sewall Wright, of the vast power of natural selection, although well brought out in recent accounts of population genetics, has certainly not been generally understood, nor its consequences realized (see p. 14). It seems to be held in some circles, as Simpson (1962) shows (and there was a public demonstration of this recently in the University of Oxford) that all those parts of zoology which are not molecular biology, biochemistry, biochemical genetics or physiology can be dismissed as 'classical' zoology, and are no longer required except at the most elementary level. With such an attitude, no advances in the study of the second aspect of organisms can be made. It is the purpose of this paper to show, by pointing out one neglected part of this study, that the time is now ripe for considerable advances in our understanding of animals. Our interpretation of the diversity of animals is at present erroneous in an important respect.

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It is commonly thought at the present day (by those who do not merely ignore such considerations) that most of the particular features of any animal are adaptive to its particular mode of life, but its general plan which it shares perhaps with an enormous number of other forms cannot be adaptive to a particular mode of life, and therefore must be due to its ancestry. This is almost certainly incorrect for four reasons. First, the belief has arisen as a carry-over from a previous epoch of ideas which are not valid. Second, it is gradually being realized that if we personally cannot see any adaptive or functional significance of some feature, this is far more likely to be due to our own abysmal ignorance than to the feature being truly non-adaptive selectively neutral or functionless. Third, everything that is known of the power of natural selection and the nature of evolution strongly suggests that there has been ample time for the complete reconstruction of the older groups to make them better adapted to their modes of life if this had been necessary; their remarkable constancy of plan combined with plasticity in pretty well every detail of that plan over hundreds of millions of years almost forces us to the conclusion that they are as they are because that is what, in competition with all the other great groups, they need to be. And last, some direct evidence is now being obtained of the highly adaptive nature of features characterizing some major groups.

This is not, of course, to say that all animals are perfectly adapted for their present modes of life. The environment is always changing, and populations cannot adapt instantaneously. You cannot change mice into men by selection in ten generations, and a major overhaul may take a long time. But if we allow a time-lag of twenty million years (for the larger animals, and no doubt much less for very small ones) or even sixty million for the clear establishment of a major change, for reasons suggested below, we still have plenty of time from the Cambrian to the present day to completely remodel the older groups if it were necessary.

The thesis I wish to put forward, therefore, is that broadly speaking, the major plans of construction shown by the older groups are soundly functional and retained merely because of that. The phyla and classes are the main possible ways of living in the face of competition from each other. Their plans are adaptive for broad functional specializations; the particular features of lesser groups are, as has long been agreed, adaptive for more particular functions. This view will not commend itself to those ardent phylogenists who are dependent upon the accepted distinction between adaptive and ancestral characters for the 'evidence' on which their phylogenies are based; it will presumably be ignored by those who are interested only in biochemistry or molecular biology. Those who are zoologists may find it worth considering. It is much more exciting than the currently accepted view, since it puts a thoroughly functional interpretation on nearly the whole of the diversity of organisms, and immediately raises an enormous number of questions about the function of widespread and profound structural features at present dismissed as merely ancestral.

#### THE DEGREE OF PERFECTION OF ANIMALS

##### *Aristotle and vestigial organs*

To find out how the present view has come to be accepted and unquestioned it is necessary to do a little historical research. The results are surprising. People from

Aristotle on to the early nineteenth century were on the whole much nearer to being right than their successors. In Britain, Richard Owen was their chief opponent for purely idealistic reasons; but his arguments were taken over by Charles Darwin and have enjoyed an undeserved observance ever since. What was the view that Owen attacked?

It was well known to Aristotle (and no doubt to many others before him) both that different sorts of animals are marvellously adapted for their different modes of life, and that in some animals there are apparently useless vestiges of organs which are fully formed and functional in others. Adaptation as an idea is immediately intelligible and its generality of application does not surprise us, although the delicacy of construction of so many devices and the complexity of behaviour shown in their utilization have been a source of astonishment and delight and a fountain of edification for many. But why these useless vestiges? Aristotle himself never explained them satisfactorily. He thought that different sorts of bird or fish, for example, were modified for different ways of life and therefore departed from the 'typical' or essential bird or fish plan; but there was a limit to the power of Nature such that no essential character of that plan could be wholly lost. Ogle (1982) comments "I take it that Aristotle was not himself clear as to his own views on the matter; that his opponents, or his own mind, had pointed out the impossibility of reconciling the existence of rudimentary organs with the strictly teleological position, and that he met the difficulty with a phrase, 'by way of token', leaving it really unexplained".

What Aristotle was convinced of, and what became orthodox doctrine for many centuries, was that by far the greatest part of the structures shown by animals were adapted to definite functions, and could be 'explained', therefore if the function of each for which it was intended, the *final cause* (in his terminology) of its existence, could be determined. So many were the evidences of adaptations for anyone to see, so marvellous their mechanism, and so satisfyingly right and fitting the aphorism that God (or Nature) makes nothing in vain—an aphorism still in serious use in some literary circles—that more concerned themselves with the attempt to determine final causes than with the explanation of occasional vestiges, even when anatomical knowledge was accurate enough to point them out. The perfection of structure for particular functions was taken as a marvellous instance of the goodness and infinite ingenuity of God, and there is a long lineage of books describing it as an aid to devotion, some by highly competent scientists. Descartes' doctrine of animals as machines, however, came to be associated with atheism, and in several books supposed instances in which structure and function did not go hand in hand were insisted on as evidence that living things were not mere machines but contained indications of a wider plan than was necessitated by functional considerations. In such highly influential works as John Ray's 'Wisdom of God manifested in the Works of Creation' (Ray, 1704) or Henry More's 'Antidote against Atheism' (More, 1655), which are the forerunners of Paley's famous 'Evidences' (Paley, 1803), perfection of structure for function is mainly insisted on, and often incorporated into prayers and other addresses to the Deity. F. J. Cole (1944) remarks caustically of Samuel Collins, who according to him was the inventor of the anatomical prayer, "We hear the Creator thanked for a variety of mercies, but it was the privilege of Samuel Collins to thank him for the neatness and skill with which the viscera were stowed away in the abdominal cavity". Collins may have been an extreme example, but of a general tendency which

stimulated work on this important subject. The doctrine of perfection of structure and function, reformulated in Aristotelean terms as the doctrine of final causes, became ever more important as a purely scientific doctrine until the early nineteenth century; Cuvier (1817) for example, was a convinced finalist and discussed the application of the doctrine in the admirable preface on scientific method in general and zoological in particular which is the first part of his 'Règne animal'. It was against this ancient and influential doctrine that Owen was campaigning. I do not propose to discuss here the origin of Owen's ideas, which are to be found in the work of the 'Naturphilosophen' but the use he made of them, since it was he who influenced Darwin.

#### *Owen on the Nature of Limbs*

The unfortunate personal relationship between Owen and Darwin has often been commented on, but almost nothing has been said on the far more important subject of what Darwin took over from Owen, agreed to, and reinterpreted in evolutionary terms.

Owen's lecture 'On the Nature of Limbs' was delivered before an evening meeting of the Royal Institution on February 9th 1849, and published soon after as a small book (Owen, 1849). He had to explain to his audience that by 'nature' in the title of his lecture he meant in effect the essential plan and structure of vertebrate limbs, and its significance; he lamented that in Germany there was a word for this (*Bedeutung*) which would be instantly understood in this context. but that he could find no exact English equivalent, partly because English anatomists had paid very little attention as yet to such subjects. He had to correct (in a footnote) the idea that the single toe of the horse corresponded to the two toes of a cow fused together, an idea still current at that time. He had to argue that some entities regarded by medical men as mere processes of particular bones were in fact bones in their own right, so to speak, as could be seen if only they would study the 'lower animals' as well as Man. He had to argue for the value of the idea of homology from segment to segment of the same vertebrate body as a guide and stimulus to the elucidation of various vertebrate structures. (He even had to argue that the right forelimb was serially homologous with the right hind-limb and not, as French anatomists had maintained, with the *left* hind-limb—a dextro-sinistral conformity.) His own interpretations were not those now accepted, and indeed were challenged very soon afterwards by T. H. Huxley. We no longer think of the pectoral girdle as the haemal arch of the occipital vertebra. All these matters strike the modern reader at once; but of greater general interest to biology are the less striking passages in which he disposes of the proponents of final causes.

His whole argument depends on a remarkable analogy between the tools of Man and the limbs of animals. He begins by giving examples of the adaptive modification of the pentadactyl limb—the 'fin' of the dugong, forelimb of the mole, wing of the bat, fore and hind legs of the horse, grasping limbs of monkeys, and finally the manipulatory forelimbs and ambulatory hindlimbs of Man. Then he says (pp. 9–10):

"Such are some of the more striking amongst the countless purposes to which the parts called 'limbs' are adapted, and such the consequent diversity of their outward shapes and proportions. We cannot be surprised at this; it

could not be otherwise: the instrument must be equal to its office. And consider the various devices that human ingenuity has conceived and human skill and perseverance have put into practice in order to obtain corresponding results!

To break his ocean-bounds the islander fabricates his craft, and glides over the water by means of the oar, the sail, or the paddle-wheel. To quit the dull earth Man inflates the balloon, and soars aloft, and, perhaps, endeavours to steer or guide his course by the action of broad expanded sheets, like wings. With the arched shield and the spade or pick he bores the tunnel: and his modes of accelerating his speed in moving over the surface of the ground are many and various. But by whatever means or instruments Man aids, or supersedes, his natural locomotive organs, such instruments are adapted expressly and immediately to the end proposed. He does not fetter himself by the trammels of any common type of locomotive instrument, and increase his pains by having to adjust the parts and compensate the proportions, so as best to perform the end required without deviating from the pattern previously laid down for all. There is no community of plan or structure between the boat and the balloon, between Stephenson's locomotive engine and Brunel's tunnelling machinery: a very remote analogy, if any, can be traced between the instruments devised by man to travel in the air and on the sea, through the earth or along its surface.

Nor should we anticipate, if animated in our researches by the quest of final causes in the belief that they were the sole governing principle of organization, a much greater amount of conformity in the construction of the natural instruments by means of which those different elements are traversed by different animals. The teleologist would rather expect to find the same direct and purposive adaptation of the limb to its office as in the machine. A deep and pregnant principle in philosophy, therefore, is concerned in the issue of such dissections, and to these, therefore, I now pass, promising that the end in view will be attained without extending the comparison beyond the framework of the limbs, or the leverage of the bones and joints".

This analogy between certain human machines and the limbs of various mammals is unquestionably an interesting and instructive one, but it can hardly bear the weight that Owen has put upon it. Man has almost no limitation in his quest for and utilization of the most diverse materials for constructing his devices, and the range of temperatures, pressures and reactions available to him is very wide. He is free, therefore, to design an immense diversity of machines highly adapted to their purposes. But all life as we know it uses water as its principal solvent, transporter and catalyst, and depends on complex organic compounds stable only between rather narrow limits of temperature. No living thing has evolved an organ *immediately* resembling the fire-box of Stephenson's locomotive engine, nor does any use steel as its skeletal material—and for good chemical and physical reasons. We *should* anticipate, therefore, that the designs available for different living devices will bear a certain general resemblance, since their range of materials is far less and their conditions of operation far narrower (to mention only these two points) than is the case with the constructions of Man.

Owen next shows by means of a diagram the skeleton of the forelimb and pectoral girdle in Man, this being the example most familiar to his audience.

Then, following out the inference from the analogy just discussed, he says (p. 11):

“When we proceed to compare with this the skeleton of the corresponding limb of the horse, ox, or other hoofed animal, the simplification of structure seems not to be in the ratio of the loss of function: almost all that the hoof can be made to do is to rest upon or beat against the ground; and yet we find in the solid ungulate limb the broad scapula, the long humerus, the radius and ulna, the carpus, the metacarpus and the digital phalanges. There is a diminution and simplification of accessory parts, but the essentials are maintained: it is obvious that the same type has governed the formation of the two limbs compared”\*.

Then he goes into the correspondence between the limbs in detail, noting that the absence of the clavicle, and the reduction of the ulna and its immobilization relative to the radius, are directly correlated with the comparative restriction of the motions the foreleg has to perform. He proceeds to demonstrate for the limbs of other mammals that the internal structure is always that of the pentadactyl limb, that the correspondence with the type is often astonishingly exact, and that there is no correlation between possession of this type of structure and any particular method of using the limb. The remarks with which he introduces each of these modifications of the limb are important for understanding his thought.

“If we had little *à priori* ground to expect so much conformity between the skeleton of the arm of man and that of the fore-limb of the horse, still less have we to anticipate such between these and the bony frame of the wide-spread wing of the bat. Yet you perceive that the essential similarity of its composition to that of the human arm is greater, the difference depending more on the proportion than on the change or suppression of parts. . . . To skim the air and to burrow in the earth would seem to require instruments as different in construction as in size and shape; but observe how closely the skeleton of the mole’s trowel conforms in the number and relative position of the parts to that of the bat’s wing! The chief change is in this,—whatever is elongated and attenuated in the bat is shortened and thickened in the mole. . . . If the dissector were little prepared on teleological grounds to meet with the full number of joints or segments in the short and seemingly simple trowel of the mole, he could still less expect to find them hidden beneath the common undivided sheath of the fin of the dugong or whale. Yet the bones of this simple form of limb offer perhaps the most striking and suggestive instance of an adherence to type, necessitated as it would seem, notwithstanding the absence of all those movements and appliances of the limb that explain the presence of the several segments, on the principle of final causes, in the horse and man”. (pp. 11–14.)

This last remark would seem to suggest that Owen, in discussing the forelimbs of the horse and man had admitted that the several parts could be explained teleologically, i.e. had discernible functions, but that this was not true for those of the other animals discussed. In fact, he does not even mention the possibility of there being any functional reason for the existence of a separated humerus or radius, and the scapula in the horse is treated most cursorily and only in relation to the loss of the clavicle. There is no attempt to do more than enumerate the

\*His references to his figures have been omitted from this and later quotations.

bones of the forelimb in the horse and man, except in noting the loss of the clavicle and the state of the ulna in the horse.

One further quotation, and Owen's attitude to the question is then sufficiently defined. He points out how remarkable it is that in the tetrapods generally there are never more than five digits on each limb, and that when the number is reduced, one can still see exactly which digits have been lost and which retained. He continues (p. 36):

“So long as the digits are developed as simple rays they are not subordinated to the typical number, but usually much exceed it, as we find in most fishes. In the skate (*Raia*), indeed, the pectoral members far surpass in bulk and seeming complexity their homologues in man, but their development is of a lower kind. It consists of a vegetative repetition,—division, bifurcation and segmentation—of mere rays, of a multiplication of essentially similar parts, without power of reciprocal action and reaction on one another; all being bound up in one common fold if integument for one simple kind of flapping motion—the only one required for an animal so low in the scale, but perfectly provided for by the form of fin in question”.

His solution is given in a particularly clear and graphic passage (pp. 84–86):

“Something also I would fain add with a view to remove or allay the scruples of those who may feel offended at any expressions that seem to imply that any part or particle of a created being could be made in vain.

Those physiologists who admit no other principle to have governed the construction of living beings than the exclusive and absolute adaptation of every part to its function, are apt to object to such remarks as have been offered regarding the composition of the skeleton of the whale's fin and of the chick's head, that “nothing is made in vain”; and they deem that adage a sufficient refutation of the idea that so many apparently superfluous bones and joints should exist in their particular order and collocation in subordination to another principle; conceiving, quite gratuitously in my opinion, the idea of conformity of type to be opposed to the idea of design.

But let us consider the meaning which in such discussions is commonly attached to the phrase “made in vain”. Were the teleologist to analyse his belief in the principle governing organization, he would, perhaps, find it to mean, that so far as he can conceive of mechanism directly adapted to a special end, he deems every organic mechanism to have been so conceived and adapted. In a majority of instances he finds the adaptation of the organ to its function square with his notions of the perfection of a machine constructed for such an end; and in the exceptional cases, where the relation of the ascertained structure of an organ is not so to be understood, he is disposed to believe that that structure may be, nevertheless, as directly needed to perform the function, although he perceives that function to be a simple mechanical action, and might conceive a more simple mechanism for performing it. The fallacy perhaps lies in judging of created organs by the analogy of made machines; but it is certain that in the instances where that analogy fails to explain the structure of an organ, such structure does not exist “in vain” if its truer comprehension lead rational and responsible beings

to a better conception of their own origin and Creator. . . . the recognition of an ideal Exemplar for the Vertebrated animals proves that the knowledge of such a being as Man must have existed before Man appeared. For the Divine mind which planned the Archetype also foreknew all its modifications”.

Only the shallowest mind can believe that in a great controversy one side is mere folly. Owen was no fool, and the strength of his case was apparently great. Yet it would seem that, as can happen to the wisest men, he was wrong, not so much because of his chain of reasoning, but because of the inadequacy of the information he was basing it on. The view of the functions of various vertebrate limbs that can be gathered from the quotations given above is far too simple to bear the superstructure that Owen raised upon it. The fin of the dugong or whale may be of a simple external appearance when compared with the hand of Man, but it is *not* a simple stiff plate capable only of being waved up and down. The hoof of the horse may merely rest on the ground or beat upon it, and so be simpler than the hand of Man, but each hoof must be picked up and put down without the whole body being raised to correspond, or much energy will be wasted in an intolerably jerky gait. The hoof must adjust itself to some extent to the different angles at which the surface of uneven ground may meet it, so that it does not slip, and yet it must bear a considerable weight—it cannot be a delicate as the sucker on the tube-foot of a starfish. Even if no horse ever curled up its legs to lie down, I think it could be argued that a single bone from the pelvis to the foot, instead of the femur and tibia, would not allow of so efficient progression as is in fact an outstanding characteristic of the horse. And no one who has ever seen a skate swimming can possibly describe its usual motion through the water as a simple flap appropriate to a very lowly creature. Owen may never have watched the swimming of a skate; it is inconceivable that he should not have ridden horses, and seen perhaps many thousands of them. I think there is no doubt, and it is no great criticism of him, that his mind was so taken up with his anatomy and the important philosophical issues it raised that he just did not think sufficiently about the actual way in which limbs are used. What he could see was adaptive, he duly recognized as such; what he could not, instead of reflecting on the need for further information before coming to a decision, he decided must be archetypal, and he used it for edification. Owen’s attitude is still a very usual one, except that what is not evidently adaptive is described as ancestral, not archetypal—and is less used for edification (although some divines have appreciated Darwin’s words about the grandeur of the evolutionary process).

#### *Darwin’s interpretation*

The effect of Owen’s arguments on Darwin is clearly set out in the section on morphology in Chapter 13 of ‘On the Origin of Species’.

“What can be more curious than that the hand of man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include the same bones, in the same relative pattern? . . . Nothing can be more hopeless than to attempt to explain the similarity of pattern in members of the same class by utility or by the doctrine of final causes. The hopelessness of the attempt has been expressly admitted by



Owen in his most interesting work on the 'Nature of Limbs'. On the ordinary view of the independent creation of each being, we can only say that so it is—that it has so pleased the Creator to construct each animal and plant”.

As will be seen from the previous section, this statement is seriously misleading in one respect. The hopelessness of the attempt is not what Owen was driven by the facts to *admit*, but what his whole lecture set out enthusiastically to *proclaim*. Gillispie (1960) has described the Naturphilosophen as fervent romantics revolting against the 'mere' objectivity of objective science (especially Newtonian physics). There is much in Owen that answers to this characterization. He was, perhaps, not a trustworthy witness in this particular cause (but I do not mean that he took up a consciously false position).

Darwin continues:

“The explanation is manifest on the theory of the natural selection of successive slight modifications—each modification being profitable in some way to the modified form, but often affecting by correlation of growth other parts of the organization. In changes of this nature there will be little or no tendency to modify the original pattern, or to transpose parts. . . . If we suppose that the ancient progenitor, the archetype as it may be called, of all mammals, had its limbs constructed on the existing general plan, for whatever purpose they served, we can at once perceive the plain signification of the homologous construction of the limbs throughout the whole class. . . . Nevertheless, it is conceivable that the general pattern of an organ might become so much obscured as to be finally lost, by the atrophy and ultimately by the complete abortion of certain parts, by the soldering together of other parts, and by the doubling or multiplication of others—variations which we know to be within the limits of possibility. In the paddles of the extinct gigantic sea-lizards, and in the mouths of certain suctorial crustaceans, the general pattern seems to have been thus to a certain extent obscured”.

Darwin, therefore, originated the evolutionary interpretation which has been followed ever since, that the general plan of the pentadactyl limb is not now adaptive, although it must have been in the common ancestor, but its modifications are adaptive. In the course of evolution the plan has been modified in different ways in different groups of mammals but has been retained as the substratum on which in each evolutionary line and in every life-history the modifications are imposed. In general, the plan or archetype common to all the diversely adapted members of a given group cannot itself be adaptive for any one mode of life, and is clearly there only by inheritance. In the section in Chapter 6 of the 'Origin' dealing with 'Organs of little apparent importance' he makes the very just remark that “we are much too ignorant in regard to the whole economy of any one organic being, to say what slight modifications would be of importance or not”. But he states in the same section that

“the chief part of the organization of every being is simply due to inheritance; and consequently, through each being assuredly is well fitted for its place in nature, many structures now have no direct relation to the habits of life of each species. Thus, we can hardly believe that the webbed feet of the upland goose or of the frigate-bird are of special use to these birds; we cannot

believe that the same bones in the arm of the monkey, in the foreleg of the horse, in the wing of the bat, and in the flipper of the seal, are of special use to these animals. We may safely attribute these structures to inheritance. But to the progenitor of the upland goose and of the frigate-bird, webbed feet no doubt were as useful as they now are to the most aquatic of existing birds. So we may believe . . . that the several bones in the limbs of the monkey, horse, and bat, which have been inherited from a common progenitor, were formerly of more special use to that progenitor, or its progenitors, than they now are to these animals having such widely diversified habits. . . . Hence every detail of structure in every living creature (making some little allowance for the direct action of physical conditions) may be viewed, either as having been of special use to some ancestral form, or as being now of special use to the descendants of this form—either directly, or indirectly through the complex laws of growth”.

When dealing with embryology in Chapter 13 he emphasizes that unless the embryo is active and free-living, and even then only to a limited degree, its plan of construction is not related to its actual requirements.

“The points of structure in which the embryos of widely different animals of the same class resemble each other often have no direct relation to their conditions of existence. We cannot, for instance, suppose that in the embryos of the vertebrata the peculiar loop-like course of the arteries near the branchial slits are related to similar conditions—in the young mammal which is nourished in the womb of its mother, in the egg of the bird which is hatched in a nest, and in the spawn of a frog under water. We have no more reason to believe in such a relation than we have to believe that the same bones in the hand of a man, wing of a bat and fin of a porpoise, are related to similar conditions of life. No one will suppose that the stripes on the whelp of a lion, or the spots on the young blackbird, are of any use to these animals, or are related to the conditions to which they are exposed.

The case, however, is different when an animal during any part of its embryonic career is active and has to provide for itself. The period of activity may come on earlier or later in life; but whenever it comes on, the adaptation of the larva to its conditions of life is just as perfect and as beautiful as in the adult animal. . . . In most cases, however, the larvae, though active, still obey more or less closely the law of common embryonic resemblance”.

#### *Insecurity of this interpretation*

It is clear from the above quotations that Darwin was much too impressed by Owen’s ideas. Translated directly into evolutionary terms they seemed to explain so much that was otherwise wholly obscure. Why should development be so often a matter of recapitulation? Why should aortic arches appear in forms as diverse as fishes, birds and mammals? Descent with gradual modification would explain it all and there was no need to puzzle about possible functions. As Darwin said, most of the features of any organism would be “simply due to inheritance”—and those that had been nearly lost would be vestigial organs. Darwin had already been so much impressed by Paley’s arguments, all pointing to evidence of functional design, that, as I have pointed out (Cain, 1954), he missed the significance of geographical variation because it seemed to affect only trivial characters. Yet there was so much in any animal apparently with no functional significance. Owen and Paley seemed to complement each other.

But there are two reasons for apparent obscurity of functions; one is indeed that a function has changed or been abolished without the structure serving it having changed to correspond; the other is that we simply do not know enough to say anything. Moreover, in the passages quoted above from the 'Origin', Darwin is confusing two rather different classes of phenomena. It may perhaps be that we can see, and state positively, from the known habits of the upland goose of South America or the frigate bird that they *never* use their webbed feet for swimming and the webs are of absolutely no other use to them. One would need a pretty comprehensive study of their life-histories before saying anything so definite. But let it be allowed that this is so; then these would be examples of a present divergence of structure and function explicable on the theory of evolution by a recent change in mode of life, and valid evidence (which is what Darwin was looking for) against any theory of fixity of species.

However, where we are dealing with structures which have persisted for hundreds of millions of years in hundreds of billions of individual life-histories, and which are still so little understood from a functional point of view, it is a very rash assertion that they are merely ancestral. Such, for example, is the pentadactyl limb. Owen's arguments are so clearly unsound precisely in this matter of actual present-day function. The flipper of a seal, for example, is not used merely as a simple flat plane: it executes complicated movements during swimming involving bending both along and across the axis. It is still used to some extent for movement on land. The use of the ends of the digits, when bent, for scratching may be of great importance in dislodging settlers. Adaptations need not be one one hundred per cent necessary for individual survival to be called adaptations, a point not well appreciated even recently, when adaptive structures have been 'explained' as the mere byproducts of physiological processes because they were thought to be not absolutely necessary, and therefore not really adaptations (Richards, 1952). However, Owen's view of the horse's limbs is so crude that he has not even recognized functionally essential features of them.

Darwin's conversion of Owen's idea to an explanation of so many features of animals was much too facile. It was based far more on ignorance of actual function than on positive knowledge, and we need not wonder, therefore, that he and Owen (and the 'Naturphilosophen') assessed the imperfection of animals, the degree to which they are not adapted for their mode of life, as far higher than anyone else had done for centuries. For some features he was surely right; those beetles on oceanic islands that have the elytra immovable so that the wings, which are present and apparently well-formed are not usable, are perhaps as good an example as any of a change in requirements rendering useless an important structure which persists (as yet) by simple inheritance. But to extend such an explanation to major features of great groups is not permissible without further evidence. Every fresh piece of work that bears on function at all shows us again and again functional significance where we might not have expected it and highlights our vast ignorance about almost all living things. Often when I have been putting forward this point of view, I have been asked 'What, then, is your explanation of such and such a structure?' and if I could not reply, the whole viewpoint was rejected. But this is merely to repeat the Owenian error; the interpretation of the course and nature of evolution is not to be based on what one individual happens not to know. Nevertheless, there is a correct feeling behind it that some positive evidence should be forthcoming. Since the Darwinian point of

view has been accepted so generally by those who have interested themselves in evolution and systematics, and the whole subject has been merely ignored by many others, direct evidence of the functional significance of characters of major groups has not yet been systematically searched for. However, there is some, and the indirect evidence is considerable and cogent.

#### THE EXTENT OF ADAPTATION

##### *The power of natural selection*

We owe to Fisher (1930a), Haldane (1932) and Sewall Wright, in books, and numerous papers, the development of the mathematics of population genetics, excellently treated by Li (1955) and Falconer (1960). Perhaps the most remarkable single conclusion is the enormous power of only a few per cent of selection to determine gene-frequencies. Except in very restricted circumstances, mutation pressure and random sampling errors can play only a very minor role, but migration, of course, if massive, can have an overwhelming effect. At the time when Sewall Wright pointed out that random processes might have a considerable effect in very small populations (Sewall Wright, 1931, 1932, 1935), it was widely believed that many characters were neutral or non-adaptive, and he helpfully suggested that genetic drift might be responsible for them. As I have pointed out (Cain, 1951a, b) there was no real basis for the idea of their neutrality. Looking at skins of closely related species of bird reposing on a museum tray, one might well be at a loss to produce an explanation for some of their interspecific differences; but a stuffed bird on a museum tray is not in the best position to show what it does with its characters. Extensive field work may be necessary before their significance is realized, even if it is great. In fact, in every case which has been carefully examined, the supposed influence of random drift, postulated on the basis of insufficient knowledge, has been greatly reduced or actually disproved for the characters under consideration. This has now happened with very diverse organisms and characters. The chromosomal inversions of *Drosophila pseudoobscura* thought by Dobzhansky and Queal to show drift from population to population were shown on more careful analysis by Wright and Dobzhansky to be responding remarkably to temperature, and the beautiful work of Dobzhansky and his school since has emphasized the extraordinary complexity of selective forces which may be acting, both within the genotype and the external environment, on a given inversion. Some of this work has been reviewed by Dobzhansky (1957, 1959). Similarly, it was widely proclaimed that the human blood groups must be of no selective significance, and therefore could be used as markers for the study of human migration; but as Huxley's review shows well (Huxley, 1955), and further work confirms (Chung, Matsunaga & Morton, 1960), this conclusion was merely due to insufficient information. The *medionigra* gene in a colony near Oxford of the moth *Panaxia dominula* originally studied by Fisher and Ford (1947) was shown by them to be highly subject to selection although in a small population fluctuating greatly in size; their work has been extended by Sheppard (1951a) and Sheppard and Cook (1962) both in the original colony and in artificial ones. Sheppard (1952b) has shown that the gene is associated with non-random mating, and Williamson (1960) has discussed its maintenance in the original population. What might seem

to be a trival and entirely neutral alteration in the colour pattern is associated with strong selection of more than one sort, ample to determine its frequency even in small populations.

In the case of the banding and colour varieties of the shell in the snails *Cepaea nemoralis* and *hortensis* it had been confidently asserted that it could not matter to a snail whether it has one band on its shell or two. Cain and Sheppard (1950, 1952, 1954), Cain (1953), and Sheppard (1951b, 1952a) were able to show that definite visual selection was exerted by predators in *C. nemoralis* and that some strong non-visual selection must also be acting to maintain the polymorphism in face of this visual pressure. Clarke (1959, 1960, 1962) has shown similar selection in *C. hortensis* and proposed an additional mode of visual selection. Lamotte (1959) (and other workers reviewed by him) has produced evidence of differential physiological response of the morphs to heat and cold. Cain and Currey (1963a, b) have now shown that considerable differences from place to place in the non-visual selective forces controlling the balance of the polymorphism are likely. Clarke and Murray (1962a, b) have been able to use a very careful survey made in 1926 by Captain C. Diver and the late Professor A. E. Boycott of morph frequencies in *Cepaea nemoralis* on the sand-dunes at Berrow (Somerset). By repeating the survey and comparing results, they have demonstrated very considerable selection in populations at first sight varying at random. This is not to say that random processes have no effect on the morph frequencies in snail populations; Goodhart (1962) has described a situation in which flooding may well have been responsible for considerable local changes. But these studies do show, as do so many other studies on genes in the wild, that merely to fail on a casual inspection to see any selective significance in a particular variation does *not* license the observer to proclaim that there is none. And more positively, they show, as indeed Fisher (1930b, 1939) had done many years before on analysing the data of Nabours on the grouse locusts *Apotettix eurycephalus* and *Paratettix texanus*, that very considerable selection coefficients (even up to 50 per cent in some combinations of genes investigated by Fisher) are actually found to act in the wild. As Sheppard (1956) has pertinently remarked, we need both the mathematical models and some knowledge of what actually goes on in the wild to determine the power of selection.

It follows from the considerations just given that even apparently trivial characters are far more likely to have their frequency and distribution determined by selection than by random effects, although these will also occur. How much more, then, should we expect character-complexes which are found throughout large groups, often comprising many millions of individuals at any one time, to be selectively determined! If they were neutral, they should vary enormously; and if the mere stability of a 'trivial' character in a single large population is presumption that selection is determining its distribution, then *a fortiori* major plans of great groups cannot be selectively neutral. Cannon (1958) has remarked 'We all have fingers and on them finger-prints. The fingers are of great functional significance obviously, but is anyone going to suggest that the particular pattern of our finger-prints helps us in any way to carry out our life processes?' This is, I believe, a valid point (almost the only one in his attack on Darwinism). It is very likely that provided there are sufficient ridges on each fingertip to make an adequate friction-pad and that they run in all directions, so that the finger is not likely to slip more readily in one direction than in another, the exact pattern is

immaterial and can be allowed to vary. The resulting variation is certainly tremendous, and this, and not relative constancy, is what we would expect of neutral characters.

But, it will be rightly said, to show that all characters are determined by selection does not show that they are adaptive. Dobzhansky (1956) had particularly urged that very many characters are mere byproducts of others that are selected for, and in themselves of no selective value or even somewhat deleterious. He reminds us that genes do not determine characters in a simple one-one correspondence; the organism is a complex and integrated whole and the alteration of the action of any gene is likely to produce all sorts of changes (pleiotropic effects) throughout the phenotype. To single out any one of these as 'the' action of the gene is incorrect. He gives as an example the three orbital bristles found in all of the more than 600 known species of the genus *Drosophila*, the most anterior of which is always proclinate (bent forwards) and the other two reclinate (bent backwards).

"Now, why should this character be retained so tenaciously in so many species? Is it really important for the flies of this genus to have one proclinate and two reclinate orbital bristles? . . . When one considers traits in which species of insects and other organisms often differ, such as the differences between *Drosophila* species mentioned above, the supposition that all or even most of them are directly useful to their possessors stretches too much one's credulity. . . . In fact, some *Drosophila* mutants have one or more of the orbital bristles missing, and the mutant flies seem to suffer no inconvenience on this account. But the processes which result in the formation of certain bristles may give rise also to the other traits, morphological and physiological, in the same organism. The proclinate or reclinate position of a bristle, though quite unimportant in itself, may be an outward visible sign of the occurrence in the organism of quite important developmental processes. The latter are not necessarily disturbed when other factors cause some particular bristle to be missing; a mutant may survive without it".

This explanation, however, does not explain. If the bristles can vary independently without ill effects, why are they not as variable as fingerprints? And why, in any case, should they always be produced by some process if not wanted, and be genetically removable without serious effects? If one action of a gene can be affected by modifiers there is no reason why two should not. No modification, of course, can be expected in exceedingly rare and heavily deleterious genes, which may well exhibit all the consequences of the alteration from the wild type. Caspari (1949) has shown in the moth *Ephestia kühniella* that different effects of the same gene may be modified differently for dominance; and presumably some could be suppressed altogether if undesirable and if the gene were common enough, as the wild type alleles normally will be. The analysis of the action of mutants, reviewed by Caspari (1952), is invaluable for investigating pleiotropic action, but we need to know more about the situation in the wild type. It will be seen from the quotations given, that Dobzhansky's argument rests entirely on his own incredulity. Now it is certainly true that nothing is known about the value of many different characters in *Drosophila*; but as long as one accepts that anything not understood is a mere pleiotrope, no investigations will be made. One possible function for bristles that suggests itself straight away is in

relation to toilet. *Drosophila* must be very liable to get covered with sticky and possible highly deleterious micro-organisms. These strong bristles near the eyes may act with others on the legs as brushes, or even have some tactile function like crude vibrissae. Dobzhansky (1952) remarks "The usefulness of a trait must be demonstrated, it cannot just be taken for granted". But equally, its uselessness cannot be taken for granted, and indirect evidence on the likelihood of its being selected for and actually adaptive cannot be ignored. In any case, the argument that flies in cultures do not seem to be affected by the loss of a bristle is inconclusive; a few per cent selection, enough to fix the character in a short time, would not have been noticed, or selection might be far more stringent in the wild.

It is interesting to compare Dobzhansky's attitude with that of Robert Hooke who in his famous 'Micrographia', published in 1665, said of the antennae of insects, "What the use of these kind of horned and tufted bodies should be, I cannot well imagine, unless they serve for smelling or hearing, though how they are adapted for either, it seems very difficult to describe; they are in almost every several kind of Flies of so various a shape, though certainly they are some very essential part of the head, and have some very notable office assigned them by Nature, since in all Insects they are to be found in one or other form". Apparently, the right attitude to enigmatic but widely-occurring organs was fully understood as long ago as the middle of the seventeenth century, at least in England.

Where comparatively trivial characters have been investigated, some very definite functional significances have turned up. One might well ask why the chick of the kittiwake *Rissa tridactyla* should have a black band on the neck, which is not found on that of other gulls. Cullen's remarkable analysis (Cullen, 1957) has shown that this and many other features of the kittiwake are directly related to its nesting on narrow ledges of cliffs instead of on the ground as do other gulls. The black band is shown off when the chick hides its beak as an appeasement gesture to prevent fights which might well end in both the birds involved falling from the ledge. Here, a wholly 'trivial' character might have a coefficient of selection of 50–100 per cent. Similarly, one would hardly expect that a difference in thickness of shell in two closely related gastropods need have much significance, yet Paine (1962) has shown that the thicker-shelled *Busycon contrarium* can open completely closed bivalves by chipping or wedging with its shell, while the thin-shelled *B. spiratum* can only take bivalves whose shells do not close completely, or other gastropods, or carrion. Shell-thickness is therefore the clue to one of the differences in habits which allow these two species to co-exist. Hecht (1952) has analysed the variation in number of the plates under the fourth toe of the gecko *Aristelliger* and shown how it varies in different age-groups in response to at least two main classes of selection; only those with a large number of plates in the adherent organ reach a large body size, and those that do are probably favoured in competition for food, mates and territory, but there is also selection against large body size, probably by predators. Kramer (1951) has made a striking study of the proportions of the hind legs and tail to the body in continental and island populations of the lizard *Lacerta serpa*. Consistent results were obtained in two widely separated areas, and indicated clearly that the proportions of the legs varied with the presence or absence of predators and with whether the islands were flat or steep, as an obvious locomotor adaptation. Shortening of the tail in island populations could be accounted for in the same way. This example is of particular importance, as variation in lizard populations of different Adriatic islands has been widely taken

as an example of non-adaptive variation presumably due to genetic drift. Ride (1959), using ciné-x-ray techniques has analysed the chewing of the Macropodinae (kangaroos) elucidated the functions of the masseteric canal, and made the first evolutionary interpretation of the very enigmatic fossil Procoptodon. Nichols (1959a, b) has not only shown how many apparently trivial features of the test of heart-urchins can be directly related to their modes of life provided one knows how deep and in what sort of substratum they burrow, but has produced a functional interpretation on one of the most famous evolutionary series of fossils, that of the chalk heart-urchin *Micraster*.

But perhaps the most remarkable functional interpretation of a 'trivial' character is given by Manton's work (Manton, 1956, 1959) on the diplopod *Polyxenus*, in which she has shown that a character formerly described as an 'ornament' (and what could sound more useless?) is almost literally the pivot of the animal's life. *Polyxenus*, is a very remarkable minute millipede which can actually walk upside-down on the ceiling of small crevices and even moult there. Manton shows that a curious Y-shaped bar of chitin on the legs enables the animals to use a very wide leg-swing in walking and develop considerable fleetness without using long legs. Speed is necessary as it has to make long journeys for its food, and short legs are an advantage in the crevices where it hides. Its gait is basically of a slow pattern, thus enabling it to have many leg-tips touching the ceiling of a crevice at once; also more secure adherence is obtained by means of special lappets at the tips. She further points out that the Y-shaped bar is also produced completely independently in some very fast-running centipedes for the same reason, namely, to strengthen the joints of a very widely-swinging leg.

To sum up this section, therefore, we can say that the theoretical power of natural selection is very great indeed, and studies in the field have shown that large coefficients are associated with what might seem very trivial characters. Where investigations have been undertaken, trivial characters have proved to be of adaptive significance in their own right. There may well be some characters which are necessary consequences of the production of others but of no selective value in themselves; but it is doubtful if any have been demonstrated to be in this state. The chances that any effect of a widespread gene of a wild-type genotype can be, or remain, neutral for long are slight indeed. Also, the evidence on which characters have been called non-adaptive is invariably wholly negative. If it is taken dogmatically that many characters *must* be non-adaptive, then of course there will be no motive to investigate them, and they will continue to be quoted as non-adaptive whether they are or not; but the positive evidence suggests an adaptive nature.

#### *Adaptive radiation and convergence*

Even where we have only a general idea of the adaptations involved and their genetic basis, we can sometimes see that adaptation is indeed affecting a very great number of characters. Adaptive radiation, the deployment of a basal stock into a large number of niches with consequent divergence of lines, is one of the most usual and pervasive of evolutionary processes, but few studies have yet appeared in which the actual adaptive nature of the divergencies is investigated. The classic work dealing with a single group is Lack's book (Lack, 1947) on the Geospizine finches of the Galapagos Islands, 'Darwin's Finches', recently greatly



supplemented by investigations by Bowman (1961). Simpson's (1950) remarkable elucidation of the evolution of mammals in South America deals with groups of a much higher taxonomic rank, with the advantages of a good fossil history. He shows how in the earliest Palaeocene probably not more than three stocks of primitive mammals, two eutherian and one marsupial, got into South America, which for most of the Tertiary was an island continent like Australia, and proceeded immediately to radiate into the available niches. The marsupials produced such generalized forms as the present-day American opossums and the rather shrewlike little *Caenolestes*, but for the most part specialized in the carnivore habit, producing weasel-like, cat-like and other types, even including a marsupial version, *Thylacosmilus*, of the 'true' sabre-toothed tigers of the northern world. Of the two eutherian stocks, one gave rise to the ground-sloths, tree sloths, ant-eaters, glyptodonts and armadillos, several of which are still extant. The other produced parallels with nearly all the large herbivores of the rest of the world—elephant-like, rodent-like, camel-like, horse-like, and others resembling big herbivores such as *Uintatheres* which are now extinct. Much later, in the late Eocene to Oligocene, some true rodents got in and produced the great radiation of caviomorph rodents well known at the present day (*Capybara*, *agouti*, *guinea pig*, *paca*, *viscacha* etc.) and some advanced lemuroids also arriving in this period produced the New World monkeys, which are generally agreed to have an independent origin from the Old World monkeys. Lastly, very late on, in the late Miocene to Recent, as several large islands became interpolated between South and southern North America and finally the Isthmus of Panama was completed, the fauna of the northern world invaded South America in force. Simpson points out that we have good fossil evidence of the consequences; broadly, those South American forms most like North American ones became extinct (this included all the remarkable herbivores and nearly all the marsupials) but those unlike anything coming in, and some very generalized forms, survived and in a few cases even managed to invade North America.

This fossil history of the South American mammalian fauna is of the first importance to all students of evolution. It is the only one which is reasonably sufficient for us to be sure of the course of events and which relates to an island continent virtually undisturbed (until near the end) either by large-scale immigration or by considerable changes in climate. The present-day and recent radiation of marsupials in Australia is deservedly famous but there is no fossil history of any but the latest part of it. The fossil history of Africa is immensely intriguing but fragmentary. And the history of North America-Eurasia, as summarized by Simpson (1947, 1953) is greatly complicated by invasions, counter-invasions and climate change.

It is not to be expected, of course, that the resemblance of different stocks occupying the same niche in different continents should be perfect, even if they are closely related and therefore very similar to start with. Circumstances will never be exactly the same. For example, the proportions of the main classes of food available may differ and so may their characteristics; if one region of savannah is much more subject to fire than another, its woody plants, becoming fire-resistant, may also become useless as a standby for food for grazers in times of great scarcity, while their bark in the other region may remain just edible. The competitors will be different in each region, and available niches may be shared out in different ways. A mode of life open to a specialist animal in one region may

be too unreliable in another to allow any form to specialize in it because of a different seasonal régime. With this in mind, the convergence actually found in the now extinct South American mammals and others is remarkable. The development of three-toed and one-toed 'horses' independently in South America and in the northern world has produced a fantastic convergence in the structure of the foot (though far less in the skull). Very small details are seen to evolve in parallel—and at widely different periods—in the true horses and in *Diadiaphorus* and *Thoatherium*, the South American convergent forms. But in fact Whitworth (1954) has shown that the single-toed 'horse' foot evolved *three* times independently; he has found it, again with astonishingly detailed similarities, in the Miocene hyracoids of East Africa. Simpson (1941) has examined the function of the sabre teeth of big carnivores and shown that, although this has been denied, they are beautifully adapted for stabbing; he points out that they have arisen three times at least, twice within the true carnivores (once in North American Eocene creodonts, once in the Oligocene to Pleistocene machairodont cats) and once in the marsupials of South America. Again, convergence extends to small details.

Within many other groups of animals convergence can be seen to affect even minute details of structure. Of particular interest is the situation in which several related lines are all progressing towards the same type or organization. Simpson (1959) reviews the evidence that the Mammalia are a polyphyletic group, in Huxley's terminology (Huxley, 1959) a grade and not a clade, that has been achieved independently in several related lines. Here we have the origin of a major taxonomic group effected by a parallelism that seems to suggest strong adaptation. H. K. Pusey (1960) has pointed out how many of the major features of mammals may be functionally correlated with a high degree of homiothermy; if so it is not surprising that they should all arise several times independently within related stocks.

It seems to be agreed that older theories of orthogenesis or innate trends in evolution are based on an insufficient examination of the fossil record, that evolution, on the contrary, is essentially opportunistic (Simpson, 1951) and that the origin of higher categories is not different in essence from that of the lowest (Mayr, 1942; Simpson, 1944, 1951), but is simply of groups which happen to take advantage of a new situation (a newly available region or an improvement in structure) and radiate. Strong convergence, therefore, is good evidence of the existence of very similar selective pressure bearing on different groups and of adaptive response to them. Now convergence, if we have (as usual) only an imperfect fossil record, may be difficult to detect. Up to now it has usually been assumed, by Darwin (see Cain, 1959) and others, that convergence will never be so good as to mislead us. We may allow that it is ecologically very unlikely that two widely different groups such as insects and brachiopods will show convergence, because it is so unlikely that similar selective pressures would act for long enough always in the same direction to produce it, and at least as unlikely that the intermediate forms would be able to persist in the face of competition from others more specialized whose niches would have to be traversed to reach the desired result. But, as remarked above, rather similar stocks may well converge greatly and in the absence of a good fossil record, give rise to much confusion. Convergence is now being suspected at all sorts of levels of the animal kingdom; to the examples I have previously given (Cain, 1959a), many more could be added,

such as Kleinenberg's (1959) acceptance of a diphyletic and Slijper's (1962) of a triphyletic origin of the Cetacea. It must be made clear that the polyphyletic origin of *all* 'natural' groups is not being asserted. It may be that some groups have been so successful in their own lines and have spread so widely that they occupy completely a given broad niche everywhere and no others can get in. If so, then there will be no convergence on them and they may well be monophyletic, even perhaps in the strictest sense. But it does not follow at all that other groups are not capable, given the opportunity, of converging into that niche. I have pointed out before (Cain, 1959b) some examples of animals that transgress the definition of their phyla in respect of major characters—a mollusc with no anus, a coelenterate with a so-called terminal pore to its gut, a protozoan (and there are several others) that is multicellular; and in a large number of groups the profound changes that have come about with the adoption of parasitism, such as those mentioned by Darwin as occurring in the mouthparts of some crustacea are evidence that even major features can be altered if necessary. It may be objected that parasitism involves only loss or hypertrophy, so that the changes are morphologically simple, but in parasitic crustacea at least this is not so, remarkable attachment systems and root-like feeding systems being developed. One can point also to the profound change in the life history of sessile tunicates from the free-living tadpole to the adult, which involves a gain as well as a loss, or the development of the mouthparts of true flies (Diptera) from the biting mouthparts of primitive insects. It is only the existence of intermediate forms that allows us to keep the Diptera and Thysanura (for example) in the same class; the whole tendency of our present system of 'natural' classification is to put together everything which can be included under some simple definition, a tendency we inherit from Linnaeus and others because it is convenient in cataloguing the enormous diversity of living things to have simple definitions of our groups (Cain, 1959a, 1962). We ignore the great diversity in each group (a good example is the classification of the marsupials as a single order (Simpson, 1962; Cain, 1959a)), manufacture a definition of the group which in some cases may be full of exceptions, and then tend to think of it as having an unalterable plan. But even if there is a constant general plan expressible in a simple definition, it does not follow that it has become incapable of alteration if the need should arise; and in some cases the diversity within major groups (in the invertebrates) is so great that we could make out classifications differently. Until a quantitative method of expressing overall differences can be produced and used to make a real map, not a highly distorted sketch-map, of the animal kingdom, our accepted classification will continue to bias our thoughts.

#### *Adaptive features of major groups*

Because of the general assumption that the major features of greater groups must be merely ancestral, there is as yet little direct evidence on their actual function. Perhaps the best available is the beautiful work of Manton (1950a, b, 1952a, b, 1954, 1956, 1958, 1959, 1961), on the locomotory adaptations of arthropods. One small piece of the huge body of work has been mentioned above, namely the explanation of the 'ornamental' Y-shaped bar on the legs of *Polyxenus*. Manton (1959) has herself summarized her work on *Peripatus*, *Polyxenus* and the *Scutigleromorpha*. Briefly, it can be said that every feature of

the skeleton investigated shows a soundly functional significance in relation to speed and power of locomotion, or the ability to push hard either forwards or dorsally in burrowing (Chilopoda), and in *Peripatus* to squeeze through extremely narrow and irregular apertures. Now if *Peripatus* is so highly modified in relation to this ability in the curious mandibles, the body wall and cuticle, the nature of the muscles, the construction of the legs, and the body cavity, it requires further investigation to see whether the excretory system, for example, is not also modified for the same reason. Similarly, Manton describes the whole anatomy of *Polyxenus* as explicable on the assumption that its ancestors were Diplopods burrowing by pushing into soil, and secondarily it has become modified for the mode of life described above (p. 18). But we might well ask, since it may be found deep in soil or under bark, whether it has retained some of the modifications for slight pushing because it needs them, in which case its anatomy will be explicable in terms of its *present* mode of life. Equally, the position of *Peripatus* as annectant between the Annelida and Arthropoda has been asserted, and questioned, simply on its comparative morphology. But if it is modified for such stringent conditions, surely very much the same result may have been attained whether it developed from annelid ancestors or simplified from arthropodan ones. Whenever structures are shown to have a functional significance, the possibility of convergence or of attainment by several routes becomes visible, and the type of argument used by De Beer (1954) and Hadzi (1953) in discussing the phylogenetic position of the Coelenterata is seen to be valueless because it ignores function. Hadzi claims that the slight bilateral symmetry of the sea-anemones must be a relic of a bilateral ancestor, which he finds in the Turbellaria; but Pantin (1960) has pointed out that this bilaterality has a function in trickle-charging the coelenteron, and therefore is not really evidence one way or the other. As functional significance is found for characters, they are abandoned as of doubtful value for phylogenetic speculation, and only the unanalysed residue is left, as may be seen very clearly in the valuable review by Morton (1963) of adaptive radiation in the Mollusca. One of the principal residual elements is the nervous system; no one seems to know exactly why ganglia and connectives are arranged as they are in invertebrates. As soon as a reason is found, the possibility of independent acquisition of (say) the ladder-like system of the Annelid-Arthropod line will be realized.

The features that Manton deals with characterize orders and subclasses, and in the case of *Peripatus* a phylum or subphylum. All indicate the importance of adaptation and the absolute necessity of knowing the ecology of the forms concerned before coming to any conclusions. *Drosophila* is so convenient an animal in so many ways that it is easy to forget its unsuitability in others. It has four different ecologies in each life-history (for egg, larva, pupa and adult) hardly one of which is well understood for any species, and functional analysis may be extremely difficult in any stage. A wider survey of the animal kingdom is necessary before probabilities of adaptation can be assessed.

#### *Imperfect adaptation*

Possible sources of imperfection in adaptation must be considered. Genetic drift had been mentioned above; it may well occur but seems unlikely to affect more than a few genes in rather restricted circumstances. Certainly, it is not likely to be effective at the level of major groups. Secular change is a far more important

cause. Organisms cannot adapt instantaneously to a change in conditions. All the factors lumped together under the name of 'genetic inertia' will hinder them. These include lack of the appropriate mutants, linkages unwanted under the new conditions and preventing recombinations, and, perhaps most important, the necessity to adapt the rest of the organism to a change in any one part. This may involve only a few trivial alterations or a good deal of reconstruction. The larger the populations involved the more rapidly will they be able to respond to selection. Haldane (1957) has pointed out, however, that selection can only act at a cost. Very heavy selection might reduce populations to comparatively low numbers, thereby slowing up their response.

There seems to be no estimate of the strength of generic inertia, but perhaps the South American mammals can give us some idea of it. If it is taken that these, on arriving in a new continent, immediately began to radiate into different niches and continued to do so without disturbance, then their evolution would be going on entirely under the influence of their own inter- and intra-specific competition, and should be representable by a set of diverging lines. (This is in fact not quite so; for example, the marsupials produced a group of rodent-like forms which did not survive after the Eocene and were replaced by eutherians.) By the end of the Eocene, most of the peculiar groups were in full course of development, although some of the more specialized forms, for example *Diadiaphorus* and *Thoatherium*, do not appear until the lower Miocene. This suggests that if nothing was holding back the development of these lines but genetic inertia, a period of about 35–40 million years was amply sufficient to see the adaptive radiation well under way. Cloud (1948) has remarked "... if diversification of multi-celled animal life did not begin previous to the Cambrian or the latest pre-Cambrian there would have been essentially no competitive pressure at this time, and virtually all ecologic niches that multicelled animals could then occupy would have been available. It is proposed as an hypothesis that the diversification of the Early Cambrian faunas may be in large part a matter of eruptive evolution, most nearly comparable to the seemingly abrupt deployment of mammalian stocks in Cenozoic time". If this is right, then the first beginnings of the major groups of invertebrates may have taken place in only a small fraction of geological time. The constancy of some of the great groups since then in their broad features suggests continual selection keeping them to what they are.

A further cause of imperfect adaptation can be called compensation. It is usually accepted that the two monotreme stocks in Australasia survived there when other mammals entered because they were already highly specialized to their modes of life; consequently they may be primitive and inefficient in some respects but their specializations compensated for this, and other groups could not invade their niches. While compensation may have occurred in this particular example, it obviously cannot apply to such a group as the Mollusca, facing competition from the Arthropoda in almost every conceivable major habitat for an enormous period of time. If one of these two groups is in any way more primitive than the other, then its primitiveness must in itself be an adaptation to some less specialized mode of life which it can pursue successfully; it cannot be merely a sign of inefficiency.

Another cause of apparent inefficiency is related to perpetually changing conditions. Those animals who by reason of living in areas with considerable seasonal changes cannot specialize highly but must, for example, take different

classes of food through the year, may seem comparatively inefficient but are in fact probably adapted as well as possible to their mode of life. While an early Eocene titanothere or proboscidean may actually be less efficient for the same mode of life as one of its descendants, less specialized forms contemporary with more specialized ones may be adapted for a different mode of life.

This point, however, can be taken much further. Any animal has to do different things at different times or at the same time. No animal can specialize entirely in running, or masticating, or conserving water, for example. Every animal is always the resultant of a balance of often conflicting selective requirements and can only be as good a compromise as possible. All the functions to be performed and all the environmental circumstances that influence the life-history must be known before one can understand the design of an animal. The sea at least, and probably by now the land as well, has been inhabited for so long that it is likely that all the basic solutions to the problem of compromise have been found out. A considerable constancy of basic plan will then be expected, because if an annelid, for example, tries to become a sponge it will come into conflict with efficient sponges already there; and any particular function in a given animal may if considered by itself be obviously improvable. But if the compromise between it and the other functions of the animal, in the face of competition, is as good as possible, no alteration will take place.

A different cause of imperfection, however, may exist. Even if the basic plan of an animal is a perfect compromise in all its major aspects, there may be some features which could be yet better but are not for developmental reasons. It might be thought, for example, that the organization of part of the mammalian embryo by means of aortic arches is unnecessarily complicated, but retained because any alteration at so early a stage would require great upheavals in the organization of so many structures in the head that it could not be carried out. It seems likely that when an animal is doing nothing but developing, it might proceed on a system of signals derived from an ancestral form which could well be arranged differently but are not, purely for historical reasons. However, we know so little about the actual mechanics of development that this may be one more argument from ignorance, and what appear merely as signals to us may have a functional reason which is not immediately apparent. Certainly, obviously useless features are cleared away from modified ontogenies—an example is the non-appearance of gill filaments and an aperture to the outside in the mammalian pharyngeal pouches. It may be true that within classes, there are a number of embryonic features which show more of ancestry than of adaptation, but the developmental features of classes, subphyla or phyla are more likely to be those best suited for producing a given basic plan. It is important that we should not, by using an argument from ignorance, make the same error in interpreting development as Owen and Darwin made in interpreting adult anatomy.

#### SOME POSSIBLE AVENUES OF APPROACH

If the great groups do represent different ways of living in competition with each other, it should be possible to suggest some lines of approach to the problem of determining their principles of design. The study of locomotion has been shown by Manton to be profitable at this level. Dr J. D. Currey has pointed out that below a certain size, the skeletal muscles may be so small in comparison with the

skeletal hard tissues that they can be accommodated inside tubes of them; but with increasing size and weight of the body they will become far too bulky for this. Where the skeleton has to resist bending, it will still be made of tubes of hard tissue, these being most economical in material and weight (as in the vertebrate femur or tibia) but the muscular tissue will have to be outside them; if the tube were so expanded as to contain them, using the same weight of material (to avoid increasing the inertia of the limb), the resistance to bending might be even greater, but the likelihood of so thin-walled and unprotected a tube being cracked by percussion would be far too high. If this is so, then for animals that have to move comparatively fast or perform precise movements it may be necessary to have two fundamentally different patterns, one for small forms with an exoskeleton, the other for much larger ones with an endoskeleton, or rather, from the functional point of view, an exosoma. Another limitation to the upper size of arthropods may well be the necessity to moult, which means that at intervals they are for a short time deprived of supporting tissue. Once given the exoskeleton, one can see that many arthropod characters would follow.

A second feature that may well be of importance is rate of metabolism. The same type of food may be found distributed in very different ways. It may, for example occur locally in masses, or be uniformly but thinly scattered; in the first case, something that can move and search efficiently enough can find enough masses to refuel for more searching, but might starve if compelled to try to utilize distributed material. A slow-moving form may be able to make do with a low but fairly constant intake. A heart-urchin moving slowly through sand may get a living by constantly taking in a very small amount of organic matter per  $\text{cm}^3$  of sand, where a more active form such as an annelid might starve.

If most echinoderms are characterized by the necessity to cut down all metabolic expense to a minimum and yet be able to move a large body around, one might think that the haemal system is an adaptation to this. If the body is large enough to require a circulatory system, but cannot afford to keep pumping a large quantity of liquid around it, an arrangement of strands along or near which amoebocytes could walk when stimulated might be efficient. An animal that has to starve for months on end might show an even greater reduction of body organs; an example would perhaps be the sea-anemones. Batham and Pantin (1950) have shown that the one-fibre-thick and slowly-contracting parietal muscular layer in the anemone *Metridium* is as efficient as would be a fourteen-fibre-thick layer of quickly-contracting frog muscle disposed in the same way. This suggests at once that there is nothing functionally primitive about the parietal muscle-layer in *Metridium*, and that there is some good reason for keeping it down to a minimum. In their brief but very illuminating discussion of hydrostatic and jointed skeletons, greatly extended by Chapman (1958) they suggest reasons for metameric segmentation in quick moving forms; the hydrostatic skeleton may be of advantage in slow moving ones if it requires less tissues to be kept up.

Metamorphosis may have several advantages. The use of a dispersal and a feeding phase is of course common, but it is usually said that the Amphibia are at a disadvantage to the Reptilia because of their necessity to come to water to breed. However, if there is no more to it than that, why are the Amphibia a markedly successful and probably expanding group in the face of so many mammals and reptiles? If the tadpole stage can be used to catch a temporary crop of food, as often seems to be the case, they may be able to tap resources of the

environment which are unavailable to any other tetrapod because they require considerable specialization in the utiliser but are too temporary to support a permanent specialist.

Murray (1962) has examined the population structure of the helioid snail *Cepaea nemoralis*, a member of a very widespread and successful group of snails. He has shown that the multiple mating and sperm storage for more than one season shown by *Cepaea* (and probably by other helioids) and hermaphroditism are adaptations to keep up the effective size of the breeding population. In such animals, which may never move more than 100 metres from their birthplace, tend to form small intra-breeding populations, and lay their eggs in clutches (so that a whole clutch at a time may be destroyed by a predator), the effective population size as defined by Sewall Wright may drop so low that there is serious danger of impoverishing the genepool of the population by inbreeding. The type of locomotion may therefore have consequences for the genitalia.

It will be noticed that while structural adaptations to climbing or swimming can be recognized fairly readily on museum specimens, especially of vertebrates about which we know something by comparison with ourselves, metabolic rate or the ecological use of metamorphosis or the degree of inbreeding, or locomotion in many invertebrates, require considerable investigation before their influence on the characters of the body can be worked out. It is not surprising that such factors as these are only now beginning to be appreciated; and it is likely that, even if the very tentative suggestions given in this section prove wrong in detail, such factors will in general supply the meaning of the higher categories.

#### CONCLUSIONS

It seems, then, that the grounds on which so much of the diversity of animals has been asserted to be non-adaptive and merely ancestral are mistaken, and based almost entirely on a lack of information. The indirect evidence available points strongly to the adaptive nature of the major plans on which animals are built, and of almost all the details. It may well be that some features are truly neutral and due only to an ancestral arrangement; the course of the recurrent laryngeal has been suggested to me as an example. But the direct evidence available, necessarily scanty, demonstrates the adaptive nature of a vast number of characters related to groups of very high as well as low rank. The sort of functions likely to be associated with the main features of the greater groups are not in general those easily appreciated without considerable study and knowledge of the exact ecology of the forms concerned. Forces making for imperfect adaptation certainly exist, but are unlikely to affect the major plans.

The working-out of the significance of the greater groups will lead to a great advance in modern systematics; but since it will require corresponding work in ecology, taxonomy, and comparative anatomy, there is little prospect of its going ahead with any speed. The present energetic concentration on molecular biology, biochemistry and physiology (all good things in themselves) to the exclusion of the wider issues of zoology and botany is likely to cast a blight on such studies in Britain for many years to come.

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## REFERENCES

- BATHAM, E. J. & PANTIN, C. F. A., 1950. Muscular and hydrostatic action in the sea anemone *Metridium senile* (L.). *Journal of Experimental Biology*, 27: 264–289.
- BOWMAN, R. I., 1961. Morphological differentiation and adaptation in the Galapagos Finches. *University of California Publication, Zoology*, 58: 1–302.
- CAIN, A. J., 1951a. So-called non-adaptive or neutral characters in evolution. *Nature, London*, 168: 424.
- CAIN, A. J., 1951b. Non-adaptive or neutral characters in evolution. *Nature, London*, 168: 1049.
- CAIN, A. J., 1953. Visual selection by tone of *Cepaea nemoralis* (L.). *Journal of Conchology*, 23: 333–336.
- CAIN, A. J., 1954. *Animal Species and their Evolution*. London: Hutchinson.
- CAIN, A. J., 1959a. Deductive and inductive methods in post-Linnaean taxonomy. *Proceedings of the Linnean Society of London*, 170: 185–217.
- CAIN, A. J., 1959b. The post-Linnaean development of taxonomy. *Proceedings of the Linnean Society of London*, 170: 234–244.
- CAIN, A. J., 1962. Zoological classification. *ASLIB Proceedings*, 14: 226–230.
- CAIN, A. J. & CURREY, J. D., 1963a. Area effects in *Cepaea*. *Philosophical Transactions of the Royal Society of London, Series B*, 246: 1–81.
- CAIN, A. J. & CURREY, J. D., 1963b. Differences in interactions between selective forces acting in the wild on certain pleiotropic genes of *Cepaea*. *Nature, London*, 197: 411–412.
- CAIN, A. J. & SHEPPARD, P. M., 1950. Selection in the polymorphic land snail *Cepaea nemoralis*. *Heredity*, 4: 275–294.
- CAIN, A. J. & SHEPPARD, P. M., 1952. The effects of natural selection on body colour in the land snail *Cepaea nemoralis*. *Heredity*, 6: 217–231.
- CAIN, A. J. & SHEPPARD, P. M., 1954. Natural selection in *Cepaea*. *Genetics*, 39: 89–116.
- CANNON, H. G., 1958. *The Evolution of Living Things*. Manchester: Manchester University Press.
- CASPARI, E., 1949. Physiological action of eye color mutants in the moths *Ephesia kühniella* and *Ptychopoda seriata*. *Quarterly Review of Biology*, 24: 185–199.
- CASPARI, E., 1952. Pleiotropic gene action. *Evolution*, 6: 1–18.
- CHAPMAN, G., 1958. The hydrostatic skeleton in the invertebrates. *Biological Reviews*, 33: 338–371.
- CHUNG, C. S., MATSUNAGA, E. & MORTON, M. E., 1960. The ABO polymorphism in Japan. *J. Genetique Humaine*, 5: 124–134.
- CLARKE, B. C., 1959. Balanced polymorphism and the diversity of sympatric species. In A. J. Cain (Ed.), *Functional and Taxonomic Importance*: 47–70. London: Systematics Association.
- CLARKE, B. C., 1960. Divergent effects of natural selection on two closely related polymorphic snails. *Heredity*, 14: 423–443.
- CLARKE, B. C., 1962. Natural selection in mixed populations of two polymorphic snails. *Heredity*, 17: 319–345.
- CLARKE, B. C. & MURRAY, J. J., 1962a. Changes of gene frequency in *Cepaea nemoralis* (L.). *Heredity*, 17: 445–465.
- CLARKE, B. C. & MURRAY, J. J., 1962b. Changes of gene frequency in *Cepaea nemoralis* (L.); the estimation of selective values. *Heredity*, 17: 467–476.
- CLOUD, P. E., 1948. Some problems and patterns of evolution exemplified by fossil invertebrates. *Evolution*, 2: 322–350.
- COLE, F. J., 1944. *A History of Comparative Anatomy: from Aristotle to the Eighteenth Century*. London: Macmillan.
- CULLEN, E., 1957. Adaptations in the kittiwake to cliff-nesting. *Ibis*, 99: 275–302.
- CUVIER, G. L. C. F. D., 1817. In Baron, *Le Règne Animal distribué d'après son Organisation pour servir de base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie comparée*: Paris: Deterville.
- DE BEER, G. R., 1954. The evolution of *Metazoa*. In J. S. Huxley, A. C. Hardy & E. B. Ford (Eds), *Evolution as a Process*. London: Allen & Unwin.
- DOBZHANSKY, T., 1956. What is an adaptive trait? *American Naturalist*, 90: 337–347.
- DOBZHANSKY, T., 1957. Mendelian population as genetic systems. *Cold Spring Harbor Symposia on Quantitative Biology*, 22: 385–393.
- DOBZHANSKY, T., 1959. Evolution of genes and genes in evolution. *Cold Spring Harbor Symposia on Quantitative Biology*, 24: 15–30.
- DOBZHANSKY, T., 1961. Taxonomy, molecular biology, and the peck order. *Evolution*, 15: 263–264.
- FALCONER, D. S., 1960. *Introduction to Quantitative Genetics*. London: Oliver and Boyd.
- FISHER, R. A., 1930a. *The Genetical Theory of Natural Selection*: London: Oxford University Press.
- FISHER, R. A., 1930b. The evolution of dominance in certain polymorphic species. *American Naturalist*, 64: 385–406.
- FISHER, R. A., 1939. Selective forces in wild populations of *Paratettix texanus*. *Annals of Eugenics, London*, 9: 109–122.
- FISHER, R. A. & FORD, E. B., 1947. The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* (L.). *Heredity*, 1: 143–174.
- GILLISPIE, C. C., 1960. *The Edge of Objectivity*. Princeton N. J.: Princeton University Press.
- GOODHART, C. B., 1962. Variation in a colony of the snail *Cepaea nemoralis* (L.). *Journal of Animal Ecology*, 31: 207–237.

- HADZI, J., 1953. A reconstruction of animal classification. *Systematic Zoology*, 2: 145–154.
- HALDANE, J. B. S., 1932. *The Causes of Evolution*. London: Longmans Green.
- HALDANE, J. B. S., 1957. The cost of natural selection. *Journal of Genetics*, 55: 511–524.
- HECHT, M. K., 1952. Natural selection in the lizard genus *Aristelliger*. *Evolution*, 6: 112–124.
- HUXLEY, J. S. (Ed.), 1940. *The New Systematics*. London: Oxford University Press.
- HUXLEY, J. S., 1955. Morphism and evolution. *Heredity*, 9: 1–52.
- HUXLEY, J. S., 1959. Clades and grades. In A. J. Cain (Ed.), *Function and Taxonomic Importance*: 21–22. London: Systematics Association.
- KLEINENBERG, S. E., 1959. On the origin of *Cepaea*. *Proceedings XV International Congress on Zoology*: 445–447.
- KRAMER, G., 1951. Body proportions of mainland and island lizards. *Evolution*, 5: 193–206.
- LACK, D., 1947. *Darwin's Finches*. Cambridge: Cambridge University Press.
- LAMOTTE, M., 1959. Polymorphism of natural populations of *Cepaea nemoralis*. *Cold Spring Harbor Symposia on Quantitative Biology*, 24: 65–84.
- LI, C. C., 1955. *Population Genetics*. Chicago: University of Chicago Press.
- MANTON, S. M., 1950a. The evolution of the locomotory mechanisms of the Arthropoda. *Proceedings of the Linnean Society of London*, 162: 22–23.
- MANTON, S. M., 1950b. The evolution of Arthropodan locomotory mechanisms. Part 1. The locomotion of *Peripatus*. *Journal of the Linnean Society of London, Zoology*, 41: 529–570.
- MANTON, S. M., 1952a. The evolution of Arthropodan locomotory mechanisms. Part 2. General introduction to the locomotory mechanisms of the Arthropoda. *Journal of the Linnean Society of London, Zoology*, 42: 93–117.
- MANTON, S. M., 1952b. The evolution of Arthropodan locomotory mechanisms. Part 3. The locomotion of the *Chilopoda* and *Paupoda*. *Journal of the Linnean Society of London, Zoology*, 42: 118–167.
- MANTON, S. M., 1954. The evolution of Arthropodan locomotory mechanisms. Part 4. The structure, habits and evolution of the *Diplopoda*. *Journal of the Linnean Society of London, Zoology*, 42: 299–368.
- MANTON, S. M., 1956. The evolution of arthropod locomotory mechanisms. Part 5. The structure, habits and evolution of the *Pselaphognatha* (*Diplopoda*). *Journal of the Linnean Society of London, Zoology*, 43: 153–187.
- MANTON, S. M., 1958. The evolution of Arthropodan locomotory mechanisms. Part 6. Habits and evolution of the *Lysiopetaloides* (*Diplopoda*), some principles of leg design in *Diplopoda* and *Chilopoda*, and limb structure of *Diplopoda*. *Journal of the Linnean Society of London, Zoology*, 43: 487–556.
- MANTON, S. M., 1959. Functional morphology and taxonomic problems of Arthropoda. In A. J. Cain (Ed.), *Function and Taxonomic Importance*: 23–32. London: Systematics Association.
- MANTON, S. M., 1961. The evolution of Arthropodan locomotory mechanisms. Part 7. Functional requirements and body design in *Colobognatha* (*Diplopoda*), together with a comparative account of Diplopod burrowing techniques, trunk musculature, and segmentation. *Journal of the Linnean Society of London, Zoology*, 44: 383–462.
- MAYR, E., 1942. *Systematics and the Origin of Species*. New York: Columbia University Press.
- MORE, H., 1655. *An Antidote against Atheism or, An Appeal to the Naturall Faculties of the Minde of Man whether there be not a GOD*. 2nd edn. Cambridge: W. Morden.
- MORTON, J., 1963. The molluscan pattern: evolutionary trends in a modern classification. *Proceedings of the Linnean Society of London*, 174: 53–72.
- MURRAY, J. J., 1962. Factors affecting gene-frequencies in some populations of *Cepaea*. Unpublished D. Phil thesis, University of Oxford.
- NICHOLS, D., 1959a. Mode of life and taxonomy in irregular sea-urchins. In A. J. Cain (Ed.), *Function and Taxonomic Importance*: 61–80. London: Systematics Association.
- NICHOLS, D., 1959b. Changes in the chalk heart-urchin *Micraster* interpreted in relation to living forms. *Philosophical Transactions of the Royal Society of London, Series B*, 242: 347–437.
- OGLE, W., 1882. *Aristotle on the Parts of Animals. Translated with Introduction and Notes*. London: Kegan Paul Trench.
- OWEN, R., 1849. *On the Nature of Limbs*. London: van Voorst.
- PAINE, R. T., 1962. Ecological diversification in sympatric gastropods of the genus *Busycon*. *Evolution*, 16: 515–523.
- PALEY, W., 1803. *Natural Theology: or, Evidences of the Existence and Attributes of THE DEITY, collected from the Appearances of Nature*. 6th edn. London: R. Faulder.
- PANTIN, C. F. A., 1960. Diploblastic animals. *Proceedings of the Linnean Society of London*, 171: 1–14.
- PUSEY, H. K., 1960. In A. J. Cain & G. A. Harrison, Phyletic weighting. *Proceedings of the Zoological Society of London*, 135: 1–31.
- RAY, J., 1704. *The Wisdom of God Manifested in the Works of the Creation*. 4th edn. London: S. Smith.
- RICHARDS, P. W., 1952. *The Tropical Rain Forest: Ch 4*. Cambridge: Cambridge University Press.
- RIDE, W. D. L., 1959. Mastication and taxonomy in the macropodine skull. In A. J. Cain (Ed.), *Function and Taxonomic Importance*: 33–59. London: Systematics Association.
- SHEPPARD, P. M., 1951a. A quantitative study of two populations of the moth *Panaxia dominula* (L.). *Heredity*, 5: 349–378.
- SHEPPARD, P. M., 1951b. Fluctuations in the selective value of certain phenotypes in the polymorphic land snail *Cepaea nemoralis* (L.). *Heredity*, 5: 125–134.
- SHEPPARD, P. M., 1952a. Natural selection in two colonies of the polymorphic land snail *Cepaea nemoralis*. *Heredity*, 6: 233–238.

- SHEPPARD, P. M., 1952b. A note on non-random mating in the moth *Panaxia dominula* (L.). *Heredity*, 6: 239–241.
- SHEPPARD, P. M., 1956. Ecology and its bearing on population genetics *Proceedings of the Royal Society of London, Series B*, 145: 308–315.
- SHEPPARD, P. M. & COOK, L. M., 1962. The manifold effects of the *medionigra* gene of the moth *Panaxia dominula* and the maintenance of polymorphism. *Heredity*, 17: 415–426.
- SIMPSON, G. G., 1941. The function of saber-like canines in carnivorous mammals. *American Museum Novitates*, 1130: 1–12.
- SIMPSON, G. G., 1944. *Tempo and Mode in Evolution*. New York: Columbia University Press.
- SIMPSON, G. G., 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85: 1–350.
- SIMPSON, G. G., 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. *Bulletin of the Geographical Society of America*, 58: 613–688.
- SIMPSON, G. G., 1950. History of the fauna of Latin America. *American Scientist*, 38: 361–389.
- SIMPSON, G. G., 1951. *The Meaning of Evolution*. New York: New American Library.
- SIMPSON, G. G., 1953. *Evolution and Geography*. Condon Lectures, Oregon State System of Higher Education, Eugene, Oregon.
- SIMPSON, G. G., 1959. Mesozoic mammals and the polyphyletic origin of mammals. *Evolution*, 13: 405–414.
- SIMPSON, G. G., 1961. *Principles of Animal Taxonomy*. New York: Columbia University Press.
- SIMPSON, G. G., 1962. The status of the study organisms. *American Scientist*, 50: 36–45.
- SLIJPER, E. J., 1962. *Whales*. London: Hutchinson.
- WHITWORTH, T., 1954. The Miocene hyracoids of East Africa. *Fossil Mammals of Africa No. 7*. London: British Museum (Natural History).
- WILLIAMSON, M. H., 1960. On the polymorphism of the moth *Panaxia dominula* (L.). *Heredity*, 15: 139–151.
- WRIGHT, S., 1931. Evolution in Mendelian populations. *Genetics*, 16: 257–266.
- WRIGHT, S., 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the VI International Congress of Genetics*, 1: 356–366.
- WRIGHT, S., 1935. Evolution in populations in approximate equilibrium. *Journal of Genetics*, 30: 257–266.