Evolution as a process / edited by Julian Huxley, A.C. Hardy, E.B. Ford.

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FOREWORD

WHILE this collection of essays was in preparation, the principal Editor, Dr. Julian Huxley, F.R.S., reached the age of sixty-five on June 22, 1952. We, the other contributors to the volume, feel it appropriate to take this opportunity of expressing our appreciation of the great service which he has rendered to biology.

Dr. Huxley's interests have been particularly directed to the study of evolution on the broadest lines and, as a young man, he was an outspoken supporter of Selection at a time when Darwinism was not generally popular. As Editor of the *New Systematics*, and as author of *Evolution, the Modern Synthesis*, we believe he did a valuable service in bringing together modern views on certain aspects of evolution when it was particularly appropriate to present them in a concise and collected form. His pioneer observations on bird behaviour, begun as early as 1912, did much to stimulate work not only on that subject but on corresponding problems in other animals. In addition, his studies on Relative Growth have thrown a new light upon certain aspects of development and of genic action, while his concept of the "cline" is proving essential to the analysis of geographical variation. Yet Dr. Huxley's greatest contribution to knowledge has been wider and more fundamental than these, for few other living scientists have so freely given their encouragement, help, and stimulating criticism to research workers in biology. There must be many, some of them leaders in diverse fields of our science, who owe much of their success to that balance of reasoned judgment and enthusiasm which he to an outstanding degree has been able to impart. It is our hope that we may still have the benefit of his inspiration as a guide for many years to come.

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JULIAN HUXLEY

The Evolutionary Process*

It is interesting to recall certain milestones in the history of the study of evolution during the last hundred years. Darwin himself convinced biologists of the fact that evolution had occurred, in part inductively, by amassing an enormous body of evidence which could not be interpreted on any other view, in part deductively, by putting forward a general theory of natural selection, which made it possible to understand in principle how evolutionary transformation could operate. T. H. Huxley was emphatic as to the value of this deductive element in Darwin's work.

Darwin himself followed up his initial triumph by extending the principle of selection in relation to domesticated animals and plants; to animal and human behaviour, notably as regards the expression of the emotions; to secondary sexual characters; and to various detailed adaptations, like those of climbing and insectivorous plants.

The main effect on zoology was the rapid development of comparative anatomy and embryology on a phylogenetic basis: this was accompanied by the growth of what have been cynically described as "forests of family trees," often highly speculative.

The detailed description of obvious adaptations, both in animals and plants, was another feature of this period, and also the study of geographical distribution against an evolutionary background.

Reaction against facile speculation set in towards the close of the century, and biologists set themselves to study what variations actually occurred in nature, and what was the precise mechanism of heredity and heritable variation. The new science of genetics came into being.

The first result of this was a widespread scepticism as to the efficacy of Darwinian selection, and the value of adaptations as evidence for past selective changes. As a consequence, the study of genetics largely ousted the study of evolution itself from the centre of the biological stage. It

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* In preparing this introductory essay, I have, by kind permission of the Editor of *The Times*, incorporated the major part of an article of mine which appeared in *The Times Literary Supplement*.

was not until about 1930 that the facts behind the chromosome theory and the mutation theory could be finally reconciled with the idea of gradual evolutionary change and the selective origin of adaptations, in what R. A. Fisher called, in the title of his important book, "The Genetical Theory of Natural Selection."

Meanwhile the details of comparative cytology and Mendelism, of ecology, of animal behaviour, and of comparative physiology and biochemistry were being explored. Paleontology too yielded a rich harvest of facts, but the paleontologists on the whole continued to prefer non-Darwinian explanations. Systematics concentrated on the necessary business of mere description and cataloguing, until the problem which Darwin saw as central in evolution, the origin of species, once more became a subject for research, together with other problems hardly envisaged earlier, such as the genetic structure of different kinds of species.

In the last couple of decades the need for synthesis has become more and more apparent. Species, chromosomes, gene-complexes, adaptations, fossil trends, ecological adjustments, ontogenetic processes, behaviour mechanisms—all had been studied in great detail; but their interrelations in a single evolutionary process had too often been neglected. Yet whenever these interrelations were studied, the result was fruitful. The synthetic study of the different aspects of evolution is perhaps the salient feature of the present period.

It is all the more curious that from certain quarters the very idea of a unitary evolutionary process has been attacked. Biologists, it is asserted, cannot study evolution as a process; they can only study an unlimited number of particular processes. This, I maintain, is an error. In the first place, a single basic mechanism underlies the whole of organic evolution —Darwinian selection acting upon the genetic mechanism. Darwinian selection is an old principle, but the way it works depends on the nature of the genetic mechanism. And modern genetics has established that this consists of unit-particles adjusted to form a unified system—the gene-complex—capable of combining constancy and flexibility in a unique manner.

In the second place, all evolution takes place in relation to the environment, including the biological environment, and its changes. There is a universal process of adaptation, though this may take very various forms, from material adjustment of the parts of the gene-complex to the development of elaborate organs serving particular biological ends. Thirdly, evolution shows the same kinds of long-term trends in all groups—specialization, advance in general efficiency, adaptive radiation, and, in most lines, restriction and final stability.

From another angle, no single component of the evolutionary process can be understood without reference to others. The origin of the horse is not an isolated phenomenon: it must be studied in relation to the adaptive radiation of the placental mammals, to the changes of climate during the Cenozoic, to the process of speciation in other groups, to the general ecology of the period, to the rate at which selection can transform the gene-complex.

Evolutionary opportunity is another general concept in our subject. The opportunities for evolutionary transformation will be different for forms of different types of construction, for forms at different stages in the process of specialization, and in regions with different degrees of biological competition.

During the last two decades, as a result of the realization of these general points, biologists have paid increasing attention to clarifying the *process* of evolution, as opposed to, or in addition to, analysing its *mechanism*.

This change of emphasis, let me repeat, is a natural evolution of the study of evolution itself. Broadly speaking, during the first third of this century attention was largely focused on the mechanism of biological transmission and transformation; the result was that, by the outbreak of the Second World War, it could be stated with some confidence that by far the most important evolutionary agency is Natural Selection, operating on the raw material of heritable variation provided by mutations. Mutations in their turn are the result of a failure of precision in the basic property of self-copying exhibited by the mendelian genes, which, aggregated in linear order within the chromosomes, constitute the physical basis of heredity; contrary to the earlier views of de Vries, Bateson and others, it is mainly small mutations which are of importance in evolution. Thanks to the work of such men as R. A. Fisher, H. J. Muller, J. B. S. Haldane, and Sewall Wright, it is now clear that selective advantages so small as to be undetectable in any one generation, are capable, when operating on the scale of geological time, of producing all the observed phenomena of biological evolution, such as the formation of new species, the adaptive radiation of groups into specialized subgroups, the succession of dominant types, and even the most apparently improbable adaptations. In fact, genetics now deals with transmission and variation on the evolutionary scale as much as within single species or individual pedigrees, and has completely justified Darwin in his application of Lyell's uniformitarian ideas to biology, as well as confirming his outstanding discovery of the principle of natural selection. Evolutionary change is almost always gradual and is almost wholly effected through selection.

There is still immense activity in the field of genetics, notably in the exploration of what genes really are, what is their chemical structure, and how they work within the cells of the body. But in the field of evolution, genetics has given its basic answer, and evolutionary biologists are free to pursue other problems.

First and foremost, the development of paleontology has at last given us a satisfactory sample picture of what actually happens in large-scale evolution—the trends and branchings-out of larger and smaller groups, the partial or total replacement of old groups and types by new ones, the succession of new dominant types, the variations of evolutionary tempo, the limitations and restrictions on change, and the relation of evolutionary change to evolutionary opportunity. Second, the progress of taxonomy has given us a picture of the process of species-formation, and of its differences in different groups of animals and plants. Third, the advance of ecology and comparative physiology, together with the rapid extension of field studies, has provided a new understanding of adaptation, its omnipresence and its protean manifestations. And, fourth, the extension of embryological studies to cover the whole process of individual ontogeny has reminded us that in a very real sense ontogeny is a necessary part of phylogeny, and that evolution must take account of the way in which the processes of individual development are canalized.

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The advances in these fields have enabled us to ask new questions, to pose old questions in a new and more precise way, and sometimes to obtain new or more satisfactory answers. In the first place we have now a much better understanding of the nature and mode of operation of natural selection. Natural selection, if perhaps unfortunately metaphorical, is a convenient shorthand phrase for the effects of the differential reproduction of different types. It results immediately and automatically from the basic property of living matter—that of self-copying, but with occasional errors. Self-copying leads to multiplication and competition; the errors in self-copying are what we call mutations, and mutations will inevitably confer different degrees of biological advantage or disadvantage on their possessors. The consequence will be differential reproduction down the generations—in other words, natural selection; with the result that favourable new mutations (or favourable new combinations of mutant genes resulting from previous mutation) will become established as normal in the stock in place of less favourable ones.

We now know a good deal about mutation—about its rate, about the kind of mutations that have actually been utilized in the evolution of higher animals and plants, and about the frequency of such potentially or actually favourable mutations and mutant genes.

Basing ourselves on this knowledge, and on the interesting branches of mathematics which have been developed to deal with problems of biological selection and transformation, we can now not merely assert with R. A. Fisher that "natural selection is a mechanism for generating an exceedingly high degree of improbability," but, with H. J. Muller, make some quantitative estimate of that degree. Muller has calculated that the most conservative odds against a higher organism, such as a man, a mammal, or even a fruit-fly, coming into existence fortuitously, without the operation of selection, by the union in one stock of all the necessary mutations, are given by a number with so many noughts that it would take an average novel to write it out, a number immensely greater than that of all the electrons and protons in the visible universe. That is a measure of the degree of our own inherent improbability—an improbability of the same order of magnitude as that of a monkey with a typewriter producing the works of Shakespeare. Just as it took the conscious activity of an outstanding human mind to produce the one, so it took two thousand million years of natural selection to generate the other.

After all, what selection does is not only to ensure the survival and establishment of a long series of exceedingly rare events (favourable mutations) but to secure, with the help of sexual reproduction, their combination in a single strain of living matter. If the rarity of a favourable mutation is 1 in 100,000, then the chance of two favourable mutations occurring in the same strain without the aid of selection is 1 in $(100{,}000)^2$ or 10,000 million, and that of 20 is 1 in $(100{,}000)^{20}$—"which is absurd."

Thus the hoary objection of the improbability of an eye or a hand or a brain being evolved "by blind chance" has lost its force: indeed, the shoe is now on the other foot, and the most apparently improbable adaptations—provided they can be regarded as conferring a biological advantage—are so many demonstrations of the immense power of natural selection operating over the stretches of geological time.

Natural selection has certain obvious limitations. It can only produce results which are of immediate biological utility to the species; and being blind and automatic, it is incapable of purposeful design or foresighted planning. In consequence its results will always be relative—to the particular environment in which the particular species of animal or plant is living, as well as to the particular structure and habits of the species. Insects that escape detection by resembling green leaves will only be evolved in the trees: in the desert, insects in need of visual protection will be selected for sandy colour or may come to resemble pebbles.

Conversely, natural selection could never produce an elephant with wings or a swallow adapted for swift running and the consumption of grasses.

As T. H. Huxley pointed out nearly three-quarters of a century ago, natural selection is the only mechanism which can at one and the same time cause one type to undergo rapid evolutionary transformation, while stabilizing another without essential change over tens or hundreds of millions of years. This relativity of selection is most obvious when a species invades a new area of the environment, where competition and predation are low; in such a case it proceeds to evolve into a number of new types, which the part of it left in the original crowded environment does not do. This is what happened with the celebrated Geospizidae of the Galapagos archipelago, the little passerine birds that were one of the chief agencies in converting Darwin to the idea of evolution. On the Galapagos the original stock evolved into an entire new family of birds, with very varied ways of life; while on the mainland the original finch-like type remained unchanged. The evolutionary opportunity differed enormously between archipelago and mainland.

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But it is time to get down to the core of the matter. For nearly a century biologists have been discussing the course of evolution. Some have emphasized the inevitability of progress, others have postulated an inner urge making for perfection. Some have denied that any animals are "higher" than others, since "lower" forms also persist; some deny progress, because specialized types tend to persist indefinitely. Some, drawing unjustified analogies from individual development, speak of racial senescence and death; others become confused as between specialization and advance in general organization.

In the *Origin of Species*, Darwin writes: "The ultimate result [of Natural Selection] is that each creature tends to become more and more improved in relation to their conditions. This improvement inevitably leads to the gradual advancement of the organization of living beings throughout the world." This idea of *improvement*, it seems, helps to provide a key to the puzzle of evolutionary progress. Biological improvement is a scientifically respectable phrase. It can properly be used to cover any increase in the efficiency of living organisms, regarded as machines for carrying on the business of living and reproducing themselves in the environment provided by this planet.

We can find close parallels in the machines invented by man. Here, the improvement may be of some small part of some machine, as when turning indicators were introduced in automobiles; or in the particular efficiency of a particular kind of machine for a special purpose, as with the increase of speed in steam locomotives; or in the general efficiency of some kind of machine, as in the improvement of steam-driven machines in general; or in the more varied utilization of some general type of machine, as with the adaptation of the internal combustion engine to all kinds of uses; or in the invasion of quite new fields by machines, as with the invention of aeroplanes or modern calculating machines; or in the total or partial supersession of one general type of machine by another more efficient type, as when sail at sea was superseded by steam, and steam in its turn by oil; or in the enlargement of the total mechanical resources of mankind, as evidenced by the advance of technology as a whole.

In the machinery of life, a small improvement of detail, like the protective resemblance of a leaf-insect to leaves, or the "telescopic" adaptation of the eyes of deep-sea fish to scarce or dim light, is usually called a special adaptation. The particular improvement of a line in relation to a special way of life, for instance of the later horse stock to grazing and rapid running on open plains, or of those extinct reptiles, the ichthyosaurs, to a carnivorous marine existence, biologists call specialization: it may take tens of millions of years before reaching maximum efficiency.

The occupation of new fields by organisms is illustrated by the invasion of the land by plants and animals, and later of the air by flying animals; or, in a more restricted way, by the evolution of the internal parasites of vertebrates, or the colonization of the abyssal zone of the sea by fish, probably in the early Cenozoic. The supersession of one main type of biological machinery by a more efficient one, as illustrated by the wholesale replacement of reptiles by mammals at the close of the Mesozoic, or by the equally spectacular replacement of the jawless "pre-fish" by the true fishes, equipped with jaws and teeth, in the Paleozoic, is called the replacement or succession of dominant types.

The extension of the use of some particular type of biological machinery is exemplified on a small scale by the history of the Geospizidae on the Galapagos, already mentioned, and on a large scale by the breaking up of each new dominant group, as it appears on the evolutionary scene, into a large number of specializations. This is the process called adaptive radiation (or deployment); both in the reptiles and later in the mammals it led to the production of carnivores and herbivores, dwarfs and giants, runners and burrowers, fliers and fish-like secondary aquatics, and so permitted the descendants of one single original type to exploit a much greater range of the environment and its resources. However, adaptive radiation also illustrates the general improvement of biological machinery, since specialized improvement for different ways of life—as for grazing in horses or for flesh-eating in the cat family—is usually accompanied by general improvements, for instance, in brain organization and intelligence.

The general advance of technology finds its biological parallel in the increased variety of biological machinery and the rise in the upper level of biological organization which was achieved during the process of evolution as a whole. This brings up the reverse side of the medal—the failure of so many types of animals and plants to continue the process of improvement. Extinction is a commoner fate than continuance, and stability more frequent than transformation and advance; creatures of obviously lower grades of organization flourish side by side with higher forms; many types have persisted essentially unchanged for tens or even hundreds of millions of years. In the dialectic of evolution, if the selective pressure making for improvement is the thesis, the restrictions on the uses of improvement are the antithesis; the actual course of evolution, including evolutionary progress, is the higher synthesis resulting from their interaction.

The restrictions on improvement are as various in type and extent as are the different manifestations of improvement. The most drastic is extinction, which overtakes such types as are unable to meet the competition of later improved types (as with many Australian marsupials in competition with introduced placental mammals, or many placental mammals in competition with man), and also those which are unable to adapt themselves to changes in the physical environment (as with the extinction of so many warm-adapted forms during the ice age, or of moisture-loving types during the great periods of desiccation in the past). In the latter case the obstacle is often the lack of genetic plasticity. The breeding systems of animals and plants may be adjusted to give extremely close adaptation to existing conditions, by decreasing the amount of outcrossing and therefore the range of variability; but this is always achieved at the expense of potential variability, and therefore of flexibility in meeting any change in conditions. The immediate evolutionary advantage gained by close adaptation automatically restricts the organism's long-term possibilities of adjustment.

Then one-sided specialization can be, and usually is, restrictive. As a type becomes thoroughly adapted to a particular way of life, as with the horse stock for grazing on open plains, or the whalebone whales for utilizing the medium-sized plankton of the open sea, there comes a time when natural selection is incapable of pushing the improvement any farther. During its 50 million years of evolution, the horse stock reduced the number of its toes, and increased the complexity of the grinding pattern of its teeth. But any further complexity of tooth-pattern would be less efficient for grinding-up grass stems, and clearly a reduction of the number of toes below one per foot would not be advantageous! The result is stability, with selection keeping the stock up to the mark instead of causing further transformations. In general, one-sided specializations show a steady improvement in relation to their particular way of life over a fairly long period of geological time, but pass into a stable state as soon as they reach a certain degree of functional adaptation. After that, they either persist on that level of improvement or are forced into extinction by the competition of new rivals.

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Thus one result of specialized improvement is an eventual restriction of any further improvement. In addition, high specialization for one mode of life restricts the possibilities of switching over to another. This results from the nature of the evolutionary mechanism. It would take an extremely large number of mutations to convert a horse's limb to the functions of grasping and tearing, let alone for climbing or flying, or to readapt a whalebone whale for the capture of large prey; not only will they never all be available at once, but any small deviations away from the existing way of life would almost always be disadvantageous. Specialization thus almost invariably forces organisms into a deepening evolutionary groove out of which it is increasingly impossible for them to climb.

Not only specializations, but also improvements in the general machinery of living, inevitably reach a limit beyond which they cannot be pushed by selection. Thus the capacity for temperature-regulation, so vital to the later evolution of higher mental faculties, did not exist before the Middle Cretaceous or thereabouts: it reached its perfection, both in birds and mammals, somewhere in the early or middle Tertiary, after a period of 30 or 35 million years, but has remained unchanged in the 25 or 30 million years since then. In general, all long-term improvements proceed by a series of finite steps, each perfected over a certain period of time, and then serving as basis for further steps.

Another type of restriction is the long-term limitation imposed by certain types of construction. Animal types which exploit the possibilities of a radial construction, like starfish or medusae, are thereby debarred from developing a true head, for this can only evolve in a bilaterally symmetrical creature: and only animals with heads have the possibility of evolving elaborate brains and eyes. But the most illuminating example is that of the insects. By adopting tracheal respiration, in which oxygen and carbon dioxide are carried directly to and from the tissues by microscopic air-tubes instead of in the blood-stream, they were able to colonize the land extremely successfully. However, for various physical and physiological reasons, tracheal respiration becomes inefficient with increased size. An insect the size of a rat would be a biological impossibility, and in point of fact no insects exist over the size of a mouse. This limitation of absolute size of course limits the size of the brain, and the small size of the brain in turn limits the power of learning and the degree of intelligence, since these demand a much larger number of nerve-cells and nerve-paths than do even the most elaborate of fixed instincts. Thus the adoption of tracheal respiration by insects imposed a drastic limitation both on their size and on their intelligence, and so made possible the evolution of higher vertebrates and the emergence of man.

It is worth noting that the long-term implications of adopting any particular plan of construction are not always restrictive. Sometimes they may be constructive, permitting the evolution of some improvement denied to other types of life. The eyes of insects provide a good example of both kinds of evolutionary implications, positive as well as negative. Everyone knows that insects have compound eyes, made up of a large number of separate units, each contributing a dot to the total visual pattern. Eyes of this type can be very efficient in detecting movement: but it is physically impossible for them to provide such a high degree of resolution as our own camera type of eye. A bee or even a dragonfly cannot see nearly as much detail as a bird or a man. On the other hand, the construction of the insect eye involves the presence of six cells arranged radially round the centre of each facet or visual unit: and since protoplasm polarizes light, this mode of construction provides the animal with a miniature set of Nicol prisms, and so with a potential organ for perceiving the direction of polarized light. In point of fact, as von Frisch has so brilliantly shown, the bees have actually utilized this potentiality, and find their way about by means of such an organ, which tells them the direction of the sun, even with an overcast sky.

It is also worth recalling that some of the most spectacular advances in evolution have been made through utilizing the consequential effects of adaptation to an extremely narrow environment. For instance the entirely new method of terrestrial locomotion possessed by snakes was the outcome of their ancestral period as burrowing and half-blind lizards. On a more important scale, the flower of life constituted by terrestrial vertebrates, sprang from a small group of rather primitive bony fish which had specialized in adaptation to life in stagnant fresh waters: when the fresh waters began to dry up in the Devonian period, one line of them survived through improving the air-breathing function of their swim-bladders and the supporting function of their primitive lobed fins

—and so became the ancestors of all amphibians, reptiles, birds, mammals, and man himself.

This brings us to the problem of progress. There have been many attempts to define biological progress, or advance in organization. It would seem that the most satisfactory definition is as follows: biological progress consists in biological improvements which permit or facilitate further improvements. Such *non-restrictive improvement* constitutes a very special and very important category of evolutionary process, and assuredly merits a special name, whether we choose to call it "progress" or not. It is the process by which "higher" types come into being, the process operating in the succession of dominant types, the process by which the upper level of improvement or biological achievement has been steadily raised during geological time. It is a rare phenomenon, and one which became increasingly so during evolution, since most evolutionary trends and processes inevitably come to a stop through some restriction or limitation. Thus there has been no improvement in birds, regarded as machines for flying, for perhaps 20 million years; none in insects for more than 30—there are ants trapped in the fossil resin that we call amber from the Oligocene which are in every way as advanced and specialized as those of to-day; and some less advanced types of organization, such as lung-fish and lamp-shells, have remained unchanged in essentials for 300 million years or more. Most evolutionary trends come to an end, either through extinction or by passing into a stable phase: during geological time, more and more avenues of unlimited advance became barred, until by the Pliocene only one path of progress remained open—that which led to man.

This last step of progress was a continuation of the trend towards increased awareness—the improvement of sense-organs and brain, leading to an increase in life's range of knowledge of its environment, a higher degree of organization of knowledge and experience, and better-adjusted behaviour. This kind of improvement became relatively as well as absolutely more important during the later stages of evolution. Indeed, it would appear that by the Pliocene, the possibilities of improving the predominantly physical aspects of living machinery—its mechanical and chemical efficiency—had been exhausted. Put rather crudely, purely physiological properties had reached the possible limit of specialization: the only road out of the evolutionary impasse was by way of brain and mind. Once more the new step was achieved by passing through a very restricted way of life. Before man could develop the cortical structure by which he achieved undisputed biological dominance, his ancestors had first to become brachiating arboreal creatures, a small and unimportant group confined to certain types of forest, and then to descend from the trees and free their hands by becoming bipedal. But once the critical point was passed at which conceptual thought and true speech could develop, a new method of evolution became possible—the method of cultural transformation, based upon the cumulative transmission of experience.

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Anatomically the human type constitutes merely one Family of one Order of one Sub-class of the Class Mammalia; biologically, he represents a new Phylum and indeed a new Kingdom. It is quite possible that even if man were to be miraculously removed from the scene, the remaining animal types would all prove to be so specialized that not one of them would be capable of the only new step which would constitute further biological progress—the step towards concept-formation, language, and a tool-making psycho-social mode of existence. It is at any rate certain that no other type can possibly find a way out of the evolutionary impasse so long as man is in existence (and this, in spite of alarmist but unscientific pronouncements on the danger of the human species annihilating itself, will certainly continue for hundreds of millions of years, until it converts itself into a new evolutionary type).

Once a type has achieved biological dominance by taking a particular step of improvement, it thereby fills what was previously an evolutionary vacuum. Accordingly no other type can take a similar step unless it does so more efficiently (in one respect or many), and, therefore, manages to compete successfully with its predecessor; and it is obvious that the very qualities which have made man so remarkably and rapidly successful would enable him not only to detect any threat to his dominant position, but to nip it in the bud.

Thus man is not only the latest dominant type to be produced during geological time, but also the only one now capable of raising the upper level of evolutionary performance, the sole potential vehicle of further evolutionary progress for life. And with man, a new method of evolutionary transformation has come into being, as different from the purely biological method of the natural selection of self-reproducing variants as that was from the methods of inorganic cosmogony. However, to extend our analysis into this new phase of evolution would be to outstep the limits of biology, as well as those of a single introductory article.

I may conclude by summarizing as briefly as may be the main principles of evolutionary transformation in the biological realm. Natural selection automatically results from the basic biological property, common to all living matter, of slightly incomplete self-copying; and it in turn automatically results in biological improvement. Biological improvement can be of any extent, from a minor adaptation in one property of a single species to a large-scale advance in general organization. Like the improvement of machines, it always proceeds in finite steps, whose upward movement is always succeeded by a stable phase of no essential change. This stable phase may form the basis for further improvements, but more frequently continues indefinitely or is cut short by extinction. Improvement thus may be, and generally is, confronted with limitations and restrictions, some of which, like the limitations on size and brain-power in insects, may be the delayed consequential effects of earlier improvements.

One particular type of improvement is that which is free from restrictions and limitations, or in other words permits further improvements: it deserves the special name of biological progress. This becomes less and less frequent with time, until recently there has been only one possible path of further progress—namely, that which led through monkey-like and ape-like forms to man. In its later stages progress as thus defined was increasingly dependent on improvements in the mechanisms for acquiring, organizing and utilizing the animal's knowledge of itself and the world around it—the sense-organs and the nervous system with its higher centres or brain. And the final step of progress which produced man was solely concerned with improvements of the brain and its capacities, physiological and mental.

The new phase of evolution thus opened up was characterized by a new relation between the organism and its environment. The human type became a microcosm which, through its capacities for awareness, was able to incorporate increasing amounts of the macrocosm into itself, to organize them in new and richer ways, and then with their aid to exert new and more powerful influences on the macrocosm. And the present situation represents a further highly remarkable point in the development of our planet—the critical point at which the evolutionary process, as now embodied in man, has for the first time become aware of itself, is studying the laws of its own unfolding, and has a dawning realization of the possibilities of its future guidance or control. In other words, evolution is on the verge of becoming internalized, conscious, and self-directing.

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After this brief attempt at a general survey I will now pass to the separate essays that make up the bulk of this book. These treat of very various aspects of the evolutionary process. R. A. Fisher very appropriately deals with the main criticisms which have been levelled against the general theory of natural selection, and the main difficulties which its opponents have raised. He points out that all of these have been in principle answered or resolved by recent developments of mendelian or particulate genetics. Selection acting upon a particulate mechanism of inheritance will not be confronted with reversion due to blending, and will permit the conservation of variability in outbreeding wild species. Selection will then not lead to fluid intergrading between species, but will tend to keep them distinct, since the harmony of the gene-complex will be broken down by crossing, so that crossing will normally be disadvantageous.

Selection, given sufficient time, is competent to produce adaptations of extreme delicacy and functional organs of extreme complexity: it is the limitations of our imaginative faculty which prevent us from realizing this fact. Fisher gives an illuminating discussion of different types of improbability, notably "the difference between probabilities viewed prior and subsequent to the events they concern"; and shows how quite small selective intensities can bring about, within ten thousand generations, a combination of characters whose establishment on the basis of mere chance would have the prodigious improbability of 10^{-79}. He further reminds us that selection is not usually a matter of life or death, but of slight differential survival; and that modern genetic study has shown, e.g. in the genetic repair of the maladjustments caused by certain recurrent mutations, that exceedingly low intensities of selection can bring about adaptive change. The essay will be greeted as a welcome reminder of the importance and power of selection as the chief transforming agency in evolution.

J. B. S. Haldane has attacked the problem from a different angle. He has concentrated on the fact that the selective "forces" (in a biological sense) acting on a population or a species, though often intense, are usually in approximate equilibrium. A study of evolutionary statics, and of the reasons why variance is conserved in a species in spite of the agencies making for uniformity, is valuable as demonstrating the stable framework within which evolutionary change can operate. Such change appears usually to be exceedingly slow, though in certain exceptional cases it may be rapid for short periods. Here we see how a study of selection on the basis of modern genetics can lead to important conclusions concerning the character and limitations of the evolutionary process.

In view of the widespread revival of interest in micro-evolutionary problems, and the fertilizing contacts that have recently been made between genetics, systematics, and natural history studies, it is natural that a number of contributors have dealt with this field. Thus Ernst Mayr has developed some thought-provoking ideas concerning evolution in different types of species, showing how important it is to take into account the differences in the type of their genetic structure. Widespread and successful species are likely to show a considerable range of variability, often in the form of clines; but, according to Mayr, they tend to be conservative in evolution. (On this point, I wonder whether, though perhaps conservative in regard to the formation of new species by splitting, they may not be progressive as regards the transformation of the species itself: this is what the work of Sewall Wright would imply.) Within such species there will be a large amount of gene-flow; and for many genes, numerous alleles are likely to be available. In such circumstances, alleles which give heterozygotes of high viability will be at a selective premium, and also those which work well on a wide range of genetic background.

If, however, a small segment of this population is isolated, which will usually not occur except on the periphery of its geographical range, the selective value of various alleles will be much altered, and selection will build up a new genetic complex, more specialized both in its internal organization and in its detailed adaptation to local conditions. Most of such isolated populations are likely to lose a great deal of their variability, and become liable to extinction if conditions change. But Mayr suggests that occasionally, during the "genetic revolution" which will often occur while the reduced gene-complex is being adjusted to the new conditions of isolation, it will happen to be altered in such a way that the species can expand into a new ecological niche; if so, it may be able to spread back into the geographical territory of the parent species and flourish there. Possibly occasional genetic revolutions of this type are the source of "real" novelty or large-scale evolutionary change.

Here is a very interesting suggestion, in which ideas drawn from pure genetics and from the details of taxonomy, may prove to shed valuable light on macro-evolution. In any case, it is a reminder of the important variations that exist in the character of the evolutionary process even in one and the same group of organisms.

E. B. Ford also deals with micro-evolution and geographical variation. He summarizes various original observations in Lepidoptera, which show how the combination of field observation, experiment in field and laboratory, and genetic analysis, may illuminate old problems, even while at the same time raising new questions. The importance of quite narrow geographical barriers, the role of the restriction of variance in small founding populations, the adaptation of large continuous populations to the mean of many ecological habitats—these are some of the points which this type of "combined operation" is in process of elucidating.

P. M. Sheppard's contribution is concerned with the same general subject, but on a narrower basis. He shows that, even in the extraordinary variability manifested by local populations of land-snails like Cepaea, selection plays a more important role than genetic drift. In such forms, it seems, polymorphism provides the original basis for adaptation to a wider range of environment than would otherwise be possible. Predator selection favours that range of variants which is least detectable visually against a particular background. In general, local populations within a species have their characteristics determined mainly by selection: the exceptions are provided by very small populations, especially when living under rapidly changing conditions. Once more, the overriding importance of selection is indicated, while, as in Mayr's argument, the door is left open for the occasional occurrence of changes which are not selective in origin, though their evolutionary future will again be subject to selective influence.

In Sheppard's example of Cepaea, it was shown that selection among the different polymorphic types is brought about in relation to the visual perception of predators. This adaptive local variation in the differently coloured and banded forms of snail is a particular illustration of what I have christened allaesthetic characters—adaptive characters whose evolutionary origin can only be understood in relation to the perceptions of other individuals of the same or other species.

In his article, H. B. Cott gives a most valuable review of the subject, so far as visual allaesthetic characters are concerned. This demonstrates how broad Darwinian principles can be applied to yield important conclusions even in the absence of genetic analysis. Granted certain capacities of visual perception, natural selection will produce certain kinds of results: and the results could not be produced by any other agency than selection. On this level of explanation, we now have a satisfactory interpretation of most of this sector of the evolutionary process. Genetic and experimental analysis would add new levels of explanation, but would not significantly alter the present picture.

The mimetic resemblance of the size and markings of parasitic cuckoos' eggs to those of their hosts is another example of allaesthetic evolution. However, this particular subject, as H. N. Southern shows in his essay, is one where a satisfactory treatment is impossible without bringing in genetic analysis and micro-taxonomy. Mimetic cuckoo species are divided into a number of so-called *gentes*, each with its own characteristic range of egg-coloration. Southern's tentative conclusion is that cuckoo gentes are infra-specific units of a unique type, intermediate between true polymorphic forms and purely geographic races or subspecies. The closeness of mimetic resemblance varies a great deal in different gentes, in some cases apparently in correlation with the degrees of discrimination exercised by the host, and therefore with the intensity of selection. More field observation, and fuller analysis in terms of population genetics, combined where possible with suitable experimentation, will clearly be needed before this problem is fully clarified. Meanwhile we see how an unusual evolutionary situation, where a parasitic species has numerous hosts, and hosts which differ in different parts of the parasite's range, may produce an unusual type of evolutionary result.

The characters employed in courtship and threat display are dealt with by N. Tinbergen; these too are allaesthetic. However, Tinbergen treats his subject from a rather different angle. He draws on recent developments in ethology and animal behaviour studies to give us a clearer picture of just how and why courtship and threat characters evolved as they have done. Courtship and threat display always act as social (allaesthetic) releasers; for this reason they will involve the development of characters which are both conspicuous and distinctive (specific). Historically, display arises either out of intention movements, when an action is only partly performed because the urge or drive to its performance exists, but at a low level, or when the opportunity for consummation has not yet been reached; or else out of so-called displacement activities, when excitation cannot issue in normal channels, owing to two opposing drives being simultaneously activated, or owing to the frustration of a strong drive. In such cases, excitation may spill over into a quite different and irrelevant system of motor activity. Thus the male stickleback will perform "displacement nest-digging" when the antagonistic drives to attack and flight are simultaneously brought into play in certain situations.

By close analysis of display activities, both in natural and controlled conditions, supplemented by their comparative study in groups of related species, it can be conclusively shown that such by-products of behaviour-pattern as intention movements and displacement activities can be secondarily utilized through selection, as releasers for new functions. For this purpose, they are ritualized and given a genetic basis of their own; they are more or less modified so that they cannot be confused with their original manifestations (the threat display of the stickleback derived from displacement-digging differs in various ways from the normal action of digging); and their effectiveness for their new functions is enhanced by the evolution of distinctive and striking colours or structures.

Comparative study may be needed to trace the origin of various display activities. Thus one type of display of male ducks derives from displacement preening; but in some species the action has been so specialized and enhanced that its origin would never be guessed without the existence of less modified types of action in related species. We have thus the possibility of establishing a comparative anatomy of the unit-organs of behaviour.

Selection will also operate to reduce the chance of matings between different species: it can do so by causing divergence of the display-characters involved, with the result that such characters are often specifically highly distinctive.

While much further analysis is needed before various details are explained, this approach has obviously clarified the subject in a very startling way. This new illumination has all been provided in the course of the last forty years.

Allaesthetic characters evolve in relation to the evolution of sensory and perceptual mechanisms in other individuals. E. N. Willmer deals with one aspect of this field, namely the evolution of colour-vision in vertebrates. He shows how complex and difficult the subject is, and how much still remains to be discovered; he also makes it clear that the evolutionary approach is a very fruitful one, both in indicating new lines of attack and in providing rational interpretations.

In any one type of higher vertebrate, the functional capacities for vision will be a compromise between the demands for high visual activity, for high sensitivity in poor light, and for discrimination of movement, of form, and of wave-length or colour. Increased visual capacity depends originally on differentiation of the sensory elements, but in later stages increasingly on the evolution of central mechanisms of discrimination and interpretation.

Colour-vision has in all likelihood been independently evolved in several different lines of vertebrates. It is probable that the differentiation of sensory elements required to discriminate colours arose in the first instance as a by-product of some primary differentiation between high-acuity and high-sensitivity elements in the retinue, such as the cones and the rods, for colour-vision will always be subordinate and secondary to form-vision. Potential colour-perceivers like hawks may, Willmer suggests, actually concentrate on black-and-white (non-colour) form-perception in most of their visual activities.

Once colour-discrimination has become a well-established visual function, it will almost inevitably provoke the development of allaesthetic colour-patterns in other members of the same species in relation to display and courtship, or in other species in relation to concealment or conspicuousness. Thus the biological significance of an apparently allaesthetic character can only be properly evaluated when we know the type of sensory and perceptual mechanism to which it is related.

Another case in which extensive field study has posed problems in a new way is that of reproductive rates, dealt with by David Lack. Here, for instance, the data of field natural history show that the number of eggs laid by a given species of bird varies with the latitude, being higher in high latitudes. Lack advances the view that basic clutch-size is adaptive, genetically adjusted by selection in relation to available food-supply; and that the modificational fluctuations in clutch-size to be seen in many species of birds are also determined by the amount of food available, rather than by the degree of crowding *per se*.

These general conclusions are supported by such recently ascertained facts that, in swifts, in wet summers the mortality of nestlings is *higher* in 3-egg than in 2-egg broods, whereas in fine summers the reverse is the case. Once more, the basic importance of selection is demonstrated.

James Fisher discusses the fact of sociality among birds from the evolutionary point of view. He points out that the social habit, in one form or another, is much commoner among birds than is usually supposed. It has even been suggested that there is a social element in territorial breeding, in the shape of the contacts between males at the territorial boundaries. Social food-seeking is probably the commonest manifestation of the social habit. Comparative study is telling us a good deal about the different ways in which the social breeding habit has evolved in different groups, while intensive observation has made it probable that, in some cases at least, sociality at breeding-time confers a reproductive advantage on the species, and will therefore be favoured by selection. On the other hand, in species like the fulmar, the lower reproductive success of newer and smaller breeding colonies appears to be due to their containing a higher proportion of younger birds, not to the so-called Fraser Darling effect resulting from the stimulus of mere numbers. Social display may also be advantageous, through the psycho-physiological stimulus which it provides. We are thus beginning to understand why such a surprisingly large number of bird species display in social groups.

We next come to the implications of developmental studies for evolution. Bernhard Rensch has given a stimulating account of his own researches and conclusions concerning the effect of increased body-size on the relative size of the brain and various of its parts, and on higher psycho-neural functions, including learning. His results indicate that increase of absolute body-size has favoured the relative size-increase of the "higher" and latest-evolved regions of the cerebral cortex, since these are positively allometric. There are a great many complications of detail, but the broad conclusion seems clear enough, and is of considerable importance. As regards psycho-neural functions, it appears that on the whole larger animals learn more slowly than small ones of the same type, but retain what they have learned for a longer period, and probably are able to learn more difficult tasks.

When this subject has been fully worked out, it will constitute one of the most original contributions of recent years to evolutionary biology. It has already demonstrated how the idea of consequential evolution, which had previously proved valuable in relation to changes of proportions, may be utilized to help in explaining the evolution of higher mental faculties in general, and of our distinctively human mental faculties in particular.

A. C. Hardy is also concerned with the relation between ontogeny and evolution. Following de Beer and Garstang, he shows that Haeckel's "Law of Recapitulation" is false, and that consequently many so-called evolutionary sequences that have been deduced from comparative anatomy and embryology should really be read in the opposite direction. He then gives a valuable review of all the main cases where the evolution of a group may with reasonable likelihood be ascribed to one form or another of paedomorphosis—the prolongation of an early phase of ontogeny, juvenile, foetal or larval, into sexually adult life by some type of heterochrony in development.

There can be no question that both the relative and the absolute rate of developmental processes may be altered genetically, and that such alterations may have important (as well as trivial) effects on the appearance or disappearance of characters, and on the pattern of the life-history as a whole. There can also, I think, be no question that paedomorphosis has played a significant role in our own evolution. Though it will not account for all the special characters we possess, notably the special enlargement of the association areas of our cortex, and the full adaptation of our feet and legs to bipedal terrestrial existence, it has certainly helped us to escape from anthropoid specialization.

It is this possibility of escaping from the blind alleys of specialization into a new period of plasticity and adaptive radiation which makes the idea of paedomorphosis so attractive in evolutionary theory. Both its possibilities and its limitations deserve the most careful exploration.

G. R. de Beer in his article supports Hadži's notion of paedomorphosis in regard to the ctenophores. Instead of the classical view that these are ancestral to Turbellarian flatworms, Hadzi would read the course of events in the opposite sense, and supposes that they are derived from flatworms by paedomorphosis of a Turbellarian larval type.

De Beer also gives a useful summary of Hadži's somewhat revolutionary theory of the origin of the Metazoa. According to this view, the earliest metazoan was not a coelenterate, but a primitive type of acoelous Turbellarian worm, derived from a multinucleate ciliate protozoan by cellularization of its body. It may never be possible to give rigorous proof or disproof of this suggestion; but we should be grateful to Hadži for reminding us that phylogenetic morphology is by no means a dead subject, and that it can still indicate interesting fields for zoologists to investigate.

Stanley Westoll gives a review of recent work on the relation between earth-movements and evolution. He shows how minor earth-movements must have been constantly changing the ecological conditions in many of the main fossil-bearing areas, so that in any such places the local disappearance of forms would usually have been the effect of emigration to other areas, accompanied by colonization by forms from elsewhere, which were better adapted to the changed conditions.

On the more important subject of major mountain-building, the consensus of modern opinion is that the idea of a few cycles of orogenesis, whose crises were contemporaneous throughout the globe, is much over-simplified. A major cycle of mountain-building in any one area may be composed of several successive minor cycles, and the major cycles of different regions may not be precisely contemporaneous.

From the evolutionary angle, while the effects of earth-movements on climate, the relative extent of land and shallow sea, etc., may influence the extinction of old lineages and the development of new types, it now seems clear that the influence is not so drastic nor the relation so simple as has often been supposed. It is rather that the environmental effects of major earth-movements provide an altered range of evolutionary opportunities; when types exist which can take advantage of the new opportunities, they will prosper and differentiate into new dominant groups, and in so doing will bring about the reduction or extinction of established groups.

It thus appears that orogenic crises cannot be regarded as the direct cause of major evolutionary change, such as widespread extinction or the rise of new groups, but that they facilitate it by providing encouragement to certain trends and lineages, and discouragement to others. And such facilitation may sometimes be decisive.

It seems clear that further study of the geological and paleontological facts, in terms of neo-Darwinian selection-theory and in the light of the general concept of evolutionary opportunity, will yield valuable results in elucidating the detailed course of the evolutionary process.

E. T. H. Corner's contribution might be described as an essay in evolutionary ecology. He develops a general thesis as to the course of evolution, not of a particular natural group of plants, but of the ecological complex represented by tropical forest. This approach has been largely neglected in the past: Corner's essay demonstrates how illuminating it may be. From one angle, the evolutionary process can be regarded as the evolution of ecological communities. This means paying attention to the evolution of new ways of life, and the interaction between their representatives. Perhaps the notions of succession and climax, so familiar in ordinary ecology, may prove fruitful in what I may call paleo-ecology also.

S. Zuckerman has contributed an exhaustive study on the correlation between different morphological characters in the evolution of higher primates, with special reference to the position of the australopithecine apes. It is frequently asserted that these are morphologically close to a stage in the evolution of man from simian ancestors. Zuckerman demonstrates that this is far from proven, and that in many of the characters crucial for human evolution, they are no different from apes. Until further specimens come to light, all we can say is that in a few other characters, where phylogenetic significance cannot be immediately assessed, they appear to resemble man more than the apes.

This important paper demonstrates how far we still are from possessing an adequate fossil documentation of the evolution of the Hominidae, let alone one comparable to that available for the horses, elephants, and many other mammalian families. It is also a useful contribution to the methodology of evolution, as showing how cautious we should be in drawing evolutionary deductions from limited morphological and paleontological data.

J. Z. Young's contribution is a new and original approach to an old problem—the relation between heredity and memory. Undoubtedly, the detailed mechanism of individual learning is wholly different from that of evolutionary adaptation, so that we must reject the pure mnemic theories of heredity and consequent Lamarckian views of men like Semon or McDougall. But, as Professor Young shows, there is a real analogy between them, in that both are concerned with adjusting the organism to changes in its environment.

Both processes can thus be examined in the light of modern communication theory, which, arising out of the study of computing machines and the like, is in process of generalizing itself to cover all cases where information (in the broadest sense of the word) is transmitted so as to secure appropriate action at a later stage.

In both cases, problems of reception, of coding and of transmission, of storage, and of decoding for action, are involved, so that we may expect to find interesting convergences in the methods evolved for dealing with them.

Such a method of approaching the problems of hereditary transmission and evolutionary adaptation may well be fruitful in suggesting what kinds of complex mechanism are to be looked for in developmental and evolutionary genetics. In any case, Professor Young's essay is a useful reminder of the value of a unitary approach in biology, and conversely of the dangers of splitting up the subject into a number of water-tight compartments.

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Some aspects of the evolutionary process are hardly touched on in the essays, notably such aspects of macro-evolution as specialization, progress, or the succession of dominant groups in time. However, the reader will have realized the many-sidedness of the evolutionary process, as well as the advantage of considering biological phenomena from an evolutionary point of view, as parts of that single process. He will also, I hope, have realized the need for further research and thought to help us to an understanding of the process as a whole. Evolution is the overriding fact for biology, the comprehensive framework to which separate biological facts and functions are related. The evolutionary approach will prompt us to ask the right questions of nature, and, when we have asked them, will help us to find the right answers.

G. R. DE BEER

The Evolution of Metazoa

Few of the most optimistic (or should it read pessimistic?) zoologists could hardly have thought it possible that, in the middle of the twentieth century, all text-books of zoology should require the drastic revision of the current theory of the origin and evolution of the Metazoa. Yet that and nothing less is the situation resulting from the researches which for half a century Jovan Hadži has made into the structure and development of the lower animals. They have led him to put forward a theory that multinuclear Protozoa evolved into Turbellaria Acoela, which latter (not the Coelenterata) would be the most primitive Metazoa. From them were descended the higher Turbellaria which gave rise to the main lines of invertebrate evolution, and, in addition and independently, to the Coelenterata and to the Ctenophora.

At first hearing, such a revolutionary view may well excite incredulity, and if it be worthy of attention at all, it certainly calls for the most rigorously critical analysis. It may therefore be of interest to present a brief account of Hadži's theory and of the evidence and considerations on which it is based.

Of all the views currently and generally held in Zoology, hallowed by a long period of acceptance and teaching, it would be hard to find one more firmly established than that which holds that the most primitive Metazoa, the animals which evolved from the Protozoa and stand on the main line of evolution towards the higher Metazoa, are the Coelenterata. The Sponges do not come into the picture, since although multicellular, they are universally admitted to be a sideline.

The Coelenterata, or most of them, are radially symmetrical, like *Hydra* and *Aurelia*, and since radial symmetry requires the establishment of only one axis of symmetry whereas bilateral symmetry requires in addition the determination of a plane, the Coelenterata have been held to be the more primitive in this respect than the higher Metazoa with their bilateral symmetry. Besides, in the embryology of many bilaterally symmetrical forms, it has been shown that the egg begins with a radial symmetry about an egg-axis, and that the plane of bilateral symmetry is only subsequently determined.

The Coelenterata have only two layers of cells, so it is usually said, and since all the higher Metazoa have three layers, the two-layered condition is held to be primitive. Furthermore, these two layers of cells in the Coelenterata surrounding a single gastro-vascular cavity which opens by means of a single mouth-aperture, give the organism the structure of a permanent gastrula, with a persistently open blastopore. And since the gastrula is that all-important stage in the development of all Metazoa, by means of which the single-layered hollow ball or blastula is converted into a double-layered sac with outer epidermis and inner gut, often by a process of invagination, so well shown in the Echinoderms, in *Sagitta* or in *Amphioxus*, there was a certain satisfaction in finding such a structure in animals held to be the most primitive of the Metazoa.

It comes, therefore, as something of a shock to find that every one of these cherished assumptions and accepted beliefs has been challenged and controverted by Jovan Hadži, as a result of his half-century of study devoted to the lower Metazoa.

Why should it be thought that the most primitive Metazoa must be radially symmetrical? Radial symmetry among Metazoa is often associated with the secondary assumption of a sessile habit and a degenerate condition, as in Tunicata, Polyzoa, and Echinodermata, and the question must be answered why the Coelenterata should be regarded as exceptions to this rule. This is all the more necessary because some Coelenterata, viz. the Anthozoa, do show a bilateral symmetry, which is confined to the internal organs such as the stomodaeum and the mesenteries. The Scyphozoa and the Hydromedusae, on the other hand, are typically radially symmetrical and only very occasionally show departures from it, which are clearly secondary. The Siphonophora, for example, exhibit an asymmetry which is clearly an accompaniment of their habit of colony-formation. Among the Hydromedusae, in *Lar sabellarum* and in *Branchiocerianthus imperator*, the tentacles may show an irregular arrangement on the body of the polyp, which is a deformation of the radial symmetry; while in the medusae of *Corymorpha nutans*, of *Euphysa aurata*, and of *Euphysa tentaculata*, the number of tentacles may be reduced to 1, 1, and 3, respectively, as a result of suppression. None of these cases can be regarded as true bilateral symmetry; they are the result of interference with radial symmetry.

Of the three main orders of the Coelenterata, the Hydromedusae, Scyphozoa and Anthozoa, the Hydromedusae have been regarded as the most primitive precisely because they are so typically radially symmetrical and their structure is so simple. The Anthozoa on the other hand have been regarded as the most advanced of the Coelenterata because their structure is the most highly developed. But if this were so, it would be difficult to account for the fact that the descendants of purely radially symmetrical animals had developed an internal bilateral symmetry. In progressive evolution, bilateral symmetry is always manifest first in the external parts, since it is these which come into contact with the surrounding medium, motion through which is the condition associated with bilateral symmetry. Conversely, it is the outer parts of the body which first show radial symmetry in the degenerating lines of evolution leading to the sessile habit. The simplicity of the structure of the Hydromedusae may well be secondary, and the only satisfactory conclusion is that the Anthozoan plan of construction is more primitive than that of the Scyphozoa and that the Anthozoa were descended from bilaterally symmetrical ancestors. It follows —and is generally recognized—that the polypoid person, which is the only one represented in the Anthozoa, is more primitive than the medusoid person found in Scyphozoa and Hydromedusae, which is clearly an adaptation to dispersal on the part of a sessile form. Those types of Hydromedusae which have lost the polypoid person altogether and only retained the medusoid form, may therefore be regarded as specialized, and the sequence in which it had been thought that the Orders of the Coelenterata evolves must be precisely reversed.

Next it is proper to consider the concept that the original Metazoa were two-layered sacs with a hollow gastro-vascular cavity, produced as a result of invagination. Curiously enough, among the Coelenterata, invagination is the most uncommon method of gastrulation, which in them more often takes place by means of delamination or immigration. But quite apart from that, except for Haeckel's theory of the Blastaea and the Gastraea as the original ancestors of the Metazoa, based on his view that the blastula and gastrula stages in the development of Metazoa represent these adult ancestral stages, there is no reason to think that the original Metazoan ancestors were two-layered or hollow at all. Indeed, it is very questionable whether the Coelenterata themselves can properly be described as two-layered. It is freely admitted in the text-books that the gelatinous mesogloea which separates the inner and outer "layers" of the body, "may contain numerous cells, which are either branched nucleated, so-called connective-tissue cells; nerve cells and fibres, muscular fibres, or cells in which calcareous skeletal spicules are developed" (G. C. Bourne: *The Anthozoa*). But since it was tacitly assumed that everything on the outer side of the mesogloea was ectoderm and everything on the inner side endoderm, and the elements in the mesogloea have come into it from one side or the other, *ex hypothesi* there could only be two layers in the Coelenterata. It was assumed that the two layers in the Coelenterata were precisely comparable with the outer and inner germ-layers found in the development of higher Metazoa, and all the cellular elements of the body such as amoebocytes, interstitial cells, and germ-cells were necessarily forced into one or other of these layers. This has had the awkward effect of situating the germ-cells in the "endoderm" in the Anthozoa and Scyphozoa, and in the "ectoderm" in the Hydromedusae. This in itself is sufficient to show that if any significance at all is to be ascribed to the germ-layers, the layers of the body of the Coelenterata as currently defined do not correspond exactly with the germ-layers of higher Metazoa, but represent a confused and independently evolved style of architecture. If it were not for the gelatinous mesogloea which separates outer from inner elements, the Coelenterata would always have been regarded as possessing a parenchyma, like Turbellaria.

With regard to the hypothetical ancestral Blastaea, it is true that if the conversion of Protozoa into Metazoa is conceived as involving the aggregation of single protozoan individuals into a hollow sphere like *Volvox*, it is easy to equate this sphere with a blastula and to imagine gastrulation as ensuing and completing the conversion. But there are the gravest objections to the view that the Metazoa were evolved by aggregation of separate protozoan individuals. This may have happened in the Sponges and, indeed, is the most likely explanation for the lack of co-ordination, integration, and individuality found in those animals. One of the most important features in the acquisition of individuality in organisms is axiation and integration throughout the body. The only way in which this can be imagined as having occurred in the transition from Protozoa to Metazoa is by means of internal subdivision of the protozoan body, by cellularization. Nor is it difficult to imagine how this might have been brought about, since there are Protozoa such as the Ciliate Infusoria, Haplozoa and some Sporozoa which possess many nuclei, and it would only be necessary to separate these by cell-walls in order to obtain the requisite organization for the primitive Metazoan. There is no necessity for a hollow digestive cavity in Ciliates, such as *Paramecium*, where food particles are ingested and digested phagocytically; and the same is true of the most primitive Turbellaria, the Acoela, which, as their name implies, have no hollow gut-cavity. Furthermore, the Acoela are imperfectly cellularized, for beneath the outermost layer or epidermis, in the more or less solid parenchyma of the body, there are irregularly-shaped syncytial masses, some of which are concerned with digestion and others with the production of the reproductive cells.

If, then, there is no compulsion to look for two-layered, hollow, radially symmetrical ancestors to play the part of the original Metazoa, and if it be allowed that these may have been bilaterally symmetrical, parenchymatous organisms in which the protoplasm of the body had not yet become differentiated into the definitive layers of higher forms, what objection can there be to the view that the Turbellaria Acoela are the modern representatives of these ancestors, doubtless specialized in many ways since then, but still the most primitive Metazoa? This is the view which Hadži has put forward. By dethroning the Coelenterata and putting the Turbellaria in their place as the most primitive Metazoa, it solves a number of difficulties regarding the Coelenterata themselves, as has been shown. But if it is to be acceptable, Hadži's theory must also provide explanations for the conversion of Protozoa into Turbellaria, for the derivation of Coelenterata from Turbellaria, for the position and affinities of the Ctenophora, and for such general questions as the correspondence of germ-layers. These points will now be considered.

Without any ambiguity or hesitation, Hadži's theory proposes the derivation of the Turbellaria from Infusorian Ciliate Protozoa. As already mentioned, some of the latter with their numerous nuclei provide an easy starting-point for such an evolution, which would have been brought about by internal compartmentalization, or cellularization of the body. In size, a member of the Turbellaria Acoela such as *Convoluta* is easily comparable with the Infusoria, for it is only one-tenth of an inch long.

It might be thought that the Infusoria, with their complicated system of conjugation, are too specialized to permit of consideration as possible ancestors for the Metazoa. It is undeniable that many of these features are peculiar to the Infusoria, but the fact remains that the fundamental characters of the processes involved in the conjugation of Infusoria are indispensable requisites for ancestors of Metazoa.

The conversion from Protozoa to Metazoa entailed some remarkable consequences for reproduction once the body, being many-celled, could no longer function as a gamete. These consequences are further complicated by the fact that the Infusoria are hermaphrodite and machinery is provided to prevent self-fertilization. Three essential steps can be made out in the conversion. The first is the adoption of the habit of conjugation, as it is called in the Infusoria; but this is really homologous with copulation between two organisms, ensuring that each will receive germ-material from the other, and therefore bringing about amphimixis. Concurrently with the habit of copulation, there is the formation of a migratory parcel of germ-material, usually known as the migratory nucleus, which represents the male gamete. In *Paramecium*, where the two individuals become interconnected by a protoplasmic bridge, the migratory nucleus does not require the acquisition of cellular individuality in order to perform its function. In other Infusoria belonging to the Ophryoscolecidae the migratory nucleus acquires cytoplasm and a flagellum, and is fully cellularized.

The stationary or female gamete in Infusoria, however, has never become cellularized, but remains nothing but a nucleus in the body of its parent. *Paramecium* in conjugation, therefore, corresponds, not to an egg-cell receiving a sperm-nucleus, but to an egg-nucleus enclosed within the cytoplasmic body of the maternal gamont-generation which has produced it; the non-sexual gamont-generation and the sexual gamete-generation having overlapped in time and in space, and been telescoped into one.

After fertilization of the stationary nucleus by the migratory nucleus, the lack of cellularization of the female gamete is responsible for the fact that the zygote produces no new individual separate from its maternal stock; instead, by cleavage divisions the nuclear structure of the Infusorian is re-established, and, subsequently, as in all Protozoa, the maternal stock-individual undergoes fission to form a number of "daughter"-individuals, potentially immortal. If the female gamete had been able to "come out" of its maternal stock-generation, which would have required the latter's cellularization, the results of fertilization would have been the cleavage of the zygote to form a new individual, separate from the maternal stock-individual which, being nothing but soma, would ultimately have died.

Of the three steps necessary for the conversion of a protozoan into a Metazoan, therefore, the Infusoria show two. The Turbellaria show all three. They are hermaphrodite and perform copulation; their body is covered with cilia; the outer layer contains a number of rod-like structures capable of discharge, the sagittocysts, which are very like the trichocysts of Infusoria on the one hand, and, on the other, the nematocysts of Coelenterata. The small size, imperfect cellularization, parenchyma, indistinct gonads, and phagocytic digestive syncytium, have already been mentioned. On its merits, the case for the derivation of Turbellaria from Ciliate Protozoa is attractive.

Next comes the question of the derivation of the Coelenterata from the Turbellaria, and in Hadži's view this took place from a Rhabdocoelid form in which were already developed (as typically in these animals) an ectodermal pharynx, a hollow gut-cavity showing many lobes, constricted between those places where the parenchyma of the body prevented it from extending outwards towards the epidermis, and tentacles containing hollow diverticula from the gut-cavity. The problem is to consider whether an organism with such a type of structure was capable of becoming converted into an Anthozoan.

The Anthozoa have an ectodermal stomodaeum or "pharynx," a hollow gastro-vascular cavity subdivided into many "lobes" by the numerous mesenteries which constrict it, and tentacles which are hollow and contain extensions of the gastro-vascular cavity. The Anthozoa also show traces of bilateral symmetry in the stomodaeum and in the mesenteries and muscle-bands; although externally they have acquired a radial symmetry. If a Rhabdocoelid Turbellarian adopted a sessile habit of life and became fixed by its aboral end, its organization already possesses all that is necessary for the construction of an Anthozoan, and some elements such as nerve-centres, solenocytes, and parenchyma would be expected to become reduced.

Hadži points out that the Anthozoa possess a macrophagous habit which he believes to have been inherited from the Rhabdocoelid Turbellarian ancestors. The tentacles of the Anthozoa would therefore be primitive, raptorial in function, and derived from the single pair found in some Rhabdocoelids by a process of multiplication around the mouth-opening which is so very commonly found in sessile animals (Polyzoa, *Phoronis*, tubicolous Polychaeta). Only in the subsequent evolution of the Coelenterata into Scyphozoa and Hydromedusae, when the microphagous habit was reassumed, did the tentacles, serving as bearers of cilia, sense-cells, and nematocysts, often lose their hollow lining which became reduced to a solid rod of cells. It is easy to see how hollow tentacles may become solid as a result of reduction in evolution, but it is very difficult to imagine solid tentacles evolving into hollow ones. The Anthozoan tentacle must be primitive.

Even those characteristic structures the nematocysts accord with Hadži's theory in spite of the fact that it is now believed that when true nematocysts are found in Rhabdocoel and Polyclad Turbellaria, they are derived from ingested hydroids. In the Acoela sagittocysts are present, and although Rhabdocoela lack them, it may as well be imagined that the Coelenterata inherited them from prototypes such as the sagittocysts in their Turbellarian ancestors. As for the protozoan ancestors of the Turbellaria, it is well known how characteristic of Infusoria are the trichocysts, from which the sagittocysts might easily have been derived.

Finally, as Hadži points out, the view generally held hitherto that epithelio-muscular cells are restricted to Coelenterata is no longer true. Bresslau has enumerated a number of Turbellaria, Acoela (*Childia baltica*, *Palmenia tvaerminnensis*), Rhabdocoela (*Rhynchoscolex*), and Alloiocoela (*Hofstenia atroviridis*, *Prorhynchus haswelli*), in which the cells of the epidermis contain muscle-fibres and present a condition more primitive than that of the differentiated epithelio-muscular cells of Coelenterata.

The Ctenophora have long been a source of difficulty to those who tried to include them among the Coelenterata, for no criteria aptly cover both. Their most characteristic feature is their planktonic habit of life and their octoradial symmetry, which does not obscure an underlying bilateral symmetry; and they undoubtedly have more than two layers of cells. The method of cleavage of the egg in Ctenophora is totally different from that found in Coelenterata. There is really no resemblance between a Ctenophore and a medusa; and altogether it may safely be said that whichever was the group from which the Ctenophora were evolved, it certainly was not the Coelenterata. On the other hand it has long been thought that there was affinity between Ctenophora and Turbellaria; but at a time when the Coelenterata were regarded as the most primitive Metazoa, and Ctenophora were regarded as Coelenterata, it was natural that the sequence of evolutionary derivation should have been read as from the Ctenophora to the Turbellaria.

As long ago as 1923, Hadži put forward the view that Ctenophora were evolved from Polyclad Turbellaria, by neotenous retention of the structural features of the larval form of the Polyclad Turbellaria, known as Müller's larva. The resemblances between Ctenophora and Polyclad Turbellaria go deep, and it is of interest to note what was said on this subject by MacBride: "In Polyclada as in Ctenophora there are large macromeres which bud off smaller micromeres, and from these last the ectoderm is formed. In both groups there is an ectodermal stomodaeum occupying the lower pole of the embryo, and at the upper pole we find the main nervous centre. Further, in both, the primary locomotor organ consists of eight ciliated ridges of ectoderm, and Lang has shown that in Müller's larva the cilia on the ciliated processes are joined edgewise so as to form combs. [F. M.] Surface has brought out clearly a hitherto unsuspected agreement between the two groups, viz. the origin of most of the so-called mesoderm. This material is really similar in both groups, consisting of stellate cells with processes, some of which are contractile. In both groups it results principally from cells budded from the lower poles of the macromeres, after the ectodermal material has been separated off; and the small cells budded from the lower poles of the macromeres of Ctenophora, after they have been almost covered by ectoderm, may well be compared to the fourth quartette of the Polyclada."

To these may be added the facts that in both Ctenophora and Polyclada, development is of a mosaic type; there is no hollow blastula stage; gastrulation occurs by epiboly; the mouth, pharynx, and gut-cavity are formed in the same manner; aboral sense-organs, statoliths, and paired tentacles are found; and there are great similarities in the gland-cells of the epidermis.

These facts can only mean that there is a close affinity between the Ctenophora and the Polyclada, and MacBride interpreted them to mean that Müller's larva represented the pelagic, Ctenophore-like adult ancestor of the Polyclada, and that the Platyhelmia were evolved from the Ctenophora. Hadži (and the present writer) prefer to regard the Ctenophora as descended from Polyclada by neotenous retention of many of the larval features of the ancestor. Some Ctenophora such as the Platyctenea, *Ctenoplana* and *Coeloplana*, when adult show a spurious similarity with Polyclad Turbellaria, which must be ascribed to convergence because, as Komai showed, the Platyctenea pass through a so-called Cydippid stage which is similar to the spherical larval stage passed through by Cydippid Ctenophora, such as *Hormiphora*, which retain the spherical, pelagic, form in the adult. The theory of the evolution of Ctenophora from Polyclada is satisfactory.

As regards the history of the germ-layers, it is clear that for those who visualize the evolution of early Metazoa in the form of a Blastaea which became converted into a Gastraea, the germ-layers can only be imagined as having originated when the gastrula was evolved as a two-layered sac, consisting of ectoderm and endoderm. And so long as the Coelenterata were regarded as consisting of only two layers, and as representing the original primitive Metazoa, the mesoderm had to be imagined as having evolved later than the ectoderm and endoderm.

But in the Infusorian Protozoa there already exist different parts of the body which may simply be called outer material, middle material, and inner material, often specialized and differentiated into organellae of a degree of complexity which is quite surprising when it is remembered that cellularization has not yet taken place in these animals. But once cellularization has taken place, the body of the resulting Metazoan possesses ectoderm, mesoderm (which Hadži prefers to call *mesohyle*, because it does not primitively form a layer at all), and endoderm, as it were ready-made, and illustrated in the Turbellaria Acoela. Being now multicellular, the zygote has to undergo the process of ontogenetic development, which re-establishes the multicellular condition out of the single fertilized egg by means of cleavage. In the development of the Turbellaria Acoela, cleavage results in the production of ectoderm, mesohyle, and endoderm, *in situ*, without the formation of any germ-layers at all. In other words, the outer, middle, and inner parts of the body are older phylogenetically than the germ-layers. The germ-layers, as defined by embryologists, are developmental devices serving the function of producing the definitive form of the organism; and as, in different animals, they have different starting-points according to the nature of the cleavage-divisions, yolk-content, etc., they may contain different materials.

One further point which may be noticed is that since mesohyle exists in Turbellaria Acoela containing crevices in the parenchyma which are the forerunners of coelomic cavities, and since these animals do not yet possess a hollow gut-cavity, the schizocoelic method of formation of coelomic cavities must be phylogenetically older than the enterocoelic method.

None of the foregoing views could possibly have been held if biology had continued to be governed by the theory of recapitulation and the theory of the germ-layers: theories which the present writer has been led to reject on independent grounds. And having discarded them, Hadži has been able to stimulate zoologists to re-examine one of the most fundamental of their beliefs, and at least to shake it. His work has been published in Slovene and in Serbian, or in German in Slovene publications, and is known only to few. It is in the hope that it may receive the attention which it deserves that this short and imperfect summary of the theories of Jovan Hadži has been prepared for the congratulatory volume to Julian Huxley, to whom the study of evolution already owes so much.

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The Evolution of Tropical Forest

IN the study of plant evolution there stand out pre-eminently a cause and its effect. How the succession of main environments, from water to land, must have been a principal cause is the subject of Church's great contribution to botany.(3) The effect lies in the conversion of these environments into "biospheres" by the plants themselves: both aspects are summed up in Church's phrase "evolution to the limit of environmental possibility." Thus, in the first planktonic stage of unicellular organisms, their minuteness gave little means of reaction on the environment. In the second, or benthic, stage, massive growths breaking the surf, overshadowing the rocks, binding the sand, and mulching at the ebb, converted the barren coasts into the modern littoral. But, in the third stage on land, the effect has been greatest. For the first time, what died fell where it stood. The saprophyte came in; soil was made; a "rhizosphere" was created; and up and up, to the limit of environmental possibility, stretched the leafing stem. It cannot be supposed that any forest, paleozoic or recent, came into existence except by gradually increasing the height and rigidity of the somata of its dominant species. Yet so simple a conclusion has still to be applied in full rigour to the evolution of land organisms. It is, indeed, seldom stated, but the making of forest is as important to biology as the undoing of it has been to anthropology.

Forest, to-day, is of two kinds. There is the coniferous or needle-leafed forest of the north temperate region, so poor systematically and ecologically as to bear the gloom of evolutionary stagnation, and there is the flowering plant or broad-leafed forest of temperate and tropical regions, which unfolds the spectacle of life. As one proceeds from the willow thickets of sub-arctic latitudes to the Equator, the broad-leafed forest becomes taller, less seasonal, and more manifold, until in the Equatorial rain-forest, where neither temperature, light, nor rainfall is deficient, where seasons, if any, are slight, and growth may be continuous, there is the greatest complexity of the living world, be it numbered in systematic categories or in modes of life. Under the most uniform conditions that the land can offer, there is the maximum contribution of living organisms. It seems paradoxical, until one recalls that these great forests have evolved, that the building of a tree gives a canopy of leafy shoots supported on a huge framework, with trunks as ladders, branches as runways, and roots tunnelling into the ground. As the forest heightens, a multitude of micro-climates and micro-habitats appear, and, as these are colonized, still more develop. The raindrops, the drips and the trickles, the bright light, the oblique and the speckled, and the high fluctuating temperatures in the canopy combine to give a maximum variety above, passing with endless diversity and gradation to the more uniform conditions on the forest-floor. And, when a tree falls, which may never have happened at first, what a space is created and what a nidus for animals and fungi, above and below ground! It is not so much the macroclimate, but the vegetation it permits that makes the theatre of sub-aerial life.

Now enters a subtlety. As the tropical forest comes to extend, its specific uniformity breaks up. Movements of pollinators (insects, bats, birds) are limited. One tree may satisfy a hive. Self-pollination of individual trees is the tendency, especially if the flowering is intermittent. Mutants, therefore, may propagate, establishing islets of new species, as the foci of new biospheres. As these become more numerous, they will cut up any original uniformity and, by reducing the likelihood of proximity of individuals of the same kind, they will promote the tendency to self-pollination and speciation. Thus, in course of time, there will arise the elaborate patchwork of families, genera and species in the modern forest, where the commoner canopy-trees, for instance, occur at the rate of one individual of a species in five acres.(7) At lower depths in the forest this isolating effect is greater, for individuals (as saplings and adults) are more numerous, and it is as surely expressed in the sensation of being lost. Close, or continuous, tropical forest, therefore, supplies in its construction and reproduction the isolation of individuals which favours speciation: and that taxonomic species can arise by genetic variation and persist by spatial and reproductive isolation is shown by the orchids, which are mainly tropical epiphytes. Great numbers of wild species and genera have been discovered on the branches of tropical trees, yet they can be cultivated together by the same methods and artificially cross-pollinated to give specific and generic hybrids, thereby breaking down their natural evolution. In contrast are the anemophilous temperate forests, for the wind as a vector of pollen has a far greater range and species are few. The complexity of tropical forest depends not only on the response of the plant in building up in the most suitable environment an immense "conglomerate of habitats," but upon the interplay of plant and animal: its evolution is a biological problem.

To-day, the lowlands of the Amazon, the Congo and the Malaysian regions present the culmination of tropical rain-forest. The Malaysian, perhaps, is the richest, as it may be the oldest, and, due most probably to its special family of canopy-trees (Dipterocarpaceae) which commonly reach a height of 200 feet, it is certainly the grandest. So lofty is it that trees grow upon trees and root down from a hundred feet or more, as do the banyans, or "strangling figs": climbers may reach 600 feet in length(2): epiphytes grow upon epiphytes: mistletoes parasitize mistletoes: parasites may have flowers 1 to 3 feet in width (*Rafflesia*): and its complexity is such that trees of all kinds may occur at the rate of 100 genera per acre.(6) Such facts give the scale on which one must meditate. In working out the problem of the flowering tree, moreover, it must be remembered that its crown expands until the limbs may be as long as the bole, unlike the majority of "big trees" among the conifers: it is not merely height or size of trunk, but spread which renders the broad-leafed canopy-trees so influential.

With regard to the origin of this forest there is no fossil evidence, inasmuch as the origin of flowering plants is a mystery. Some place their origin in the pre-Cretaceous period of the Mesozoic: a few refer to the Paleozoic. When the record begins in the Cretaceous, flowering plants appear in modern variety, with magnolias, plane-trees, bread-fruit trees, and palms.(10) At that time, the Indo-Malaysian flora reached across Europe to Greenland, whence it has shrunk to its present state through deterioration of the climate.(9) Still less is known of the geological history of the Amazon and Congo forests, except that they must have extended in modern dress since Eocene times. Morphological evidence concerning the origin of the flower is also unsatisfactory and highly conflicting, so that the two extreme views have reached stalemate. The continental, or Germanic, school considers that primitive flowering plants resembled conifers in their small leaves and minute anemophilous "flowers," but the static nature of gymnosperm forest is overlooked. The other, and mainly English, view considers the cycad and the fossil seed-fern, with massive stem, large fern-like leaves, and stalwart reproductive structures, as nearer to the prototype that evolved flowers and simple leaves by reduction. Consideration of modern plants, however, shows that the type of flower has no immediate significance for the evolution of their life-forms. Trees with large, elaborate flowers occur side by side with trees with minute, simple flowers: similarly among climbers, cushion-plants, epiphytes, water-plants, and so on. The flower is a speciality, intercalated as a means of pollination between the initial vegetation and the final fruiting, and these are the phases, somatic and reproductive, that are primarily concerned in the evolution of the tropical forest, once the flower had given its possessors a general advantage.

Among popular and true conceptions of the tropics are brilliance, ferocity, gigantism, quickening of "tempo," lusciousness, and odoriferousness. All these are displayed by an Indo-Malaysian tree, the durian, to taste the fruit of which, according to Wallace in his *Malay Archipelago*, was worth a visit to the East.(11) Like huge horse-chestnuts, studded with spines and weighing up to twelve pounds, the fruits hang from the lofty branches until they ripen, crash down, split, and allow the creamy pulp round the seeds to be eaten. The pulp turns rancid in a few days, and in a few more the big seeds have begun to sprout, for they have no dormancy. Ripe durians vary from olive-yellow to golden orange, not unlike pineapples, and they emit a pervasive aroma, suggesting drains, gas pipes and onions to the uninitiated. In the forest wild animals congregate, from elephant, tiger and monkey to squirrel and scavenging insect, attracted by the smell, to eat what they can of this reputed aphrodisiac, and men build shelters up the trunks to secure their portion of the feast.

Durian-time offers a key to forest biology. Why do such fruits exist? Why, indeed, are there horse-chestnuts which, had they pulp round the seeds, would resemble miniature durians? The horse-chestnut splits and drops one or two large seeds, but they could germinate as well if the fruit fell without ever opening. The durian, however, is an attraction to other organisms, and it is one of the lessons of "durianology" that the ways of temperate plants must be read in the light of tropical methods.

Botanically a durian-fruit is a capsule. The pulp is the aril, such as envelops also the seed of the yew and spindle-tree. One species of *Durio*, at least, has a red fruit and red pulp embedding the black seeds. Now, this red and, often, spiny capsule, opening to display the red and black seeds attached along its split edges, is found throughout the main series of flowering plants, whether dicotyledon or monocotyledon, as a mechanism for animal dispersal. It occurs most conspicuously and characteristically among tropical woody plants or palm-like monocotyledons, though the peony-fruit is a small and somewhat modified derivative. Set against the background of green foliage, the colours are most striking, the red varying to orange or yellow, and the black of the seed to blue-black, dark purple or dark brown: the seed of an Indian *Polygala* has been likened to "the pupil and iris of the eye in a red fleshy setting."(8) But, compared with other kinds of fruit, the arillate is rare and so sporadic as to suggest that it is a relic rather than an incipient novelty. In fact, there are more examples of rudimentary, or vestigial, arils and of coloured, dehiscent fruits than there are of fully functional, arillate fruits. There are even cases of indehiscent fruits with the aril, more or less developed and coloured, inside the hard woody stone, where it could not operate as an attraction, as in some Leguminosae and Lecythidaceae. Further, in most families which have some genera with arillate fruits, there are transitions among the species of the genus to the exarillate condition and even to the usual berries, drupes, and dry fruits, which are more typical of the family. The evolution of fruits must have been polyphyletic, therefore, among the families of flowering plants, either from the arillate fruit to the exarillate with dry, detachable seed and to the nut, which functions as a seed, or vice versa. On morphological grounds the arillate fruit appears as the primitive state, because its construction is so much alike in many families as to be almost indistinguishable, whereas their other kinds of fruit bear the family marks. With one exception (Scitamineae), moreover, arillate fruits are very rare in families with the advanced feature of the inferior ovary: they occur more typically in families with the primitive apocarpous ovary. On morphological grounds, too, the dehiscent and many-seeded fruit must be antecedent to the indehiscent and few-seeded. Similarly, the seed without an abscission layer for detachment and without the faculty of dormancy must be antecedent to that with a special abscission layer and with the secondary properties of dormancy. Biologically, the transition from the arillate to the exarillate fruits seems the natural process, because the alternative presents the intermediate state, with undetached seed and incipient functionless aril, as actually detrimental, having no means of dispersal or opportunity for germination until the fruit-stalk and the seed-stalk have decayed. The view that the arillate fruit is upgrade cannot account, either, for the presence of arils inside the stones of drupes: nor can it explain the rarity of this most attractive method of seed-dispersal. Though durian-time may be spectacular, though pigeons may flock to breakfast on the arils (or *mace*) of the wild nutmeg trees, the distribution of which is largely determined by them, and the tropical American leguminous trees, *Swartzia*, may dangle the most juicy seeds out of their pods, yet trees with arillate fruits make up only 1 per cent, or less, of a tropical flora, just as the yew and one or two other exotic conifers are the only gymnosperms with arils. Finally, it is most improbable that so many different families, and even individual genera within a family, should now be evolving a new feature, the aril, polyphyletically, when the geological record shows that in all major aspects the evolution of flowering plants has been at a standstill since the Cretaceous.

The first, and overwhelming, postulate of the durian-theory, therefore, is that a red durian-fruit exemplifies the primitive fruit of flowering plants.(5) From a spectacular mechanism, greatly attractive to avian and mammalian eyes, the primitive fruit has suffered the loss of the aril, of the spines, of dehiscence, of fleshiness, and of colour: it has become smaller, woodier, and fewer-seeded. Thus the modern array of berries, drupes, dry capsules, nuts, achenes, and winged fruits have come into existence, polyphyletically in the families, if not in the large tree-genera themselves. From a process invoking animal dispersal, flowering plants have passed to the simple, and obvious, method of dropping inedible, dormant, seeds to roll, blow, and float around. The process shows how the complex may be simplified with improved efficiency, and how, as Church maintained, evolution has proceeded among plants by the successful conversion of failures in the ancestral equipment.

A capsule in botany presupposes a cluster of bean-like fruits, or follicles, developed from the apocarpous ovary of the flower. So, the durian-capsule implies, as its antecedent, a bunch of large, red, banana-like fruits, each opening to display the red and black seeds, and the whole immense structure derived from a single flower. Such fruit-clusters occur in the leguminous tree *Archidendron*, of Queensland, New Guinea and New Caledonia, which was so named because, almost alone in this great series of plants, it has the primitive radially symmetrical flower, many stamens, and many carpels. That it should have the primitive fruit is therefore not strange, because it is clearly a relic: but its fruits seem to have lost the aril, and they are borne on the trunk of the tree: that is, it is cauliflorous. Smaller, but arillate, clusters occur in the Anonaceous trees *Xylopia*, where they are also more or less cauliflorous. To be borne on the leafy stem, such a fruit-cluster, measured in feet rather than inches, implies a massive primary construction of the stem. Thus the first postulate of the durian-theory leads at once from the fruit to the vegetative form.

Massive, radially constructed twigs characterize woody, and stout herbaceous, plants which have large, compound or fern-like leaves. In many tropical families there is, in fact, a very curious kind of small tree which has a stout primary stem terminated by a rosette of fern-like leaves: it may be unbranched or have a few branches like the main stem: and its low stature is caused very largely by the lack of internodes. This is the cycad-form, and that of the tree-fern and the paleozoic seed-fern. It is exemplified more robustly by the palm, and it can be recognized as a transient, sapling phase in many lofty and more normal trees. Because of its thick primary stem, due to the massive growing point, it can be referred to as the pachycaul type. So the second postulate of the durian theory is that broad-leafed tropical forest has evolved from pachycaul plants, 10 to 20 feet high, unbranched or, at most, with a few massive branches which arose at a wide angle, ascended steeply as replicas of the main stem, and bore in the midst of the terminal rosette of fern-like leaves the bunch of arillate fruits. Such a plant no longer exists, but its traces occur in the vegetative and reproductive construction of many families of flowering plants, where they have generally been regarded as oddities, e.g. the habit of the papaya or pawpaw (*Carica*), the fruit of the peony, the mace of the nutmeg, the stout buds of the horse-chestnut, or the jointed stalk of the orange-leaf. Among modern pachycaul plants, moreover, the most interesting traces of the arillate fruit are to be found, though such survivors have evolved their own peculiarities, often parallel to those of derivative tree-forms. The second postulate, therefore, gives the prototype of flowering plants a growth-form in accordance with the theory of floral evolution which ascribes a massive flower to the primitive state, and it is strikingly at variance with that which attributes unwarranted powers of evolution to the small-leafed gymnosperms.

The pachycaul tree, as a starting-point, now enables one to read in modern tropical forest the manner in which it must have evolved, for this vegetative form still exists in the undergrowth. Reduction in size of the growing point would give thinner twigs with fewer leaves, developing one at a time, and would thus permit internodal extension and increase in height without the necessity of having to make more leaves. Reduction of the compound leaf to the simple leaf with single blade, for which there is abundant evidence among many genera of tropical trees, conforms with the reduction of the growing point, and, together, they give the leptocaul, or thin-stemmed, character of the modern twig. Reduction of the apical growing-point may also have permitted the evolution of axillary buds and branch-systems. Thus, the upward struggle for the light, so predominant in forest biology, was intensified as the modern twig and branch-systems were gradually evolved. A canopy began to be raised on trunks and branches, and the pachycaul became an undergrowth tree or was transformed into herbaceous, saprophytic and parasitic forms on the forest floor. Taller trunks with thinner branches, however, require more or better lignification to support the weight and strain: such lignification implies slower decay until more active saprophytes evolve: the rubble accumulates in the forest and makes the establishment of seedlings more difficult, as well as the passage of animals. Herein lies the value of the big seed, retained as one of the traces of "durianism" to the present day, as the factor for forest-regeneration: the large food-store enables the plumule rapidly to elongate and bring the young leaves into the open, as in the 3-foot plumule of *Dimorphandra* (Leguminosae) in Surinam. But, as the leader and branches of the tree transform into slender twigs, carrying the crown upwards and away from the water-supply, less and less is it possible to reproduce by the old method depending on a large food- and water-supply for each flower and its fruit. Either flowers and fruits become smaller to conform with the lengthened twigs, and more efficient, as in most modern trees, or they retain the ancestral massiveness and are produced on the older, matured parts with greater food-store, as the branches and trunk: thus, cauliflory is introduced, as in the durian itself, *Archidendron*, and the giant parasite *Rafflesia*. Again, the apparent simplicity of the modern twig, as that of the beech, is the outcome of a long process of reduction-simplification involved in the evolution of side-branches. Tropical families of trees show the many ways in which side-branching has evolved, all converging to the apparently simple leptocaul state.

As the fruit becomes smaller, two selective tendencies arise, towards one large seed per fruit or towards many small seeds. The first reduces the number of offspring per parent, but retains their forest-value as big seeds, whereas the second increases the number, while jeopardizing their chance of survival, for small seeds need places for germination which are at least temporarily bare, as bark, or soil or rock exposed by rain-wash, river-subsidence, and so on. Thus, as long bare trunks and branches evolved, a new xerophytic habitat was opened to epiphytes with small seeds. Then, as small seeds dried off in the fruit become resistant to further desiccation, small-seeded trees, as well as epiphytes, would become the pioneers beyond the climate of the rain-forest. Into these seasonal forests the large-seeded trees could slowly travel to establish the climax-forests of temperate and subtropical countries, just as oak and hazel follow the small-seeded willow, birch and alder in the modern north temperate succession.

In the first place branches were radially constructed, like the parent stem, and were steeply ascending. Later, as the leptocaul characters appeared, oblique and horizontal sprays of foliage evolved as the most umbrageous effects. But, as the canopy was raised, its water-supply became a problem: intermittent growth, intermittent flowering, and even deciduousness become factors in the equipment of the tropical rain-forest tree.

So it is possible to continue in increasing detail and complexity, but enough has been mentioned to prove how realistically the evolution of tropical forest can be inferred from the great wealth of living plants that it harbours. In increasing their height, flowering plants have created and solved their own problems, thereby building a new environment of extreme complexity, disposing of the old and wasteful method of reproduction by large arillate fruits and producing, in the long run, the physiological and structural equipment needed for the evolution of temperate, broad-leafed forest on the one hand, and grassland on the other. As Church stated, "Every morphological *phenomenon* which can be isolated by deduction and observation must be the *response* of the living organism to some special *factor* of biological environment, appearing as an *adaptation* of preceding organization, and requiring for its elaboration some special physiological *mechanism*. Hence in dealing with any and every structural detail of plant-soma it should be necessary to attempt to isolate the biological factors concerned, as also the mechanism of the response.(4) Mutation, aided by the manner of speciation inherent in dense animal-pollinated forest, must have been rigorously selected in this tumultuous process of trees seeding upon trees, and has resulted in the unbelievable variety of present-day tropical rain-forest. It is the very oddness of the durian on the modern scene which gives the clue, not merely for disentangling the structural peculiarities of the modern flora, but for relating them with the living forms of plants in their stations in the forest. Systematic botany shows, as one would expect, that the evolution of the canopy-tree has been largely homoplastic and polyphyletic. Thus the Cretaceous forests were modern, systematically, for the beginnings of the families of flowering plants must go back to the soft-wooded pachycaul stage, of which there is no fossil evidence.

Corroboration comes from an unexpected source. Water-lilies are flowering plants that have become aquatic. Two genera, *Victoria* and *Nymphaea*, have arils, but instead of being fleshy, they are membranous air-containers floating the water-borne seeds: in other genera the aril is lost. Now, if *Victoria regia* could be taken out of the water and lignified, or strengthened, to hold itself upright, and if its compound leaves and aril-mechanism were restored, it would be an extremely thorny, massive, unbranched plant of low stature, with spiny arillate capsules, altogether resembling the prototype postulated by the durian-theory. *Gunnera* is another example, yet further removed. But such odd plants provide "the story of the survivors" (Church), disclosing primitiveness in modern specialized dress.

In the humble beginnings of the broad-leafed tropical forest, there must have been plenty for vegetarians. There were not special feasts, as the durian now offers, but daily feasts from any flowering plant which, when the spines permitted, called only for the most elementary scrambling, climbing, jumping, flapping, or standing on the hind-legs: large brutes may have pushed the plants down. As the primitive trees heightened, a canopy was raised where every branch bore red arillate fruits at the expiry of its growth, and thus the arboreal habitat came into existence, to which many vertebrates and countless insects became specialized, never to set foot on ground again. As the forest heightened further, the food supply fell off until, as now, barely 1 per cent of the trees and climbers have arillate fruits. Though the new kinds of leaves, buds, flowers and honey (from floral and extra-floral nectaries), as well as the modified fruits and seeds themselves, supplied food, yet this great decline in rich arils must have seriously affected the animal life, leading either to extinction or to change of diet. It may be wondered, indeed, to what extent a diet of arils, rich for instance in carotenoids, may have contributed to biochemical evolution. Simple camouflage of the fruit and mechanical protection gave place to distastefulness and poisons, as visual and manipulative acuity increased, and some of these poisons came to permeate the plants. The early animal life, lead on by such attractive fruits, surely over-reached itself and promoted the increasing inedibility of the plants as a counter-measure, inasmuch as it is sure now that a tropical plant will be eaten out, if it has not some degree of unpalatability or a habit of growth able to survive being eaten back. Wild bananas, by suckering, withstand the onslaught of elephants, and their very hard seeds must prevent too thorough mastication of the fruit (as do those of palms eaten by elephants): hybridization, however, has restored the ancestral edibility of the fruit to the cultivated banana, though at the expense of fertility. The insect-fauna must have increased enormously with the complication of the forest, for it would not have been affected by the decline in fruit supply, and thus, as now, it became an important intermediary between the tree and the vertebrate. Nevertheless, one must conclude that the larger animal life of the forest progressively diminished as the canopy was raised out of reach and as the fruit supply fell off. On the forest-floor, however, a new environment was opened by the rhizomatous and tuberous herbaceous undergrowth which, in contrast, must have assisted the evolution of such as rodents, pigs and deer with their attendant carnivores.

While the forest was still of moderate stature, perhaps 50 to 100 feet high, the branches would have been in the main steeply ascending, bearing the terminal rosettes of leaves. This tree form with ascending foliage suggests climbing and gliding rather than running, jumping and brachiating, for which the later horizontal branch systems provide the spring-boards, platforms and bars. Thus the way of the flying lemur in gliding through openings and scrambling up the trunks again seems a natural transition to the agility of bats and monkeys. Their habitats and, perhaps, that of squirrels must have come at a relatively late stage when the forest was becoming really tall. Moreover, if the food supply provided by the early forests invited animal life, the later forests offered refuge as well, as shown by the nesting of birds and the voice of the gibbon, which expresses a joy from aloft inconceivable to men in tigerridden country. Perhaps, too, as the senses of the vertebrates developed in the arboreal habitat, this retreat provided the greater sleep which the primate, or anthropoid, brain needed.

Spines, evidencing the depredations of animals, may seem a topic for old-fashioned natural history, but they are not to be so lightly dismissed. The orang-utang, in Beccari's picture,(1) cannot open the durian! *Victoria regia* is one of the spiniest plants, only the roots, the upper sides of the leaves, and the insides of the flowers being without a dense armour: what the spines lacerate will be food for the piraña fish. Palms, too, are among the thorniest plants and, contrary also to the usual association of thorns with deserts, the thorniest palms occur in the swampiest forests. Now palms, more than any other flowering plants, have the appearance of the pachycaul prototype, and in their biology, as yet too little appreciated, much primitive natural history of the forest is retained. They have large, edible, terminal buds (often the only vegetative bud on the stem), and large fruit clusters, offering immense quantities of food, as well as edible young inflorescences and young leaves. A strong casing of leaf-bases protects the bud, and spines on the leaf stalks and stems render them unclimbable. The spines may be six inches long, or more, and set in deflexed combs, or in whorls pointing alternately upwards and downwards. The spiniest palms, too, retain the durian-spines on the fruit as an armour of backwardly imbricating scales. Only small and relatively innocuous animals can jump or fly on to the crowns of such palms: large animals can get the fruits only when they have fallen. The thorny, or sharp and slippery, edges of the leaf stalks may even be connected with an immunity from flying foxes, which cause serious defoliation where they hang up to rest. Yet many palms have passed on to woodiness or chemical unpalatability and become thornless: others are thornless and survive because of the absence of large animals, as on oceanic islands. Thus the coconut palm, transplanted to the continental shelf of Malaysia, is prone to devastation by honey bears. The durian theory envisages iguanodon wrestling with palms, the ants that plague the creatures lacerated by the thorns, and the sloth in its immunity from ants and its humble diet of leaves, just as the theory can revive the thorny, fossil seed ferns.

Small, dormant seeds, with their secondary features, must have been a comparatively late refinement of the flowering plant, yet they occurred already in the Cretaceous period, as shown by the presence of the plane-tree. It was the step, however, which finally liberated the herb, by permitting small fruits and seeds to be produced on slender, precocious and seasonal shoots: it emancipated, also, the pioneering plants with small dormant seeds drifting on to the bare earth. Thus, grasses, sedges, composites, orchids, gentians and heaths, which make up so much of the modern landscape that it is difficult to imagine a world without them, appear as late novelties in the progress of flowering plants. Perhaps their perfection may date from the Miocene, when the world climate altered, the Indo-Malaysian forest was in retreat, and the savannah herbivores began to appear. It need not occasion surprise, therefore, that some forest bamboos, with many primitive features of the grass family, have large fleshy fruits, like red pears, and large seeds that germinate without dormancy. But the tall bamboo with long hollow internodes is a forest speciality, as is the gibbon. Its prototype with solid stem and short internodes is seen rather in the maize and sugar-cane, showing again how agriculture, in its effort to restore the waning edibility of plants, selects the primitive features. The durian theory can contemplate the hairless arboreal mammal that lurched from the forest in its increasing austerity, to slaughter the wild herds, to harvest the wild grain, and to hack down the testimony of his origin.

While all these changes have been wrought upon the forest so as to render the results at first sight unconnected, one reflex persisted. A stimulus to the repast for birds and primates, at least, has been the colour of the fruit. On redness their eyes have feasted: with blackness they have been frightened. Redness is attractive and stimulant: with green, it is gay; but the combination with black becomes diabolical, long after the horrors and delights of the forest have been forgotten. It may seem a far cry from a tomato to a sunrise, or from a durian to a petticoat, but redness in human experience seems referable to the dim origin of durianism.

What has prevented a simple approach to forest evolution has been the academic chase after the primitive flower; practically, it is the impenetrable tangle at the edge of the forest. This "green wall," as it is popularly called, is just the dense canopy brought to the ground level where the forest has been stopped. Inside there is an architecture of trunks and branches on their foundation of roots, as a living edifice that has evolved and retained among its stories pieces in ancient styles, to appear as the bizarre, the grotesque, and the ornate. At the top, there is the main protoplasmic factory with its tangle of twigs, leaves, tendrils, spikes and grapnels, and from what is written on this living wall it should be possible to read the steps in its attainment down to the lowest stories. In the history there will be met, as if they were interpreters, such acmes of its expression as apes, bats, elephants, durians, nutmegs, orchids, butterflies and birds of paradise: but what they mean and have meant will not be understood until botany and zoology combine in the biology of the tropical forest.

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HUGH B. COTT*

Allaesthetic Selection and its Evolutionary Aspects

I. ALLAESTHETIC CHARACTERS IN RELATION TO ANIMAL RESEMBLANCES

To anyone interested in zoology, whether from the point of view of paleontology or systematics, of functional morphology or biochemistry, of embryology or ecology, one of the most obvious yet arresting phenomena is the astonishing diversity—of size and organization, function and behaviour—found among animals. Not less interesting to the student of evolution are the resemblances to one another which we see in animals of different species.

(1) The commonest and most familiar class of resemblance is that which is an expression of phylogenetic relationship—as found in varying degrees throughout the hierarchy of natural classification, from the close similarities between conspecific races and congeneric species to the basic similarity of plan found among members of a phylum. Such resemblances differ from all others in being fundamental, as opposed to the superficial similarities, independent of affinity, to be mentioned below.

(2) In a second class, the likeness is fortuitous or accidental and without any biological significance. Bashford Dean (1908) has drawn attention to a number of these meaningless coincidences—as seen in the Japanese crab *Dorippe* on whose carapace an Oriental face is portrayed; or the whale's "ear-bone" which suggests in profile the face of a Scandinavian fisherman; or the larval crane-fly *Tipula abdominalis* which in end-view is said to look like a cuttlefish.

(3) A third class is that often exhibited by unrelated animals which have adopted, and are adapted to, a similar mode of life. Convergence is found at all levels of affinity—in different families of an order, as in the

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tree-frogs *Hyla* and *Polypedates*; in different orders of a class, as in the fossorial *Talpa*, *Spalax* and *Notoryctes*; in different classes of a phylum as in a shark, ichthyosaur and cetacean; or even in different phyla, as in a humming-bird and Humming-bird Hawk Moth.

(4) In a different category are the adventitious resemblances independently acquired by unrelated animals whose *appearance* has been modified in response to a similar biological need. For example, animals of many diverse groups—including fishes, toads, leaf-insects, butterflies, moths, bugs and grasshoppers—bear a striking likeness to leaves, and so indirectly come to resemble one another. Or again, different syncryptic animals resemble sticks, or sea-weed, and so come to look alike.

(5) A fifth category embraces visual resemblances between animals which, unlike those just mentioned, so far from being adventitious, are believed to have survival value and to have been evolved for their own sake. Such are the mimetic Batesian and Müllerian associations, where the likeness between different species is itself the end achieved through evolution.

Relation to adaptation	Degree of resemblance	Class of resemblance	Biological significance	Relation to appearance
non-adaptive characters	fundamental	Phylogenetic	adventitious	indifferent characters
	superficial	Fortuitous		
adaptive characters		Convergent		
		Syncryptic		allaesthetic characters
		Mimetic	advantageous	

Various relationships seen in animal resemblances.

If we review these five classes of phenomena, it will be seen that the first two are unconnected with adaptation, while the remaining three, indirectly or directly, are expressions of adaptation. From a different point of view we may note that in the first three classes the similarity of appearance is either inherent or superimposed upon the animals by chance or similarity of habit. On the other hand, syncryptic and mimetic resemblances stand apart from the others, having this in common—that appearance has been an essential factor in their evolution. In short, they are examples of a large group of phenomena, for which Huxley (1938a) has proposed the useful and embracing term "allaesthetic characters"—"which exert their biological effect via the distance receptors of another individual, i.e. those of smell, hearing and sight." The present essay is concerned with visual aspects of the subject, but it should be remembered that parallel phenomena occur in the auditory and olfactory fields.

2. ALLAESTHETIC CHARACTERS IN RELATION TO BEHAVIOUR PATTERNS

Bearing in mind the distinction between the several classes of resemblance above-mentioned, we may note that it is sometimes difficult to determine the standing of particular examples. The history of zoology contains many instances of confusion between features due on the one hand to affinity and on the other to convergence—of a failure to interpret correctly the status of characters that are, respectively, primitive and fundamental, or analogous and superficial. Similarly, it is often difficult to assess the significance of likenesses falling within the fortuitous and mimetic groups. An excellent illustration of this difficulty is provided by the remarkable South American homopterous bug *Laternaria servillei*: the likeness which this creature undoubtedly bears to an alligator's head has been variously regarded as a meaningless freak of nature, or as a character subserving false warning in the Batesian sense (Poulton, 1924).

While the verdict on such doubtful cases must ultimately rest upon the results of observations and experiments, much indirect light is thrown upon the problem by recent studies of animal behaviour. Thus it is now clear, from the work of Lack, Lorenz, Noble, Russell, Tinbergen and others, that in certain circumstances many animals—including birds, lizards, fishes and various invertebrates—recognize objects in a way very different from a human observer. The reactions of such animals are often limited to one or a few simple sign-stimuli, whether of posture or pattern, colour or movement, and not to all the visual elements of the situation. Thus, to mention but a few examples: The male *Gasterosteus aculeatus* will react differently to a crude model-stickleback, according to its posture: in the "head-down" position the model elicits fight; in the "head-up" position, mating activity (Tinbergen, 1948). Or again, simple patches of colour, almost irrespective of form, may be sufficient to release patterns of innate behaviour—as shown by the threat display which may be elicited in the male Robin by a mere bundle of red breast-feathers (Lack, 1943); and in the male *Lacerta viridis* by a crude clay model with a blue throat (Kitzler, 1941); or by feeding-reactions of young Herring-gulls in response to the red patch on the parent's mandible or to crude models similarly coloured (Tinbergen and Perdeck, 1950); or by characters valent in sex-recognition, such as the presence or absence of the black "moustache" in the Flicker (*Colaptes auratus*) (Noble, 1936). In some cases form is the significant releaser: thus many birds show incubation responses to rounded objects other than eggs (Kirkman, 1937). In others, birds react to form combined with movement, as shown by the escape-reactions elicited by the sight of overhead dummy "birds-of-prey"—"short-neck" being the valent stimulus irrespective of the shape of wings and tail, or colour (Lorenz, 1940).

The bearing of such work upon the theories of adaptive coloration has been discussed by Carter (1946, 1948), who points out that a resemblance which includes the valent characters for a particular predator will be effective even though in other respects the resemblance is lacking; but where an animal is susceptible to attack by many species, more complex resemblances may be built up by a combination of the different valent characters thus required. "We can thus see," he writes, "how the astonishingly accurate resemblances we find in nature may have originated from very partial resemblances which, in spite of their incompleteness, would still have had some value." Such considerations help towards an explanation of the further fact, that while conspicuous patterns which serve as releasers demand, and generally exhibit, only some striking distinctiveness, those on the other hand which subserve cryptic resemblance—in order to be effective as a protection—often exhibit much accuracy in detail.

3. ALLAESTHETIC CHARACTERS IN RELATION TO VISUAL PERCEPTION

Studies of adaptive coloration and visual perception have shown that there exists a close correlation between allaesthetic characters themselves and the sensory equipment and habits of the animals towards which they are directed, and in relation to which they have evolved. Such characters therefore assume a new interest in the indirect light they throw upon questions of comparative psychology and sense perception. For example, among the colour-blind lower placentals, visible colour itself is limited to sober ranges of melanic pigments—from black through grey to white, and from dark brown through russet and tawny tones to buff. True reds, purples, and blues occur only in the Primates—which are the only mammals known to have a well-developed colour-sense (Walls, 1942). Similarly, the varied and saturated hues of many birds, lizards, fishes, and entomophilous flowers postulate a colour-sense in the vertebrates and insects concerned with these advertisements—a sense that is borne out by experimental evidence.

The particular optical properties of the structures displayed have a correlative in the particular receptors of the animals which they are destined to attract. Thus, bees are blind to red, but have a range of colour-vision extending into the ultra-violet: and it is significant that bee-pollinated flowers fall into three main colour groups—orange-yellow, blue-violet, and white. Those in the first two reflect light which acts as an efficient colour-advertisement to the bee, while flower petals in the last group generally reflect little ultra-violet light and thus also appear coloured and attractive to the bee (Hertz, 1937, 1939). Pure red is absent from bee advertisements; on the other hand, red is an efficient stimulant to diurnal birds, as to man, and it is more than a coincidence that red plays a dominant role in bird-stimuli—whether their function is attractive, in the form of bird-pollinated flowers (Werth, 1915; Pickens, 1930); or repellent, in the shape of aposematic insect-prey.

Many fossorial desert mammals (*Gerbillus*, *Jaculus*, etc.) and lizards (*Uromastix*, etc.) shelter in burrows by day, and are only exposed to predatory attack (by colour-blind nocturnal enemies) when they emerge to feed at night. Hence it has been argued that their tone-matching coloration is non-adaptive. This is a fallacy which takes no account of the highly specialized vision of nocturnal enemies. For example, the astonishing powers of vision in owls has been established by Dice (1945, 1947), whose experiments show that the Barn Owl and other species are able to detect at six feet and pounce upon dead mice under an illumination of 0·000,000,73 foot-candles: the intensity of starlight is about 0·000,08 foot-candles—a brightness far above the owls' effective threshold.

Again, in the darkness of the abyss, it will be noted that the three groups of animals—cephalopods, arthopods, and vertebrates—possessing the most complex and efficient photogenic organs, are also those in which the eye (whether of the compound or camera type) attains its highest development. Incidentally, the structure of the more complex luminous organs is superficially similar to that of an eye—the pigmented reflector, photogenic transmitter and lens in the one corresponding to the pigment layer, photochemical receptor and lens in the other: indeed, photogenic organs of animals studied in the laboratory have in the past sometimes been mistaken for eyes. As Harvey (1940) remarks, these organs are eyes in reverse: "chemical production of light is the converse of the chemical detection of light. The lantern . . . is an organ of chemiphotic change; the eye of photochemical change."

4. ALLAESTHETIC CHARACTERS IN RELATION TO CONDITIONS OF LIFE

It is also evident that visual stimuli are correlated with the conditions of life under which they take effect. Characters adapted to arrest attention—subserving distraction display, or distance recognition, threat or warning—must be immediately conspicuous or specifically distinctive (Lorenz, 1935): in such rôles, crude colours and simple patterns are found. On the other hand, colours which are employed solely or mainly in epigamic display and used at close range, like the plumes of birds-of-paradise or the ocelli of various game-birds, tend to be detailed, delicate and beautiful rather than merely conspicuous (Huxley, 1938c). Similarly in the field of concealment, the extraordinary degree of detail and perfection attained by many insects and other animals in their resemblance to bark, lichen, leaves, twigs or other objects, is adapted to near-vision in their potential enemies—and its evolution almost presupposes in birds those exceptional powers of visual acuity—perhaps two or three times that of man (Pumphrey, 1948)—which on other grounds we know them to possess.

Again, sign-stimuli which would be effective in one environment may be ineffective in another. In dimly-lit surroundings (where rod-vision comes into play), white is the most revealing colour, and finds its place as a crepuscular advertisement. For example, the mouths of various passerine nestlings reared in holes are marked with white or pale tints, rather than the saturated colours found in open situations: the fleshy flange bordering the gape of the young Jackdaw is white; so is that of the Splendid Glossy Starling (*Lamprocolius splendidus*) (Swynnerton, 1916). Pycraft (1909) has suggested an advertising function for white coloration in the eggs of hole-nesting birds, the conspicuousness preventing inadvertent damage to the clutch by the returning parent. White is again seen as an aposematic advertisement in the nocturnal skunks. Such characters have their parallel in the war-time use of white to mark the rear of vehicles or the edge of railway-platforms during black-out conditions. On the other hand, where total darkness prevails, no coloration can take effect, and we may note that animals of caves and the abyss, and those that are wholly fossorial, or internal parasites, are self-coloured or unpigmented, and totally lack such attributes as countershading or pattern.

The over-riding importance of habit in enhancing visual effects is seen in every aspect of visual adaptation. For example, specialized cryptic coloration is typically an attribute of creatures which—like most geometrid larvae—rest motionless by day in harmonious surroundings; while aposematic species on the contrary are typically diurnal and (like flowers) exhibit themselves to the best advantage, frequently advertising their presence by sounds and odours as well as by displays of colour.

Among cryptic animals the widespread correlation between colour and attitude is well illustrated by the habit of orientation in bark-like moths which adopt postures that bring their disruptive wing-design in relation to the background configuration (Cott, 1940); or by cases of inverted posture of sphingid larvae where countershading is also inverted. Süffert (1932) has demonstrated that the larva of *Colias edusa* reacts to light direction, and will move from the upper to the lower surface of a stem when illuminated from beneath.

Many birds and other animals adopt, like the nightjars and bitterns, specialized and "unusual" cryptic attitudes in response to enemies. Thus, fledglings of the Black-backed Pied Shrike (*Hemipus picatus leggei*) which are reared in a nest concealed with lichens and bark-flakes on a horizontal branch, face one another in the nest with their beaks pointing upwards and nearly meeting in the centre, and thus sit motionless with half-closed eyes—their coloration and attitude causing the nest with its contents to resemble a snag produced by the falling off of a branch (Phillips, 1940).

Of special interest are the habits of animals which enhance either concealment or conspicuousness by the use of extraneous objects. Many invertebrates habitually masquerade in garments borrowed from their surroundings. In these cases the cryptic appearance depends absolutely upon highly specialized behaviour, such creatures instinctively covering themselves with a clothing of leaf-fragments, sticks, or weed—as various beetles, caterpillars and dressing-crabs, which often carry on the body hooked bristles or spines that do duty as clothes-pegs. Shelford (1902) has described a geometrid larva from Borneo which adorns itself with flower-buds (which also form its food): these were always renewed as they withered. If the disguise is removed from a spider-crab's carapace, the animal will at once begin to clothe itself again; and if the crab is removed into a new environment it will assume a new disguise. We may also note that while the bottom-living spider-crabs decorate themselves throughout life, beginning to use foreign material directly they emerge from the megalopal cuticle, swimming-crabs do not dress at any stage (Lebour, 1928).

Conversely, some animals—instead of assuming a dress which suits their surroundings—alter their surroundings to suit their own coloration. Thus, the silvery young of the Malayan spider *Cyclosa insulana* rests on a silvery silk platform; but as the animal grows older and becomes light brown in colour, it changes its habits, coating the platform with brown debris (Bristowe, 1941).

In an advertising context, we must here mention the remarkable animal associations in which one partner benefits through adventitious aposematism, so well illustrated by associations between certain tropical birds and wasps; these have their parallel in the sea, where stinging anemones, rather than stinging aculeates, play the role of protector to the hermit-crabs which solicit their company. Among animals themselves conspicuous, or such as display conspicuously, specialized behaviour is to be found in group after group, and in relation to the several functions subserving advertisement—such as threat, warning, epigamic and distraction display, mimicry and allurement (see Armstrong, 1947; Cott, 1940; Huxley, 1938; and others).

5. ALLAESTHETIC CHARACTERS IN RELATION TO COLOUR CONFLICT

Allaesthetic characters fall into two main functional groups, cryptic and phaneric. Those in the first category, which tend towards effacement, operate exclusively in the inter-specific struggle for existence, in the relations between predator and prey (protective or *procryptic* and aggressive or *anticryptic* characters). Those in the second category, which tend towards advertisement, subserve on the other hand many diverse functions, both inter-specific and intra-specific—in the relations between predator and prey (warning or *proaposematic*, adventitious warning or *allosematic*, Müllerian mimicry or *synaposematic*, Batesian mimicry or *pseudaposematic*, and distraction display or *parasematic*); in those between rival males (recognition and stimulation of the mate or *gamosematic*, and threat or *antaposematic*); in those between parent and offspring (feeding releasers or *endepisematic*); and in those between members of the same species (recognition and social or *synepisematic* characters). Thus both concealment and conspicuousness may carry biological advantages. Yet, for obvious reasons, these two types of coloration are antagonistic, if not mutually exclusive. This conflict between the rival claims of cryptic and phaneric coloration is met in various ways, here illustrated mainly by examples from birds.

Firstly, the conspicuous phase may be transitory. In many animals where the coloration is predominantly cryptic in the resting attitude, hidden advertising characters are exposed either in movement and especially in flight, or in specific display attitudes. Such are the group-recognition marks on secondary wing-feathers, rump and rectrices of many plovers and waders; the warning or distraction displays of owls, nightjars, ducks and many other birds; the buccal feeding-releasers of passerine nestlings; and the flash colours of such forms as *Draco*, *Phyllomedusa* and many cryptic grasshoppers—such a dual-purpose dress being well illustrated among birds by the deserticolous Bifasciated Lark (*Alaemon alaudipes*) which is isabelline at rest but predominantly black and white on the wing. Again, the newly-hatched young of *Vanellus vanellus*, *Pluvialis aegyptius* and other plovers carry a conspicuous badge of white down on the nape: when an intruder enters the breeding-ground, the highly cryptic offspring scatter and crouch motionless, with the nape-patch hidden; but when the danger has passed, the chicks stand up or run, with the head deflected so as to expose the nape, which doubtless acts as a recognition mark enabling the parent to recognize or reassemble her brood. Other animals, by a change of posture, can instantly transform their appearance from cryptic to aposematic: for example, the Brazilian sphyngid larva *Leucorhampha ornatus*, normally stick-like and inconspicuous, translates itself, under provocation, into the likeness of a "snake" (Moss, 1920).

Alternatively, the problem of colour conflict may be met by the exhibition of two rival sets of coloration in different groups of individuals within the species, rather than on different parts of the body in the same individual. In such cases the advertising dress is generally worn by the less vulnerable or less valuable members of the species, i.e. males or adults; and the cryptic dress by the more valuable or defenceless members, i.e. females or young. Among sexually dimorphic game-birds, ducks and others which nest in the open, it is typically the male that has utilized the biological advantages of conspicuousness, whether for purposes of display or distraction; while the female, upon whom devolves the duty of incubation, has been forced to take the evolutionary road leading to concealment. Parallel conditions obtain in the parent-child relationship: for instance, the young of many ground-nesting species such as Oystercatcher, Avocet, and of gulls and terns, in which adults of both sexes are conspicuous, are themselves highly cryptic.

Such temporary or inter-individual segregation of effacing and revealing functions is essentially related to the selective pressure imposed upon species by predators; and we may here note the interesting point made by Mottram (1915)—that marked sexual dimorphism is only found among birds specially liable to attack of enemies; and that among relatively non-vulnerable species, such as large birds possessed of fighting strength, or formidable powers of offence, and colonial species with corporate defence in the flock, secondary sexual dimorphism rarely occurs. Here the opposing claims no longer operate, and the way lies open for the untrammelled use of advertisement by both sexes—as seen in the coloration of albatrosses, penguins, gannets, frigate birds, swans, cockatoos, ravens and many others. On the other hand, with small or otherwise defenceless species, the conflict between cryptic and sematic needs is acute. Such birds may take one or other of two evolutionary roads; many, like larks, pipits, partridges, quails, coursers, stone-curlews, and nightjars, forgo the advantages of conspicuousness, both sexes being typically cryptic, as is generally true of ground-nesting species in which incubation is shared by both parents; sematic characters are then often auditory. Another line of adaptation has led in the opposite direction, and it would appear that where advertisement has been developed in otherwise defenceless species, such as the black-and-white desert chats *Oenanthe leucopyga* and *O. lugens*, it is often associated with distastefulness of the flesh (Cott, 1946).

In this respect, birds fall into line with many other groups of animals, for which a broad correlation has been established between cryptic coloration and relative palatability on the one hand, and between conspicuousness and deterrent attributes on the other. Such a relationship, supported by a great body of experimental and observational evidence (Marshall and Poulton, 1902; Swynnerton, 1919; Hale Carpenter, 1921; Poulton, 1929, 1932; Morton Jones, 1932, 1934, 1937; Cott, 1932, 1934; Kluijver, 1933; Carrick, 1936; and others) is found among many groups of animals, including tectibranch molluscs (Garstang, 1889–90), Ephemeridae (Mottram, 1918), spiders (Bristowe, 1941) and Amphibia (Cott, 1940). Recent work has extended the application of this principle to the eggs of birds. Observations by members of an egg-panel (Low Temperature Research Station, Cambridge) and experiments carried out with the hedgehog, rat, ferret and cat, show that egg-species differ widely in acceptability, that there is an inverse relation between relative palatability and vulnerability of the clutch, and that the coloration of the shell is related to the palatability of its contents—cryptic eggs tending to belong to the higher, and distinctively-marked eggs to the lower edibility grades (Cott, 1949, 1951b, 1952, 1953 and unpublished results).

6. ALLAESTHETIC CHARACTERS IN RELATION TO OPTICAL PRINCIPLES

Concealment is achieved by the very devices (including general resemblance, obliterative shading, disruptive and coincident patterns, correlated with structural and behavioural adaptations) which, for optical reasons, best serve to obliterate the visual clues upon which detection depends, namely—differences of colour and tone, effects of light and shade, surface-continuity and defined contour, cast shadows, and movement. Conversely, the opposite devices enhancing these visual clues are those employed where conspicuousness is biologically advantageous.

The general colour resemblance of the object to its background is a first step towards effacement, and is achieved by a wide range of mechanisms and organisms. A feature of such visual effects is that they may be produced by the most diverse means. For example, cryptic green coloration may be variously due to chlorophyll in the alimentary canal showing through the transparent body-wall, as in the larva of *Phlogophora meticulosa* (Poulton, 1934); to modified chlorophyll-pigments derived by caterpillars from their food (Poulton, 1893); to synthesized green pigments unrelated to chlorophyll, as in stick-insects, locusts and some caterpillars (Faure, 1932; Giersberg, 1928; Meyer, 1930); to structural effects, as in the green plumage of birds other than plantain-eaters (Musophagidae); to the combined effects of non-green pigments and structure, as in many tree-frogs (Noble, 1931); or to a mosaic of black and yellow scales, which in the wings of the Orange-tip Butterfly (*Euchloë cardamines*) thus exhibit an arrangement of pigment analogous to that used by the Impressionist School of painters (Wigglesworth, 1928).

In many cases colour resemblance is the result of elaborate physiological mechanisms or of specialized habits—as seen in colour changes associated with the life-history or with the seasons; in morphological and physiological colour change; in the use of adventitious material as a dress (see above); in differentially coloured races adapted to particular background-colours (including the phenomenon of industrial melanism); and in specialized habitat selection. Very striking are the clearly-defined habitat preferences shown by various birds like the desert larks *Ammomanes*, *Mirafra* and *Spizocorys* for soils of different colours: not only do the various species and races resemble the colour of their habitat—whether black lava or red earth or white sand—but also the birds are extremely reluctant to leave their own terrain and cannot be driven on to adjoining ground of a different colour (Meinertzhagen, 1940; Niethammer, 1940).

Many insects well illustrate the same principle. Thus Popham (1941) has shown that habitat selection in relation to colour occurs in corixid bugs. Stick-like geometrid larvae habitually take up positions where their special resemblance is enhanced by place and posture; while, as I am informed by Professor G. C. Varley, the Buff-tip Moth (*Phalera bucephala*) habitually rests on the ground amongst fallen sticks—in the very surroundings where its broken-stick-like form would be least likely to attract attention.

Sometimes a particular optical principle is variously applied in different animals and then may produce opposite visual results. For example, the effect of countershading, which is the basic principle of coloration for innumerable species of very diverse groups, is to obliterate relief and so optically to flatten solidity of form. But graded tones may also be used with contrary effect, as for example on the underside of a butterfly's wing, thereby making the flat surface appear to be curved or bent in different planes—an effect strictly parallel to that used in pictorial art. Moreover, the same animal may utilize graded effects of colour in opposite ways: this is well seen in the male Three-spined Stickleback, which in the off-season is countershaded according to Thayer's well-known principle, while in the breeding-season it becomes pale silvery-blue above and deep red below—thus achieving a total reversal of the normal tonal arrangement and exhibiting itself in exaggerated relief.

Or again, among disruptive patterns, which serve to prevent or to delay the first recognition of an object by sight, the commonest optical-psychological effect is to break up what is really a continuous surface into what appears to be a number of discontinuous surfaces. But in coincident patterns (Cott, 1940) disruption produces precisely the opposite results, in that the pattern serves to unite, visually, a number of adjacent but discontinuous surfaces—in various animals spanning the spaces between folded leg-segments, or between leg and back, or between tegmen and femur; bridging the gulf between upper and lower jaws, or crossing the slit of the closed orbit from lid to lid, or sweeping across the under surfaces of two, or the outspread upper surfaces of all four wings. In their distribution, such patterns exhibit a complete disregard for the different histological and anatomical elements upon which they are superimposed, being essentially of a type appealing to appearance only.

A special application of coincident patterns is seen in the concealment of the eye in many fishes, frogs, lizards, snakes and birds. Unmodified, the eye of a vertebrate, with its black pupil surrounded by a circular coloured iris, is a veritable target and the essence of conspicuousness. Frequently such eyes are obliterated by the use of coincident patterns incorporating black elements nicely adjusted to the position and size of the pupil, and sweeping unbroken across iris and conjunctiva to continue outwards on the surrounding scales, skin or feathers. Since few objects possess greater inherent conspicuousness than the pattern of an eye, it is of considerable interest to find that while true eyes may be so effectively concealed, the visual eye-pattern has itself been exploited as an advertisement—taking as it does a prominent place in display characters, which subserve many diverse functions such as warning or threat, distraction or epigamic display, and evolving independently in group after group of animals—including mantids, butterflies, moths, cephalopods, fishes, frogs, turtles, lizards and birds. Moreover, it often happens that a single individual will utilize both mechanisms, having—as in the fish *Chaetodon capistratus*—the eye effectively obliterated, and its place taken by a large dummy "eye" at the rear of the body.

Such contrary effects are again seen in relation to cast shadows. In the patchwork configuration which the observer sees in nature, shadows play an important part—indeed, the shadow of a cryptic animal may well be far more conspicuous than the body which casts it. Hence it is not surprising to find in the animal kingdom various modifications of coloration, habit and structure, whose function is directed on the one hand towards shadow elimination, and on the other towards the presentation of false-shadows which simulate real ones but are due only to pigmentation. When at rest, certain butterflies orientate the body in relation to the sun, and thus reduce their shadow's size (Longstaff, 1906;

Swynnerton, 1926): others like the Grayling (*Satyrus semele*) tilt the wings over in a more or less pronounced list, so that their cryptic under-surface screens the shadow which they cast. Dorsoventrally flattened animals are in any case adapted by their form in this respect. Nevertheless many such creatures attain yet more effective concealment by crouching low—either habitually when at rest, as in the case of flat-fishes, skates and various bark-dwelling bugs, moths and geckos; or instinctively when in danger, as is the case with the young of Stone-Curlew, Ringed Plover, Oyster-Catcher, and of various tropical crabs like *Ocypoda*. But we must note that many of these animals incorporate in their cryptic dress patches of pigment which themselves simulate the natural shadowed-interspaces of their habitat.

More remarkable than the above instances of cryptic posture are those animals which have evolved special flaps or frills that serve effectively to fill in the space between the lower edge of the body and its substratum, and thus to mask any tell-tale furrow. Such structural modifications are found in many stick-like caterpillars, such as those of the Early Thorn (*Selenia bilunaria*), Brimstone (*Opisthograptis luteolata*) and Peppered Moth (*Pachys betularia*) (Cott, 1951a), which carry a fringe of fleshy tubercles on each side between the posterior clasping legs: this frill, as was pointed out by Poulton (1890), neutralizes the shade between the insect and its food-plant so that the caterpillar—itself wonderfully twig-like—appears to grow out of the branch upon which it rests. In other species such as the Red Underwing (*Catocala nupta*), which lie with their whole length applied to the twig, the frill extends the whole length of the body. Thus the structures are in each case distributed where, as a defence against hostile vision, they are needed.

Sometimes special behaviour ensures the best disposition of the camouflage net. For example, the Angler-fish *Lophius piscatorius* carries a fringing frill, composed of tags of skin, round the jaws and body. Not only is this curtain cryptic in function, but the fish arranges it in such a way that it becomes draped after the fashion of the garnished nets used in war-time to camouflage vehicles. Wilson (1937) has described how the Angler first shovels a hollow in the sea bed with its pectoral and pelvic fins, then settles down with the head raised: as the head is then smartly lowered, the outflow of water spreads the net, which thus effectively joins the upper surface of the fish to the sea bed which it resembles. The bark gecko *Uroplates* is an equally striking example: here lateral flanges unite the body and tail to the tree trunk—and Webb (1947) relates how the only specimen found by him in Madagascar was obtained when, in putting his hand for support on a tree, he placed it right on top of a *Uroplates*.

Conversely, structural modifications may produce real shadows where these assist in disguise, as in the remarkable forest-dwelling leaf-like *Bufo typhonius* of Brazil and *B. superciliaris* of Africa. The first-named toad is so depressed as to appear extremely thin, but the effect is enhanced by a lateral flange or fold extending backwards from the eye, along the flank and down the outer side of the thigh: this causes the ventral surface to be thrown into deep shadow, the animal's side simulating a leaf-edge, while a few jet-black spots on the back give the exact appearance of holes in a leaf (Cott, 1926). In *B. superciliaris* the upper parts are again flat and pale-tinted, while below the superciliary-ridge and flank-fold the colour abruptly changes to a deep chestnut, there producing the optical illusion of a clear-cut shadow beneath the underside of a fallen leaf.

7. ALLAESTHETIC CHARACTERS IN RELATION TO ANATOMY AND AFFINITY

A number of significant facts emerge when we consider the relation of visual adaptation to anatomy and to affinity. For instance, disruptive designs and, notably, coincident patterns, as already mentioned, are of a kind that disregards underlying details of structure—which thus become visually subordinate to the appearance superimposed upon them. On the other hand, where a particular organ or part of the body is itself modified and used as an allaesthetic unit, as in many organs associated with display, we find the nicest agreement between the disposition of the conspicuous colours and the shape of the structure bearing them. In short, where structure hinders the allaesthetic effect, its details are disregarded or misrepresented; where it enhances the effect, its aid is enlisted, and the different structures are invoked and used rather than contradicted and over-ridden—in either case, anatomy becomes the servant of appearance.

The superficial nature of visual characters is well illustrated by pseudaposematic resemblances. Thus, among ant-mimics the appearance of an extra "waist" may be produced (as in different species of spiders) by a real (morphological) constriction either on the cephalothorax or abdomen; or (as in various stout-bodied ant-mimicking insects) by a simulated (visual) constriction depicted as a pattern on the body or folded wings. Again, as Poulton (1898) pointed out, in the South American association of butterflies and moths mimicking ithomine models with transparent wings, transparency has been achieved in several ways: the wing scales may be reduced in shape, size, or number; they may stand up on edge, or they may themselves be transparent; while in the clear-wing moths which mimic Hymenoptera, the scales are loosely attached and are shed soon after emergence of the imago.

In their relations to phylogenetic affinity, allaesthetic characters have all the attributes of adaptation—as expressed for example by the complementary phenomena of convergence and radiation. A striking instance of cryptic convergence is provided by various animals of sandy habitats. Many such creatures—including desert vipers, geckos, lizards, bustards, sandgrouse, coursers, larks, many birds' eggs, jerboas and other mammals, scorpions, spiders, racing-crabs, flatfishes and rays—though differing widely in systematic position and physiology and though they may live in arid conditions of a desert or in water over sandy shores, show similar adaptation to the one visual feature common to all their habitats, namely a sandy coloration: and we may note that this colour is itself displayed on such diverse structures as chitin, scales, feathers, hair and shell. Even were it not for other evidence, it would be difficult to account for such facts except on the view that appearance in these organisms is related to the ultimate need for concealment. At other levels, we see physiological convergence in the independent evolution of mechanisms for colour change in animals of three phyla and many orders; and behavioural convergence in the responses of animals to visual releasers, or in the analogous displays of unrelated species.

Conversely, allaesthetic radiation is seen in the divergent structures, patterns and behaviour evolved among related animals having different habitats or conditions of life. In the matter of appearance, closely related species often diverge widely from one another—until, as in the extreme cases of mimicry and special resemblance, members of one group appear superficially to have affinities with members of an alien group. Mimetic resemblances are essentially independent of affinity (as they are of anatomy), occurring between species belonging to different families or even phyla (as in snake-like sphingid larvae), while special cryptic resemblance often involves similarities between members of the plant and animal kingdoms.

Allaesthetic radiation occurs in group after group of animals, and is well illustrated by the larvae of Sphingidae (Moss, 1920), spiders (Bristowe, 1941), and Asilid flies (Carpenter and Ford, 1933). Thus, various mimetic Asilidae bear a marked resemblance to xylocopid bees—being broad-bodied and hairy, with pigmented wings: while their non-mimetic relatives are slender-bodied and naked, with narrow transparent wings. Or again, the eggs of non-parasitic cuckoos are typically white: but eggs of different parasitic species frequently bear the closest resemblance to those of the foster-species; while the eggs of certain species of cuckoos are themselves markedly dimorphic or polymorphic in relation to clutches of the different birds upon which they are foisted (Stuart Baker, 1942).

8. ALLAESTHETIC CHARACTERS IN RELATION TO SURVIVAL VALUE

The assumption that the physiological, structural and behavioural devices which make for concealment or hinder recognition are in fact protective in function, has often been challenged. For example, various other explanations have been offered to account for morphological and physiological colour change—such as an appeal to advantages from the absorption or reflection of solar radiation by the skin (Fuchs, 1914). "These perversions of scientific thinking," Sumner (1945) writes, "spring from the insistence by a certain type of mind upon finding an immediate physiological explanation for every organic phenomenon."

Much of the criticism directed against theories of adaptive coloration reveals a failure to distinguish between "proximate" factors affecting physiological control and "ultimate" factors affecting survival value. As Lack (1947) points out in another context, "Obviously the type of physiological control has been evolved in relation to survival value, but the external factors affecting the former are not necessarily those determining the latter." This point is well illustrated with reference to the breeding seasons of birds (Lack, *ibid.*, Thomson, 1950), where the determining factors are of two kinds: those, such as length of daylight, rainfall and humidity, which provide the physiological timing mechanism; and those, such as state of vegetation, nest-sites and food-supply, which give ultimate survival value to seasonal reproduction.

Other critics, including Verne (1926), Uvarov (1932), McAtee (1932), and Shull (1936) whose approach is "deterministic," tend to reject an adaptive interpretation of coloration in animals as "teleological" or "anthropomorphic," though just why it is unscientific to hold that concealing coloration does protect, is not clear. However, extensive experiments carried out in recent years—notably those of Sumner, Isely and Popham—provide the most convincing proof of the survival value of concealment.

Over fifty years ago Poulton and Sanders (1898) demonstrated that pupae of *Vanessa urticae* were in far greater danger from birds, when suspended from a surface against which they stood out conspicuously, than when they were in situations affording concealment. Similar results were obtained by di Cesnola (1904) who in experiments with *Mantis religiosa*, exposed the brown form (usually found upon sunburnt grass) and the green form (usually found on green grass) against backgrounds on which they were variously concealed and revealed: casualties due to bird predation were confined entirely to individuals exposed in situations from which they differed in colour. In 1921, Gerould subjected the normal green and mutant blue-green larvae of *Colias philodice* in the open to the attack of birds: after ten days the survivors were found to belong almost exclusively to the normal grass-green form, birds having eliminated all but two of the blue-green individuals. Young (1916), again, proved the selective value of cryptic coloration in experiments in which crows, buzzards and other birds were offered a choice of prey exhibited against backgrounds giving varying degrees of contrast. In an extensive series of tests, Isely (1938) subjected to bird-predation different species of white, black, red-brown and green grasshoppers in various combinations against white, black, brown and green backgrounds: "protected" as compared with "non-protected" individuals were eaten in the following proportions—by bantams, 80 to 157; by wild birds, 39 to 96; by turkeys, 27 to 73. Very significant are the results of Sumner's (1934b, 1935a, b) extensive experiments in which more than 3,500 "black" and "white" individuals of the fish *Gambusia* were exposed to attack by a penguin, night-heron and sun-fish: the number of casualties among fish which contrasted more strongly was nearly twice that of individuals which contrasted less strongly with the background. Broadly similar are the results obtained by Dice (1947) in his work with owls and deer-mice; and by Moss (1933) using pupae of *Pieris brassicae* as bird-prey: both of these workers again demonstrated differential elimination in favour of the situation which afforded concealment. Intensive selection against "non-protected" bugs was again conclusively demonstrated by Popham (1941, 1943, 1947) in his exhaustive work with *Corixa* in relation to such predators as dragon-fly larvae, *Dytiscus*, Rudd and Minnow: thus, in one series of his tests, casualties among the less conspicuous as compared with the more-conspicuous prey were in the proportion of 49 to 151 individuals.

Little attention has yet been paid to the complementary aspect of the concealment theory—the advantage to predators. The simple yet ingenious experiment conducted by Bristowe (1941) to test the value of concealment in the aggressive rôle is therefore of special interest. Bristowe placed an equal number of black and yellow dummies of the normally yellow spider *Misumena* on the flower-heads of dandelion—one dummy to a flower, and the two kinds arranged alternately. During a half-hour period insect visits (by honey-bees, *Halictus*, syrphid and muscid flies) were distributed as follows: 56 to flowers with an inconspicuous (yellow) dummy; and 7 to flowers with a black (conspicuous) dummy.

Most of the above-mentioned examples relate to selection against very large differences in colour and background, but it should be borne in mind that smaller differences giving far lower rates of selective advantage would still be effective (Fisher, 1930; Wright, 1931).

Lack of space forbids more than passing reference to other important classes of biologically advantageous coloration such as those which—on the phaneric side—subserve various functions in the intra-specific relations of animals, whether between rival males or the opposite sexes or between parent and offspring. Here again, though the evidence is of a different nature, recent observations and experiments leave no doubt as to the survival value of allaesthetic characters—in their various manifestations of threat, sex-recognition, epigamic display, mutual rituals, social facilitation, nest-relief ceremonies and so on. Armstrong's comprehensive work (1947) provides a mine of information in this field; functional aspects of display, both in relation to threat and warning, and to the opposite sexes, have been reviewed by Huxley (1938 a, b, c); and the physiological aspects summarized by Marshall (1936). Thus, it is now known that in birds visual characters serve (at different psycho-physiological levels) to stimulate ovulation (Matthews, 1939); to synchronize the reproductive cycle of male and female—sometimes through the cumulative effect of display of colonial species (Darling, 1938); to excite sexual emotion and the readiness to mate, and to maintain the emotional bond between the sexes after mating (Huxley, 1914, 1923)—and thus in various ways to promote effective reproduction.

9. ALLAESTHETIC CHARACTERS IN RELATION TO APPLIED USES OF COLOUR BY MAN

Since visual sign-stimuli are essentially related to a seeing public, it is not surprising to find many analogies between natural adaptations and applied inventions—in this as in other fields. Innumerable devices used in everyday life, by primitive and civilized man, in sport and war, for courtship or commerce, are merely rediscovered arrangements and applications of allaesthetic characters that have reached a high, and indeed often a far higher, degree of perfection in the animal world. The biological principles of concealment, disguise and habitat selection find a direct application in war-camouflage (Cott, 1938); warning displays, recognition characters and mimicry find various expressions in pictorial art, warning signs, and advertising. An excellent example of such parallelism is seen in the use of lights. Considered as an advertisement designed to attract attention and facilitate recognition, an intermittent flash is more arresting and distinctive than a steady glow. This principle is of course applied in the flashing navigation lights of harbours and airports. Now as Harvey (1940) has pointed out, the ability to control light is a fundamental characteristic of animals. The various mechanisms by means of which the intermittent flash is produced in photogenic organs form a fascinating study. In some fishes such as *Echiostoma* and *Argyropelecus*, the flashing is due to the appearance and disappearance of light in the organ itself which is under nervous or humoral control (as in the switching on and off of an electric light). In the ostracod *Cypridina hilgendorfi*, granules of luciferin and luciferase are extruded to the exterior and light up outside the body (as in the burning of a firework). In yet other cases, steady luminescence caused by symbiotic bacteria is made to appear intermittent, by secondary controlling mechanisms. In *Coelorhynchus* and *Hymenocephalus* the brightness is increased or decreased by the movement of pigment in a superimposed screen of chromatophores (as in the use of filters or diaphragms in optical equipment). Again, *Photoblepharon* and *Anomalops* both carry permanently luminous bacteria in a cheek-organ: but in the former, the organ can be occluded by a shutter of black-pigmented tissue which closes over it like an eyelid (as in the dark-shutter of a bulls'-eye lantern); and in the latter, the organ itself can be rotated downwards into a pocket (as in the dipping of a car's head-lights or the revolving beam of a light-house).

We have given grounds in the foregoing pages for the belief that the biological needs of security, subsistence and reproduction have exerted, through the operation of natural selection, striking modifications in the appearance of animals—modifications which involve form, coloration and behaviour. When we review the range of these widespread and highly specialized appearances and activities, it becomes increasingly evident that such characters must ultimately be interpreted in terms of the perception of other animals—that the significance of the phenomena lies in the visual perceptions which they produce in the observer. In short, allaesthetic characters have evolved in relation to, and are directed towards, a seeing public, being of a kind inconceivable or impossible of achievement in a dark world where the faculty of vision had never emerged, and, indeed, in animal nature before the evolution of an image-forming eye.

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JAMES FISHER

Evolution and Bird Sociality

THAT birds are a class of fundamentally social animals is an idea that has only slowly emerged from the sea of ornithology. Lashed by the winds of the territory theory, the tides of the aggressive theory of bird behaviour have run long and deep, breached some walls and left some floods behind. The inundation has, of course, deeply enriched and fertilized our knowledge and understanding of birds. To two pioneer workers must go the credit for the wonderful awakening of human interest in bird behaviour, and for the eventual and unequivocal surrender by academic biology to the notion that birds are the most observable of all wild animals, and that their study is not only respectable but desirable.

In establishing upon such a strong foundation of research and logical argument the ideas that much bird display is aggressive, much bird coloration intimidative, and that a defended territory is the property of most bird pairs, Huxley and Howard led the way to investigations which are now professionally occupying some scores of trained zoologists at the universities of many countries; as well as an uncountable number of amateurs whose published work is often of academic quality. Excellent recent summaries of the state of our knowledge of bird display and behaviour have been published, of which perhaps the most important is that of Armstrong (1947). Yet it would be hard to guess from this scholarly work, or from several other similar contemporary summaries, that birds are social animals.

It is true that the masterly work done in recent years in Europe by Lorenz (1935, 1938) and Tinbergen (1939) has been largely on the behaviour of overtly social birds such as geese, jackdaws, night-herons and herring-gulls, but this work has largely concerned the role of the individual within this social network. As example, a recent general discussion by Tinbergen on the biological significance of bird behaviour (1952c, pp. 370–1) does not mention sociality. It has taken a long time for the general studies of W. C. Allee (1931, 1938), based mainly on invertebrates, to carry the idea of the universality of sociality to ornithologists, and for F. Fraser Darling to tread the path from prophet (1938) to oracle (1952). He goes so far as to say that the term "aggressive behaviour" could be dropped for a great deal of true display; that in his opinion so-called fighting, and singing, are forms of social stimulation; that "territorialism is one aspect of social behaviour." One of his theses is that "one of the important functions of territory in breeding birds is the provision of *periphery*"—edge along which the bird is in relation with a neighbour. From this he regards the mosaic of territories, in a very proper sense, as units in a social network; and believes that this sociality, as expressed in the relationships and social conventions (display and song) enjoyed by the neighbours, has survival value.

The thesis that sociality is fundamental (the rule and not the exception) among birds, acquires merit if it can be shown that the most successful species, in the biological sense, possess it. This they unquestionably do. It is not known which is the most numerous bird in the world, but (Fisher, 1940), it is certainly a sea bird, and probably Wilson's petrel (*Oceanites oceanicus*), which nests in sometimes fantastic numbers on the Antarctic continent and sub-Antarctic islands. It is social in its breeding-grounds, and also flocks at some of its feeding-grounds, including those in the northern hemisphere farthest removed from its home, e.g. Long Island Sound. All oceanic birds, for that matter, are social on their breeding-grounds: there are about two hundred species belonging to five different orders. It is idle to suggest, moreover (as some have) that their sociality is an inevitable consequence of the limitation of breeding-grounds: for most, there is plenty of unoccupied suitable cliff-, beach- or island-space, and only at a few remote oceanic islands is there apparent saturation, and a "shift" system by which different species have different seasons so that they occupy the breeding-ground in turns.

Thus the conquerors of the world's most "difficult" bird habitat, the sea—the birds that have put the ocean storms and winds to their use and benefit by becoming sail planes—are social animals. We shall find that the most successful land birds are also social animals.

If we accept the reasonable definition that a bird with a particularly wide distribution and a high population is successful, we may examine the "heavy" end of the avifauna of a country. The population of such an avifauna probably has a log-normal distribution (Williams, 1953, Fisher, 1952b), and 10 per cent of the breeding species account for about 90 per cent of the population. In England and Wales the fourteen most successful (or at least populous) birds are chaffinch, blackbird, starling, robin, house-sparrow, hedge-sparrow, song-thrush, meadow-pipit, rook, yellow-hammer, wren, whitethroat, willow-warbler and wood-pigeon (Nicholson, 1932).

Now nearly all these birds can be shown to be overtly social in at least some part of the year; and the rest, we shall see, as territorial birds, are covertly social. Of the former, the chaffinch and the yellow-hammer maintain winter flocks, hunting organizations in which they make foraging tours of the countryside. Chaffinches sometimes have flocks predominantly of one sex, as was recognized in the eighteenth century by White (1789). Blackbirds normally act as "orthodox" territorial birds, but have liaison habits with their neighbours, particularly in autumn and winter, when they appear to behave socially and even to flock. Starlings have intensely social winter habits, using roosts in tens of thousands. Rooks, which are our commonest large birds (there are probably between one and three-quarters and two million breeding adults in England and Wales), have two levels of social organization; the spring rookery, an aggregation of individuals, and the autumn roost, a rookery of rookeries, to which thousands of individuals, usually from about eight miles radius (and more in Scotland) adhere. Few British rooks migrate, but many European rooks do so—and do so in flocks. Wood-pigeons migrate and spend the winter in flocks, having social roosts; and there is some evidence of breeding season sociality—of nests very close to each other, in certain places. The house-sparrow's yearly life is surprisingly little known; it is a social feeder and has sometimes very strong tendencies to be a social breeder.

The rest of these successful birds are territorial species. All of them, being common, cover the country—but even in areas of suitable habitat, in times of plenty, do not cover it wholly or evenly. They form what can only be called colonies, each a mosaic of territories. Darling quotes most aptly from the work of Lack (1948) on the robin and May (1949) on the willow-warbler, amongst others, to show that these "territorialists" have themselves demonstrated that a bunch of occupied territories by its very nature acts as a magnet to unsettled birds and attracts them into the network of neighbourhood.

That is it: the effect of the holding of territory by common passerines is to create "neighbourhoods" of individuals which are masters of their own definite and limited property, but which are bound firmly, and *socially*, to their next door neighbours by what in human terms would be described as a dear enemy or rival friend situation, but which in bird terms should more safely be described as mutual stimulation.

It is necessary to examine the possible advantages of some different kinds of sociality; there has been a good deal of confusion about them in the literature. Thus of flocking for "maintenance" (i.e. non-breeding and particularly feeding) purposes Darling (1952) states, "we do not know for sure whether these aggregations have survival value," while, ever since his pioneer observations on herring-gulls *Larus argentatus* (1938) he has believed that for reproductive purposes social stimulation is of value in synchronizing the breeding of the members of a colony and increasing their reproductive output. While, in my opinion, sociality is of biological value in both spheres, I believe that it is easier to prove it so in maintenance activities; and that there is a more economical and simple explanation for the differential breeding efficiency that Darling observed in his pioneer work on gulls and fulmars (*Fulmarus glacialis*).

Briefly to recapitulate his observations, while living on Priest Island in the Summer Isles in Wester Ross, he carefully noted the exact status and fate of its four herring-gull and two lesser black-back (*Larus fuscus*) colonies and its two fulmar groups, except that in 1937 he was unable properly to watch two of the herring-gull colonies because they were invaded by overlapping lesser black-backs. His observations can be summarized as follows:

HERRING-GULL

Colony	No. 1		No. 2	No. 3	No. 4	
Year	1936	1937	1936	1936	1936	1937
Number of birds	84–90	130–150	30–34	20	4	6
Number of nests made	48	69	14	8	2	3
Number of eggs laid	84	189	26	16	0	9
First egg-date (May)	7	9	12	18	–	13
Period (days) of egg-laying	17	17	23	26	–	15
Number of eggs hatched	72	181	22	14	0	8
Number of young fledged	35	76	8	3	0	1
Per cent of eggs fledged	48·6	41·4	36·4	21·4	–	12·5

LESSER BLACK-BACK

Colony	No. 1		No. 2	
Year	1936	1937	1936	1937
Number of birds	72–80	120	18	30
Number of nests made	46	82	10	19
Number of eggs laid	78	163	15	43
First egg-date (May)	15	17	23	19
Period (days) of egg-laying	24 (18)	23	21	25
Number of eggs hatched	72	155	14	41
Number of young fledged	40–45	75–90	8	22
Per cent of eggs fledged	55·5–62·5	48·4–58·0	59·1	53·6

Fulmar

Group	No. 1		No. 2	
Year	1936	1937	1936	1937
Peak number of birds	12	20	6	8
Arrival of first bird	27 Apr.	13 Mar.	after 27 Apr.	20 Apr.
Peak number first noted	?	7 May	?	30 Apr.
Number of "nest-sites" occupied	6	10	3	4
Number of eggs seen	0	8	0	0
First egg-date	–	1 June	–	–

These were the facts which inspired Darling's excellent ideas that the size of bird-colonies affects the amount of stimulus with which their members mutually stimulate each other, and that in larger colonies there is a tendency for a greater percentage of the members to breed, for the breeding season to be more compact, and for the production of a greater proportion of successfully fledged young. Darling also suggested, from the fulmar evidence, that in "colonies" of some species there might be a threshold number of individuals whose presence was necessary to create enough neighbour stimulus for any egg-laying to begin at all. While his ideas may, I believe, be correct, at least as regards general reproductive efficiency under some conditions, I do not think the facts he quoted are enough to prove them (the difference between the reproductive efficiency of any of his gull colonies could have been expected by chance more often than once in twenty times), and even when the differences in reproductive efficiency or breeding season of colonies of a social species of different size can be unequivocally demonstrated—as it has for many species, including the fulmar (Fisher, 1952), since the publication of Darling's *Bird Flocks and the Breeding Cycle* (1938)—the differences can be more economically explained on the supposition that smaller colonies contain a higher percentage of young birds than larger colonies, and have a smaller breeding efficiency and later or longer breeding season because these young birds are young.

This explanation was applied, though as Lack points out (1943) "rather as an afterthought," to the evidence in Fisher and Waterston (1941), in which in fulmar colonies producing under ten eggs a year, an aggregate of 532 pairs produced 126 eggs (23·6 per cent); in colonies producing ten or more but under a hundred eggs 734 pairs produced 308 eggs (41·8 per cent); and in colonies producing a hundred eggs a year or more the egg production was probably as much as 75 per cent. At that time we certainly regarded these figures as corroboration of Darling's idea and had not fully realized how very much better they fitted the "young pioneer" theory, though we pointed out that they might do so. So, more emphatically, did Lack, and Richdale (1949).

Upon re-analysis of the fulmar evidence, including new material, Fisher (1952) found the following:

Under ten egg colonies: 646 nest sites produced 194 eggs (30 per cent), 726 sites produced 134 young (18·5 per cent).

Ten to ninety-nine egg colonies: 1,096 sites produced 561 eggs (51 per cent), 2,093 sites produced 775 young (37 per cent). Of 47 young seen newly-hatched, 43 flew (91 per cent).

Over a hundred egg colonies: for every hundred paris that occupy sites in early June it seems probable that over 90 eggs are laid, 70 young or more hatch, and over 50 young eventually fly.

The reproductive output of the different sized fulmar colonies can be summarized thus:

Colony size	Sites occupied at spring or summer peak	eggs laid	eggs hatched	young fledged
Under 10 eggs .	100	30	?	18·5
Under 100 eggs .	100	51	40	37
100 or more eggs	100	over 90	70 or over	over 50

Matching this analysis with the information I had collected about the fulmar's astonishing spread in Britain (in years round 1949 it was pioneering about thirty new breeding-places every year), I became persuaded to the "young-pioneer" theory; and quite convinced of it when I had read the work of Richdale (1949, 1949b, 1950) on penguins and albatrosses. He particularly criticizes the "threshold" suggestion of Darling, and points out (1949) that in New Zealand and places south the following social sea-bird species "will each nest singly and in keeping with normal laying dates": the erect-crested penguin *Eudyptes sclateri*, the drooping-crested penguin *E. pachyrhynchus*, the yellow-eyed penguin *Megadyptes antipodes*, the gentoo penguin *Pygoscelis papua*, the ringed penguin *P. antarctica*, the royal albatross *Diomedea epomophora* and Peale's, or the mottled petrel *Pterodroma inexpectata*. Similarly in Britain and places north I have notes from personal observation and the literature of the breeding or at least egg-laying of single pairs of the following social breeding sea-birds: cormorant *Phalacrocorax carbo*, shag *P. aristotelis*, gannet *Sula bassana*, storm-petrel *Hydrobates pelagicus*, fulmar *Fulmarus glacialis*, black tern *Chlidonias niger*, gull-billed tern *Gelochelidon nilotica*, Caspian tern *Hydroprogne caspia*, Sandwich tern *Sterna sandvicensis*, roseate tern *S. dougallii*, common tern *S. hirundo*, arctic tern *S. macrura*, little tern *S. albifrons*, Sabine's gull *Xema sabini*, Ross's gull *Rhodostethia rosea*, black-headed gull *L. ridibundus*, common gull *L. canus*, herring-gull *L. argentatus*, lesser black-back *L. fuscus*, great black-back *L. marinus*, glaucous gull *L. hyperboreus*, kittiwake *Rissa tridactyla*, razorbill *Alca torda*, great auk *A. impennis*, guillemot *Uria aalge*, Brünnich's guillemot *U. lomvia* and puffin *Fratercula arctica*. The skuas *Stercorarius* spp. and tystie *Cepphus grylle* which often breed singly are not truly social breeders: apart from them my list includes practically all the breeding sea-birds of northern Europe and the Arctic, and there is good but not formally conclusive evidence that the remainder, which include such highly social species as Leach's petrel *Oceanodroma leucorrhoa* and the Manx shearwater *Puffinus puffinus*, may also occasionally breed singly.

Thus an examination of the "Fraser Darling effect" shows that its working is not so simple as originally stated, and that in particular the "threshold number" hypothesis is incorrect and the analysis of the differential breeding efficiency and breeding season of the colonies of different sizes must include some assessment of the proportion of adolescents in those colonies before final conclusions can be reached about the value of general social stimulus.

To recapitulate, it is an interesting, and perhaps significant fact, that two of the three sea-birds of Darling's original study were species at that time increasing and spreading (the fulmar dynamically so). Such evidence as there is of the increase and spread of social species of animals shows that most, and sometimes all of the pioneering of new breeding-places is performed by young. Tending by instinct to return to the place where they were hatched or born,* they encounter adults already in occupation —their parents, or their parents' subsequent mates or mates' mates—whose intimidative display-power, greater than theirs at least in the early part of the season, is likely to drive them away rather than to "encourage" them to take up a neighbouring nest site. If they were truly adults it would be more likely to do the latter, if young with relatively lower drive, the former. Thus we have a situation in which new colonies are founded by young with weak drive. At these small colonies the birds arrive late, breed inefficiently or not at all, and depart early. The evidence, and particularly the statistical evidence, that I have collected for the fulmar fits this "young-founders" hypothesis better than it fits the "threshold" hypothesis of Darling, though he not unnaturally quotes (1952, p. 187) my findings in support of his ideas.

An important aspect of bird-breeding sociality which was not embraced by the original Darling hypothesis is that of dispersal. There is, of course, an inherent contradiction between sociality and dispersal, yet arguing

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* Lockley (1942, pp. 134–5) believes that young Manx shearwaters do not necessarily return to where they were hatched. Owing to the poor durability of the rings he used at that stage of his work his early evidence was inconclusive; but recently (he informs me) he has proved that some hatched on Skokholm return there, while others have been caught on Lundy and Skomer.

teleologically (as it is legitimate to do here) it is necessary to the long-term survival of an animal species which reproduces itself normally in social communities for it to be able to start new communities. By what mechanism can the members of such a species overcome their inherent sociality, the imprinting upon them in early youth of the place of their birth, the instinct or disposition to navigate after adolescence to this place? Can it be that the "aggressive" displays of members of a colony have a differential impact upon those other members which they greet, depending on the age of those members, namely to drive away at least some adolescents, yet to attract adults and older adolescents to a neighbourhood? Can it also be that the displays of the (presumably) young members of new, pioneer colonies are attractive to other young birds in an opposite way to displays of the adult members of established colonies? Does the world of birds, indeed, parallel that of humans in which the young part from the community to seek their fortunes in response to mutual repulsion and often form new communities with other young in response to mutual attraction? Have we here a dispersal mechanism and a source through exogamy of genetic novelty that confers biological advantage and balances the risks inherent in the conservatism of the traditional colony with those inherent in pioneering? These are questions almost unanswerable in the light of our present knowledge, but perhaps worth a moment's thought. There is no more conservative and traditional colony nester than the gannet, yet (Fisher and Vevers, 1943–44, 1952; Fisher and Venables, 1938) the two colonies of Shetland, now large, have been *continuously* colonized from outside Shetland for more than thirty years. The colonization of the British Isles from outside (probably from Iceland and the Faeroes) by fulmars was continuous and certain from 1878 to 1914, and has almost certainly continued ever since (Fisher, 1952). Few land birds have so rigid a social organization as the rook, yet there seems to be some self-regulating mechanism by which rookeries whose size comes to exceed the carrying capacity of the land within operational range "explode" into dispersed satellites; and even the great roosts may divide, become abandoned suddenly. Just how these social units adjust themselves to new environmental situations we do not know, but I am sure that part of the mechanism will be found in a differential response to displays by adults and adolescents.

I have written enough, I hope, to show that the situation, so boldly and originally simplified by Fraser Darling, is more confused than that pioneer student of bird sociality thought, and that a key to the problems may lie more in the study of the differences between old birds and young than in those of plain populations. The populations of social birds are proving, incidentally, to be less easy to count accurately than has been generally assumed (by the writer as much as anybody); their fluctuations through the season and through the years are nearly always great, and often unpredictable. Yet upon the close and intricate study of the history and age-group composition of such populations all the answers to these many questions depend. It is interesting to note that the most detailed and careful of the few such studies as have so far been made are the private ventures in Wales of Lockley and in New Zealand of Richdale. What possibilities open up when permanent, sea-waterproof colour rings can be made, and when all the individuals in a large British sea-bird colony can be known and recognized and studied over a long period!

The biological value of breeding sociality is still imperfectly understood. Darling (1952) states, "There is not space to go through the body of work published in the last ten years which supports the biological survival value of social stimulation." While most people believe—myself, certainly—that social stimulation (*a*) exists and (*b*) confers a biological benefit, most people will surely find this statement of Darling's disingenuous, for of published work in the last ten years that formally *proves* the biological survival value of social stimulation there is (so far as I can find) none. The situation, on the contrary, resembles very much the stage often found in mathematics, where for many years an axiom proposed by common sense eludes formal proof. In avian sociality, the foremost such axiom is the fundamental axiom of Darling himself, which has come to be known as the "Fraser Darling Effect." Among the most recent to point out that this is "as yet hypothetical" is N. Tinbergen (1952).

It is not enough to suggest that breeding sociality protects bird species against predators, for to bring all eggs or young together at the same stage may be to save them from those predators that the guardian adults can drive away, acting alone or in concert (such as small mammals or birds) only to render them particularly vulnerable to those which the guardians cannot drive away (such as Man and members of the Canidae).* It is not enough to suggest that "more stimulus" produces a greater reproductive output—this can be proved only by an observational experiment on colonies of different sizes but of exactly the same age-group, and no such experiment has been made. The best that can be done, at the present state of our knowledge, is to suggest that breeding sociality serves to introduce potential mates, and in very general terms ensures a continuity of reproduction through the provision of a meeting-ground. I started this essay with the universality of sociality as my thesis, and dwelt on the (paradoxical) social nature of territory. Sociality, territory, aggressiveness, courtship, concealment, exhibitionism, submissiveness, threat—all are dogged by their own contradictions and

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* See the valuable discussion of P. L. Errington (1946).

opposites; and the art of understanding bird behaviour, as Tinbergen so clearly hints (1952, 1952b), is the art of understanding the compromise or balance between different drives.

Is the biological advantage of sociality in "maintenance activities" easier to see than that of breeding sociality? Contrary to Darling (1952, p. 186) I find this so, though the demonstration of this apparent truth seems likewise to derive from "common sense" rather than from logical or formal proof. Mutual aid, co-operation, and the continuity and systematization of beneficial activities seem to be relatively easy to demonstrate among most of the many birds that flock for feeding purposes. The examples really *are* too numerous to mention. A hundred years ago H. W. Bates (1863), who travelled in the forests of the Amazon in 1848–59, noted that "The birds of the country are gregarious, at least during the season when they are most readily found; but the frugivorous kinds are to be met with only when certain wild fruits are ripe." The mixed flocks include both fruit eaters such as parrots, toucans, trogons and bell-birds, and insect eaters. It is easy to understand the advantage of flocking for fruit eaters in a tropical forest where there are literally hundreds of species of fruiting trees, distributed in a scattered mosaic—any tree in season found by the flock can be fully exploited; and a flock can find a fruiting tree at the right stage more easily than can an individual. Moreover, the insect eaters benefit from the general "stir-up" of animal life in the foliage, awakened and driven out of cover as much by the fruit eaters as by themselves. Incidentally this argument applies to the flocks of tits in Britain, which Colquhoun and Morley (1943) believe forage together "more merely for the sake of feeding, because each species tends to have its own vertical niche in the flock and is therefore feeding at a different level from the others." I do not quite understand their difficulties, for disturbed insects are no respecters of levels!

The efficiency with which a flocking system ensures the thorough and even exploitation of the food crop can be readily seen when large flocks of wild geese or rooks are studied. A goose flock steadily grazes across a water meadow, the geese at the rear of the advancing vanguard line exercising "pressure" continually from the back with the result that the rate of walking advance of the flock is such that those in front are bound to leave grass to those at the back of quality as good as their own sample. Rooks have a different system; in large feeding flocks those at the back sometimes "leap-frog" those at the front in their excitement, so that on (rather rare) occasions a flock may actually leap-frog itself out of a good field into a bad one, before some elements detect a mistake and begin a reverse movement. Such rare lapses excepted, the result is a cleaner sweep of the crop than could have resulted from the independent and separate enterprise of the flock's individuals. In the sea, as on land, the food of sea-birds is distributed differentially, in swarms of plankton, and in shoals of fish. That a flock can (*a*) detect and (*b*) exploit a swarm more efficiently and thoroughly than individuals seems entirely obvious. Some sea-birds such as double-crested cormorants (Bartholomew, 1942) or pelicans may indulge in mass fishing in formation, co-operating in driving shoals of prey before them.

If I may express myself teleologically, many sea-birds must be social feeders because a social flock is the best device for keeping in touch with a prey that lives in flocks or shoals, or with a human affair which periodically discharges valuable food such as a trawler or a whale factory-ship or a chain of fishing villages. Some very mobile species of sea-birds, such as fulmars, often give the impression of being individually dispersed when in fact the individuals are all part of a "stretched flock"*—a great network of beaters spread to the limit of practical neighbour watching, so that the discovery of one can become the prey of all the hunters of a wide sea area.

However, the biological value of some kinds of flocks is less easy to detect than that of the previous examples, and many must share the difficulty of Hesse, Allee and Schmidt (1937, pp. 450–1) in identifying the advantage in the extraordinary gregariousness of certain plainsland and desert herbivorous mammals and birds, such as ratites, and some bustards, galliform birds and sand-grouse.

. . . . .

To sum up: sociality is almost universal among birds, in their breeding-life, their feeding-life, or both. All successful and numerous species appear to be in some way sociable. Perhaps only certain predatory birds at the top of the food pyramid (a biologically precarious and vulnerable postion) experience no sociality; otherwise all are probably sociable—even possession of aggressively-disputed territory can be, paradoxically, shown or at least held to be a form of sociality.

However, the universality of sociality among birds is rather easier to demonstrate than its biological value. The benefits of breeding sociality, which common sense accepts, become elusive if pursued in argument, largely because of the lack of satisfactory evidence from observation and experiment. In particular the ideas of Fraser Darling,

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* The classic example of a "stretched flock" is that of vultures, never better described than by H. B. Tristram (1859):

"The Griffon who first descries his quarry descends from his elevation at once. Another, sweeping the horizon at a still greater distance, observes his neighbour's movements and follows his course. A third, still further removed, follows the flight of the second; he is traced by another; and so a perpetual succession is kept up so long as a morsel of flesh remains over which to consort."

which have stimulated our thought on this subject for the last fourteen years, must be re-examined in the light of the certainty that birds of different ages behave differently, and the probability that this explains (at least partly) the differential breeding success of colonies of different sizes. The benefits of feeding sociality (or "sociality in maintenance activities," as it has been called!) are usually easier to demonstrate, though many cases are at present not understood.

One thing seems clear; that we should consider the evolution of bird population groups as well as that of individuals. It seems likely that soon somebody will prove that bird "aggregations of a certain size enjoy various advantages over single individuals." I use the words of Huxley (1942, pp. 479–80), who points out that once aggregations enjoy advantage over individuals "selection will encourage behaviour making for aggregation and the aggregation itself will become a target for selection." The study of bird populations in the future may uncover the nature of their self-regulating mechanisms. If we admit bird sociality, we must admit these mechanisms: but what they consist of we can at present hardly begin to guess.

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Retrospect of the Criticisms of the Theory of Natural Selection

THE objections and difficulties felt in respect of Darwin's views seem to fall historically into four comparatively distinct periods; (*a*) the difficulties which he himself felt during the period when the theory was developing in his mind, all of which seem to flow from his acceptance of the blending theory of inheritance, as I have tried to make clear in the first chapter of *The Genetical Theory of Natural Selection*. There I discussed in particular the difficulty which he felt with respect to the maintenance of heritable variability in wild species, and point out that the problem is completely resolved, and the contradictory inferences to which it appears to lead are reconciled, when the "blending" is replaced by the "particulate" theory of inheritance. A second difficulty which flows from the same source is that Darwin had no deductive basis from which to infer the quantitative efficacy of a selective process in producing evolutionary change. Being unwilling to burden his theory beyond what the most cautious use of the analogy of man's achievements in modifying domesticated plants and animals would justify, he was undoubtedly led consistently to underrate the rapidity with which, in favourable circumstances, evolutionary changes can be brought about by natural selection.

(*b*) The objections of the second period are those which Darwin discusses at some length, as difficulties of the theory, in the sixth chapter of the *Origin*, and were evidently brought to Darwin's notice principally by scientific friends and sympathizers with whom he had discussed his theory. They are difficulties, not of natural selection in particular, but of organic evolution in general, and seem to be due to two principal causes; (i) to the misapprehension induced by earlier evolutionary speculations of the Lamarckian type, which led men to conceive of hereditary transmission as fluid and indefinite, as is well illustrated by the discussion of the difficulty "that species are well defined and not connected by innumerable gradations," and (ii) by the very magnitude of the conception of organic evolution itself, when considered in its entirety. The call on the imaginative faculty required to conceive of the intermediate stages, which must have connected widely diverse groups of animals and plants, must have been, and must always be, an immense one to minds not already prepared by a knowledge of the diversity and intricate adaptations of analogous forms. The elaboration and perfection of special adaptations such as the electric apparatus of fishes, or the organs of flight, or of vision, the neuter castes in insects, and the detailed appropriateness of instinctive behaviour, the design of any of which might have baffled human ingenuity, were thus felt to be objections to the theory from the very magnitude of the evolutionary vision which they revealed, although in themselves they afforded the strongest corroboration of the view that evolutionary change was caused by, or rather consisted in, the improvement of adaptations.

(*c*) The objections of the third period represent the reactions of the more conservative or recalcitrant biologists, or, for this period, perhaps one should say essayists, to the growing acceptance of Darwin's views. They introduce no new intellectual element. At their best, and when free from misapprehensions as to the nature of the theory they are attacking, they consist almost exclusively of special elaborations of "cases of special difficulty" of the kind we have referred to under (*b* ii), that is to say, of the discussion of some peculiar phenomenon, of the physiology, or the ecology, or the homologues of which little was known, and challenging the evolutionist to say how *that* was produced by natural selection. It is, perhaps, because the selectionists of this period were incidentally fighting the battle for evolution in general, that it so seldom appears to have been realized that the difficulties, such as they are, are such as must be faced by any evolutionary thinker, and are indeed far more formidable to any evolutionist who ignores the aid provided by selection theory towards their solution.

(*d*) The fourth stage was ushered in by the assumption, widely disseminated among the earlier geneticists, that the discovery of Mendel's laws of inheritance was unfavourable, or even fatal, to the theory of natural selection. To demonstrate how little basis there is for this opinion was one of the main purposes of my book. The asserted support of an experimental science did, however, for many years have the effect of reviving in the minds of critics many of the older difficulties and objections, though in a derivative and sadly degenerate condition. The logical cogency of the arguments adduced has indeed shown a progressive decadence from the first stage to the last; and, though I am unwilling to pillory otherwise excellent modern writers, it will be necessary, when we have considered the more substantial difficulties of the earlier periods, to give some examples of the manner in which they have in comparatively recent times been presented to the public.

The first difficulty discussed by Darwin in the *Origin* is that existing species are well defined and are not connected by innumerable gradations. This point should be clearly distinguished from the discontinuity of species in the geological record. The modern reader will probably have some difficulty in imagining on what suppositions the evolutionist is expected to infer that contemporary species should not be distinct. To understand how it came to be discussed as a difficulty in connection with Darwin's views, we must recognize it as an inevitable survival of the controversies engendered by evolutionary speculation of the Lamarckian type. In these, exposure to the current differences of environment, accidentally formed habits, and mental or physical exertion of any kind, were supposed to produce hereditary effects. With such a vague and fluid notion of inheritance, the evolutionist might indeed have anticipated that the variations of the existing species must spread indefinitely in all directions, and that systematic classification should be shown, as more and more material was accumulated, to be logically impossible.

The point is one that must have been pressed upon Darwin by Lyell. Indeed in his *Principles of Geology* (Volume II, Chapter I), Lyell had given a discussion of Lamarck's speculations under the remarkably illuminating heading "Whether species have a real existence in Nature," and summarizes Lamarck's argument upon the point in the words:

> The greater the abundance of natural objects assembled together, the more do we discover proofs that everything passes by insensible shades into something else; that even the more remarkable differences are evanescent, and that Nature has, for the most part, left us nothing at our disposal for establishing distinctions, save trifling and, in some respects, puerile particularities.

Since Darwin had not entirely freed himself of the Lamarckian assumption, it is not unnatural that he should have felt that there was sufficient point in the difficulty to deserve discussion, and should have discussed it with characteristic care and candour. It is probably only for this reason, though none the less remarkable, that it should have come to be considered by later writers as a difficulty opposed to the theory of natural selection.

If, in the belief that the inheritance we observe is in fact a simple process of transmission of relatively permanent elements of the germinal material, we seek for the grounds on which an evolutionist could infer a confusion of specific types, it appears that he must postulate either a completely asexual process of reproduction, or fertility and habitual mating between different species. Something approaching this latter condition does seem to exist in certain so-called polymorphic genera of plants, in which, as we might infer, classification on traditional taxonomic lines appears to be impossible. On the contrary the vast majority both of plants and animals consist of groups between which breeding is impossible or exceedingly rare, but within which there is a constant interchange of germinal material, on a scale which ensures some community of ancestry between almost every two individuals, within a period no greater than a hundred generations. With this community of ancestry in view, the reason for the possibility of systematic classification becomes readily apparent; no other consequence could be anticipated than that such classes should be divisible into distinct groups, which, when the systematicist has learnt to recognize the special criteria of each group, will seem to him easily distinguishable. A similar process of training the powers of observation is gone through with respect to quite different characters by the practical geneticist, when he learns to distinguish the effects of different individual genes. In both cases all degrees of difficulty are encountered, and the worker may need to be sustained for some time by the faith that the material he is examining really contains objective distinctions, which he may learn to recognize. The justification of this faith would seem to be, in the one case, the particulate nature of the heritable elements, and in the other the constancy of heritable differences ensured by the historical distinctness in ancestry of the intrabreeding groups.

The suggestion, sometimes stated frankly, sometimes hinted obliquely, that the Darwinian theory rendered systematic classification nugatory, or, in converse, that the success of systematic Biology is unfavourable to Darwin's views, is still alive in modern writings on Biology. It is one of the curiosities of the situation that the systematists appealed to are invariably evolutionists, although holding very diverse opinions as to the causes of evolutionary change, and that the objection which is valid against the views of Lamarck is invariably spoken of as a point against those of Darwin. Thus in 1901, alluding to the reaction of systematists to the *Origin*, Bateson thought it worth while to write:

> Should there not be something disquieting in the fact that among the workers who come most in contact with specific differences, are to be found the only men who have failed to be persuaded of the unreality of those differences?

It would, of course, have been impossible to state baldly that Darwin tried to persuade men of science of the unreality of specific differences. Darwin persuaded men of their transmutability, and it would be difficult to find a systematist to differ from him in this matter.

Such confusion is not, however, confined to professed opponents of the selection theory. In his *Short History of Biology* (1931), C. Singer (p. 548) states, with no suggestion that his views are not fully representative of modern opinion:

> Darwinian theory demanded that species should produce endless variations, some, at least, adapted to the needs of the organism. It was an essential corollary that species could not be exactly delimited. They would tend always to be giving off varieties which would gradually pass into new species. Thus the work of the systematist was merely formal, at least when regarded *sub specie aeternitatis*. The systematist, according to the Darwinian view, is not really distinguishing species from each other, but only species as they happen to exist at his particular point of time. Since new species must be ever in process of formation, we ought to be able to trace the process.

We here see one of the bases of Lamarck's theory transmuted into a corollary of Darwin's. The historian makes no similar comments on the teaching of Lamarck, who really did attack the possibility of systematic classification. He does not realize that the Darwinian view, if by this he means, as is probable, natural selection as contrasted with the Lamarckian hypothesis, implies the reality of specific distinctions, and why the recognition of real entities is "merely formal" unless the entities themselves are eternal he does not attempt to explain. The whole passage illustrates the chaos into which an originally rational discussion may fall through reliance upon thought at second-hand.

With these examples of careless and consequently confused thought before us, it is not surprising that others, whose acquaintanceship with biological ideas is more remotely derivative, should have been led into unqualified, though completely indefensible assertion. The *History of Biological Theories* by Professor Radl of Prague, commences the chapter of Species (XXVIII) with the following amazing sentences:

> Darwin's attack on the constancy of species failed. Only his most faithful disciples—Haeckel, Schleiden, Schmidt and Carpenter—accepted the suggestion that there are no species; Haeckel and Carpenter were the only workers who tried to follow up this idea practically, and in this they had no lasting success. The other Darwinists hold in theory that the word "species" does not correspond to any existing reality, but in practice they go on discovering new species, as was done in pre-Darwinian days.

As a philosopher it is surprising that Professor Radl should have confounded *inconstancy* with *non-existence*. In conjunction with this slip, which his logical training might have obviated, his stricture, that the majority of biologists, who reject the doctrines of the constancy of species, should be so incapable of rational thought as to hold in theory what is disproved by their daily practice, deserves to be put on record for its unconscious humour.

The cases of special difficulty, which were advanced in great numbers, and which were discussed by Darwin, and by his supporters and opponents at very considerable length, are all closely similar in the kind of difficulty which they present, although this difficulty may be framed in three distinguishable phases.

(*a*) An organ, such as the wing of a bat, belonging to a group somewhat widely separated from its nearest allies, may be so specialized for the particular functions to which it is adapted as to bear little resemblance to the prototype, as illustrated by the fore-limb of an insectivore, from which it must be presumed to have arisen. The difficulty felt here is that of imagining a series of organisms presenting organs of intermediate grades connecting these widely separated extremes.

(*b*) An organ of extreme perfection, such as the eye in the higher vertebrates, may show such perfect and detailed adaptation to its important function that by comparison with the obstacles which the design of such an apparatus would present to human ingenuity, the mind is staggered by the effort of conceiving it as the product of so undirected a process as trial and error.

(*c*) Some organs of seemingly trifling importance are yet so clearly adapted to the function they perform that they cannot be regarded as accidental. In these cases it may be asked how can the efficacy of this trifling function have ever been a matter of life and death to the organism, and so have determined its survival in the struggle for existence.

Of these three types of objection the first is opposed to evolutionary theory of all kinds, while the second and third, though I have stated them in the form in which they should be presented to a selectionist, can only be evaded by evolutionists of other schools by postulating a creative power in living matter equivalent to the ingenuity of a benevolent creator. They are all, in somewhat different ways, difficulties less of the reason than of the imagination. The cogency and wealth of illustration with which Darwin was able to deal with these cases was, perhaps, the largest factor in persuading biologists of the truth of his views, and would in itself to a great extent explain the enormous influence which he exerted upon biological opinion. The difficulty of imagining the intermediate stages in the evolution of the wing of a bat Darwin met by pointing to the existence in Nature, not of the intermediate stages themselves, which must necessarily be extinct, but of the analogues of a chain of intermediate adaptations, in the flying squirrels and in *Galeopithecus*, in which less specialized means for gaining assistance from the air, in leaping and gliding, indicate a series of stages, each of practical service to its possessor, without the latter enjoying the advantages of true flight. In considering such a series of stages it becomes apparent that it is the theory of evolution by continuous adaptation, amid the extraordinary diversity of the expedients which are in fact useful to different animals, which makes such transitions possible. What would be incredible in such a case would be a non-adaptive orthogenetic urge leading straight from the fore-limb of an insectivore to the wing of a bat through some thousands of generations of intermediate types encumbered with useless appendages; or, to allude to a rival absurdity, the appearance of the bat's wing by a *saltation* among a litter of primitive insectivorous mammals.

Singer, to whose *Short History of Biology* we have before alluded, repeats this particular difficulty as though it had been never mentioned by Darwin. Of "a series of fallacies and some erroneous assumptions" which he ascribes to Darwin the second is:

> (*b*) That a natural variation should confer an advantage is not enough to secure its perpetuation. The advantage must be effective and moreover it must be transmissible. Now it is difficult to believe that the earlier stages of some developments are effective. A wing, for instance, so little developed as to confer no power of flight, or at least of gliding, would be no advantage.

It might perhaps have been expected that an historian of science would use such words as "fallacy" and "assumption" in their logical senses, rather than as terms of general disparagement for opinions he disagrees with. "Assumption" is a curious word to apply to an opinion, the grounds for which occupy half a chapter in so compact a book as the *Origin*. The reader will appreciate the wildness with which the word "fallacy" is used if he attempts, as a mental exercise, to set up a logical process based on accepted observational facts, disproving the "fallacy" that the wing of a bat has been evolved through a continuous series of forms, changing at every stage, in the direction of improved adaptation to the needs of the organism.

The second type of difficulty is encountered with respect to organs of extreme perfection, of which Darwin chooses the eye as an example. Examples of this difficulty, however, if for the moment, we assume the paradox that examples of extremely minute and intricate adaptation can be regarded as difficulties of a theory, which makes adaptation the mainspring of evolutionary change—could now be easily multiplied. For not only have morphological structures showing such adaptation been described in greater detail, but the study of the regulation and development of organisms has brought to light physiological mechanisms which rival them in the perfection of their aptitude. Darwin clearly recognized in this case that the principal difficulty lay in the limitations of the imaginative faculty. In the *Origin* he writes (Chapter VI):

> Reason tells me, that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case; if further, the eye ever varies and the variations be inherited, as is likewise certainly the case; and if such variations should be useful to any animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, should not be considered as subversive of the theory.

It would be impossible to add to the cogency of this sentence, yet we may perhaps attempt to probe the difficulty more closely by examining it under the aspect of the improbability of chance variations ever conspiring to achieve what we should naturally regard as a finished triumph of design. This aspect is the better worth examining since, in the writer's opinion, it was Darwin's chief contribution, not only to Biology but to the whole of natural science, to have brought to light a process by which contingencies *a priori* improbable, are given, in the process of time, an increasing probability, until it is their non-occurrence rather than their occurrence which becomes highly improbable.

Consideration of the conditions prevailing in bisexual organisms shows that in a species without great differential fertility, and maintaining a stationary population, the chance of an organism leaving at least one offspring of his own sex has a calculable value of about $\frac{5}{8}$. Let the reader imagine that this simple condition were true of his own species, and attempt to calculate the prior probability that a hundred generations of his ancestry in the direct male line should each have left at least one son. The odds against such a contingency as it would have appeared to his hundredth ancestor (about the time of King Solomon) would require for their expression forty-four figures of the decimal notation; yet this improbable event has certainly happened. It is not easy, however, to conceive of the remoteness of the contingency as given by a number enormously great beyond our ordinary experience. In a large lottery with a million tickets the chance that a number chosen at random should gain the first prize is an almost inconceivably larger probability than that of a hundred successive males each leaving a son. To match the probability we have calculated we should need to consider the chance that seven numbers chosen at random should give the first prize-winner, the second, and so on down to the seventh, in the right order, and even then the probability of one hundred ancestors all leaving male issue would be only about a twenty-fifth as great.

This example only illustrates the difference between probabilities viewed prior and subsequent to the events they concern. Probability is, in essence, merely a statement of relative frequency. A frequent consequence of any action is a probable consequence; a rare result is an improbable one. The peculiarity of natural selection with which we are concerned is that it constantly modifies the frequency with which different types of organism come into existence, and consequently the probability of all the types of organism which might appear, whether such types are actually in existence or not. The rate at which the probability is modified will not be as great as that illustrated by the continuance of the male line, but, with selective intensities of the order of 1 per cent the lapse of 10,000 generations will suffice to bring about changes of probability of the same magnitude. And ten thousand generations is not a long period in the evolutionary history of most species.

Very large numbers are often referred to as "astronomical," and indeed astronomy has done much to stretch the human imagination in respect of magnitude of time and distance. In respect of probability ratios measuring intricacy of design, quite commonplace biological situations involve ratios as large as the largest commonly conceived by astronomers. Some astronomers believe that the universe is finite, and contains a finite number of particles (protons). This number may be illustrated as follows: A largish helping of salt contains about a gram of matter, and this would contain about a million million particles the size of a bacterium, while each bacterium contains a million million protons. A million million grams would give a sizeable hill, and ten thousand million million of these would make up the earth. Astronomically the earth appears to be a rather insignificant body. The solar system is about a million times heavier, and the sun is one of about a hundred thousand million, or perhaps four times as many, which make up the galaxy. Our galaxy seems to be a large one, as galaxies go, but there are at least two million others, and astronomers who believe that the universe is finite have made estimates of the total weight that it contains substantially larger than would be found by multiplying these figures together. The probability 10^{-79} of picking at random one particular proton out of the totality of those present in the universe may be used as a standard of comparison. A combination of characters of this order of improbability might become the prevalent condition within ten thousand generations under the action of a selective intensity of rather less than 2 per cent. Such changes have probably occurred in most living species within comparatively recent times.

That these considerations of probability are not altogether irrelevant to modern discussions may be made clear by a quotation from Professor Berg's *Nomogenesis*:

> As a case in point, what is the probability of the test in the appendicularians (free-swimming tunicates) being accidentally formed? These animals inhabit a very complicated test, which is secreted by peculiar large epithelial cells, known as

> oikoplasts. In *Oikopleura albicans* the test is provided with a sieve for filtering minute organisms of the nannoplankton, an entrapping apparatus, a funnel, etc. Among the oikoplasts of this appendicularian there are two large groups—one for the secretion of the entrapping apparatus, another for the formation of the sieve (Lohmann, 1909). The test may be cast off and formed anew several times during one day, being secreted by the ectoderm. Can such a chance variation of two groups of cells be conceived, as should lead to the formation of a purposive apparatus harmonious in all its parts? If we share this point of view on probability, we are bound to say that the probability of an accidental occurrence of even one useful character in such a complicated organ as the eye, the ear or the brain is insignificantly small. A new character, accidentally produced, is very likely to *injure* a complex mechanism; to expect that it will *improve* it would be in the highest degree injudicious. But probability will very nearly approach zero, if we remember that an accidental variation of one character is insufficient for that purpose: a useful variation in the retina, for example, should be connected with variations in the whole apparatus simultaneously: not only a series of other parts of the eye, but likewise the corresponding centres in the brain should vary in the direction of usefulness. The probability that all useful variations will simultaneously occur in all the parts is the probability of a miracle. Repeating Darwin's words, it might be said, "To admit all this is, as it seems to me, to enter into the realms of a miracle, and to leave those of science. (*Origin of Species*, sixth edition, p. 204.) We might just as well expect that if the wheels, screws and other component parts of the mechanism of a watch were to be put into a vessel, we could, by the simple process of shaking, get them to combine in such a manner as to become a watch that would function as such.

It appears that this is an argument which the theory of natural selection is singularly well fitted to meet. Berg's statement of the improbability of such adaptive mechanisms as biologists have brought to light, arising by chance without selection, does not appear to be over-strained. What is strange is that he adduces it as an argument against selection theory, rather than in opposition to such theories as that of saltations, or of orthogenesis, which assume that evolutionary modification takes place by reason of causes other than the adaptive improvement of the organism. The quotation from Darwin, it may be noted, is drawn from Darwin's criticism of the saltationist theory of M. Mivart. Its citation by Berg shows how entirely in the course of time the point of an argument may become obscured.

We may now turn to the difficulty felt with respect to adaptive organs, the importance of which to the organism appears to be trifling. This difficulty has not been prominent in recent evolutionary writings, though it was taken seriously by Darwin. It is, however, valuable for the light which it throws on the logical position of argument based upon structural features, and on the difficulty of attaining to a just appreciation of the relative certainty or uncertainty of our judgements.

In the first place it should be noted that the difficulty only arises when we have already satisfied ourselves that the organ in question is in fact adapted to a specific purpose. If the adaptation itself is in question the criticism we are concerned with here cannot be developed. The selectionist is bound by no obligation to show that all characters are adaptive. Anyone, however, who rejects the alternative methods by which adaptation might conceivably have been acquired, i.e. by Lamarckism, or by the special intervention of the Creator, must be prepared to claim that all genuinely adaptive characters have become so through selection. If, therefore, it can be confidently asserted that an examination of such a structure as a giraffe's tail shows features and details which can only be interpreted upon the view that it is a protective fly-whisk, then, if this function really is unimportant in the life history of the species, it may rationally be argued that, since natural selection depends on life or death, it cannot be the means by which the organ has come to be adaptively modified to fulfil so unimportant a function.

It will be observed that the argument depends on the judgement of unimportance, and to the question of what weight can be given to such a judgement we shall be obliged to return. Its rhetorical force, however, springs from the negation that admittedly very important matters like life and death can be influenced by trifling differences, and in this aspect the argument embodies a widespread fallacy which it is of some importance to expose. It may be admitted that death and reproduction afford the final criteria by which the existence and magnitude of any injury or disability may be tested, without admitting, however, that such a test is immediately applicable in the absence of impossibly exact knowledge of every detail of the life-history and its contingencies. In cases where it is arguable whether the supposed injury really is injurious this is indeed the only test on which we could rely. If it were urged, for example, that infestation by vermin conferred the advantage of a beneficial stimulus leading to an alert and vigilant activity, sufficient to outweigh its more obvious disadvantages, the only possible final test would lie in the relative survival and reproduction of the infested compared with the uninfested animals. In practice, however, this final test cannot be applied. Still less, if we are convinced that vermin or blood-sucking flies are really injurious, can we apply it to assess the magnitude of the injury. We can only form a judgement that the injury is more or less important, and it is easy to see that the judgement that it is very unimportant compared to the death of the organism, even if this judgement is unquestioned, is an entirely inadequate basis for the assertion that it does not inflict a selective disadvantage.

The case to which the life and death test is most immediately applicable is that of capture by or escape from a predator. If we consider no outcome to such an encounter, other than escape or death, then it is manifest that the amount of difference in alertness, speed or endurance, which may decide the issue, is smaller than any assignable quantity. The difference needed to determine life or death is, in mathematical strictness, infinitesimal. For, however small the difference which we choose to consider, a finite number of increments of this magnitude will suffice, in any particular case, to determine the difference between easy capture, at the one extreme, and easy escape at the other. And some particular one of these increments, however small they may have been chosen, will therefore have sufficed to bridge the gulf between death and safety. Obviously, small advantages will make the critical difference more seldom than large ones. On our postulates, "hairbreadth" escapes may be rare, but are certainly not imaginary.

If, on the contrary, intermediate results of the encounter are to be considered, such as injury not resulting in death, a finite difference in fitness will be needed to determine the whole difference between death and complete escape; but in these cases smaller differences in fitness will determine such selective advantage as there may be in uninjured escape over escape with injury, in escape with slight injury over escape with severe injury, and in escape with severe injury over capture and death. In all cases, therefore, the disabilities from which an animal suffers will entail consequences expressible as a finite increase of the death rates or a finite decrease of the rates of reproduction. And the fact that natural selection acts by life or death, by the survival of the fittest and by the destruction of the less well fitted individuals, though it adds great rhetorical emphasis to the difficulty we are considering, does not carry us a step farther than the general recognition that all modifications that confer advantages, however slight, or which avert injuries, however apparently trivial, will be favoured by natural selection in proportion to the magnitude of their actual effects upon survival and reproduction.

We may, none the less, in so far as our judgement can be relied on, make a broad distinction between characters of great apparent importance to the life of the individual and those the apparent importance of which is much less considerable. In the case of characters of great importance, such as acuteness of vision, and of the other chief senses in the higher animals, we may infer that any appreciable differences in adaptation will be favoured by selections of a high numerical intensity, leading to a proportionately rapid genetic progress in the species. Again, in such cases, we may recognize that even small and intricate refinements of design, which add to the efficiency of the sensory apparatus, will confer a sufficient selective advantage to ensure their gradual establishment in the long course of evolutionary progress. On the other hand, with characters influencing only slightly the efficiency of the organism in its various necessary activities, evolutionary progress could only be expected to be rapid in adaptations of a relatively simple character, and especially in characters which, like human stature, are determined by an abundant supply of factorial differences. Intricate adaptations, involving a great complexity of genetic substitutions to render them efficient would only be established, or even maintained in the species, by the agency of selective forces, the intensity of which may be thought of broadly, as proportional to their complexity.

The difficulty of high adaptation of unimportant organs may therefore be genuinely felt in cases where we have substantial reasons for believing, (i) that the bionomic function is in fact unimportant, and (ii) that the adaptation is so intricate and has required so many gene-substitutions to build it up, that it could only have come into existence through the agency of selective intensities more powerful than any that our knowledge of the bionomics of the species permits us to postulate. The difficulty of adducing evidence sufficient on these two points to support a cogent argument will be obvious as soon as the form of the argument is carefully stated. A biologist who wished to satisfy himself, in the case of the giraffe, that a partial protection from the attacks of flies was, in reality, of trivial importance, would be obliged to investigate the loss of nutriment caused actually or potentially by these pests, and the frequency with which injuries to the skin due to other causes were aggravated by them. He would have to study whether the irritation and disturbance caused by their attacks harass the animals and interfere with the efficiency of their normal activities, their feeding, mating, herd reactions, vigilance, or sleep. He would have to discover whether the flies included blood-suckers merely, or insects which were internal parasites during their larval stages, whether they were the vectors of such parasites, and whether they infected the blood of their host with the germs of any distemper or disease. In the course of these investigations he would doubtless discover additional questions which required answering before an opinion could be formed as to the advantage of killing or driving away a proportion of the insects to the attacks of which the giraffe would otherwise be exposed. But the great extensions which have taken place during the last two generations in our knowledge, both of the insects and of micro-organisms, have made the considerations urged above sufficiently obvious, and almost unnecessary to the present generation. It is perhaps for this reason that modern writers have not chosen to revive this particular class of the difficulties discussed by Darwin, although it is the class which is most particularly an objection to selection theory, rather than to theories of evolution in general.

The difficulty of forming a judgement of bionomic utility is, however, only one half of the problem of comparing this utility with the magnitude of the task of bringing into existence, by a process of genetic substitution, an adaptation of an observed degree of structural complexity. Psychologically the impression of the ingenuity of an adaptation is much heightened when it is one of a kind of which we had not before suspected the existence, as though we should say, "How clever of natural selection to have thought of that!" The purely human difficulty of perceiving the need of a contrivance, or of the possibility of improving one, and of studying the situation with a view to designing its execution, is thus added to the real difficulties which the evolutionary forces have overcome, which consist only of bringing about the series of genic substitutions by which it has been in fact built up. Even when we discard these extraneous and anthropocentric elements, however, much knowledge of the common effects of genic variations, and of the developmental mechanisms by which they are brought about, is needed to form a judgement of the amount of genetic complexity to be ascribed to an observed adaptation. It has been beautifully shown by J. S. Huxley (*Problems of Relative Growth*, 1932) that relatively simple modifications in the system of growth-gradients (by which the form of organisms, both in their general structure and in that of their parts, is governed in the later stages of development) will bring about harmoniously adapted modification of form, involving numerous structural elements, and which might have appeared to require equally numerous modifications of the germinal material. The principle appears to be applicable with conspicuous success to many cases of sexual dimorphism in the Crustacea and to the polymorphic neuter castes of the social insects. It would, I believe, be an entire overstatement to deny an extreme degree of genetic complexity in the evolutionary development of some structures such as the eye. A better understanding, however, of the developmental process, may well show that conspicuous phylogenetic changes in the external form can be brought about more simply than many far less striking adaptations in detail of the organism to its environment, or of its parts to their mutual reactions.

A third point may also be considered in this connection. In cases where adequate judgements can be formed, both of the bionomic utility of an adaptive modification, and of the comparative simplicity or complexity of the genic substitutions by which it can be brought about, we shall be in a position to estimate the *relative* speed of evolutionary change. Even so, however, our data for translating this knowledge into that of absolute speed, measured in generations, or in geological epochs, is as it happens, very meagre. The hard parts surviving as fossils seldom supply a means of assessing the exactitude of adaptation to the prevailing conditions, whereas the gross changes which are observable in the size and proportion of parts are certainly in themselves the kind of modification which the very faintest selective intensities would be competent to accomplish. I do, however, suggest that an indirect basis of comparison is afforded by the modifications which have apparently taken place in the heterozygotes of certain rare, but recurrent, mutations. In those, exceptionally minute selective intensities, not easily to be accounted as more than a ten-thousandth of those at work on the evolutionary improvement of the species as a whole, have apparently sufficed to repair serious maladaptations in very numerous instances, in some of which, at least, the process of repair seems to have been completed since the separation of nearly allied species. It is not unreasonable to hope that, as this source of information becomes more fully explored, it will provide a basis of comparison for assessing the actual rates of modification possible to characters of very different kinds under the action of known selective intensities.

E. B. FORD

Problems in the Evolution of Geographical Races

The object of this article is to discuss the bearing of some recent experimental and observational data upon the evolution of geographical races in animals. They illustrate certain aspects only of this problem; that is to say, those which seem to have been insufficiently developed or call for further investigation at an early date. No attempt is made to provide even a brief general survey of the subject, for this can be obtained from other sources (e.g. Huxley, 1942; Mayr, 1947; Dobzhansky, 1951).

One of the most fruitful ideas which has in recent years illuminated the analysis of geographical variation is the concept of the *cline*. This word was suggested by Julian Huxley (1939) to denote a gradual and continuous change in a character over a considerable area as the result of its adjustment to changing conditions, whether geographical (geoclines), ecological (ecoclines) or of other types, each of which can be distinguished by an appropriate prefix. The need for, and easy application of, this term was shown by its rapid adoption in biological literature. So well has it become known that to-day familiarity with its use can safely be assumed and it is appropriate here only to pay a tribute to the foresight which coined it.

The fact that clines, of various types, are of frequent occurrence in animal and plant subspecies is increasingly recognized, but information on some of the problems involved in their evolution, especially the kinds of isolation which give rise to them and their genetics, is defective.

The view of Mayr (1947) is to-day generally accepted that, apart from polyploidy, some type of geographical isolation is essential for the formation of distinct races. Now it is clear that, in addition to major barriers, the free flow of genes through a population may be impeded either by mere distance, or by the occurrence of minor discontinuities each of which may be too slight to produce an abrupt response, though their cumulative effect may be considerable if they subdivide a gradually changing habitat.

The importance of mere distance as an isolating mechanism has been demonstrated on several occasions, but information on the subject is still scanty. Some work on the butterfly *Coenonympha tullia*, Müller (Satyridae), though still incomplete, indicates the type of effect involved. This is a northern species, occurring on the mainland of Britain from the extreme north of Scotland as far south as Shropshire and Staffordshire in central England (where it has lately become nearly extinct) and northern and mid-Wales. It inhabits moors and marshes from sea level up to about 1,800 feet, but is absent from agricultural land. Thus, at least in the southern part of its range, it is to-day subdivided into widely separated colonies, but the population must have been a more or less continuous one in the recent (historical) past, very possibly up to the more rapid changes in land usage which have taken place from the latter part of the eighteenth century onwards. Even now it is subject to little geographical isolation in the far north. The species passes through a long cline in a northerly to southerly direction in which the colour darkens and the spots enlarge: this is to some extent reversed in a subsidiary cline west from Shropshire and Staffordshire into Wales.

When males from Merioneth were crossed with females from Scotland, five of the thirty-six female offspring so produced were intersexual and these appeared in two out of three families which were reared (the third contained only seven females). All of the forty-five male offspring were sexually normal (Ford, 1949). It is to be noticed that this result is in accord with the prediction of Haldane (1922) that when one sex of a cross between species or subspecies is absent, rare or abnormal, it will be the heterogametic one, which is the female in the Lepidoptera. It indicates that the balance of sex genes is differently built up at the distant ends of what must, two hundred years ago, have been a fairly continuous cline. To-day the breaks in it are far more considerable in England than in Scotland, yet when specimens from Merioneth and Cumberland (near the Scotch border) were crossed, no sexual abnormalities appeared (48 males, 58 females), suggesting that distance rather than modern isolation is responsible for the degree of subspeciation which is here indicated. Pairings between Cumberland and northern Scotch specimens failed: indeed the small numbers obtained throughout were due to the technical difficulties of the material, the specimens being extremely unwilling to mate, and not easy to rear, in artificial conditions.

Thus owing to the distance between the ends of an extensive distribution, a non-migratory species such as *C. tullia* may build up a gene-complex gradually adjusted to the changing conditions across its habitat. This may produce a cline in speciation, reflected in the production of increasing sexual abnormalities in the heterogametic sex, and eventually its lethality, followed by abnormalities of the homogametic sex, and finally general sterility, as individuals that have been more and more widely isolated by distance are crossed in the laboratory.

We are extremely deficient in information upon the second aspect of isolation which has been mentioned: the importance of minor ecological and other barriers in micro-evolution. It is very desirable that the pressing need for data upon this subject should be appreciated by field workers, for it has been greatly neglected, while much attention has been given to the more spectacular, but less general, problems of migration. The influence of such minor barriers may be detected in several ways: by the study of gene-frequencies, by marking methods and by direct observation.

Dowdeswell, Fisher and Ford (1949) have assessed the effect of minor ecological barriers by marking specimens, a method which might profitably be extended to many forms. Their work was carried out on the butterfly *Maniola jurtina* L. (Satyridae) on the uninhabited island of Tean, Isles of Scilly. This is approximately half a mile long and is divided into a sequence of five ecological habitats of two distinct types. Three of them are areas of long grass, bracken and bramble, where *M. jurtina* flourishes. These are separated from one another by two strips of short, almost lawn-like, turf 210 and 130 yards long respectively, from which it is absent. By the technique of marking (with cellulose paint), release and recapture, it was possible to estimate approximately the number of insects in the three populations as somewhat over 15,000, 3,000 and 500 specimens. Each butterfly that was recaptured was in addition given a mark to denote the area in which it had been found so that an indication was obtained of the amount of movement from one colony to another. During the course of the work 183 marked insects were recaught, but only three of them had changed their areas. This tendency to localization was confirmed by direct observation. The work occupied three weeks during which we walked over the regions of short turf a number of times each day, but only once did we see a specimen of *M. jurtina* crossing either of them, though it was flying freely in its three appropriate habitats. This is quite a powerful active insect on the wing, capable of passing in a few minutes from one to another of its colonies on the island and frequently traversing greater distances within the larger of them than would be required to do so. Yet evidently the small strips of unsuitable terrain were a serious barrier to its distribution.

It is indeed by no means impossible that the mere subdivision of a piece of country by hedges may to a significant degree localize the movement even of flying insects and so check the free flow of genes throughout a population. Should the nature of the ground or its ecology change progressively across the area in question, such apparently insignificant barriers might contribute materially to the formation of a cline.

There can be no doubt also that some organisms will be subject to much potential environmental variation as a result of the different conditions to which they are exposed. This may well be expressed as actual diversity during the colonization of a new habitat, but it is likely that a species will become buffered against such environmental effects after it has established itself. For these will tend to be at random relative to the needs of the organism, and selection, operating only upon genetic variability, controls the phenotype by acting upon the genotype. Even when a purely environmental variation chances to fit in harmoniously with the adjustment of an organism to a particular locality, it can only be improved or modified by selection which must act upon genetic variability. This, therefore, will tend to transfer the production of the character in question from environmental to genetic control.

Thus the lower altitude races of the butterfly *Pieris napi bryoniae* O. have two broods in the year while the high altitude ones are single-brooded. There is indeed an obvious environmental basis for this because of the relatively short period suitable for active larval life at the higher elevations. Yet Müller and Kautz (1940) have shown that the differences in the number of broods is genetic, for single broodedness is retained by the mountain race when reared in warm conditions in the laboratory.

It is noteworthy, indeed, how stabilized are some forms of a species against great environmental differences within their habitats, though they may differ widely from one locality to another elsewhere in their range. Thus in our work on the butterfly *Maniola jurtina* we find the same distribution of female spotting (on the underside of the hind-wings) maintained throughout southern England, from mid-Devon to the East Coast, in spite of the great diversity in climate, soil and ecology. Yet female spotting has widely different frequency-distributions in the extreme South-West (West Devon and Cornwall) and in the Isles of Scilly: a district which, in comparison with the rest of southern England, appears relatively uniform. Irrelevant as this character seems, and indeed may be, to the needs of the organism, it is clear from these observations that it must be genetic and that the genes controlling it have selective value (Dowdeswell and Ford, 1952). Indeed, only in very small populations of a few hundreds can the random survival of characters become of any importance compared with selection, in spite of much that has been written on the effect of genetic "drift" (Fisher and Ford, 1947; Sheppard, 1951).

Racial differences, especially in animals, have so far been little studied genetically. We may expect that those falling within a cline, except of the polymorph-ratio type, will most usually be controlled on a multifactorial or polygenic basis, though this may involve the selective adjustment of the gene-complex to the expression of single genes. Indeed, that is the situation responsible for the gradual change in the patterns of polymorphic mimics in response to the diverse geographical races of the species which they copy, or to the intrusion of new models into some part of their distribution. Thus on the West Coast of Africa *Hypolimnas dubius* Beauv. is dimorphic: one form, *dubius*, copies *Amauris psyttalea damoclides* Stand. and the other, *anthedon* Dbl., is a mimic of the western race of *Amauris niavius* (*niavius* L.). On the East Coast, however, the *dubius* form is represented by *mima* Trim., which differs from it both in colour and pattern to resemble a different species, *Amauris echeria* Stoll., while *anthedon* follows the geographical race of its model *A. niavius dominicanus* Trim., and is known as *wahlbergi* Wallengr. In both areas the dimorphism is, as expected, unifactorial and I have shown that, in spite of an apparent contradiction, the corresponding *anthedon* and *wahlbergi* forms are recessives (Ford, 1952a). However, in some parts of Central Africa these forms of *H. dubius* are intermediate between the West and East Coast races.

In order to support his particular theory of "parallel mutation" (in the unusual sense in which he employs the term), Goldschmidt (1945) is driven to suppose that the different polymorphic forms of a mimic must be controlled by multiple allelomorphs, and he rejects the concept of the adjustment of the effects of a "switch gene" by selection operating on the gene-complex. His theory of multiple allelomorphs is greatly strained when it has to account for a series of intermediates between geographical races of mimics and models, whereas the selective adjustment of the effects of a gene is in harmony with these facts and has been established experimentally in the laboratory (Ford, 1940; Fisher and Holt, 1943; and others).

It would not be difficult to design an experiment to determine whether or not the corresponding West and East Coast forms of *Hypolimnas dubius* are due to multiple allelomorphs at the same locus. Such a test would have far-reaching theoretical results since it would cast a deciding vote in favour of the views on the genetics of mimicry supported by Fisher and Ford on the one hand, and by Goldschmidt on the other. That such important yet simple data on these or some of the many other comparable forms are not available, indicates the great need for genetic work on mimetic insects. This has so far been handicapped by the fact that the appropriate species are mainly tropical; for they are not easy to rear in temperate climates, while the facilities for such work in the the tropics are so far negligible, though there is certainly no reason why they should continue to be so.

Furthermore, the genetics of geographic races in general have everywhere received but scanty attention, and there are as yet little data which allow us to interpret the phenomena of zoogeography in genetic terms. The need for a comparative genetic study of subspecies and distinct races is evident enough; but it is equally necessary to apply such an analysis to the situation in which the same form occurs in isolated areas. For we are in almost complete ignorance of what in terms of genetics is meant by "the same" in such circumstances. An example will make this clear. The moth *Triphaena comes* Hb. (Agrotidae) is monomorphic in England and southern Scotland, the fore-wings being ochreous brown and the hind-wings yellow with a black sub-marginal band. In northern Scotland, however, this is a dimorphic species, for a dark form, *curtisii* Newmn., occurs in addition to the normal one and in some areas occupies 50 per cent, or perhaps more, of the population. Unlike the ordinary *comes* it is very variable: the fore-wings may range from a mahogany shade to intense black and the hind-wings are clouded with black scales, slightly in some specimens but very heavily in others.

As early as 1905, Bacot showed that *curtisii* is nearly but not quite dominant. This has now been confirmed in material derived both from the Outer Hebrides (Barra) and from Orkney. These islands are very isolated from one another, yet I could see no consistent differences between the forms obtained from them even when several hundred bred specimens were available for comparison. Moreover, in both places *curtisii* proved to be unifactorial, nearly dominant, and due to the same gene (or to an allelomorph of it: the data do not distinguish this possibility). Yet the corresponding adjustments of each population to that gene, giving it nearly complete dominance, had not been produced in the same way, for the "dominance modifiers" utilized in Barra and Orkney are different. This fact which became evident when the *curtisii* gene was brought into a gene-complex half of which was of Barra and half of Orkney origin, for an unclassifiable series was then obtained ranging from extreme dark *curtisii* to the normally recessive *comes* (Ford, 1952b). In this instance, therefore, it was possible to attach a genetic meaning to the statement that "the same" form of a species occurs in two isolated localities: a result which places its taxonomic status in a somewhat new light.

The balanced adjustment of the gene-complex within two geographical races is well illustrated by those which, after a presumed period of isolation, have extended their ranges and met. In these circumstances, it has several times been shown that the intermediates produced by crossing are restricted to a narrow belt, where the two original forms come into contact, instead of spreading and giving rise to a hybrid population. For, almost by definition, the mixture between two gene-complexes each harmoniously but differently adjusted by selection will be at a disadvantage compared with either one of them: a situation demonstrated, for example, by Sumner (1930) for the coastal and inland races of the mouse *Peromyscus polionotus*.

It is to be noticed also that the combination of two genes, each having advantages in certain districts, or races, may be subject to heavy counter-selection. Thus Bovey (1941), who has made an extensive geographical and genetic study of the European moth *Zygaena ephialtes* L. (Zygaenidae), shows that the form *peucedani* is found almost exclusively in the West (France) and the alternative one, *ephialtes*, in the South (e.g. Italy), though over considerable areas in Europe the two fly together. They are controlled on a unifactorial basis, *peucedani* being dominant. He also showed that red colouring is a simple and complete dominant to yellow. The *ephialtes* population may consist of mixed red and yellow specimens, but in some districts only the red are found and in others only the yellow. Consequently, it is clear that in nature either form or either colour may be at an advantage. Yet the gene for yellow colouring cannot satisfactorily be combined with that for the *peucedani* pattern, for yellow specimens of this form are always rare and local and are produced only where red and yellow *ephialtes* and red *peucedani* fly together.

We are at present almost completely ignorant of the effects for which particular genes are utilized in one geographical race and rejected in another or of what type of disadvantage accrues from combining certain of them. Those modifying the habits of the organism must be particularly important in the evolution of geographical races, but information is almost always lacking in regard to this sphere of their action, owing partly to the technical difficulties of studying it. Only in the few instances so far detected in which a gene affecting habit controls also some other easily recognized quality has it yet proved possible to follow its distribution. The best example is provided by the butterfly *Colias chrysotheme* Esp. (Pieridae). This species is monomorphic (yellow) in the male, and dimorphic (yellow or white) in the female. The white females are the less common and are simple dominants, the gene concerned being autosomal and sex-controlled. Hovanitz (1948) showed that it influences the habits of the insect, in addition to its colour, for the white females are more active than the yellow in the early morning and towards evening: they are also the earlier to emerge from the pupa (Hovanitz, 1944b). As might be anticipated, these effects adjust the polymorphism of the species in relation to its geographical distribution, for the white females prove to be relatively the commoner both at higher latitudes and higher elevations (Hovanitz, 1944a and c, 1945).

A balanced polymorphism provides a sensitive mechanism by which a species can adjust itself to the different environmental conditions which exist within its distribution, whether this be a continuous or a discontinuous one. The result may be a polymorph-ratio cline, as in the chromosomally controlled polymorphism of *Drosophila pseudoobscura*, so fully studied by Dobzhansky (see his general survey, 1951). In that species, a number of different gene arrangements in the third chromosome are found at all levels in the Sierra Nevada of California, but the frequencies of two of them are closely related to altitude; for "Arrowhead" increases from 25 per cent at 850 feet to 50 per cent at 10,000 feet, while "Standard" declines from 46 per cent to 10 per cent over the same vertical range. A similar but much more extreme polymorphism characterizes the entire and very extensive distribution of this insect in North America. It has now been shown that these arrangements of genes are of adaptive significance (Dobzhansky, 1948), a fact which the correlation of some of them with altitude itself demonstrates.

As already indicated, when a species occurs over a wide range in which the environment changes progressively, it tends to form a cline, while mere distance may allow the accumulation of genic differences and so initiate subspeciation. At the other extreme, the subdivision of a population into quite small isolated, or semi-isolated units, is favourable to its rapid evolutionary adjustment in different directions because of the diversity of environmental conditions to which the various colonies are exposed, and to each of which they can be adapted. Furthermore, marked fluctuations in numbers, to which such small groups are particularly liable, will greatly accelerate this process.

An intermediate situation arises in some larger habitats throughout which the environment changes not progressively but in an irregular way. This seems to be the one least favourable to rapid evolutionary modification, as the populations which colonize such places must be fitted to the average of the conditions which they include. Communities of this kind tend to be relatively alike when contrasted with the various adjustments which may be achieved by quite small isolated units, each of which can be more closely adapted to its own local conditions. A comparison between sets of these larger and more uniform, and smaller but more dissimilar, populations might, therefore, suggest the occurrence of genetic "drift" in the latter, though such a conclusion would be erroneous.

We are at present finding a situation of this kind in our work on female spotting in the butterfly *Maniola jurtina* in the Isles of Scilly, where we have examined the frequency-distributions of spot-numbers on several "small" and "large" islands respectively, the one type having at least twelve times the area of the other. The populations on the small islands have diverged widely from one another as judged on this character. On the other hand, those on the three largest islands are almost identical: a striking fact in view of the circumstance that small islands, whose populations have quite different values, lie between them (Dowdeswell and Ford, 1952, and in Press). The superficial parallel with the results postulated by the supporters of genetic "drift" as an agent in the evolution of small isolated or semi-isolated populations is sufficiently obvious. Yet we have good evidence of the selective importance of the genes which determine female spotting (Dowdeswell and Ford, *l.c.*), while several of the small populations involved are numerically so great as to fall quite beyond the possible limits claimed for the action of drift. Thus when actually estimated (in 1946), the largest of the three colonies on one of the small islands (Tean), comprised more than 15,000 individuals, while that on another of them, St. Helens, must be much larger.

Experimental analysis, on the lines exemplified by some of the examples quoted in this article, has been insufficiently applied to the study of geographical variation. Modern techniques are making it possible to obtain data on the isolating effects of minor ecological barriers, upon the genetics of local races, and upon the micro-evolution of small populations. Only with the further accumulation of results obtained by such means can the older concepts of geographical variation, obtained largely by the taxonomic study of museum specimens, be reinterpreted in the light of modern biological theory.

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J. B. S. HALDANE

The Statics of Evolution

EVOLUTION is a dynamical process. It is due to the joint action on populations, over very many generations, of various processes, including, probably, some of which we do not yet know. One of these is heredity, that is to say the process by which one or two parents produce offspring like themselves. Among its essential features is the reproduction, from genes or extranuclear bodies, of like genes or extranuclear bodies. Another such process is mutation, the name given to the fact that genes and the like are sometimes changed in such a way that they are reproduced in their changed form. A very fundamental one is selection, which means all those processes which ensure that organisms with certain sets of genes leave more progeny than those with different sets. We also have to consider the effects of migration, of the mating system, and so on.

The history of our ideas about evolution is very peculiar, as may be seen by comparing it with the history of our ideas on astronomy or geology. Newton, just as much as Ptolemy or Kidinnu, regarded the solar system as something given, whose changes were calculable, but which was essentially in a steady state. Newton was able to calculate the planetary positions for some time in the past and future, but looked to divine intervention, if necessary, to prevent the possible disastrous consequences of attraction between the different planets. Such intervention might be needed, he thought, to keep the system much as it is now. Laplace showed (or thought he had showed) that interplanetary attractions would not lead to any great changes in the present orbits of the planets, and, therefore, informed Napoleon that he was able to dispense with the hypothesis of divine intervention. In fact we do not know the very long-term effects of relativistic corrections to Newton's laws, but Laplace was right if we think in periods of the order of ten million years, and very probably if we think in periods of a thousand million.

It was reserved for Charles Darwin's son George to find a cause, namely tidal friction, which could produce large and progressive, though slow, changes in the solar system. Other causes have since been suggested.

Similarly in geology the statics of mountains, and even the rate of their erosion, were studied before it was realized that mountain ranges represent a stage in the fruitful conflict between erosion and orogenesis.

But heredity was not well understood when Darwin wrote. Both Lamarck and Darwin greatly overestimated the importance of mutation (though, of course, they did not use this word for the environmental effects which they believed to be inherited on a very large scale). And natural selection as an influence which may change a population was first seriously discussed by Darwin, who had to invoke it in order to explain evolution in which he had been led to believe on other grounds. Only in recent years had it been observed and measured.

In fact, evolution is an almost unimaginably slow process. Darwin in the first edition of *The Origin of Species* gave a scale nearly three times too long. He later omitted the passage in question (p. 244 in Watts's reprint). In fact he was much more nearly right than his contemporaries. Haldane (1949a) has given some measures of the actual rate. In fairly rapidly evolving lines like the dinosaurs and the ancestors of the horses, measurable lengths, such as those between homologous points on homologous teeth or body lengths in general, changed by quantities of the order of 1 per cent to 10 per cent per million years. For a ratio of lengths, which can be regarded as a measure of shape, 2 per cent is a representative figure. In a few cases, such as human skull height, and the size of eocene nummulites, the rates were a good deal quicker. Often they were far slower.

This means that no measurable evolutionary changes are to be expected in most species in 10,000 years, let alone in a human lifetime. Such changes as occur in these short periods are likely to be reversible, like the contemporary retreat of the glaciers or the marine flooding of the English Fens in Roman times.

This extreme slowness might be due to two causes. The "forces" at work might be extremely small, like the effect of tidal friction on the earth's rotation. Or they might be large, but nearly in equilibrium. Both these alternatives are true in different cases. Thus natural mutation by itself can only change a population slowly. If we suspend natural selection by giving mutants as good a chance to breed as the "wild type" of a species they will spread at rates of about 10^{-5} per generation. To get rapid changes (say within ten generations) we must reverse the process of natural selection by artificial selection in favour of the mutants. On the other hand, natural selection is an intense "force." It can and does change a population cyclically in the course of a year where generations are about monthly. But it consists of many components, which on the whole balance one another.

In the bulk of this essay I propose to neglect evolution, as being a process almost unobservable in a lifetime, and consider the processes which bring it about as being, at any moment, almost in equilibrium. Actually, evolution is probably proceeding with unparalleled speed at the moment. After the series of violent climatic changes of the Pleistocene, man has altered the ecological conditions of most animal and plant species, including his own. In spite of this I believe that the approximate equilibrium deserves investigation.

Within any population of any species we find variation. Some of it is due to environmental differences during the lifetime of the individuals concerned. These differences are rarely inherited when the progeny is placed in a uniform environment; but they are sometimes inherited, polyploidy in plants being a conspicuous example. If they are inherited, they have to pass the test of natural selection.

Other differences are inherited, often according to Mendel's law. These are most conspicuous in polymorphic species such as the snails *Cepea nemoralis* and *hortensis* with their wide range of colours and patterns. But immunology makes it clear that the members of most, if not all, species of mammals and birds differ in the make-up of their antigenic colloids to such an extent that grafts are very rarely possible from one individual to another, and that the differences between the antigens are determined by genes and not to any measurable extent by the environment.

Metrical characters like length of tail or life, number of hairs per square centimetre or of mistakes made before a task is learned, are usually found to be determined both by nature and nurture, that is to say by inherited genes and plasmatic bodies, and by the environment of the individual. We have very inadequate data except on men and animals living under artificial conditions, but it seems likely that in most cases both nature and nurture contribute enough to variation for neither to be negligible, and in several cases in poultry the heritability of a character is nearly a half, that is to say they are about equally important.

Why does this congenital element in variation persist? That is the central problem of evolutionary statics. Darwin thought that it was largely due to variations in the environments of immediate ancestors. But if so it would not persist for many generations when the environment was made more uniform. Fisher (1930) pointed out that Mendelian inheritance ensures that in so far as a character is genetically determined, its variance will be conserved under random mating, and under some types of partial inbreeding, in a large population, provided that it confers no selective advantage. Some types of plasmatic inheritance, by the way, have the same effect. Fisher's remark is true and important, but it only applies to selectively neutral characters, that is to say to characters which are of little evolutionary importance. It is, like the uniform motion of a body under no forces, a prerequisite for further discussion, but it no more explains the conservation of heritable variation in important characters like stature than Newton's first law explains why rivers keep on flowing. If there is an optimum size in a given environment, why does not natural selection make populations uniform as regards the genes which determine it? Why, in general, is there any genetical diversity except as regards characters, if such exist, which are of no selective value?

This question has been answered, though there is no reason to suppose that the answer is complete. Before giving the answer, we may make the elementary point that natural selection weeds out extremes. For example, ducks' eggs or human babies much lighter or heavier than the average are less viable than those of average weight. The fact that the optimum is usually near the mean implies that the population studied is nearly in equilibrium under natural selection.

The factors which are responsible for genetical variation include the following:

1. Spatial clines.*—If genotype α is suited to environment A and β to environment B, two things may happen. If mobility is low, each genotype may persist in some or most of the environment in which it is the "favoured race," with a zone of hybrids, which may or may not be intermediate, between them. If mobility is relatively high, one of the genotypes may disappear. Geographical clines are well known, and are probably stable. We know much less about the topographical clines between plant varieties in comparatively close localities where, as Gregor (1946), for example, showed, different ecotypes may exist. The danger that a minority may be swamped by hybridization may be serious, and too great mobility of pollen or seed in plants, or of animals at any stage of their life cycle, must prevent the formation of such local ecotypes. This is, perhaps, one reason why plants and animal species which migrate with great difficulty persist in competition with species which do so readily.

Another type of cline is found where the characters determined by α and β are not obviously adaptive, but produce a hybrid less fit than either. This is so when α and β differ in respect of an inversion, a translocation, or otherwise cytologically, or in respect of an antigen, like the D antigen at the Rh locus in man, which produces incompatibility

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* This word, due to J. S. Huxley, has passed completely into the vocabulary of biology. One cannot pay a colleague a greater compliment than to assume that every reader is familiar with what was once his original idea. To give a reference implies that it requires explanation.

between mother and foetus. A similar case must arise when α and β differ in respect of evocators of responses (e.g. epigamic characters or innate courting behaviour) and in the innate capacity for response to such characters or behaviour. Thus Seitz (1948) found that males of *Tilapia heudeloti* and *T. natalensis* display at females of either species, but females normally respond only to males of their own, apparently on a basis of colour differences. The differences may not be sufficient to sterilize the hybrid on the one hand, or prevent mating altogether on the other. If not there will be a zone in which hybrids probably less fit than either "pure" race occur. Clearly such races are possibly incipient species, as a sufficient number of such differences would isolate them completely as regards mating. The important point, which I owe to conversation with Dr. H. Spurway, is that the characters concerned need in no way be adaptive. α and β might thrive just as well if they were transferred to environments B and A, but the cline would persist. Thus we see a possible origin for some of the differences between related species which many systematists regard as non-adaptive.

2. Temporal clines.—In the course of evolution some genes are replaced by their allelomorphs. It seems possible that genes for a major character, say hair density, may be replaced rather rapidly in response to environmental change, but that this is followed by a much slower replacement of genes at many other loci which yield an organism better physiologically balanced. If this is so replacement of this kind may be going on, and account for a good deal of minor diversity as regards genes of slight selective advantage. It is clear, however, in view of the slowness of evolution, that this particular cause of diversity is hypothetical, except for Lepidopteran melanism over short periods.

3. Heterosis.—In some cases the heterozygote for a pair of genes may be fitter than either homozygote. This may merely be because it gives an optimal value for some particular metrical character. But Wright (1935) showed that this cause could only keep one locus segregating for any one character, e.g. stature. A more general reason may be as follows: When each of a pair of allelomorphs makes a substance, say an enzyme, it may be advantageous to have a mixture of two enzymes with slightly different capacities (e.g. pH optima), thus rendering the organism more adaptable. If the heterozygote is fitter than either homozygote, both genes will persist, unless inbreeding is heavy, even when one is lethal. The same is true for structural differences between chromosomes. Thus *Drosophila pseudoobscura* populations are generally polymorphic for inversions in one chromosome, *Drosophila subobscura* for inversions in three. In a few plants such as *Oenothera* species almost all individuals may be heterozygous for an elaborate system of translocations.

4. Sexuality and Self-Sterility Factors.—Most animals are polymorphic for sex. In hermaphrodite plants and in ciliates a species may have anything from two to several hundred "mating types," a member of each of which is more or less completely sterile with members of its own type, but fertile with some or all of the others. This diversity may be determined by genes at one or more loci, or as in some ciliates, in ways not fully understood. Such a polymorphism is on the whole stable. On the one hand the rarer is a mating type the less is the chance that two members of it will mate or attempt to do so, so it will tend to become commoner. On the other hand a genic change producing self-fertility will expose the self-fertile organisms to the dangers of inbreeding. Nevertheless, the work of Crosby (1949) suggests that in special circumstances such genes may spread in nature, and a self-sterile species become self-fertile. It is at least possible that sexuality and self-sterility mechanisms encourage the other types of polymorphism. Polymorphism in one sex only is not uncommon in insects.

5. Where sex is determined by a chromosome some genes show the classical type of sex-linkage. Where males are haploid, all genes do so. A sex-linked recessive raising the fitness of males (or whichever sex is heterogametic or haploid) will spread to some extent even if it very seriously lowers that of females; and an equilibrium is possible, even though at a later stage a suitable "switch mechanism" may convert the character in question into a sex-limited one. This case is, however, still hypothetical.

6. Conflict between Mutation and Selection.—A large number of the rarer human congenital abnormalities are "dominants," the homozygous mutant being unknown or lethal, the heterozygote abnormal. Others are sex-linked recessives. The genes in question are rapidly eliminated by natural selection, new ones appearing by mutation. It can be shown that unless the mutation rate changes rapidly, equilibrium is soon reached. For autosomal recessives the same process occurs, but much more slowly. These genes may be lethal, or reduce the viability to 25 per cent or less of the normal. But a precisely similar equilibrium must be reached if they only reduce it by 1 per cent or less, except that in this case the abnormal condition cannot be very rare.

It is at least possible that a good deal of the "normal" variation in a species is due to this cause. This possibility will be considerably increased if the statements of the modern Russian school are confirmed. Unfortunately the data on which these are based are not translated into languages which I understand; but it appears that they claim to have obtained adaptive inheritable changes in a number of plants. It is probable that genes which for any reason are induced to greater or less activity than usual might alter in consequence, such alterations being particularly likely to appear as mutations in the germ line where, as in higher plants, the germ cells are directly descended from the highly active cells of the growing point. If so the genes, or whatever else is the material basis of such mutations, would be sources of variation in the Darwinian sense, but being adapted to abnormal conditions, would be eliminated by selection if they did not mutate back to normality in a normal environment.

Even if mutation rates are seldom as great as 10^{-4} per generation, and often less than 10^{-6}, there must be large numbers of mutant genes due to recent mutation in a population. Thus if 1,000 loci each had a mutation rate of 10^{-6} to recessive mutants with a fitness of 0·99, each of these recessives would have a zygotic frequency of 10^{-4} in a random mating population, a gametic frequency of 0·01, and an average individual in an outbred species would be heterozygous for twenty of them. Judging from the frequency of visible recessives on inbreeding wild *Drosophila* this may well be the case. How much of the variation found in a metrical character is due to this cause is quite unknown.

7. Selection by Labile Pathogens.—The genetics of the immunity of wheat to rusts (especially *Puccinia graminis*) has received much attention. A particular genotype can be immune to one strain of a rust but susceptible to another. The difference frequently depends on a single gene substitution. After a type of wheat immune to all the local types of rust has been widely bred for some years it is often found that a new type of rust arises which can attack it. We do not know whether the new rust has appeared by immigration, mutation, or genetic segregation.

In a natural population of hosts and pathogens composed of many genotypes there will be selection for pathogens adapted to common biochemical types, and against those only adapted to rare ones. The selection among the host plants will be in the opposite direction. Thus both host and pathogen will constantly alter their prevailing genotype, in so far as it affects the host-parasite relation. The same is probably true of animals and their parasites. This process will favour a diversity of types in the host, and probably in the pathogen also. It is, perhaps, too rapid and too reversible to be regarded as evolution, but it cannot be without effect on evolution, particularly by favouring divergence of separated populations. Haldane (1949b) has some further remarks on this topic.

8. Non-Darwinian Selection.—The above is a particular case of what I venture to call non-Darwinian selection. Darwin wrote of "favoured races," where we should now write of favoured genotypes. However,

the relative fitness of two genotypes may depend on their frequency. This is so for the Rh locus in man, where the rarer gene is at a disadvantage. In a social animal some genetic diversity may be desirable, but there is an optimal frequency for a particular type. In some cases such a situation may lead to equilibrium; but we know too little as yet to specify them.

Mimetic polymorphism may be due to this cause. If a mimic devoid of unpleasant taste is rare compared with its unpleasant model it will rarely be eaten. If it is commoner, predators will have to kill a number of both species before (if ever) they learn to avoid the pattern common to them. Thus if mimicry confers some slight disadvantage, for example, in lowering sexual recognition, a balance may be struck, mimics only forming a fraction of the potentially mimicking species. This case is, however, still hypothetical.

Another case of this type which may not be very rare occurs where a gene influences the haploid generation in a higher plant and also the diploid generation or the triploid endosperm, one influence being favourable, the other unfavourable. Here a balance may be struck if the unfavourable zygotic character is recessive.

9. Non-Mendelian Inheritance.—If the mechanism of segregation is so disturbed that a heterozygote does not produce equal numbers of the two types of gamete, it is clear that one gene or chromosomal arrangement will tend to spread at the expense of the other. Such cases have been observed in mice for lethal "genes" at the brachyury locus (Chesley and Dunn, 1936), in *Drosophila pseudoobscura* for the abnormal X-chromosome associated with abnormal sex ratios (Wallace, 1948), and for a fragment in *Secole* (Östergren, 1945). In each of these cases the gene or chromosomal arrangement favoured by segregation lowers fitness, and an equilibrium is reached. But in other cases selection may be unable to check such a spread. If so such a process could lead to the degeneration or extinction of a species.

10. Neutral Genes.—If there are selectively neutral genes their frequencies will be determined by mutation rates. If, which is much more probable, there are genes whose selective advantage or disadvantage is numerically smaller than their mutation rates, frequencies will mainly depend on the latter, but the progress to equilibrium will be a matter of millions of generations, and will constantly be interfered with by chance effects.

My own very tentative opinion is that heterosis will be found to be the main cause of genetic variation within most species. I may be prejudiced by having worked with *Drosophila subobscura* in which structural heterozygosis is almost, if not quite, obligatory. Heterosis is clearly not a major cause of variation in self-fertilized plant species, or in animal species broken up into very small endogamous groups. Nevertheless, the devices for cross-fertilization in so many plants are evidence for its importance; but very much more work is needed before any general conclusion can be reached.

If the views here stated are true, much of the rather speculative human biology which passes under the name of eugenics will turn out to be incorrect. Various types of human being, such as giants, dwarfs, idiots, saints, mathematicians, murderers, and musical composers, are rare, and there is evidence that, in a given social background, membership of each of these classes is to some extent genetically determined. The innate endowments needed in a first-rate musician or mathematician are obviously rare. We should like to make them common. It is doubtful whether such an attempt is likely to succeed until we know how rare they are in fact, and still more why they are so rare. Part of the reason is almost certainly that exceptional genotypes are relatively infertile. This does not mean that natural selection is so altering populations that they are becoming rarer (though this is, of course, a possibility). It seems to me that the best provisional hypothesis is that populations are nearly in stable equilibrium as regards the genes concerned. If so we have less to fear from the sterility of highly endowed types and less to hope from eugenics than has often been thought. I do not suggest that the problem of eugenics is insoluble. But I suspect that contemporary programmes for its solution may be no more likely to succeed than was Leonardo da Vinci's flying machine.

Wright (1949) in a series of papers of which the citation gives a bibliography, has pointed out that in small populations all allelomorphs but one at any locus may be lost by chance. Thus a species broken up into small endogamous populations will tend to consist of favourable combinations of genes occupying "adaptive peaks." Fisher and Ford (1947) have attacked this conception. It appears, however, to have at least a greater validity than Fisher's "conservation of variance," and in fact Fisher (1922) calculated the rate of disappearance of heterozygotes with a comparatively negligible error. Fisher, however, seems to hold that isolated populations are generally so large that the effects postulated by Wright would act so slowly that immigration and other causes would overcome them.

Weber's (1950) results on local mouse populations appear to support Wright's view, but the matter will possibly be settled when the antigenic variation in a natural species has been studied as closely as that of men and cattle. If members of local populations are commonly found to be alike in antigenic structure while the populations differ between themselves, it will be hard to doubt the substantial truth of Wright's views. If the opposite is found to be the case, it will appear that their importance has been exaggerated.

Spurway (1953) believes that this process has been particularly important when species extended their area. The first few individuals to cross a barrier would leave relatively vast numbers of progeny, and if they carried inversions or translocations, these would become too well established to be swamped by later migration, even if the later migrants brought in new genes. This extension of Wright's theory will probably stand or fall with the main theory.

Let me emphasize one point, the intensity of natural selection in populations is approximate equilibrium. Haemophilics have about a quarter of the chance of normals of leaving offspring, achondroplasics less than a quarter. The fitness of females homozygous for the sex ratio "gene" in *Drosophila pseudoobscura* is about 39 per cent of the normal at 16·5 °C, 5 per cent at 25 °C. But haemophilia has persisted, though as a rarity, for at least two thousand years, and the frequency of the sex ratio inversion in natural populations may be as high as 30 per cent. We are not dealing with slow processes, but with processes which, if not opposed, could radically alter a species in a hundred generations. This means that it is entirely possible to measure the intensity of natural selection in a natural population, provided that it is approximately balanced in one of the ways listed above, or perhaps by some other process not as yet understood. The work of Cain and Sheppard (1950) offers a beautiful example of such a measurement, as yet unfortunately on such a small scale that the measurement lacks precision. Animal colorations are often protective in a given environment, but laboratory experiments will never measure the intensity of selection for coloration in nature. It is important to know that, say, owls will pick out 20 per cent more light than dark mice out of equal numbers against a given background. If 10 per cent of all mouse deaths were due to owls this would give an increased death rate of 2 per cent in the light mice, if only 1 per cent were so killed the difference would only be 0·2 per cent. On the other hand Sheppard (1951) found that of marked snails released in a wood 3·4 per cent were killed by the thrushes in forty days, the yellow snails being predominantly killed when the background was brown, the brown snails when it was green. Until such populations have been followed through several years the intensity of selection cannot be measured, but it probably exceeds 1 per cent per snail generation, and might possibly reach 10 per cent. It is not impossible that such changes did occur with a rapidity of this order when the first fish left the water, and they are probably happening now in domestic animals.

Once a few "main" genes have been altered, so as to produce a type of organism which can perpetuate itself in a new environment, hundreds or thousands of other genes will probably change their frequencies more gradually, making the original change less and less readily reversible as a more harmonious type of organism is built up. Perhaps only when this process is over—and it may take millions of years—is adaptive radiation in the new environment likely. Such "quantum" evolution, as Simpson (1944) calls it, is doubtless rare, but it may have happened. The more normal process is far slower, and will be harder to imitate experimentally.

I believe (thanks to the arguments of Dr. H. Spurway) that one of the most hopeful fields for the study of evolution is in the domestication of animals and perhaps also of plants. It appears to be a common observation that only a few out of a number of specimens of a species captured will breed in captivity. Here we at once have at least a *prima facie* case for intense selection. The subsequent morphological changes may be very rapid (cf. Castle, 1947). They are a response (whether selective, as I think, or Lamarckian) to the new environment, and occur whether or not there is conscious artificial selection.

I have, however, strayed from my chosen topic. I have tried to present a species as something in equilibrium under fairly intense "forces." The struggle between selection for fertility and longevity, for example, may be an intense one, in the sense that different genotypes of nearly equal net fitness differ greatly in these respects. Palaeontology suggests that over long periods the equilibrium may be altered very gradually. Gene frequencies will slowly alter, and allelomorphs be replaced by others with very similar effects, for example the different members of the Agouti series in related rodent species and subspecies. But the very fact that the equilibrium is between processes which can produce very rapid change suggests that it may sometimes be upset, as a mountain can be produced by a million years of folding and ten million of erosion, but also by ten years of eruption.

I am quite sure that our views on evolution would be very different had biologists studied genetics and natural selection before and not after most of them were convinced that evolution had occurred; and even now it may sometimes be worth while seeing what sort of picture we should form if we considered the statics, rather than the dynamics, of populations.

ADDENDUM, NOVEMBER 1952

I think that the observed fact of heterosis may prove to be an important key to the understanding of evolutionary progress. Evidence is accumulating that different allelomorphs at the same locus make slightly different types of large molecule (antigens and enzymes in particular). Thus selection for heterozygosis means selection for greater biochemical complexity. In particular since different genes are active in different tissues, and perhaps even in the same cell at different times, it means that there is selection in favour of greater differentiability and greater adaptability of cells. Apart from special cases like *Oenothera*, selection for heterozygosis can only achieve the optimal biochemical complexity in a tiny minority of a species. But duplication of whole chromosomes or of chromosomal sections can achieve it in all members. The former process seems to be commoner in plants, the latter in animals.

Here then we have an evolutionary process, discovered by Darwin, which offers an explanation for progressive evolution or "aristogenesis" as a result of natural selection. Outbreeding has of course the further function of allowing recombination of genes. This is its only function in such Protozoa as *Paramecium* which rapidly become homozygous by autogamy, since they have no possibility of tissue differentiation. In multicellular organisms it has the further function indicated above.

From this point of view we may say that in every case where heterosis keeps each of a pair of allelomorphs in existence the species is waiting for the possibility of evolving in such a way that every member of it may possess both the genes in question. This possibility is only given by a suitable cytological change. If it is correct that when such a change has occurred, one gene can be used in one tissue, the other in another tissue, a mutation inactivating either of them will cause homoeosis (e.g. *proboscipedia* in *Drosophila melanogaster*).

On this view then, heterosis is seen not merely as the index of a conflict between selection and segregation, but as a condition now found in some members of a species, but foreshadowing an evolutionary possibility for all its descendants.

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A. C. HARDY

Escape from Specialization

AT one time or another we must all have imagined ourselves possessed of some Olympian power enabling us to look down and see the whole past course of evolution spread out before us as branching lines of succession. We shall have succeeded in forming a picture of the mighty spectacle only if we have thought of it in a highly artificial and diagrammatic fashion, and not attempted to visualize the sequence of the vast populations which have swarmed upon the earth in turn; we must have represented them by lines of individuals: samples of each race taken at intervals as they are gradually modified with the passage of time. If we imagine ourselves viewing evolution like this we shall have a vision of countless streams of life dividing again and again into new avenues as they advance from the past towards the present; but we shall also see that there are quite as many lines coming to an end as there are new ones branching out. At some points in time, in periods of great change, we shall see many more lines dying out than new ones beginning; such periods, however, are usually followed by others of innovation and rapid adaptive radiation, as when the great outburst of mammals followed the speedy decline of the reptiles at the end of the mesozoic era.

Julian Huxley in his essay on *The Uniqueness of Man* sees the process in a particularly vivid way; he sees it as a maze in which the animal kingdom has been caught; and suggests that there is now only one way out to future progress: that which man is taking. Every other path is thought of as having led to too great a specialization and so being closed to further advance. "Evolution," he writes, "is thus seen as an enormous number of blind alleys, with a very occasional path to progress. It is like a maze in which almost all the turnings are wrong turnings. The goal of the evolutionary maze, however, is not a central chamber, but a road which will lead indefinitely onwards."

I would indeed seem ungracious if my contribution to this volume were thought to be put forward in any spirit of attack upon Dr. Huxley's suggestion. I agree with him that Man, now in a unique position, may well modify the world to such an extent, and so dominate all lower forms of life, that the initiation of other new major lines of evolution may now become impossible. What I want to question is the idea that all other paths in the maze, leaving out the question of man's possible interference, are really blind alleys; in other words, I am doubting whether specialization must inevitably lead either to the extinction of the race or to its stagnation in the path of progress. In doubting this I am not of course criticizing Huxley's opinion in particular; he has given us a most graphic representation of the widely accepted view that specialization must lead to a dead-end from which there is no escape.

The views I wish here to discuss are not really my own, but are those of my father-in-law, the late Professor Walter Garstang; I wish to stress them here because their full significance for evolution theory has so far, I think, been realized by only a few. It must of course be true that times out of number specialization has indeed led to an evolutionary *cul-de-sac* or even to racial extinction; occasionally, however, a very unusual process has intervened and enabled one line or another to escape from such an ending and pass on to quite another road: perhaps to progress and radiation. How can it be done? Can evolution be put into reverse so that the race retreats backwards away from specialization down the pathway up which it came? Not exactly, but something very like it. Garstang has shown us the key with which such animals may sometimes escape from the maze; it is to be found in his conception of paedomorphosis linked with that of neoteny. I think it likely that some of the most successful advances in evolutionary progress have been due to this factor and that some of the major groups in the animal kingdom might never have been evolved without it. The thesis I wish to argue is the suggestion that this element is in fact one of cardinal importance in the general process of evolution and especially in the field which G. G. Simpson would call mega-evolution.

Garstang came to find this key through his rejection of Haeckel's so-called "Biologentic Law" or the theory of Recapitulation, and this rejection in turn was primarily due to his great interest in the pelagic larvae produced by so many different kinds of invertebrate animals living on the sea-bed. He could never believe that the trochophores, veligers, plutei and the like could represent ancient and relatively simple ancestral *adult* forms which had once been entirely planktonic and only later taken to a benthic life and evolved into worms, molluscs and other invertebrate stocks. When Garstang was beginning to revolt against the Haeckelian doctrine MacBride had just published his *Textbook of Invertebrate Embryology* (1914). At the beginning of his book MacBride writes:

"If this 'law' (i.e. Haeckel's) can be substantiated the interest in embryology becomes immense, it binds all the innumerable phenomena of development into one coherent scheme, and opens the door to the hope that we may yet be able to sketch the main history of life on the earth." At the end of his book, which treats pre-eminently with these planktonic larval forms, he gives judgement as follows: "The first and most far-reaching conclusion we may draw, is that, in general, the *larval phase* of development represents a former condition of the *adults* of the stock to which it belongs." Many zoologists at that time held such views, but not Garstang. As an undergraduate attending the Easter vacation course at the Plymouth marine laboratory in 1920, it was my good fortune to hear a remarkable impromptu lecture he gave to the class on the significance of these marine larval forms. He left us in no doubt that they, far from representing ancestral types, were special developmental adaptations thrown up by sessile bottom-living creatures to spread the species far and wide in the ocean currents, just as rooted plants may scatter their seeds in the winds. In making a survey of the larvae of many different groups he pointed out how in each there is a compromise and adjustment between two rival needs—or, in other words, two competing selective advantages: on the one hand to grow up into the adult so as to reproduce the species as quickly as possible, and on the other to remain floating as long as practicable so as to distribute the species over the widest possible range. He was one of the first to see that selection will be acting just as powerfully upon the developmental stages as upon the adult end-product. The young stages, varying as much as the older ones, may be modified in quite a different direction from that in which the adult structure is adapted, especially if larva and adult inhabit two very different zones of life; the greater the contrast, the greater, of course, will be the metamorphosis involved.

Garstang realized, before anyone else, the profound influence which such larval adaptations might have on the course of evolution; it was this that brought him into conflict with the many who still firmly believed in Haeckel's ill-named "law" and thought of evolution only in terms of *adult* forms. Did not evolution consist in always adding something new to the adult end of development, and was not development gradually compressed, as it were, or speeded up, to make room for each new addition? So thought the recapitulationists who looked upon development as the rapid passage of the organism through a sequence of slightly modified past adult forms. Garstang led the revolt in his paper to the Linnean Society in 1922 (published 1923). Here he called zoologists back to the almost forgotten laws which the great Von Baer had propounded just a century before: laws which expressed the view that the life-histories of animals along their whole lengths tend to deviate more and more from the course of development which was followed by a distant ancestor. In his paper he used the term *paedomorphosis* for the first time; in it he crystallized the new idea which came to him: the idea that the adaptations to larval or young life might not only have a profound influence on the adults of the race but upon the whole future evolution of the stock. "Ontogeny," he boldly says, "does not recapitulate Phylogeny: it creates it."

The importance of the idea of paedomorphosis was only dimly foreshadowed in his paper of 1922; he gave the first striking example of it in his famous paper on "The Morphology of the Tunicata and its bearing on the Phylogeny of the Chordates" which he published in 1928. Here he put forward his view that the Chordates were derived by paedomorphosis from the pelagic larval forms of a *sedentary* invertebrate animal; and that the modern Ascidians are *not* degenerate animals, as was usually held, but are living much as the original ancestors of the group must have lived: sending up their pelagic larvae to spread the species far and wide. Here he coupled the idea of paedomorphosis with that of neoteny—the acceleration of the development of the reproductive organs in relation to the rest of the body so that the animal becomes sexually mature in a larval condition. He imagined the sessile, perhaps somewhat echinoderm-like ancestor of the Chordates sending up its planktonic larvae and then he imagined these larvae being subjected to the two rival selective influences already mentioned: one tending to keep it afloat as long as possible for purposes of distribution and the other tending to accelerate the development of the gonads. He imagined these larvae becoming equipped, as indeed are the larvae of the modern ascidians, with a tadpole-like muscular tail which is a more powerful swimming organ than the ciliated bands with which such larvae are usually provided. He imagined this more efficient active larva prolonging its pelagic phase and actually becoming sexually mature by neoteny while still swimming in the plankton; thus he supposed that the stock, after long periods of time, became one in which the adults never settled down on the bottom at all! Evolution takes the remarkable step—or rather stride—from an apparently lowly sedentary form to become an active free-swimming type: the forerunner of a new race to lead on to the vertebrates—to fish—to man.

Instead of past adult forms determining the course of development of later members of the race as the recapitulationists believed, we see it suggested that larval novelties may give rise to a new major line in evolution. A monstrous piece of speculation some may say. Speculation, no doubt, it is—but no more so than the idea of recapitulation—and moreover it is based upon a much more substantial array of facts. There is one group of tunicates, the Larvacea, which has every appearance of having been evolved in just the same way in which Garstang supposed the chordates as a whole to have come into being; they are little tadpole-like forms not dissimilar to the larvae of the typical sedentary ascidians, but they have become sexually mature while still swimming actively in the plankton and they never develop further. They are the little forms such as Oikopleura which secrete their marvellous "houses" of jelly which serve as most complicated filtering devices for sieving out from the water the very finest living particles on which they feed. There can be no reasonable doubt that the Larvacea at any rate, as their name implies, are modified larval forms; they are neotenous. There *is* some doubt as to whether they were so derived from the larvae of the typical bottom-living ascidians or, as Garstang himself believed, from the larvae of those forms such as the Doliolids which as adults have themselves taken to a floating pelagic life; this, however, is a detail compared with the importance of having a case exactly parallel to that of the supposed origin of the chordates in general. Some may object to the parallel on the grounds that the Larvacea are but a small specialized group; if a naturalist from some other planet had visited the earth and seen the little paedomorphic chordates in their very early days he might well have failed to see any future in them.

For those who are not zoologists perhaps a brief digression to give a more familiar example of neoteny may be desirable to make Garstang's ideas clearer. The North American Salamander *Amblystoma tigrinum* in its fully developed condition, as found in the United States, has lost its gills, breathes by lungs and spends most of its time on land; in Mexico, however, this same species usually becomes sexually mature and breeds in a condition of body which is really larval: this is the Axolotl, which keeps its external gills and its gill-slits and remains in the water. This condition of neoteny is brought about in some cases, as here, by a relative retardation in the rate of development of the rest of the body as compared with that of the reproductive organs, or in others by the reverse process of an acceleration in the development of the latter; the result is the same. In the Axolotl we see a species which is only partially neotenous, for it may be converted, either in nature or experiment, into the fully adult *Amblystoma*. Some other newt-like forms such as *Necturus* and *Proteus* are permanently in the neotenous condition; here we see an evolutionary step brought about by the fixing of this change in the relative rate of development of body and gonads. It has been known since the work on sex determination in the gipsy moth by Goldschmidt and that on the development of the eye-coloration of the amphipod crustacean *Gammarus*, by Ford and Huxley, that Mendelian genes can affect the *rates* of different developmental processes: accelerating or retarding the appearance of some characters or parts of the body in relation to others; this explains the mechanism of neoteny.

Let us now return to Garstang's view on the origin of the chordate or vertebrate stocks. He did not imagine that the main chordate stock arose from ancestors which were actually like the modern ascidians; he believed, however, that the ascidian tadpole gave the clue. As long ago as 1894 he had made a most illuminating comparison between the early chordate embryo and the larvae of the echinoderms. He had not at that time suggested the origin of one from the other by paedomorphosis; he had then only stressed their similarity and likely relationship. In his great paper of 1928 he suggested that the chordate stock had arisen from some invertebrate ancestor in the far distant past which had had a common origin with the echinoderms on the one hand and the ascidians on the other. So important is this contribution to zoological theory that I shall emphasize it by quoting an excellent appreciation of it in Dr. de Beer's book *Embryos and Ancestors* (pp. 52–4):

> Garstang was the first to look for the trace of the ancestors of the vertebrates in early instead of adult stages of invertebrates; and he focussed his attention on the larvae of Echinoderms (starfish, sea-urchins, sea-cucumbers, etc.). He showed that if the ciliated bands on the larva (auricularia) of a sea-cucumber were to become accentuated and rise up as ridges leaving a groove between them, and if these ridges were to fuse, converting the groove into a tube, a structure would be produced which has all the relations of the vertebrate nervous system, including such details as the neurenteric canal. Not only this, but the two modifications of the vertebrate nervous system which are found in Amphioxus and all higher forms on the one hand, and in sea-squirts on the other, can be based on differences which are found in the disposition of the ciliated bands on different kinds of Echinoderm larvae. This theory of the origin of the vertebrate nervous system has several advantages. In the first place it avoids the difficulties which beset any attempt to derive it from the existing nervous systems of any other invertebrate. It also agrees with the principle of neurobiotaxis, according to which a concentration of nervous tissue takes place in the region of greatest stimulation. If the ancestors of the vertebrates had crawled about on their ventral surfaces like most invertebrates, one would expect their nervous system to be ventral, like that of most of the invertebrates. But the nervous system of vertebrates is dorsal, and it is precisely the dorsal side of the body which would receive the greatest stimulation in a form swimming freely in the sea, the stimuli being the rays of light penetrating through from the surface. Not only is the auricularia free-swimming, but it bears an unmistakable resemblance to the tornaria larva of *Balanoglossus* and *Balanoglossus* is an undoubted relative of *Amphioxus* and the early vertebrates (or chordates as they may more correctly be termed). But the resemblance between the Echinoderm larva and the chordate goes further still, for the former has an adoral ciliated band formed partly from the inner layer of the body; and in a corresponding position the chordates have a ciliated band called the endostyle, which is looped in the same peculiar

> manner as the other. The middle layer of the body arises in three tiers or segments in the Echinoderm larva and in *Balanoglossus*, and indications of this tripartite arrangement are present in *Amphioxus*. Further, the body-cavity of the Echinoderm larva is in communication with the outside by a pore, as in *Balanoglossus*, *Amphioxus*, and several other chordates. In fact, if the nervous system and endostyle are formed in the way suggested, all that is required to turn the Echinoderm larva into a chordate is the formation of the notochord and the piercing of the gill-slits.

de Beer more than anyone else has recognized and acknowledged the importance of Garstang's conception of paedomorphosis and has himself coined another term to stand beside it—gerontomorphosis—to signify evolutionary changes brought about by modification of adult structures. His brilliant book *Embryos and Ancestors* (called *Embryology and Evolution* in its original form) is largely a discussion and analysis of those two factors in the process of evolution. To paedomorphosis he assigns the larger steps in the course of evolutionary change and to gerontomorphosis the smaller ones.

Professor J. Z. Young declares strongly in favour of Garstang's views in his *Life of Vertebrates* (p. 74):

> The problem which remains is in fact not "How have sea-squirts been formed from vertebrates?" but "How have vertebrates eliminated the sea-squirt stage from their life-history?" It is wholly reasonable to consider that this has been accomplished by paedomorphosis. . . .
>
> Larva and adult, it must be remembered, possess the same genotype; the remarkable feature in all animals with metamorphosis is the difference between the two stages, not the similarity. Any characteristic may appear at either larval or adult stage or be transferred by evolutionary selection from one to the other. There is no serious objection to the view that the early adult free-swimming chordates arose by paedomorphosis of some tunicate-like metamorphosing form. If the creatures abandoned the habit of fixation it would be possible for characters previously present separately in larva and adult to become combined in a single stage. This is indeed what has happened in the Appendicularia (Larvacea).

Garstang's ideas, although they cannot be proved to be true in any particular case, have enabled us to see that specialization need not always be the end of evolutionary progress. However specialized the *adults* of a stock may have become in relation to life in some particular environment, it is still open to their young stages to become modified in some quite other way and then by neoteny to produce a new paedomorphic line leading perhaps to a quite new type of animal—perhaps a new Order, Class or even Phylum. It may be of interest to bring together in one brief review the other more important possible instances of this.

For more than a century two opposing views have been held as to the nature of those remarkable animals the Siphonophores: on the one hand there has been the "poly-organ" or "medusome" hypothesis which supposed them to be highly developed medusae complicated by secondary budding, and on the other "the poly-person" or "swimming hydroid-colony" hypothesis. In a very thorough analysis of the problem, bringing together a great array of facts, published only two years before his eightieth birthday, Garstang (1946) does not favour either view but comes to a new and original interpretation. He shows that there is more than a superficial resemblance between the conaria larva of *Velella* and the developing hydranth of the solitary hydroid *Corymorpha*. In *Tubularia*, one of the hydroids in which the free-swimming medusoid phase has been suppressed to become a mere sporosac, we see a new planktonic phase developed afresh to take the medusa's place as a means of dispersal: a floating larval polyp, the actinula, which, after drifting for a time in the ocean currents, settles down to become the sessile adult. Now if we imagine a large Corymorpha-like hydroid to produce a similar actinula-like larva, that larva must be the very image of the conaria larva of *Velella*. Further, if we imagine that, through a long succession of generations, such larvae tend to remain floating for longer and longer periods and at the same time neoteny should set in, so that they become mature without forming their anchoring stem and thus remain floating forms—why then indeed we should have Velella-like Siphonophores. Few, I believe, of those who have studied Garstang's paper can doubt that this is the most likely origin of the Disconanth forms (i.e. Chondrophorida); with perhaps less certainty he then goes on to show how the rest of the Siphonophores—the Siphonanths—may also, but quite independently, have arisen from actinula-like larvae of colonial hydroids which then became permanently floating colonies.

Dr. de Beer in another essay in the present volume has called our attention to the view put forward by Hadži that the Ctenophora are derived by neoteny from the eight-lobed planktonic larva—the Müller's larva—of the Polyclad Turbellaria; Hadži first published this view in 1923. Quite independently Garstang had come to the same view which he expressed in one of his comic verses "Mulleria and the Ctenophore." It may be of interest to relate that when collecting his verses for publication after his death I found that this little poem was certainly written in or before 1922, in which year he had submitted it and several others to the editor of *Nature*; I found Sir Richard Gregory's letter, together with the verses, regretting he was unable to accept them as he considered them of too specialized an interest for his readers, that was dated May 22, 1922. They and others have now been published in a little volume entitled *Larval Forms and other Zoological Verses* (Basil Blackwell, Oxford, 1951). Characteristically he presents his theory in charming pantomime, as an imaginary encounter and conversation between a

Müller's larva and a Ctenophore; I don't believe he has put it forward in any other form. A resemblance between the early development of a polyclad Turbellarian and that of a Ctenophore had of course been discussed before, notably by Lang (1889), who also observed that the cilia on the eight ciliated processes of the Müller's larva are joined edgewise to form combs. It was then thought that the Müller's larva represented a Ctenophore-like ancestor of the Polyclada; it is just as reasonable that the exact opposite may be true, as Hadži and Garstang both believe.

Garstang and Robert Gurney (1938) in a joint essay on the evolution of the Crustacea make passing reference to their view that the Cladocera are paedomorphic forms. I have never seen the metanauplius of Apus alive, but who can look upon a detailed drawing of such a larva—with its swimming second antennae, its minute maxillulae and rudimentary maxillae, and its four or five pairs of foliaceous thoracic limbs—and not be forcibly reminded of a water-flea? Yes, surely the Cladocera are precocious metanauplii which have become mature without growing up. While Apus and its close allies are now among the rarer Crustacea, the Cladocera are the most successful of all fresh-water forms; it seems that they leapt the barrier from the path leading towards stagnation and have blossomed out into a new glory of their own.

A few years later in his monograph on the *Larvae of the Decapod Crustacea* (1942) the late Dr. Robert Gurney put forward a most exciting phylogenetic idea; he suggested that the Copepoda—that great sub-class of the Crustacea which above all others have supplied the teeming populations of the marine plankton in all the waters of the world—and been very successful in freshwater too—have been derived by arrested development from the protozoean larva of some early prawn-like Decapod. He was always very reluctant to speculate and he put forward his idea with great caution. Let me quote his actual words:

> Something should be said here of a possible relation between the Decapoda and the Copepoda. It has been said that, throughout the Copepoda, there is a stage in which three pairs of thoracic appendages are present and the abdomen is unsegmented. It may be no more than a coincidence, but it seems reasonable to assume that it is a fact of phylogenetic significance, that the first Protozoea of Decapoda corresponds precisely with this grade of development. Apart from the exact correspondence in number of somites and appendages there are other points of agreement in detail which may be significant.
>
> In the first place there is in the Protozoea a caudal fork as in the Copepoda, and this fork bears, in both cases, six setae. It is true that seven is the usual number found in Decapods on either side of the telson in the first Zoea; but six are found in some Protozoeas, and the fact that there are six in the embryonic cuticle of the Caridea shows that this is really the primitive number.

The antenna of the Penaeid Protozoea bears a remarkable resemblance to that of the Copepoda. The endopod is, as in Copepoda, of two segments; but the arrangement of the setae suggests that it was primitively of three segments, as it is in the Cirripede Nauplius. In the exopod eleven segments can be found, but the basal segmentation is uncertain. From the fourth segment each bears an inner seta, with three on the terminal segment—ten in all. In other Decapoda the segmentation is much reduced, but ten setae remain as a rule, and it is clear that there is correspondence with the antenna of the Protozoea.

It may seem that undue importance is attached to coincidences in arrangement and number of setae; but they do show a very remarkable consistency which cannot be without significance. . . .

Although the swimming legs of the Copepoda are entirely different from those of the Decapoda at any stage of their development, there is evidence that they have been derived, by suppression of segmentation, or arrested development, from a more primitive form of limb with nine segments, such as there is in Decapoda. All nine segments can still be seen in the maxillipedes of some Copepods (Gurney, 1931, p. 63).

In the Protozoea the third thoracic appendage is rudimentary, whereas it is a functional biramous limb in the Copepodid, and in the Euphausiacea only one maxillipede is developed in the corresponding stage. In the latter the compression of the thoracic somites, with general shortening of the body, is evidently a secondary modification which has led also to suppression of maxillipedes 2 and 3, and it seems probable that a larva with three pairs of functional maxillipedes is more primitive than one with fewer. Three pairs are always present in the first larva of Caridea which corresponds to the Protozoea. The universality of this stage, modified though it may become, gives good reason to believe that it is a deep-rooted ancestral stage, and it is suggested that it actually corresponds to the first Copepodid stage of Copepoda.

While it must be admitted that evidence of this kind is not very substantial, it does justify putting forward the speculation that the Copepoda have arisen by arrested development from a larval form having the general characters of the Decapod Protozoea.

Most zoologists, I think, on examining the evidence will agree that Gurney in his modesty has put forward his views on this possible relationship with a caution that is almost an understatement. Dr. W. T. Calman, our greatest authority on the Crustacea, writing to me upon Dr. Gurney's death, referred to this idea as "one of his most promising suggestions" and he himself had written as early as 1909, when discussing cephalic appendages in his *Crustacea* volume of Lankester's *Treatise on Zoology* (p. 26) that "it is possible, however, that in these characters the Copepoda are persistently larval rather than phylogenetically primitive. . . ." It is indeed remarkable, not to say romantic, that in early life Gurney should have singled out from all the many groups of Crustacea these two, the Copepoda and the Decapoda, to be the objects of his life's research; and then, only towards the end of his work, that he should come to find that the evidence, which he had been so carefully collecting, was pointing to the conclusion that these two groups, hitherto regarded as so widely separated and at first sight so fundamentally different, are in fact perhaps the most closely related of all the Crustacean orders.

In looking at examples of possible paedomorphosis I am passing upwards in the animal kingdom. We now come to a striking comparison between the adult form of an insect and the larva of a myriapod made by de Beer in his book *Embryos and Ancestors*. He shows how the larval millipede upon hatching has only three pairs of walking legs properly developed, and these are on the three segments immediately following the head, just like the three pairs of limbs on the thorax of an insect; the remaining segments of the larval body bear only rudimentary stumps of limbs, as in fact do the abdominal segments of the most primitive living insects of to-day. As the little millipede grows up, more and more pairs of limbs are fully developed. If we imagine the growth of the millipede being arrested and it becoming sexually mature by neoteny in the six-legged stage, then we are presented with an insect of the primitive wingless type. There are, as de Beer says, many other considerations, such as the tracheal and malpighian tubes which they have in common, that point to the insects being evolved from myriapod-like ancestors. "At the same time," he points out, "insects could not have been derived from adult Myriapoda for the structure of the latter is too specialized and peculiar." As in both the sea and fresh water, so on the land, the most successful group of arthropods appears to owe its origin to the process of paedomorphosis. In passing let us remember that some insects themselves are neotenous, as for example the female glow-worm which retains its larval form.

Now let us return to the Vertebrate stock from where we started with that first example which Garstang showed us. Apart from the very origin of the Chordate stock there are other interesting examples of possible paedomorphosis at different levels within it. We have already noted the neotenous origin of the pelagic Larvacea and have briefly mentioned that Garstang himself derived them not from the larvae of the more typical sedentary ascidians, but from the more specialized pelagic members of the group: the Doliolidae. Dr. E. W. Knight-Jones in his recent paper "On the nervous system of *Saccoglossus cambriensis*," published in *The Philosophical Transactions of the Royal Society* has expressed his opinion that enteropneusts such as *Balanoglossus* are also derived paedomorphically from other larvae of early chordate forms but in quite a different way. He refers to the points of resemblance between the ciliated larvae of the Echinodermata, the Enteropneusta and Amphioxus which suggests that the common ancestor of the chordates and echinoderms had a trimetameric, bilaterally symmetrical, ciliated larva; this general form and symmetry persist in the adult enteropneust and lead him to think that "it seems highly probable that paedomorphosis has played a part in the evolution of the group." I will quote him further:

> The essential peculiarity of the Enteropneusta is that neurulation is never completed. In other chordates which have little yolk (Urochordata, Cephalochordata and some Amphibia) the neural folds fuse posteriorly over the blastopore, enclosing the neurenteric canal, the anus appears *de novo* and the tail is formed. In the Enteropneusta the neural folds, where these appear (Morgan 1891; 1894), fuse only in the collar region, leaving open anterior and posterior neuropores. They do not enclose the blastopore, which becomes the anus, and dorsal tail-formation never begins.
>
> The neurocord differs from the neural tube of other chordates in two important respects, its shortness in being confined to one metamere and its shape in transverse section, but as Van der Horst (1927–39) pointed out, its shortness may be explained as the result of arrested development, whilst the neural tube does not develop its normal shape without a notochord beneath it and myotomes on each side . . .

He goes on to show that it would be reasonable to suppose that the Enteropneusts were derived from some more generalized chordates which had a ciliated larva with three pairs of coelomic pouches and the rudiments of a notochord and neural tube. The enteropneust he believes was evolved firstly by having its development arrested at a stage when its neural tube had only closed in the middle somite, and secondly by the front and hind somites becoming greatly modified for a burrowing life: the front one elongated for locomotion through the mud or sand and the hind one enormously lengthened to provide a gut long enough to extract sufficient organic matter from the "soil" passed through it. The middle somite and its neurocord have remained by comparison absurdly short. He then shows how the nerve rings of *Saccoglossus* encircling the body at either end of the neurocord may be compared to the neural folds of vertebrates or to the ciliated circum-oral band of the Tornaria larva. He writes:

> The presence of these nerve tracts is therefore relevant to Garstang's (1894) hypothesis, that the neural folds of vertebrates may have been derived from the ciliated band of a larva like the Auricularia, an idea which received some support when Assheton (1896) showed that the neural folds are particularly strongly ciliated in embryos of *Rana*. In vertebrate embryos there are closely associated with the neural folds only those ganglion cells which belong especially to the sensory system; the bulk of the presumptive nervous tissue is associated not with the folds themselves, but with the neural plate between, which appears to represent the original dorsal or aboral surface. In Enteropneusta most of the surface of the body is aboral to the ciliated band, and to the anterior and prebranchial nerve-rings, so the greater part of the richly nervous epidermis may well be homologous with the neural plate of vertebrates.

What now of Amphioxus? Young, on p. 46 of his *Life of Vertebrates* (1950), considers the possibility that it may be a paedomorphic form, but soon dismisses it. He writes:

> The closeness with which its organization corresponds to that of later forms might give rise to a suspicion that it is not an ancestral type but a simplified derivative of the vertebrates, perhaps a paedomorphic form. It possesses, however, sufficient peculiar features to make this view very unlikely. Neoteny might explain the regular segmentation, separate dorsal and ventral roots, and other features, but can hardly account for the method of obtaining food, for the condition of the skin, or for the presence of nephridia. We may therefore feel fairly safe in assuming that *Amphioxus* shows us approximately the condition of the early fish-like chordates living in the Silurian some 400 million years ago, and that it has undergone relatively little change in all the time since.

Among a number of comic verses which Garstang is known to have written either in 1922 or earlier, and to which I have already referred (p.129), is one entitled "The Axolotl and the Ammocoete." In this he begins by describing the often uncertain neotenous condition of the Axolotl and the permanent neoteny of the Perennibranchiate Amphibia; and then, looking at the Ammocoete (the larva of the Lamprey), he suggests that if *it* should become neotenous we should have to revise our ideas of the ancestral position of the Lancelet (*Amphioxus*):

Now look at Ammocoetes there, reclining in the mud,
Preparing thyroid extract to secure his tiny food:
If just a touch of sunshine more should make his gonads grow,
The Lancelet's claims to ancestry would get a nasty blow!

To derive Amphioxus from an Ammocoete is to get over the first of the objections to the idea of its origin by paedomorphosis referred to by Young above; the Ammocoete larva is of course a plankton feeder complete with endostyle and peripharyngeal bands similar to *Amphioxus*. Garstang returned to this idea in 1947. In the interval Stensio by his wonderful reconstructions of early fossil vertebrates had shown that the Cephalaspids (Ostracoderms) were clearly related to the stock of the modern lampreys. Just as the modern lampreys have an ammocoete larva, Garstang considered it likely that the Cephalaspids also had a plankton-feeding larva of a similar sort. In November 1947 he wrote a letter intended for publication in *Nature* under the title "Amphioxus, a Cephalaspid paedomorph." I came across the letter, still in its stamped and addressed envelope, among his papers after his death. I remember him telling me how on the day he was going to post it he came across a reference to the paper by Holmgren and Stensio (1936) and on looking it up found that they had already made many of the points of comparison that he was making between *Amphioxus* and a Cephalaspid, but without concluding it was paedomorphic. He held up the letter, but from further notes I have found among his papers it is clear that he intended rewriting it and again submitting it to *Nature*. He kept carbon copies of many of his letters to scientific friends on matters of zoological interest. On December 8, 1948, he wrote in a letter thus:

> I agree that it (is) "unlikely" that Amphioxus is a paedomorphic Gnathostome, but these (referred to earlier in the letter) and other correspondences render the hypothesis at least tenable that A. is a paedomorphic Cephalaspid.
>
> I was hoping that you might take the matter up, but if not, I think I shall have to expand my letter to *Nature*, publish it and draw the shock of criticism upon my own head!

That entry is the last one in his book of carbon copies; he died soon afterwards on February 23, 1949, without leaving a revised draft of his *Nature* letter. Knowing that he intended to publish it in a modified form, I believe it will be of considerable interest to students to have available his original draft; as it is too long and technical to be quoted in full in the middle of this more general essay, I add the full text of it in an appendix at the end.

After reading this unpublished letter of 1947 it is interesting to read the quite independent views of Professor A. S. Romer on p. 19 of his *The Vertebrate Body* (1949) where he is discussing the vertebrate pedigree:

> This larva (the ammocoete) shows marked similarities to Amphioxus, a fact which to some demonstrates the ancestral position of the cephalochordates. The majority opinion has been that Amphioxus, although departing to some degree from the directly ancestral pattern, represents a stage in evolution preceding that of vertebrates.
>
> There is, however, a second possible interpretation, namely, that Amphioxus is not really primitive, but a degenerate descendant of primitive vertebrates. We see in many animals the phenomenon known as *neoteny*, in which a larva lingers long before finally changing into an adult, or that of *paedogenesis*, in which the larval animal becomes sexually mature and breeds without ever reaching the adult condition. It is possible that paedogenesis has occurred here and that Amphioxus represents the permanent larva of some early vertebrate type; its simplicity may be due to arrested development.

Neoteny has apparently occurred recently and independently in a number of different stocks of lampreys. There are in different parts of the world pairs of apparently related forms, one species migrating to the sea and the other remaining much longer, sometimes several years, in the ammocoete form and only becoming adult for a short period at the end of its life without going to the sea at all.

As we pass up the vertebrate stock we come across a number of examples of possible neoteny or paedomorphosis. In discussing the present day Dipnoi, J. Z. Young in his *Life of Vertebrates* (p. 262) writes:

> An interesting feature is that the Müllerian duct is very well developed in the male. This is one of several details (lack of ossification, unconstricted notochord) which raises the suspicion that the living Dipnoi have acquired their special characters by a process of paedomorphosis or partial neoteny, that is to say, becoming sexually mature in an early stage of morphogenesis.

Among the Amphibia it is of course the Urodeles which show this condition *par excellence*. In his last great book *Evolution Emerging* (p. 253), W. K. Gregory writes:

> Viewing the modern urodeles as a whole it seems probable that all are to a varying extent neotenic or paedogenetic forms which have retained more or less the larval adaptations for water-living, including the larval cartilaginous skeleton.

The ostrich and other flightless birds which have miniature wings and retain into adult life the down plumage characteristic of the nestlings of other species may perhaps be regarded in these respects as gigantic neotenous chickens.

Gregory has recently (1947) put forward an interesting speculation on the phylogeny of the monotreme mammals suggesting that they are really much nearer in origin to early (and then apparently egg-laying) marsupials than to the Triassic pro-mammals and that some of the apparently "reptilian" features may be due in part to neoteny or paedomorphosis. He summarizes his views in *Evolution Emerging*, p. 363, as follows:

> According to this principle, certain ancient embryonic features which are ordinarily passed through before the adult stage are sometimes retained in the adult by the lagging of later growth stages either in vigor or in timing. In other words, the right and left oviducts, which in vertebrates generally are completely separate in the embryonic stages, may, in the monotremes, have simply failed to unite in the mid-line and thus made possible a seeming reversion to a reptilian stage. This initial check in development then permitted (according to this hypothesis) a partial and incomplete resurgence of the latent embryonic forces which in earlier ages would have produced a premammalian, not a mammalian, adult. The strength of this hypothesis, as applied to the case of the monotremes, lies chiefly in the great number and variety of the points of close agreement between the adult monotremes and the marsupials in such features as the arrangement of the cranial foramina, the mode of development and adult construction of the auditory ossicles and internal ear, the close general resemblance of foetal monotremes to foetal marsupials, rather than to embryo reptiles, the wholly marsupial stage of the brain, etc.

Finally we come to the evolution of Man himself and to-day we find the views of Bolk concerning the process he termed foetalization, which is really the equivalent of Garstang's term paedomorphosis, very widely held. These views are known so well that I need not discuss them in detail, but for any reader to whom they are not familiar I will quote briefly from de Beer's admirable account of them in his *Embryos and Ancestors*:

> Bolk has shown that many of the features of the adult structure of man show resemblances to those of the embryonic structure of the anthropoid apes, and the same point of view has been expressed by Devaux. These features include the relatively high brain-weight, the position of the foramen magnum and the cranial flexure, the retarded closure of the sutures between the bones of the skull, the dentition, the flatness of the face (orthognathy), the hairlessness of the body, the light colour of the skin, and a number of other features.
>
> The axis of the head forms a right angle with that of the trunk in the embryo of all mammals (and of nearly all vertebrates, for that matter), and this bend is known as the cranial flexure. Whereas in mammals other than man the axis of the head is rotated during later development so that the animal's head points in a direction which is a continuation of the line of its backbone, in man the cranial flexure is retained so that his head points in a direction at right angles to the axis of his body. Since the direction in which his head points, i.e. his line of sight, is horizontal, the position of the body will be vertical; and so man's erect attitude is associated with the retention during ontogeny of a condition which in other mammals is embryonic and temporary, as it must have been in man's ancestors. The erect posture of man is, in Bolk's view, a consequence of neoteny of the shape of the head.

It must not be pretended of course that paedomorphosis itself can account for the most essential character of Man—his new mental capacities; we may, however, say that these could not have been evolved without paedomorphosis.

Among dogs we see a similar process although not involving the cranial flexure; in the King Charles Spaniel we see the bulging high forehead and short upturned jaws, which are of course foetal characters, persisting into adult life. Dr. Tinbergen in his recent book on *The Study of Instinctive Behaviour* has wickedly reminded us that such dogs as these are particularly popular with women who want children but have not got them; these little lap-dogs have the baby face that is so adorable!

It has been my object in this essay to bring together all the more reasonable examples of paedomorphosis which have received some support from prominent zoologists. Having completed my survey, I was preparing to pass to my conclusion when at this point I stopped for a moment to glance at the new issue of *Nature* which had just arrived: that of June 14, 1952. What an extraordinary coincidence! Here is a letter from Professor Hadži of Ljubljana University, Yugoslavia (to whom we have already referred in relation to the Ctenophora), entitled "Application of the Principles of Phylembryogenesis to the Protista."

After discussing the general importance of the principles of paedomorphosis and neoteny he says:

> The question may be asked whether these principles can be applied to the ancestors of the multicellular organisms, that is, to the Protista. In these there is no ontogeny but only a succession of different generations during the life-cycle. . . . Analysis and comparison of a few examples selected from among Protista and multicellular forms have revealed which are the corresponding phases in the life-cycle of Protista and in the ontogenies of multicellular organisms.
>
> In the Protista, the chief phases (some of which also comprise sub-phases) take the form of generations, such as the vegetative, progamic, gametic and metagamic generations.

I can only pick out a few sentences from his long letter to illustrate his idea in merest outline.

> Comparisons of the life-cycles of various types of Protista have shown with certainty that evolutionary changes have occurred in all phases or stages of the life-cycles. Larger and more rapid changes involve whole generations, while smaller and slower changes, having the character of adaptations, may be effected within single phases or generations. It therefore seems legitimate to apply the modalities of the development of multicellular organisms (phylembryogenesis of Sewertzoff, paedomorphosis of Garstang, gerontomorphosis of de Beer) to the conditions in the Protista. . . .

(after discussing the case of *Paramecium* he goes on):

> My second example, which I should go so far as to call a case of paedomorphosis, is to be found among the Folliculinidae (Infusoria, Heterotricha). Here the entire sexual part of the life-cycle (progamic, gametic and metagamic phases) has vanished, and a new, free, vegetative phase has appeared instead, because the old vegetative phase or generation has become sessile.
>
> It is probable that bacteria and viruses may be found to provide examples among the Protista of the applicability of these principles. In such cases, the macro-evolutionary changes would be of a retrogressive character associated with the specialization in adaptation to saprobiotic and parasitic modes of life.

Without further thought I should not like to commit myself as accepting the validity of these parallels between the phases in the life-cycles of Protista and the stages in the development of Metazoa; Professor Hadži has certainly made a suggestion well worth considering and there can be no logical reason why something like neoteny may not be found among the Protozoa. It seems that there is no grade of organism to which the principle of paedomorphosis could not apply provided only that the conditions of genetical make up and selective advantage are appropriate. As we have seen there is already an impressive list of animal groups which may have been evolved in this way: Siphonophora, Ctenophora, Cladocera, Copepoda, Insecta, the Chordata as a whole, and (within the Chordata) the Larvacea, Enteropneusta, Cephalochordata (Amphioxus), some lampreys, the recent Dipnoi, the Urodeles, the Monotremata and Man himself. Other groups may well be included in the list as more is known of them, for example some of the Archiannelida may very likely be paedomorphic rather than primitive and Professor Young in *The Life of Vertebrates* (p. 74) suggests that the molluscs as a whole may be so derived. I do not wish to imply that I regard all of these cases as proved, but there are, I think, a sufficient number for which paedomorphosis supplies the most reasonable explanation of their origin to make one realize that this process is one of outstanding evolutionary significance.

However highly specialized a race of animals may have become in its typical adult condition, provided it has a less or differently specialized young or larval form (which naturally will already be well adapted to its particular mode of living), and has a gene-complex which may sooner or later produce neoteny, then given sufficient time it stands a chance of escape from its path to extinction. In the great majority of stocks the end must come before this rare opportunity of paedomorphosis can intervene; but in a very small minority the chance comes earlier, before it is too late, and such lines are switched by selection to new pathways with fresh possibilities of adaptive radiation. So vast is the span of time available, that, rare as they may be, these escapes from specialization seem likely to have provided some of the more fundamental innovations in the course of evolution.

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APPENDIX

The following is the text of the note which the late Professor Walter Garstang had intended sending for publication to *Nature* in November 1947 but withheld after finding that he had been anticipated in a number of points by Holmgren and Stensio in 1936 (*Kranium und Visceralskelett der Akranier, Cyclostomen und Fische. Handt. vergl. Anat.*, iv, pp. 233–500). As recorded in the foregoing essay, he clearly intended to publish it in a modified form, but died before he could do so and without leaving a revised draft. It is here published as originally written because it is felt it will be of great interest to students of chordate evolution.

AMPHIOXUS A CEPHALASPID PAEDOMORPH

When recently reconsidering the relations between *Amphioxus* and Ascidians I was struck by the fact that the curious "ventral fin" of *Amphioxus* with its double series of so-called "finrays" has never been explained, although Lankester for a time regarded it as the fused extremities of "epipleural fins." Actually neither this nor the so-called "dorsal fin," with its single series of "finrays" in their "finray boxes," is sufficiently elevated or flexible to serve functionally as a fin. The only real fin in *Amphioxus* is the caudal, and that has neither finrays nor boxes. Moreover in *Asymmetron*, doubtless in consequence of its longer pelagic phase (the "*Amphioxides*" of Goldschmidt) this fin extends to a greater or less extent, both dorsally and ventrally, along these ridges, and partly or entirely suppresses both "finrays" and "boxes" in its path. Compare the ventrals in the series: *A.* (*Heteropleuron*) *maldivense*, Cooper, 1903, with both boxes and single finrays; *A.* (*Heteropleuron*) *cultellum* in Kirkaldy, 1895, with boxes but no finrays; *A. lucayanum*, Andrews, 1893, with neither boxes nor finrays. Clearly the dorsal and ventral "fins" have been incorrectly named.

On the other hand the "finray boxes" seem to be quite comparable with the connective tissue pockets in which the bony scales of Teleosts are developed, and the "finrays" may well be uncalcified representatives of the scutes and scales commonly figured in illustrations of Ostracoderms—the scutes in a single dorsal series, the scales in a pair of ventrolateral rows (cf. Smith Woodward, 1898, Fig. 10; Moy-Thomas, 1939, Fig. 3, after Kiaer and Stensio).

It is unnecessary to stress the obvious general affinity between *Amphioxus* and Cyclostomes, but a peculiarity of their larval forms deserves more attention. In the Ammocoete only the hinder part of the endostyle is median: it is produced in front as a right and left pair of anterior horns, each with the structure of half an endostyle, and continuous with, but distinct from, the peripharyngeal bands. It is thus essentially similar to the V-shaped endostyle of the larval *Amphioxus* (Willey, 1891). This forked condition is never shown by Ascidians. It may be thought to have been provoked by special conditions in each case (thyroid transformation in the Ammocoete, asymmetrical dislocation in *Amphioxus*), but it so clearly recalls the primitive loop of the Echinoderm adoral band that it must be either a reversion or a retention of that hypothetically ancestral larval condition. In either event it indicates a special similarity of constitution.

A further resemblance is seen in the development of the embryo. Both are hatched at a very small size in an embryonic, blind, and inactive condition, but, while ample yolk enables the Ammocoete to complete its development without external food, *Amphioxus* is compelled to collect microplankton when its body is so slender that only one set of gill slits can be accommodated. Some twenty years ago (1928) I drew attention to this point in an explanation of its asymmetry, and advanced the hypothesis that *Amphioxus* has undergone a secondary reduction of yolk in its eggs which entailed the precocious feeding. I can now be less abstract by claiming *Amphioxus* to be a modified Ammocoete—not the modern Ammocoete of lamprey parentage, but the corresponding larva of some Ostracoderm fish the adults of which had a dorsal row of scutes and a pair of ventrolateral scale-rows, the rudiments of which would doubtless be laid down in the larva.

From Stensio's brilliant revelation of the structure of Cephalaspids I believe this family may have included the actual ancestors of the Cephalochorda. The shovel-like head-shield suggests arenicolous habits as in *Limulus* and *Apus*, and the edges of the shield seem to have been adapted for gliding over the surface layer. The metapleures of *Amphioxus* have similar relations to the rostrum (if allowance be made for the arrested development of the left one in consequence of the left-sided larval mouth), and, previous to the closure of the atrium, they overhang the gill-pores on each side exactly as in Stensio's figure of *Kieraspis* (Moy-Thomas, *l.c.* Fig. 4B). They are no longer "gliders," however, for *Amphioxus* has since gone underground, but, being turgid with fluid, they function as fenders or buffers, especially during its lightning-like dives into the sand. That they originally served as gliders is supported by the fact that each metapleure in the young larva is bordered by a band of epidermal sense-organs, as interpreted by Gibson (1909, pp. 228, 238, Figs. 8–12, mtp.). These sink inside before the metamorphosis, and apparently take up secondary positions underneath the pleurocoele (Fig. 18), where they may conceivably act as pressure-recorders, though further investigation is necessary before anything definite can be said.

Incidentally it is worth mentioning that the Ammocoete of the lamprey has the same vigorous escape tactics as the adult *Amphioxus*.

That Cyclostomes may exhibit conditions of *presque-neoténie* is well known in the case of the brook lamprey (*P. planeri*) which lives as an Ammocoete for two, three, or four years and dies within a month or two after metamorphosis and reproduction.

A similar life-history is believed to have characterized some of the Ostracoderms, since, according to Heintz (cited by Moy-Thomas, p. 9), the exoskeletal plates of Palaeaspidae show no growth after their formation.

If it is objected that the Ostracoderms were freshwater animals, I need only say that a predominant freshwater habitat is not inconsistent with periodic visits to the sea for spawning, as exemplified by the freshwater eel. Moreover *Myxine* is entirely marine, and related Ostracoderms may have lived in Silurian seas. The sharp discontinuities between the freshwater families indicate the existence of unknown connecting links, possibly with more friable exoskeletons, less completely fossilized in shore deposits.

WALTER GARSTANG.

Oxford, November 11, 1947.

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DAVID LACK

The Evolution of Reproductive Rates

The reproductive rate differs considerably in different species of animals. Some, such as man or a tsetse fly, produce only one young at a birth, while at the other extreme various fish and marine invertebrates lay well over a million eggs at a spawning. The variations are quite large even within one class of animals. In birds, for instance, the average clutch-size of different species varies between 1 and 15. Even within the same species the variations may be far from negligible. Thus the average clutch-size of different populations of the Great Tit *Parus major* varies from 3 to 12 (Lack, 1950), and of the copepod *Arctodiaptomus bacillifer* from 6 to 60 (Hutchinson, 1951).

In the past, variations in the reproductive rate have usually been explained as due to differences in the mortality rate. Migratory birds have larger clutches than resident species because they have to undergo the additional danger of a long journey. Elephants have only one young at a birth because they are long-lived and, if they had more, they would quickly overpopulate Africa. Flatfish lay vastly more eggs than skates to compensate for the vastly heavier mortality among their fry. So runs the argument, which appears in a variety of explicit and implicit forms through the zoological literature. The fact is undoubted: those species with a lower reproductive rate have a lower mortality rate; but the explanation must be wrong. The reproductive rate is a product of evolution, and if the theory of natural selection be accepted, then the number of eggs laid by each species should be that which results in the maximum number of surviving offspring; and those genotypes with a higher egg-number than the normal should be eliminated by selection. Is this statement true? If it is true, what is the selective disadvantage of genotypes with a higher egg-number than the normal? And why should some species lay many more eggs than others?

This question can be answered with some confidence for nidicolous birds. First, it should be made clear that clutch-size is far below the normal limit of egg production; if the eggs are taken when laid, the bird readily lays others in their place, but these other eggs are not laid unless the first are taken. Secondly, the limit is not set by the number of eggs that the sitting bird can incubate, for hatching success is similar for clutches of all sizes found in nature, including those well above the normal (Lack, 1947, 1948a, 1950). The true answer, at least for nidicolous species, is that clutch-size has been adapted through natural selection to correspond with the maximum number of offspring for which the parents can, on the average, find enough food without seriously harming themselves. The evidence for this conclusion will be summarized in succeeding paragraphs. Two types of variation are involved, hereditary variations acted upon by selection, and phenotypic variations adapted to the conditions at the time. It is simplest to consider first some cases in which phenotypic variations can be neglected or excluded.

In England, the Common Swift *Apus apus* lays either 2 or 3 eggs, 2 more often than 3. The parents feed their young on air-borne insects, which almost disappear in continued bad weather, when young Swifts often starve to death. An analysis of the mortality among nestling Swifts in four colonies in southern England in 1946–50 showed that in broods starting with 2 young 82 per cent safely left the nest, whereas in broods starting with 3 young only 45 per cent safely left the nest. Nearly all the losses were due to starvation, broods of 3 suffering more than broods of 2 because the food was at first shared among three mouths instead of two. As a result, broods of 2 gave rise on the average to 1·6, and broods of 3 to 1·4, survivors per brood (Lack and Lack, 1951). Hence 2 was a slightly more efficient clutch-size than 3; and had any Swift laid 4 eggs, one may suppose that a yet higher proportion of the young would have starved, so that fewer, not more, young would have been raised per brood. Broods of 2 were more successful than broods of 3 particularly in wet summers like that of 1948, while in fine summers such as 1949, the average number of young raised per brood was higher from broods of 3 than 2. This makes it understandable how both individuals laying clutches of 2, and others laying clutches of 3, persist in the population. A closely similar result was obtained in a study of the Alpine Swift *Apus melba*, in which the average number of young raised per brood was highest for broods of 3, and the commonest clutch-size found in nature was likewise 3 (Lack and Arn, 1947). In these analyses late broods, which are of smaller size, were omitted.

In passerine birds, unlike Swifts, the nestling mortality proved to be similar in broods of all sizes. But considerable variations were found in the weight of the young when they left the nest, presumably due to differences in the amount of food received, and this might influence their subsequent chances of survival. It was then found that, in the Starling *Sturnus vulgaris*, the mortality-rate after the young left the nest was above average in young from broods of above average size. In first broods in Switzerland, the post-fledging mortality rose with increasing brood-size in such a way that the average number of survivors per brood was similar from broods starting with 5, 6, 7 or 8 young (Lack, 1948a). Hence 5 was the most efficient clutch-size in the Swiss Starling, and it was also the commonest size found in nature, thus supporting the view that clutch-size has been evolved through natural selection.

The above argument presumes the existence of hereditary variations in clutch-size. There is as yet no proof of the latter, though it seems likely on general grounds that specific differences in clutch-size have a hereditary basis. Further, in a breeding colony of the Starling in Holland, the clutches laid in successive years by particular ringed females were less variable in size than those of the colony as a whole, and the same was found in colonies of Common and Alpine Swifts, and in the Great Tits breeding in a Dutch wood (Lack *et al.*, *loc. cit.*, Kluijver, 1951). This suggests that different individuals differ somewhat in the hereditary factors influencing clutch-size. Each individual was not, however, completely consistent; its clutch-size varied within small limits. Hence within the hereditarily determined limits, some of the variations in clutch-size are evidently phenotypic.

In the Song-Thrush *Turdus ericetorum* and Great Tit *Parus major*, unlike the Starling, the mortality-rate of the young after they left the nest did not vary appreciably with brood-size. Hence the average number of survivors per brood was highest from the largest brood-sizes found in nature (Lack, 1949, 1950). Were then the largest brood-sizes the most efficient? In that case, why should not every individual of the species lay a clutch of the largest size? The answer, I suggest, is that, within the specific limits, larger clutches tend to be laid when prospects are more favourable, and smaller clutches when prospects are less favourable, for raising young. If the clutch-size could be perfectly adjusted to the food situation, then the survival-rate would be similar for the young from broods of all sizes. This raises two problems. The first concerns survival value: are the phenotypic modifications in clutch-size adapted to the food prospects for the young? The second concerns the physiological mechanism: How are such modifications brought about? The first question will be considered in some detail, the second only briefly.

There is suggestive evidence in various types of birds that clutch-size can be modified adaptively (within limits) to suit the feeding conditions under which the young will be raised. For instance, in those hawks and owls which prey on voles of the genus *Microtus*, the average clutch-size is half as large again, and sometimes twice as large, during a vole plague as in a year when voles are scarce (Lack, 1947–48). Again, in the arid parts of Africa and Australia, various passerine and other species have smaller clutches in years of low rainfall than in years of high rainfall when food of all kinds is more abundant (Moreau, 1944).

In many European species, clutch-size varies regularly with the time of year. For instance in single-brooded species, any late clutches are usually smaller than the rest. The breeding season of single-brooded species is presumably adapted to coincide with the most favourable time of year for raising young; hence late broods will tend to be raised in poorer conditions, and the smaller size of late clutches may well be adaptive. This probably holds in the Alpine Swift, in which clutches laid at the normal season average 2·7 and late clutches 2·2 eggs, while the mortality from starvation is higher in late than normal broods of the same size (Lack and Arn, 1947).

In some double-brooded species, the average clutch-size declines steadily as the season progresses, and this also may be adaptive. Thus in the Great Tit at Oxford, where the average clutch-size declines from the start to the end of the breeding season, the caterpillars on which the birds feed their young become scarcer from about the time that the first broods leave the nests, while the mortality of the young from starvation is much higher in second than first broods (Gibb, *in progress*). Likewise in the Starling in Switzerland, the commonest size of first broods is 5, but of late broods 4. In second broods, the mortality of the young after they left the nest was higher in broods of 5 and 6 than in broods of 4, and 4 proved to be the most efficient brood-size; whereas in first broods, as already mentioned, 5 was the most efficient size. Similar results were obtained in a comparison of early and late broods in England, where the most efficient brood-size was again the commonest found in nature (Lack, 1948a).

In various other double or treble-brooded species, the average clutch-size rises from April to early June and thereafter declines, hence the second broods are larger than either the first or third (Lack, 1947–48, 1949). The food supply of these species has not been investigated, but another factor, day-length, perhaps has some influence, for with a longer working day the parents can collect more food, and hence, other things being equal, they can raise a rather larger brood. The increase in day-length may also be one of the factors responsible for the marked increase in average clutch-size shown by many species of birds between the tropics and the North Temperate regions (Moreau, 1944; Lack, 1947–48).

Extensive studies of the Great Tit have revealed not only seasonal and regional variations in clutch-size, but also differences between woods in the same region, and differences in the same wood in successive years (Kluijver, 1951; Lack, 1950, 1952). In a wood near Oxford, Gibb (*in progress*) found that the clutch-size of first broods was lower each successive year from 1948 (when the average was 12·3) to 1951 (when it was 7·8 eggs), and that the abundance of the caterpillars on which the Great Tit fed its young also fell off each year. In Holland, Kluijver (1951) found that both the local and the annual variations in clutch-size were partly explicable through an inverse correlation with population density; but the difference was not large, since in any one wood the average was only about ½ egg smaller in years when the population was well above normal than in years when it was well below normal (Lack, 1952). Some other factor must have contributed to the observed differences in clutch-size, and this may have been the food situation, which Kluijver did not study. (Possibly, therefore, the influence of population density was indirect, due to its influence on food.)

To sum up, the available evidence suggests that the variations in clutch-size found in birds are closely adapted to the number of young that the parents can feed. The limits of clutch-size in each species are probably determined by the action of selection on hereditary differences, and some of the regional differences between populations of the same species may also have a hereditary basis. In addition, clutch-size can often be modified phenotypically to suit the immediate conditions. The physiological mechanisms involved have not been studied. In some cases, notably the vole-predators, clutch-size is probably modified by the food situation at the time of laying. In other cases this is not so. Thus the small second broods of the Great Tit are laid when their caterpillar food is most abundant. It should be stressed that, in birds, the clutch is laid some 2–4 weeks before the young require food. To be effective, therefore, any modification in clutch-size must be "anticipatory." The proximate factors involved are not as yet known.

To what extent do the conclusions reached for birds hold in other classes of animals? The closest parallels may be expected in mammals, which resemble birds in having a small family fed by one or both parents. One point is clearer in mammals than birds, since hereditary variations in litter-size have been established for the Rabbit *Oryctolagus cuniculus* and several other species. Since the litters of domestic breeds are larger than those of the wild type, mutations for larger litter-size must be eliminated in the wild by selection. This implies that the number of young surviving from litters above normal size is lower than from litters of normal size, a point which has not been studied under natural conditions. There are, however, suggestive data from the laboratory for the Guinea-pig *Cavia porcellus*. In this species the mortality among the young was found to rise steeply with increasing litter-size, in such a way that the average number of young weaned per litter was highest with a litter of 5; with 6 young in the litter fewer, not more, young were raised (Wright and Eaton, 1929; Lack, 1948b).

The most efficient litter for the laboratory Guinea-pig being 5, it might be thought that this size would have been favoured by natural selection, but in fact the commonest observed size was 3. The discrepancy is probably due to three causes. First, mortality was studied in the laboratory; it would doubtless be higher in the wild. Secondly, mortality was recorded only up to weaning. At weaning, the young from larger litters had a lower average weight than those from smaller litters, hence the subsequent mortality may well have been higher among the young from large than small litters. Thirdly, some of the variations in litter-size were adaptive modifications, smaller litters being produced in poorer, and larger litters in better, feeding conditions. Under these circumstances, the survival-rate from larger litters will be better, and that from smaller litters poorer, than would otherwise be the case. Altogether, the results for the Guinea-pig provide close parallels with those discussed earlier for passerine birds.

Various mammals show seasonal variations in litter-size comparable with those found in birds, though they have not been studied in relation to feeding conditions (Lack, 1948b). An adaptive modification related to food supply is found in the Arctic Fox *Alopex lagopus* in Greenland. The inland populations of this species prey primarily on the Lemming *Dicrostonyx groenlandicus*, and have much larger litters than usual in years when Lemmings are particularly abundant. The coastal populations prey primarily on marine organisms and do not show this variation (Braestrup, 1941).

Outside birds and mammals, the only animals which regularly feed their young are the social insects, in which the number of eggs laid is closely related to the food situation. In both termites and social hymenoptera, the queen lays comparatively few eggs in the early stages of the colony, but the number is vastly increased when there are many workers to help in feeding the larvae (Bodenheimer, 1937).

At first sight it would seem that the factors limiting the reproductive rate must be completely different in those animals which do not feed their young. In fish and invertebrates, it is often claimed that the number of eggs laid is correlated inversely with the degree of safety of the larvae. Thus marine invertebrates with a high degree of brood-protection lay 10–100 eggs, those with a crude type of brood-protection lay 100–

1,000 eggs, and those with no brood-protection lay 1,000–500,000,000 eggs (Thorson, 1950). Similar correlations hold in fish and in insects, but as mentioned earlier, the conventional deduction from these facts is wrong. Natural selection cannot favour the evolution of a smaller egg-number as such. There must be some compensating advantage, and this, I suggest, is a larger size of egg. As between different species, a given food intake by the adult can be utilized to produce many small eggs or a few large ones, and in each species the compromise actually evolved will be that which leads to the maximum number of surviving offspring.

In fact, a smaller egg-number is usually associated with eggs of larger size. Thus in marine invertebrates, the species with brood-protection produce a few large eggs rich in yolk, while those with pelagic larvae produce many small eggs poor in yolk (Thorson, 1950). The advantage of pelagic plankton-feeding larvae is that, being in a medium rich in food, they do not need a large internal food-store, hence the parents can produce a large number of small eggs; the disadvantage is the heavy predation. The advantage of brood-protection is the comparative safety from predators, but the embryos or larvae subsist on internal food-stores, hence the eggs must be large, and this means that the parents can produce fewer. Parallel considerations apply in fish and in insects, in which large eggs are found in viviparous species and others in which a larva of large size at hatching is advantageous. In phanerogamic plants, likewise, some species have many seeds with small food-stores, while others have few seeds with large food-stores.

In birds, clutch-size is well below the physiological limit of egg-production, and the limit is set by the amount of food which the parents can supply to their young. In fish and invertebrates (also in higher plants), on the other hand, the number of eggs laid is probably the physiological maximum, but this maximum is greatly influenced by the size of the eggs, and in particular by the size of the food-store, hence the amount of food that the adults can supply for their offspring again plays a vital role, the difference being that in these other groups, unlike birds, the food is provided wholly beforehand. When comparing different types of invertebrates or fish, an exact correlation between egg-number and egg-size cannot be expected, as the number of eggs laid is probably influenced by several other important factors. These include the ability of the adult organism to obtain food before laying, and also its subsequent survival; proportionately more eggs may be expected from species which die soon after laying than from those which survive to breed again.

In birds it was found that, because of the many variables involved, a study of interordinal or interspecific differences in clutch-size was not nearly so illuminating as a study of intraspecific differences (Lack, 1947–48). In other groups of animals, unfortunately, intraspecific variations in egg-number have been little studied. An exception is the recent review by Hutchinson (1951) of researches on freshwater copepods, from which the following facts are taken. In the Scheinsee, Germany, *Eudiaptomus gracilis* has an average "clutch" of 11 in April, which falls gradually during the summer to 3 in early August, then rises again to 8·8 in early November, and falls again to 5–6 during the winter. In Denmark, the same species usually carries 25–30 eggs in spring but only 6–8 in summer and autumn, both these values being smaller in one particular lake. Hence this species shows both local and seasonal variations in egg-number, and the same holds for other species in northern Europe, U.S.A. and Ceylon.

The reasons for these variations have not been established, but, at least in some cases, the food supply apparently varies in a similar way to the clutch-size, in northern Europe, for instance, reaching a peak in spring and declining in summer. The position is not, however, as simple as this might suggest. Thus in three species of copepods studied by Wesenberg-Lund in Denmark, not only does the egg-number decrease, but the size of the eggs increases, between spring and summer, and Hutchinson calculated that in *Eudiaptomus graciloides*, the summer clutch of about 4 eggs represents a similar egg-volume to the spring clutch of 9–18 eggs. The larvae hatch from these large summer eggs at a later stage of their development. It may therefore be suggested that the large egg-size is adaptive and due to the fact that, when food is scarce, the larvae have a greater chance of survival if they have a larger internal food-store and hatch out at a later stage; but the production of eggs of larger size inevitably means a smaller number of eggs. Here, then, within one species, is an inverse correlation between egg-number and egg-size similar to that found earlier when different families or orders of marine animals were compared, and with the same suggested significance. A similar case occurs in *Daphnia*, in which the larger number of small "summer" eggs poor in yolk contrasts with the smaller number of large "winter" eggs rich in yolk. It may be noted that in fresh-water crustacea, as in birds, the clutch is formed in anticipation of the food situation for the young. Such "anticipatory" adaptation is a characteristic result of natural selection.

This relationship between egg-number and egg-size helps to explain an otherwise puzzling situation found in a very different group of animals, the lizards. In the Wall Lizard *Lacerta sicula*, Kramer (1946) found that the number of eggs laid per clutch on islands off the Italian coast was 2–4, whereas on the adjacent mainland, subspecies of the same species usually laid 4–7 eggs. Genetic crosses between the insular and mainland subspecies showed that this difference was hereditary, the hybrids having clutches of intermediate size. Now the insular lizards not only laid smaller clutches, but had eggs of larger size than those of the mainland lizards. On the islands, the lizards have no predators so far as known, but food and water are sparse, while on the mainland both enemies and food are abundant. A larger egg is probably advantageous for the insular forms, as the young are larger at hatching, and so are better able to withstand food and water shortage. The smaller clutch of the insular lizards is, in my view, an incidental consequence of natural selection favouring eggs of larger size.

A similar difference has been found in California for lizards of the genus *Sceloporus*. High in the mountains, where enemies are absent but food is short, *S. graciosus* has an average of 3·3 eggs per clutch, but in the plains, where enemies abound, the related *S. occidentalis* has an average of 8·5 eggs (Stebbins and Roberts, 1946; Stebbins, 1948). The reason is not that *S. occidentalis* lays more eggs because its young have more enemies, but that, where enemies are absent, the lizard populations are limited by food shortage, and so eggs of larger size are at a selective advantage; and larger eggs mean fewer. (This interpretation is mine, not that of Kramer or Stebbins.) Once again, therefore, there is an inverse correlation between egg-number and egg-size, and the size of the eggs has been evolved in relation to the food situation for the young.

One further, and quite different, factor is claimed to influence the reproductive rate of lower animals. Fecundity, it is said, varies inversely with population density. This claim is based on population studies made in the laboratory with cultures of *Lucilia* (Nicholson, 1950) and *Drosophila* (Pearl, 1932; Sang, 1950) among diptera, of *Tribolium* and other flour-beetles (Park, 1941; Boyce, 1946; Crombie, 1947) and of *Hyalella* (Wilder, 1940) and *Daphnia* (Pratt, 1943) among crustacea.

In *Lucilia*, Nicholson clearly showed that the females laid fewer eggs when the cultures were crowded. He also showed that with a limited food supply the number of larvae which survived to become adults was larger when the culture was started at a low than a high density. Indeed, if the initial density of larvae was too high, none survived, as the food supply became exhausted before they could complete their development. Now *Lucilia*, the Sheep Blowfly, is a mobile animal which, in nature, lays its eggs in a circumscribed habitat such as the flesh of a living or dead sheep. Since, as shown by Nicholson, the larvae die when overcrowded, there must be strong survival value in any behaviour which prevents the adult flies from laying their eggs where too many eggs or larvae are already present, and under natural conditions *Lucilia* presumably reacts to overcrowding by suspending laying and flying off to seek some other place in which to lay.

I would suggest, therefore, that the crowding in Nicholson's experiments was unnatural, and that their true significance is rather different from that claimed. Similarly in *Drosophila*, I would interpret the decline in fecundity with rising population density in the culture bottles as part of the response which, in nature, leads the females to cease laying where the food supply for the larvae is dwindling, and to go elsewhere. In support of this view, the natural breeding-places of *Drosophila*, sap-smears and the like, are evidently much more circumscribed than a laboratory culture bottle, or they would have been found more often; yet as Sang (1950) points out, stunted adults (indicating undernourishment as larvae) are rarely if ever found in nature, though they are common in the laboratory. Further, Sang has shown that the decline in fecundity with rising population density is due, not to population density as such, but partly to a change in the nature of the culture medium through the action of the larvae already present, and partly to a decline in the quantity of food present.

There is a parallel to these findings in the experiments of Salt (1936) on the chalcid *Trichogramma evanescens*, which parasitizes the eggs of the flour-moth *Sitotroga cerealella*. Normally *Trichogramma* lays one egg in each host. When it was supplied with many hosts, egg-laying proceeded apace. If, however, only a few hosts were provided, these were parasitized, but egg-laying was then restrained for about eight hours. After this, the parasite began to lay more than one egg in each host, but had it been unconfined in nature, it would presumably have moved elsewhere in search of unparasitized hosts. The survival value of the behaviour is clear, since Salt found that if 2 or 3 eggs were laid in one host, only one adult usually emerged, while if more than 4 eggs were laid in one host, only one stunted adult, or none at all, emerged.

In flour-beetles, part of the apparent decline in fecundity with rising population density is due to a rise in egg-mortality through accidental cannibalism, but there is also a genuine decrease in the number of eggs laid. This, also, is due not to a high population density as such, but to a resulting shortage sometimes of food, and sometimes of places in which to place the eggs (Crombie, 1947).*

Similarly in crustacea, the data reviewed by Hutchinson (*loc. cit.*) indicate that clutch-size is influenced by food supply, but not by popu-

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* In a paper seen only after this MS. was completed, Voute (1937–38) showed that the fecundity of the rice-eating weevil *Calandra oryzae* decreased above a certain population density, and that at this same density the beetles started to emigrate. This supports my interpretation of the situation in *Lucilia* and *Drosophila*.

lation density as such. In the copepod *Phyllodiaptomus annae* in Ceylon, for instance, clutch-size is highest at the start of the reproductive season in June and thereafter falls steadily, but population density first rises and then falls during this time. Likewise in European freshwater copepods, clutch-size falls from April onwards, but population density first rises and then falls. Hence clutch-size bears no constant relationship to population density. Hutchinson also cites Slobodkin (*unpublished*) that food supply controls fecundity in *Daphnia obtusa*.

Summarizing, the decline in fecundity as the population increases in a laboratory culture is really a response which, in nature, prevents or reduces egg-laying where or when there will be insufficient food for the larvae to develop. It is not primarily a response to a high population density as such, though the latter is often associated with a dwindling food supply. It seems very possible that the inverse correlation mentioned earlier between clutch-size and population density in the Great Tit *Parus major* has a similar explanation. Provided that the population is not restricted by shortage of nest-holes, the Great Tit breeds at a much higher density in broadleaved than coniferous woods (Kluijver, 1951). This indicates that broadleaved woods provide it with much more favourable conditions, so the question arises as to why any Great Tits breed in conifers. The answer is, I suggest, that broadleaved woods become progressively less favourable for raising young as the tit population increases, until a point is reached at which an empty coniferous wood provides better conditions. This view is supported by Kluijver's finding that the average clutch-size is higher in coniferous woods (the less favoured habitat) than in *crowded* broadleaved woods.

The situation in the Great Tit is much complicated by local and annual fluctuations in the food supply (Lack, 1952); the available evidence suggests that clutch-size is influenced by the food situation, rather than by population density as such. This also applies to those hawks and owls which prey on *Microtus*. Where there is a vole plague, these species not only have larger clutches than usual, but they congregate to breed in much larger numbers than usual. Hence their clutch-size varies directly, not inversely, with population density. The relevant point, of course, is that both their population density and their clutch-size are greatly influenced by the food supply, and any direct or indirect influence of density on clutch-size is negligible.

The vole-predators, also cone-crop feeders like the Crossbill *Loxia curvirostra* and locust-predators like the Rose-coloured Starling *Pastor roseus*, are unusual among birds in that, in any given locality, the food for their young varies greatly in abundance from year to year. Correlated with this, the species concerned are nomadic, moving out of areas where food is sparse, and congregating to breed where food is abundant. In most other birds, the food for the young varies much less, and such species tend to be much more evenly dispersed when breeding. This dispersion was formerly attributed to territorial behaviour (Howard, 1920), but there are grave objections to this view. In particular it is necessary to postulate, as Howard saw, that territory-size is specific. Indeed Howard claimed that it was specific, but actually it varies with the conditions, as shown above for the Great Tit.

Further, a rather even dispersion for breeding is characteristic not only of territorial but also of colonial species, such as the Heron *Ardea cinerea.* In the Upper Thames valley, for instance, there is a small heronry about every five miles. Despite the attraction for this species of colonial breeding, the birds do not collect into one large colony, and there is evidently a severe restriction on the size of each colony. Further, the upper limit of size varies markedly in different parts of England and the Continent, presumably in accordance with food supply.

There is no reason to think that, in the Heron, some individuals expel others from the colonies. The simplest explanation of the dispersion of the colonies is that those individuals seeking breeding sites avoid settling where there are already many pairs present in relation to the food supply. The same explanation may well hold in territorial species, with the hostility of settled pairs perhaps playing a subsidiary role. Bird-ringing shows that, except in the few nomadic species, adult birds tend to breed where they bred in the previous year, probably because the advantage of returning to a known place outweighs the possible chance of finding a new place that is richer in food. In species of this type, the only individuals seeking breeding sites are those breeding for the first time, together with a few older individuals which have found their site of the previous year untenable. Hence dispersion is brought about mainly by individuals breeding for the first time. Kluijver's findings for the Great Tit show that the attractiveness of any particular place depends not only on the nature of the habitat, but on the number of pairs already present, and the observed decline in the reproductive rate with increasing population density shows that there will be survival value in avoiding crowded places. To conclude, therefore, the significance of breeding dispersion in birds is probably similar to the tendency among invertebrates to avoid laying eggs where the chances of larval survival are reduced.

SUMMARY

(1) The thesis advanced here is that the reproductive rate of animals, like other characters, is a product of natural selection, hence that each

species lays that number of eggs which results in the maximum number of surviving offspring.

(2) In nidicolous birds, clutch-size is limited by the number of young that the parents can feed. With broods above normal size, fewer, not more, young are raised per brood. In many species, clutch-size can be modified within limits to suit the particular feeding conditions. Similar considerations hold for mammals; and in social insects the number of eggs laid is adapted to the number of workers, i.e. to the food supply.

(3) In animals which do not feed their young, the number of eggs laid is probably the maximum that the parent can produce, but this is greatly influenced by the size of the eggs, in particular by the size of the food-store. An inverse correlation between egg-number and egg-size is found not only when comparisons are made between different types of animals, but also in the seasonal variations in egg-number within one species of freshwater crustacean, and in the local hereditary differences between lizard populations.

(4) The decline in fecundity with rising population density, found in both birds and invertebrates, is primarily a response to a dwindling food supply for the young, and not to population density as such. As part of this response, birds, diptera and other mobile animals move away from places where conditions are less favourable, and so tend to be dispersed rather evenly for breeding.

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ERNST MAYR

Change of Genetic Environment and Evolution

THAT mutation, recombination, selection and isolation are the four cornerstones of evolution is now generally acknowledged. The way in which these factors interact in the various evolutionary processes and the role played by diverse subsidiary factors are, however, by no means fully clarified. In particular, the role of one factor, a sudden change in the genetic environment, seems never to have been properly considered. That this factor might be exceedingly important in the evolutionary process occurred to me when studying a puzzling phenomenon, frequently encountered by the systematist, the conspicuous difference of most peripherally isolated populations of species.

Let us look, for instance, at the range of the Papuan kingfishers of the *Tanysiptera hydrocharis-galatea* group (Fig. 1). It is typical for hundreds of similar cases. On the mainland of New Guinea three subspecies occur which are very similar to each other. But whenever we find a representative of this group on an island, it is so different that five of the six Papuan island forms were described as separate species and four are still so regarded.

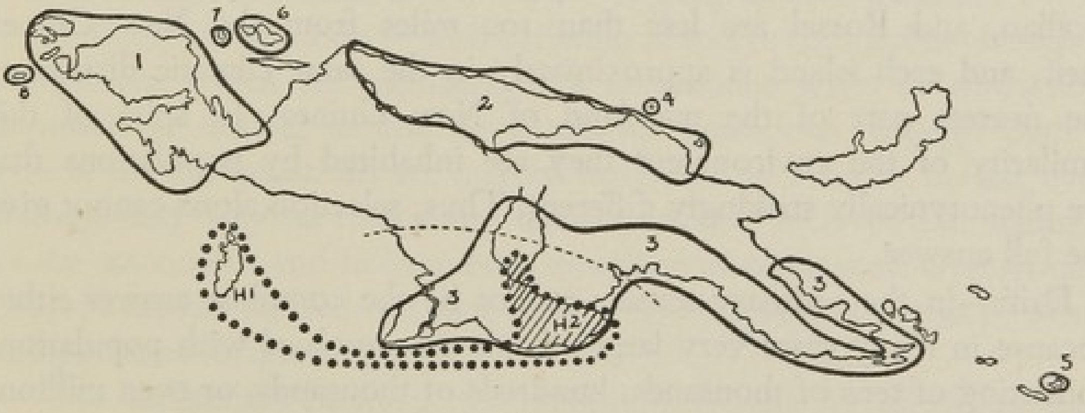

FIG. 1

EVOLUTIONARY GENE-FLOW

For such a striking dissimilarity of peripherally isolated populations two reasons are usually cited: difference of physical and biotic environment or genetic drift. It seems to me that neither of these factors nor a combination of the two can provide a full explanation, even though both may be involved.

Let us first look at the possible effects of the environment. New Guinea is a tropical continent. If it were projected on the map of Europe, it would reach from England to the Black Sea. In north-western New Guinea (near the Equator) it is exceedingly humid and without pronounced seasons; nearly the same amount of rain falls in every month of the year. In south-east New Guinea (Port Moresby) most of the rainfall is condensed into a short rainy season, while it is dry the rest of the year. The biotic environments in the extreme areas of New Guinea are as drastically different as the physical environments, only heavy rain forest in some areas, much monsoon forest in others. Still, the populations of *T. galatea* which occur at the two ends of New Guinea are hardly distinguishable.

A similar situation is found in numerous other species; if there are subspecific differences within New Guinea they are often merely matters of degree. We can generalize and say that strong environmental differences may not lead to conspicuous morphological differentiation. (This statement does not deny the physiological adaptation of the populations to their respective ranges.)

What is the situation with respect to the islands? Numfor, Biak, Koffiao, and Rossel are less than 100 miles from the New Guinea shelf, and each island is approximately in the same climatic district as the nearest part of the mainland of New Guinea. In spite of this similarity of the environment they are inhabited by populations that are phenotypically strikingly different. Thus, selection alone cannot give the full answer.

Drift—in the ordinary sense—cannot be the complete answer either because in many cases very large islands are involved with populations consisting of tens of thousands, hundreds of thousands, or even millions of individuals (see below).

The phenomenon of conspicuous divergence of peripherally isolated populations, so well illustrated by the *Tanysiptera hydrocharis-galatea* group, is familiar to every taxonomist. Scores, if not hundreds, of examples can be found in every monograph or checklist. We may mention merely a few more:

The kingfisher *Halcyon australasia* is virtually without geographical variation all over Australia (*sancta*), but has subspecies on New Zealand, New Caledonia, the Loyalty Islands, and very strikingly different subspecies in the Lesser Sunda Islands.

The hawk *Accipiter novaehollandiae* shows little evidence of geographical variation in New Guinea but has endemic subspecies on many islands east and west of New Guinea, five subspecies in the Bismarck Archipelago, and five in the Solomon Islands, in a total land area considerably smaller than the area of New Guinea.

A comparison of the disrupted Mediterranean ranges of many amphibians, insects (e.g. *Bombus*), and lower invertebrates (e.g. *Dugesia gonocephala*) with the contiguous ranges of the same species in the temperate parts of the Palearctic region shows the same. The lizards (*Lacerta*) of the Mediterranean area have only few slight subspecies on the mainland, but scores on islands. The four species of *Peromyscus* most closely related to *P. maniculatus*, are (or have been until recently) peripherally isolated.

It would lead too far to quote here more cases; all would merely be variations on the same theme. I have spoken in earlier publications of the "law of peripheral populations." This is not entirely accurate. Peripheral populations are not outstandingly different if they are part of a continuous series of populations. Only "peripherally isolated" populations show the pronounced deviations from the species "type," illustrated by the above-given examples.

THE STRUCTURE OF SPECIES

It is evident that there are two types of geographical variation.

(1) Ecotypic variation.—This variation adapts to the local environment populations which are members of a continuous series of contiguous populations. Owing to the never-ceasing gene-flow through such a system these populations are merely variations on a single theme, even though they may be sufficiently distinct to have received the attention of the taxonomist and to have been described as subspecies. Goldschmidt (1940: 182) has singled out *such* subspecies to attack the concept of the subspecies as incipient species.

"The differences between two subspecies are usually clinal, merging into each other. . . . While the characters of subspecies are of a gradient type, the species limit is characterized by a gap. . . . The subspecies do not merge into the species either actually or ideally. . . . Subspecies are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species."

These statements are correct so long as they are applied only to those subspecies that are subdivisions of a widespread array of continuous populations. Such subspecies, indeed, are not incipient species. Incipient species require isolation (see under 2).

The variation in such a system of contiguous populations is characteristically "ecotypical," that is, adaptive within the established "type." It is characterized by clines, and most variation within such a system obeys the various ecological rules. That the evolutionary changes due to this type of variation do not necessarily lead to species formation has been long recognized by systematists.

"Clines indicate continuities, but since species formation requires discontinuities, we might formulate a rule: *The more clines are found in a region, the less active is species formation.* We can prove this if we compare regions in which clines are frequent with those in which they are rare" (Mayr, 1942: 97).

Nevertheless there may be an accumulation of considerable genetic differences at the opposite ends of a cline. Nothing illustrates this better than the well-known overlapping circles of races as well as reduced fertility among geographical races. A secondary isolation of such populations may quickly lead to completion of species formation (see below).

(2) "Typostrophic"* variation.—Isolated populations, such as the ones illustrated above, show a type of variation so different from that of contiguous populations that we may be dealing with something entirely new. These peripheral populations often have not only the characteristic features of incipient species, but what is more important they often are species or incipient species of an entirely new type. That is, they may have morphological or ecological features which deviate quite strikingly and unexpectedly from the "parental" pattern.

A comparison of the two kinds of geographical variation, as well as of the populations produced by them, leads inevitably to the question: What is the factor that distinguishes the isolated population from the population which is part of a large group of populations? We shall attempt to answer this in the next section.

THE EFFECT OF GENE-FLOW

Of the many factors that are of importance to the evolutionist, gene-flow is perhaps the most neglected one. In a given wild population genetic novelties may occur through mutation or through immigration from outside populations (with recombination making available an unlimited assortment of these factors). While there are numerous studies on all aspects of mutation, virtually nothing is known on the genetics

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* A term used by the paleontologist Schindewolf to denote the origin of a real evolutionary novelty, a new "type."

of gene-flow. In fact, the technique of the geneticist is built on the avoidance of gene-flow or of immigration, hence the stoppers on *Drosophila* bottles and the wire netting of mouse cages. Whenever gene-flow occurs in spite of all precautions it is called "contamination," and the contaminated cultures are carefully destroyed. Since the genetics of gene-flow has not yet been studied in the laboratory, a determination of its importance depends either on field work, such as done by Timofeeff-Ressovsky, Dobzhansky, and Ford, or on guesses. In orthodox genetics the effects of gene-flow are usually presented as the addition of the immigrated genes to the gene pool of the local population and their subsequent gradual elimination in so far as they are inferior to the other genes of the gene pool. Such a purely additive treatment of gene-flow is not correct, as we shall presently discuss, since it neglects the fact that a gene pool is not an unconnected "pile of genes," but a well-integrated, balanced system.

For a further analysis of this problem it is of vital importance to determine how great the amount of gene-flow is as compared with mutation. I venture the guess that the total amount of genetic change contributed by immigration to a given local breeding population of a prosperous widespread species is many times that contributed by mutation occurring among the members of this population.*

Since gene-flow is due to the movement of individuals which are the carriers of genes, the phenomenon of dispersal becomes of interest to the geneticist. This was clearly realized by Timofeeff-Ressovsky, Dobzhansky, Ford, and other population geneticists. To measure the amount of gene-flow through a study of dispersal, as was attempted by naturalists and geneticists, encounters various difficulties.

The chief difficulty is that at best one can determine only what percentage of individuals in a population are immigrants, but not how genetically similar or different these immigrants are as compared with the members of the "native" population. The amount of genetic difference depends largely on the distance (within the species range) from which these immigrants have come. The usual assumption is that individuals settle within a predictable and rather narrow circle around their place of birth. In studies of non-colonial bird populations it is usually found that 30–40 per cent of the individuals that newly settle in a study area are born within the study area, the remainder being new arrivals. It is usually assumed that most of these come from the immediately adjacent area. This assumption is based on the further assumption that the dispersal curve is essentially a normal curve. Bateman

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* It has no bearing on the present argument that the genetic differences of the immigrants are ultimately also due to mutation.

(1950), however, has summarized numerous data, including his own and those of Dobzhansky and Wright, which indicate that the dispersal curve is not normal but leptocurtic and probably not even symmetrical but strongly skewed. In fact, so far as birds are concerned, there are some indications that the populations in many species are composed of two kinds of individuals, those with a strong locality sense and those with little or none. It is possible that the latter, perhaps up to 10–30 per cent of the population (differing from species to species) may settle in any suitable spot up to 100 kilometres or more of the place of birth. Dobzhansky and Wright (1947) likewise suggest for *D. pseudoobscura* the possibility of a composite dispersal curve. Previous calculations of the amount of gene-flow have tended to ignore this minority of long-distance colonists, which are nevertheless of considerable importance in counteracting the effects of local selection-pressures. Such long-distance dispersal has been established not only by bird banders, but is very characteristic for the spreading of expanding species like the Serin Finch (*Serinus serinus*) or the Ring Dove (*Streptopelia decaocto*). Individuals from far distant populations, even though few in number, are apt to contribute many new genetic factors to a population.

In previous discussions of the genetic effects of long-range dispersal attention was focused almost entirely on the fate of the alien genes in the new gene-complexes. Since they are usually from regions with rather different selective factors, such alien genes are apt to be of inferior viability in the new environment and will be eliminated sooner or later. Little or no thought, however, was given to the effects of these alien genes on the relative viability of the genes of the gene-complex into which they were introduced. It appears probable that the frequent introduction of such alien genes into a gene pool will lead to selection of such "native" genes as are tolerant to combination with such alien genes, that is, which produce viable heterozygotes with a great assortment of alien alleles or gene combinations.

A further effect of such gene-flow is that it disturbs the integration of local gene-complexes in response to local selection-pressures. Although all populations are somewhat ecotypical, such infiltration of alien genes may prevent a complete response of the gene-complex to the local selection-pressure and may therefore act as a conservative ("stabilizing") element in the whole evolutionary picture.

Several proofs can be cited for the reality of this effect of gene-flow. Dr. R. A. Fisher kindly called my attention to a case described by Turesson where in a specialized habitat no specific ecotype developed because the location was too small and therefore too much exposed to gene-flow from adjacent localities. But, even where a local ecological race develops, its great variability is evidence for the continued inflow of genes from adjacent populations (see the cases described by Clausen, Hiesey and Keck and those summarized by Stebbins, 1950).

Particularly instructive are the races of small mammals in the southwestern United States that live on lava flows. Endemic blackish races develop on small lava-flows only if they are completely surrounded by sandy desert. If they are in contact (on more than $\frac{1}{10}$ of their circumference) with areas of desert rocks there will be too much gene-flow to permit the development of endemic black races (Dice and Blossom, 1937; Hooper, 1941). When two soils of different colours come in contact, the effects of gene-flow will be noticeable for many miles on either or, at least, on one side of the zone of contact as shown by Sumner, Dice, Blair, Hayne, and others. It is evident in all these cases that local selection-pressure is partially neutralized by the effects of gene-flow.

Selection will be able to work unimpeded only if the selective agent simultaneously eliminates dispersal. Contact poisons for insects, as for instance, DDT are indeed such an agent. In a population, which is being selected for DDT resistance, all non-resistant flies that enter the population are eliminated before they can counteract through their genes the genetic process of the continued improvement of the DDT resistance.

These considerations finally elucidate a problem which has been a great puzzle to all naturalists and zoogeographers, namely, the problem of the borderline of species. The species-border is the line beyond which the selective factors of the environment prevent the successful reproduction of the species. However, it is well known to naturalists that through dispersal from the species range a considerable number of individuals settle down annually beyond the normal species-border where they attempt to reproduce. Some even succeed in establishing new colonies, but these are sooner or later eliminated in an adverse season. This has the result that the species border, though fluctuating, remains at a dynamic, stable line. What has been puzzling is the fact that the natural selection in the belt immediately beyond the previously existing borderline has not been able to produce a population adapted to the local conditions, in the same way as the application of DDT produces a DDT-resistant strain of flies. This is particularly puzzling since conditions beyond the borderline differ from conditions within the species border usually only slightly and in degree. This puzzle can be considered solved if we assume that this process of adaptation by selection is annually disrupted by the infiltration of alien genes and gene-combinations from the interior of the species range which prevents the selection of a stabilized gene-complex adapted to the conditions of the border region.

THE GENETIC ENVIRONMENT

The reason for the importance of gene-flow and of isolation is implied in much of the recent genetic work but has never been fully stated. Classical genetics studied the genetic changes at a given gene locus as well as the physiological and selective effects of such changes. Since—for the sake of simplifying the analysis—each locus was studied separately, the genetic factors of an organism were treated as so many beans in a large bag. That this is not so is now known to every geneticist, but "bean-bag" thinking is still widespread. The fact is, of course, that genes do not exist in "splendid isolation," but are parts of an integrated system. In order to appreciate the complexity of this system it is necessary to recall some of the recent studies.

The normal model of genetic change, presented in most evolutionary studies, is that of a gene p, originally in homozygous condition, on which mutation pressure (or immigration pressure) is exerted by an allele q. A maximum of 50 per cent heterozygotes may occur under these conditions (if both alleles are of equal frequency). Numerous studies indicate, however, that such a situation in which there are only two competing alleles may be the exception rather than the rule. At many loci there are simultaneously three, four, five, or more alleles available.

Two alleles produce one kind of heterozygote, 3 alleles 3 (ab, ac, bc), 4 alleles 6, 5 alleles 10, and 6 alleles 15 kinds of heterozygotes. The series expands very rapidly: 15, 21, 28, 36, 45, 55, etc. The number of homozygotes (under the simplified assumption of equal frequency of the various alleles) is $\frac{1}{n}$, so that with 5 alleles present, only $\frac{1}{5} = 20$ per cent of the genotypes might be homozygotes. It is quite evident from these considerations that the heterozygotes are of much greater importance in such a system than the homozygotes, and the more so, the greater the number of alleles.

In view of the considerable morphological uniformity of samples from most natural species, it may be denied that multiple alleles are frequent in nature. This may be true for some loci, but it is certainly not true for others. Even alleles that produce lethal homozygotes may be indistinguishable as heterozygotes, and it is known that lethals are frequent in many wild populations. A consideration of the so-called *isoalleles* (Stern) is important in this connection. Isoalleles are alleles that are phenotypically indistinguishable in homozygous condition from the "normal" wild-type allele but have different expression when placed in heterozygous combination with tester alleles. Only few studies have been made so far to determine the frequency of isoalleles (Stern, Timofeeff, Spencer), but, as Spencer's summary indicates (Spencer, 1944), isoalleles appear to be amazingly common at some loci. The fact that there are different frequencies of hereditary diseases in different human races may in part also be due to different mutation-rates in different isoalleles.

Still more important than are the multiple alleles is the fact that during development all genes are members of a team. Not only has every gene that has been thoroughly studied been found to have pleiotropic effects, but it has also been found that every character is produced by the joint action of many genes. It is immaterial in this connection what particular genetic theory one adheres to: major genes and modifiers, genes and polygenes, switch genes and gene complexes, position effects, and non-localized genes. They all agree in the essential point which is that the action of a given gene is strongly influenced by its genetic background, its genetic "co-actors." And what is true for the function of a gene is true also for its selective value. A gene which is of high selective advantage on one genetic background may be selected against on another genetic background. *The selective value or viability of a gene is thus not an intrinsic property but is the sum-total of the viabilities on all the genetic backgrounds that occur in a population.*

THE COADAPTED SYSTEM

The concept that the viability of a given allele depends on its genetic background is not new. It has been emphasized by several students of this problem. Sewall Wright (1931: 155), for instance, stated: "The selection coefficient of a particular gene is really a function not only of the relative frequencies and momentary selection coefficients of its different allelomorphs, but also of the entire system of frequencies and selection coefficients of non-allelomorphs." Recently Dobzhansky has supplied experimental proof for coadapted selective changes in chromosomes or gene-arrangements (Dobzhansky, 1950; Dobzhansky and Levene, 1951). The relativity of such viabilities is most convincingly illustrated by the findings of Wallace and King (1951) in irradiated Drosophila populations. They find "that while an examination of the individual chromosomes of a population may reveal that these are generally "deleterious" when homozygous, an examination of pairs of unrelated chromosomes from the same population may reveal that these pairs are distinctly superior." Muller's (1948) work on dosage effects and much other genetic work points in the same direction.

Such a well-integrated, coadapted gene-complex constitutes an evolutionary unit in spite of its intrinsic variability. Any disharmonious gene or gene-combination which attempts to become incorporated in such a gene-complex will be discriminated against by selection. There is much evidence for this, partly from experiments and partly from a study of natural populations. That the offspring of crosses among species or other only distantly related populations produce inferior gene-combinations has long been known to students of hybridization. This is often true even in cases where there is superficial heterosis. In the cases of back-crosses of F_1 hybrids with one of the parents, it is often found that only those back-crosses are viable that are close to the parental type.

That gene-complexes are well integrated units is the explanation of a phenomenon that has long been a puzzle to naturalists. There are many cases known where two incipient species come together in an allopatric zone of hybridization after a previous extrinsic barrier has been removed. Sometimes this zone is wide, but more often it is very narrow, even though all the available evidence indicates that the zone has existed for thousands of years. The border between the carrion crow and the hooded crow (*Corvus corone* and *cornix*) is an excellent example. Peus (1950) discusses such a case in a flea. In these and many similar cases it appears that the gene-complexes which come together are so well balanced within themselves that combinations with alien genes lead to combinations of inferior viability and are eliminated by selection. This counter-selection reduces introgressive gene-flow drastically.

Even a gene-mutation which leads to an improvement in the phenotype may have difficulties in such a system because it will take a long period before it is fully fitted into the total pleiotropic-buffered gene-complex. Simpson's findings that the tooth elongation in fossil horses was of the order of only one millimetre per one million years is a suitable illustration of this process. To be of real value such an improvement in the teeth has to be correlated with a strengthening of the upper and lower jaw and with numerous other readjustments of the skeleton, the muscles, and presumably even the viscera and the nervous system. All these changes require a rather thorough overhauling of the total gene-complex. It is not often that selection permits a single structure to rush far ahead of the other parts of the system to which it belongs.

The better integrated such a gene-complex is, the smaller the chance that a novel mutation will lead to an improvement. As Schmalhausen, Heuts, and others have pointed out, much of selection is stabilizing. A widespread species, with many local populations among which there is active gene exchange, tends to be very conservative.

Even though a species may have many local races (ecotypes), it arrives sooner or later at a geographical line, its species border, beyond which it cannot expand. As stated above, and other things being equal, this appears to be due to the fact that even the border populations are tied by gene-flow to the integrated gene-complex of the main body of the species. This applies to horizontal as well as to vertical (altitudinal) distributions. In most species there is a limit to ecotypic adaptation. It has long been known, for instance, that the validity of the so-called ecological rules (Bergmann's rule, Allen's rule, etc.), so far as it exists at all, is restricted to intraspecific variation. Subspecies of birds living in a cool climate tend to be of larger body size than subspecies living in the warmer parts of the range of the same species. However, a more northerly *species* is by no means always larger than its nearest more southern relative. The same is true for altitudinal variation. As Rand and others have shown, there is a steady increase of size with altitude within most sedentary species of birds with a wide altitudinal range. However, again, this does not necessarily apply to full species which replace each other altitudinally, as Dr. Rand pointed out to me. In 15 such pairs of bird species from New Guinea, the higher species was larger in 5 cases, of equal size in 3 cases, and smaller in 7 cases. It appears as if in these latter cases expansion into the higher altitudes was made possible on an altogether different physiological (and hence genetic) basis. The gene-flow through the lower altitude species was too stabilizing to permit range expansion into the higher altitude. (There is enough altitudinal overlap between the members of nearly all of these pairs to permit neglect of Gause's rule in this particular problem.)

CHANGES OF THE GENETIC ENVIRONMENT

The make-up of the well-integrated gene-complex, discussed in the previous section, as well as the continuous immigration of alien genes from adjacent or far distant populations, makes it evident that genes with either or both of the following two properties will be specially favoured by selection.

(1) Genes which produce heterozygotes of high viability, preferably viability superior to the homozygotes.

(2) Genes which produce viable combinations on the greatest number of different genetic backgrounds.

The former phenomenon leads to balanced polymorphism, first postulated by R. A. Fisher, the widespread occurrence of which has been abundantly confirmed in recent years. Dobzhansky and Levene (1951) have shown how quickly natural selection can produce such heterosis in cases where it was previously absent.

The selective advantage of genes that do well on a great variety of genetic backgrounds, "jack-of-all-trades" genes, does not seem to have received much attention in the genetic literature. The richer a population is in genetic factors (multiple allelic heterozygosity on many loci), the more important such genes are. A "good mixer," rather than a good "soloist," has a tremendous advantage in such a system.

This all may change dramatically when a few individuals are taken out of the stream of genes and placed in isolation. Let us illustrate this again with reference to the kingfishers of the *Tanysiptera galatea* complex. Let us assume, for instance, that Numfor Island, previously without *Tanysiptera*, was colonized by a couple of pairs of New Guinea birds. What changed in the conditions? The climate of Numfor is much like that of the opposite coast of New Guinea, thus the selection-pressure by the physical environment will remain much as it was in the previous range. The flora is somewhat different and the fauna is somewhat impoverished but the only potentially serious predator, *Accipiter novaehollandiae*, occurs both on Numfor and New Guinea. The physical and biotic environments are thus rather similar in both places. A third environment, however, the genetic environment, is strikingly different. The Numfor population is geographically and hence also genetically completely isolated from all other populations of the species (perhaps a few New Guinea individuals may get there every ten years), while *every New Guinea population is in the midst of a continuous stream of genes flowing back and forth across the entire island continent.* While the number of possible contacts of a given gene with other genes is exceedingly high in New Guinea, it is drastically reduced among the founders of the Numfor population.

The total sum of the relative selective values of each allele may be changed because the number of possible genetic interactions of this allele is much reduced. To illustrate the situation diagrammatically we might group the total number of possible genetic backgrounds of the parental populations in ten classes, x_1 to x_{10}. Let us further assume that in the population there are two alleles, of which one (a_1) is of broad, general efficiency on many genetic backgrounds, while the other allele (a_2) is very superior on some genetic backgrounds but inferior or even lethal on others. We are assuming arbitrarily for the sake of illustration an extreme situation. Most genes would presumably be ranged somewhere between the extremes of a_1 and a_2. The selective values of the two alleles a_1 and a_2 on the 10 backgrounds might be as in Table 1 on p. 169.

The total selective value of both alleles is identical, allowing for the relative frequencies (q) of the carriers of the genetic backgrounds x_1–x_{10} in the population. If the founding of the Numfor population was made by individuals with only the genetic backgrounds x_1–x_4, each being present with equal frequency ($q = 0{\cdot}25$), the total viability of the alleles a_1 and a_2 suddenly changes to $1{\cdot}075$ for a, and to $2{\cdot}5075$ for a_2. Instead of retaining equal viability, the viability of a_2 is now $2\frac{1}{2}$ times

TABLE 1

Arbitrary values of the frequencies (q) of ten classes of genetic backgrounds (x_1–x_{10}) in a population and of the viabilities (w) of alleles a_1 and a_2 on these ten backgrounds. The total viabilities of a_1 and a_2 are about equal in this population (1·102).

	x_1		x_2		x_3		x_4		x_5	
	q	w	q	w	q	w	q	w	q	w
a_1	0·1	1·1	0·05	1·2	0·02	0·9	0·17	1·1	0·12	1·3
	0·110		0·06		0·018		0·187		0·156	
a_2	0·1	1·33	0·05	3·4	0·02	2·8	0·17	2·5	0·12	0·4
	0·133		0·17		0·056		0·425		0·048	

	x_6		x_7		x_8		x_9		x_{10}	
	q	w	q	w	q	w	q	w	q	w
a_1	0·09	0·4	0·07	1·4	0·06	1·8	0·19	1·2	0·13	0·08
	0·036		0·098		0·108		0·228		0·101	
a_2	0·09	0·1	0·07	1·0	0·06	0·5	0·19	0·3	0·13	0·8
	0·009		0·07		0·03		0·057		0·104	

that of a_1. It is evident that a formidable selection-pressure will be exerted against a_1 which presumably will soon lead to its elimination from the new population. Even if the two alleles in question are less different in kind than a_1 and a_2, it is very unlikely that their selective values will remain unchanged (Fig. 2).

One of the obvious effects of the sudden reduction of population size in the founder population will be a strong increase in the frequency of homozygotes. As a consequence, homozygotes will be much more exposed to selection and those genes will be favoured which are specially viable in homozygous condition. Thus, the "soloist" is now the favourite rather than the "good mixer."

We come thus to the important conclusion that *the mere change of the genetic environment may change the selective value of a gene very considerably.*

Isolating a few individuals (the "founders") from a variable population which is situated in the midst of the stream of genes which flows ceaselessly through every widespread species will produce a sudden change of the genetic environment of most loci. This change, in fact, is the most drastic genetic change (except for polyploidy and hybridization) which may occur in a natural population, since it may affect all loci at once. Indeed, it may have the character of a veritable "genetic revolution." Furthermore, this "genetic revolution," released by the isolation of the founder population, may well have the character of a chain reaction. Changes in any locus will in turn affect the selective values at many other loci, until finally the system has reached a new state of equilibrium.

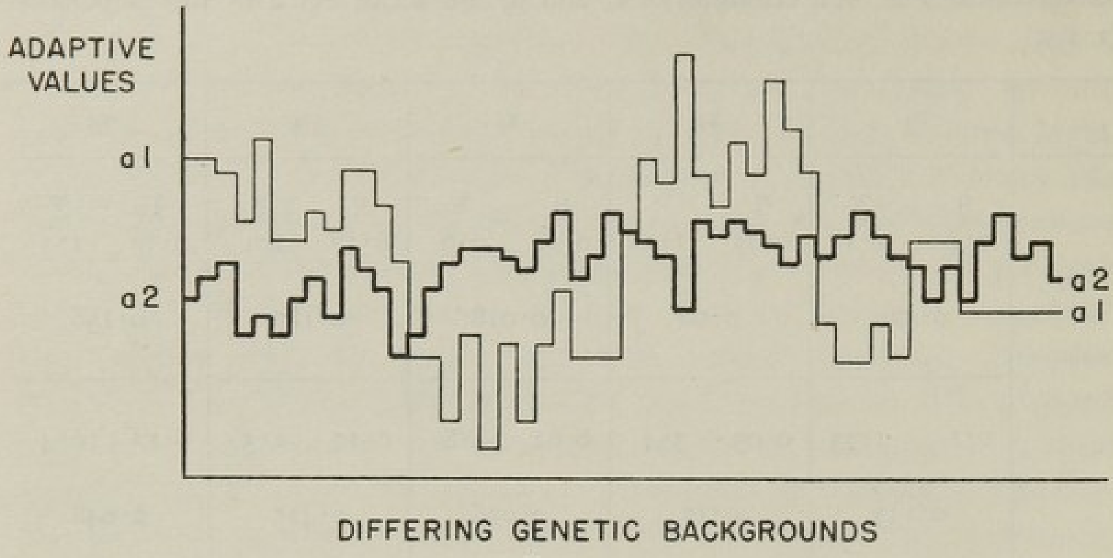

FIG. 2

THE ROLE OF THE PHYSICAL AND BIOTIC ENVIRONMENT

Focusing our attention on the decisive effects of interrupted gene-flow should not make us forget the important synergistic role of selection by the new physical and biotic environment. Selection on an island differs in two ways from selection on the mainland. The selection-pressure itself is different, since the environment (particularly the biotic one!) is inevitably somewhat different. Secondly, this selection can express itself more directly because its effects are not continuously disturbed by the inflow of alien genes. Selection, then, on an island will, if anything, produce even more conspicuous results than on a mainland.

The amazingly great differences among populations of adjacent islands, e.g. *Tanysiptera carolinae* (Numfor) and *riedelii* (Biak), indicate that the accidents of gene assortment during the "genetic revolution" of the isolated population may be more important than the "directive" force of the similar environment of adjacent islands.

It should be emphasized that such a "genetic revolution" in the founder population is only a potentiality but does not need to happen every time a population is isolated, if the genetic constitution of the founders does not favour it. The amount of the genetic revolution is unpredictable since it depends on many factors. It proceeds at the most rapid rate,

(1) if the parental population was particularly variable and subject to much gene-flow,

(2) if the founder population contained genes of very uneven selective values in different genetic environments and particularly genes that contribute high viability in homozygous condition,

(3) if the founders happened to have many genes of particularly high selective value in the new environment, and

(4) if the new physical and biotic environment is capable of setting up and maintaining divergence producing selective pressures and, in particular, if it permits a shift into a vacant ecological niche somewhat different from the parental one!

The fact that neither the Starling (*Sturnus vulgaris*) nor the House Sparrow (*Passer domesticus*) after their introduction in North America, nor many of the introduced agricultural pests have shown indications of a drastic evolutionary change confirms that the isolation of a population is not by itself a guarantee for a drastic change. Perhaps these colonies regained large population size too quickly. As has been shown by Ford and others (Ford and Ford, 1930), there is an increase in variability and a relaxation of selection in a rapidly expanding population. This relaxation of selection may mitigate or even counteract at first some of the effects of the sudden isolation. Perhaps this explains why there is apparently a lag between isolation and the differentiation of the isolated populations. One might expect the isolated populations to change conspicuously within the first two or three generations, but this is usually not the case. The fact that the gene-complex as a whole has to remain well integrated at all times (cf. tooth elongation in fossil horses) is another retarding factor.

FRACTIONING OF A CONTINUOUS SPECIES RANGE

Not all population discontinuities in nature originate by the colonization of islands. Sometimes they arise by the contraction of a species range and the separation of a previously continuous area into separate ranges. If a continuous large species range is split, let us say, into two wide ranges, A and B, both will contain a similar rich mixture of isoalleles, polymorph genes, pleiotropic factors, and polygenes. It will take some time before the interruption of gene-flow between the two population groups will make itself felt. But eventually some of the genes in A will disappear that had continuously drifted in from B (where they are superior) and vice versa. Also in view of the randomness of mutation, it is unlikely that the same mutations will occur in the two areas with identical frequencies. The result will be an increasing genetic divergence, accelerated by the different selection factors (of the external and genetic environment) in the two areas until the two population groups have again reached equilibrium.

If the respective environments remain rather similar and if the gene-complexes that were fractioned by a secondary discontinuity were particularly well balanced, they may diverge only very slowly after separation. There are many cases known, particularly among plants, where striking geographical discontinuities have not led to much of an evolutionary change in the separated populations. Stebbins (1950) has called attention to many such cases as, for instance, to that of the American and Asiatic *Platanus* which have not even reached reproductive isolation in spite of many millions of years of geographic isolation. It is evident from such cases that the length of the period of separation and the amount of genetic divergence are not always very closely correlated. Why some gene-complexes are so stable, while others evolve rapidly is still an unsolved problem. It appears very probable that differences in selection-pressures are not the complete answer.

It is possible that the difference in the mode of speciation (founder population versus fractioned species range) contributes to the differences in species patterns found in nature. It is well known among systematists that in some taxonomic groups there are many very similar species (including sibling species), while in certain other groups (e.g. Cerambycidae) most species are so different from each other that many of them are placed in monotypic genera. It would be interesting to determine whether most speciation in the former cases had proceeded via fractioning of initially large populations, while founders gave rise to many of the monotypic genera. Too many additional factors enter the picture to permit any generalization, but the possibility that the mode of speciation is one of these factors should not be entirely ignored.

GENETIC VARIABILITY

During a genetic revolution the population will pass from one well integrated and rather conservative condition through a highly unstable period to another new period of balanced integration. The new balance will be reached after a great loss of genetic variability. There are several sources of loss:

(1) The founders represent only a segment of the variability of the

parental population. (2) During the period of rapid readjustment, alleles that had been previously of equal viability will change their relative viability, like a_1 and a_2 discussed above, and the inferior ones will become eliminated. (3) Recessives will have a much greater chance to become homozygous in the reduced population and thus become more exposed to selection. As a consequence of these gene-loss inducing factors, a population may result which is not only very different genetically from the parental population but also genetically comparatively invariable. Much that is known about island populations supports the validity of this conclusion.

The evolutionist takes, on the whole, a dim view of the future prospects of populations with depleted genetic variability. Such populations are not very plastic. If they live on an island (in the broad sense of the word), they will probably be successful as long as conditions remain stationary. However, such populations rarely have the capacity to adapt themselves to severe environmental shocks. The arrival of a new competitor or of a new enemy or a drastic change of vegetation or of the physical environment is apt to lead to extinction. It is no coincidence that even though less than 20 per cent of all species of birds are island birds, more than 90 per cent of all bird species that have become extinct in historical times are island species. An island bird thus has at least fifty times as great a chance to become extinct as a mainland bird. Only part of this extinction can be attributed to the small size of the range of these island species.

Permanent genetic depauperization and eventual extinction are, however, not the inevitable fate of island populations. An occasional population succeeds in making an ecological shift during the "genetic revolution" and during the period of relaxed selection accompanying the phase of rapid expansion. It may become adapted to a new ecological niche or even to a major new ecological zone. If such a population can colonize the nearest adjacent "mainland," it may find this ecological niche or zone unoccupied and be able to invade it. Once it starts spreading over wide areas it can again start accumulating additional genetic variability so that in due time it may be as full of heterozygosity and concealed variability as the ancestral species with which it may now be sympatric.

We may illustrate this diagrammatically (Fig. 3).

Genetically depauperized populations have the best chance of survival in an unsaturated environment, an environment relatively free of competitors and enemies. This is the reason why speciation of this type has played such an important role on "vacant" archipelagos, such as the Galapagos or the Hawaiian Islands, or in "empty" lakes. Similar considerations may apply to the apparent bursts of speciation encountered by the paleontologist whenever a new major "type" appeared on the scene and entered a "vacant" ecological zone.

It has been questioned whether any natural population can pass through a genetic bottleneck of reduced variability (Fig. 3, B or C).

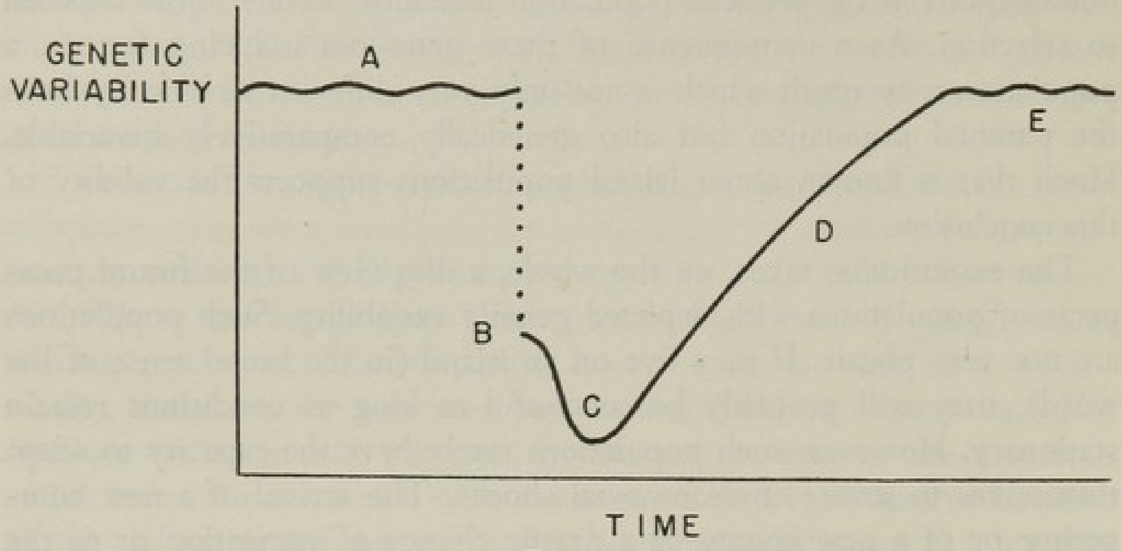

FIG. 3

However, there is abundant evidence that this *is* possible. Less than twenty pairs of the European Starling were introduced to the United States in 1890; and only a fraction of them bred successfully. It took more than fifteen years before they began to increase materially, but now (only forty years after they really started to spread) they are one of the most common birds of North America having increased to an estimated number of over fifty million individuals. The story of the House Sparrow (*Passer domesticus*), the Japanese beetle, the potato beetle, or of any other kind of successful introduction is the same. But there are also many cases of spontaneous founding of new species ranges. The Australian White-eyes (*Zosterops lateralis*), a small flock of which found its way in 1856 from Australia to New Zealand, is now the most common land bird in New Zealand, having settled the outlying islands as well. Finally, it is now well established that most, if not all, the birds of the Australian region got there island-hopping across the Malay Archipelago. The result has been a rich fauna of successful species, genera, and even families. All of them must have gone at one stage or repeatedly through a genetically extremely depauperized condition. The adaptive radiation of birds, insects, and other animals on isolated archipelagos, like the Galapagos Islands or Hawaii, is further proof. It is thus evident that populations can get through such a bottleneck and still become the progenitors of successful stocks.

Not enough quantitative analyses of species structure have been made to determine the average number of peripherally isolated incipient species in various groups of animals. Many species have none; others have five or six. Since most of the parental species have—speaking in terms of geological time—a long life-expectancy, there is only little opportunity for replacement, unless a population succeeds in entering a novel ecological niche. Thus, in spite of the continuous budding off of peripheral populations undergoing major or minor "genetic revolutions" as described above, only few will play a role in long-term evolution, perhaps one in fifty. The odds are very much against a successful passing through the bottleneck of reduced variability (Fig. 3) as well as the reaching of a new level of high variability and of an unoccupied ecological niche.

PERIPHERAL POPULATIONS AND MACROEVOLUTION

The peripherally isolated population has various attributes that are of great interest not only to the student of speciation but also to those who study major evolutionary changes. It seems to me that many puzzling phenomena, particularly those that concern paleontologists, are elucidated by a consideration of these populations. This concerns primarily the phenomena of unequal (and particularly very rapid) evolutionary rates, breaks in evolutionary sequences and apparent saltations, and finally the origin of new "types."

Evolutionary rates. It is now realized that the rate of evolutionary change is closely correlated with population structure. Evolutionary transformation would tend to be very slow in large panmictic populations, if such should exist in nature. A more rapid rate of evolutionary change will be induced by a different population structure. "A fine-scaled structure of partial isolation without marked environmental differences presents the most favourable condition for transformation as a single species" (Sewall Wright, 1951, summarizing earlier work). It seems to me, however, that even such a system is comparatively slow and conservative because it is rich in diverse genetic factors, including multiple alleles and, as Heuts (1951) points out, there will be a premium for constancy in such a system. Genetic factors will be selected for their ability to form viable combinations with the greatest number of other genetic factors.

It is very doubtful whether the population structure cited by Sewall Wright is favourable enough to explain the sudden, sometimes almost precipitous, changes of evolutionary rates which have been so puzzling to paleontologists. The (relative!) suddenness of these changes is unquestionable and even Simpson, who on the whole is successful in explaining evolution within the framework of the current genetic theory, found it necessary to coin a special term, quantum evolution, for this type of rapid evolutionary change.

Two kinds of explanations for rapid evolution have most often been given previously, a genetic and an ecological one, but both are unconvincing. Previous genetic interpretations are based on the occurrence of macromutations ("systemic mutations") or on mutational avalanches. Either type of event would have exceedingly slim chances of success in a population which is part of a connected system of populations with undiminished gene-flow. Equally unlikely is an ecological explanation based exclusively on a cataclysmic change of selective factors. Mountain building, shifts of climatic belts and similar events are by far too slow to account for "quantum evolution."

The genetic reorganization of peripherally isolated populations, on the other hand, does permit evolutionary changes that are many times more rapid than the changes within populations that are part of a continuous system. Here then is a mechanism which would permit the rapid emergence of macroevolutionary novelties without any conflict with the observed facts of genetics.

Phylogenetic saltations. Many paleontologists have postulated various kinds of typostrophic "saltations" in order to explain the absence of crucial steps from the fossil record. If these changes have taken place in small peripherally isolated populations, it would explain why they are not found by paleontologists. In fact, peripheral populations are neglected even by the taxonomists of most living faunas because they are comparatively small, isolated, and often in far distant or inaccessible places. In birds, however where they have been well studied, it is quite evident that they are not only incipient species but in many instances also incipient genera and higher categories. It has been pointed out earlier (Mayr, 1942; Rensch, 1947) that the problem of the origin of higher categories is inseparable from the problem of the origin of new species. Those who have denied this seem to be unfamiliar with the facts. It is, of course, inadmissible to apply the term speciation to subspeciation within continuously ranging populations and use this as evidence for denying that speciation could have anything to do with the origin of the higher categories. As stated above, the clinal variation within continuous populations is not of the type that normally leads to the origin of major evolutionary novelties. Such are found only in isolated allopatric peripheral populations.

As an example may serve the drongo species *Dicrurus hottentottus.* Though we are dealing here merely with inconsequential plumage features (Fig. 4), it is noteworthy not only that every aberrant population is peripheral but also that several of these populations have been considered by avian taxonomists to be generically distinct.

As stated above, most of these populations will eventually die out without playing a major role in the evolutionary picture. Only a very occasional one will be able to reach a vacant ecological zone. This agrees with the observed evidence, since the number of real evolutionary inventions ("new types") in the history of the earth is quite small in comparison with the total number of forms occurring at any one time.

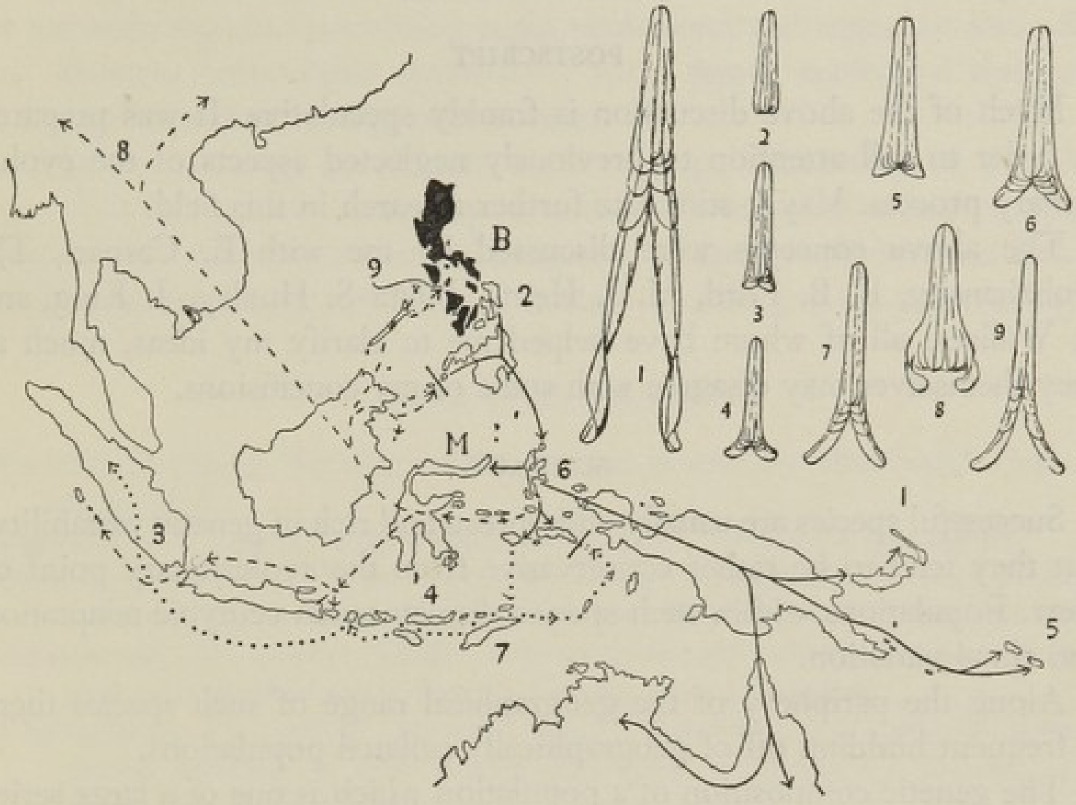

FIG. 4

As soon as such a population has completed its genetic reconstruction and ecological transformation, it is ready to break out of its isolation and invade new areas. Only then will it become widespread and is likely to be found in the fossil record. But then it is already too late to record the evolutionary change through which it has gone. All the paleontologist finds is the fact that one widespread numerous species was replaced or succeeded by a rather different species which is again widespread and numerous. Contrary to the belief of many paleontologists, such an apparent "jump" is consistent with the accepted genetic theory, as detailed above.

Ecological shifts.—Oceanic archipelagos are the best place to observe the results of sudden ecological shifts of populations in living faunas. A particularly convincing case has been described by Amadon (1947) in a Hawaiian honeycreeper. Here is an allopatric population which has not only undergone a change in bill structure but also in feeding habits. It has truly switched into an entirely new ecological niche. I visualize all major evolutionary novelties to occur in a similar manner. E. Zimmerman has described the case of a species of dragonflies, isolated on the Hawaiian Islands, in which the larva has entered into a totally new niche. It no longer lives in water like the larvae of all other dragonflies, but in the moist humus and plant debris on the forest floor. It could well become the progenitor of an entirely new type of insect.

POSTSCRIPT

Much of the above discussion is frankly speculative. It was prepared in order to call attention to previously neglected aspects of the evolutionary process. May it stimulate further research in this field.

The above concepts were discussed by me with E. Caspari, Th. Dobzhansky, E. B. Ford, M. J. Heuts, Julian S. Huxley, J. King, and B. Wallace, all of whom have helped me to clarify my ideas, much as they themselves may disagree with some of my conclusions.

SUMMARY

Successful species are usually widespread and rich in genetic variability, but they tend to be rather conservative from the evolutionary point of view. Populations within such species display much ecotypic adaptation and clinal variation.

Along the periphery of the geographical range of such species there is frequent budding off of geographically isolated populations.

The genetic composition of a population which is one of a large series of contiguous populations of a widespread species is continuously affected by the immigration of genes derived from adjacent or far distant populations.

In such a population there will be a selective premium on genes which do well on a great variety of genetic backgrounds and which are thus adapted to cope with the continuous influx of alien genes.

The selective value of many genes will change drastically on the altered genetic background ("genetic environment") of a newly founded peripherally isolated population. This will lead to a rapid change of gene-frequencies simultaneously at many loci ("genetic revolution"), assisted by the selective effects of the change in the physical and biotic environment of the isolated area.

Furthermore, a different set of genes is apt to be superior in such an area in which gene-flow does not interfere with selection by the local environment.

Isolated populations are relatively invariable genetically for various reasons, and appear to become vulnerable to extinction, particularly if they live for long periods in a very uniform environment.

An occasional one of such populations may succeed during the period of genetic reorganization to enter a previously unoccupied ecological niche and to expand into this niche. As such a population becomes more and more numerous, it builds up again its previously depleted genetic variability.

The period of genetic reorganization and relaxed selection-pressure is not only a period permitting rapid evolutionary change, but also offers an otherwise unavailable opportunity for a drastic ecological change of a somewhat unbalanced genetic system.

Rapidly evolving peripherally isolated populations may be the place of origin of many evolutionary novelties. Their isolation and comparatively small size may explain phenomena of rapid evolution and lack of documentation in the fossil record, hitherto puzzling to the paleontologist.

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Fig. 1. Species and subspecies of the *Tanysiptera hydrocharis-galatea*-group. The subspecies 1, 2, and 3 of *galatea* on the mainland of New Guinea are exceedingly similar to each other. The subspecies *vulcani* (4) and *rosseliana* (5) are much more distinct. The populations on Biak (6), Numfor (7), and Koffiao (8) have reached species level. The form of Aru Island, *hydrocharis* (H_1), has also reached species rank and now coexists in South New Guinea (H_2) (shaded area) with a subspecies of *galatea* (3). (From Mayr, 1942.)

Fig. 2. Diagrammatic presentation of the relative selective value of alleles a_1 and a_2 on many different genetic backgrounds. On some a_1 is superior, on others a_2; a_1 has a more even viability on many backgrounds; a_2 is very superior on some and very inferior on others.

Fig. 3. Levels of genetic variability. A, in parental species, B, in founder population, C, after "genetic revolution," D, during recovery period, E, after a new level is reached.

Fig. 4. Geographic variation of the form of the tail in the polytypic drongo species *Dicrurus hottentottus*. The central populations, such as those on Sumbawa (4) and Halmahera (6), have a normal drongo tail. Nearly all peripherally isolated populations have a more or less aberrant tail, as those on Samar (2), Sumatra (3), San Cristobal (5), the Asiatic mainland (8), Timor (7), Tablas, Philippines (9), and New Ireland (1). The populations of Asia (8), New Ireland (1), Tablas (9), and Kei, near Timor (7) were once considered generically distinct. (From Mayr and Vaurie, 1948.)

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The Relation between the Evolution of Central Nervous Functions and the Body Size of Animals

I. GENERAL EVOLUTIONARY PROGRESS AND COPE'S RULE AS FACTORS IN THE EVOLUTION OF CENTRAL NERVOUS FUNCTIONS

IN the course of evolution the nervous processes have become increasingly complicated. Once a network of neurons for the conduction of excitation was developed (on the phylogenetic level of the Coelenterata), the behaviour of animals could be controlled by an increasing number of reflexes. Later, the development of nerve-centres made possible the origin of complicated instincts with a genetic basis and the increasing utilization of associations and experience. The higher the animal in the animal kingdom, the more the fixed hereditary instincts are reduced in favour of actions guided by experience. In the course of such an action there are alternative motor responses to the stimuli present in the situation, of which the most favourable is chosen. On the highest level of development the actions guided by experience become partially replaced by actions guided by insight, i.e. by recognition of causal connections, thus enabling experience to be generalized. Such a series—reflexes, instincts, actions guided by experience, actions guided by insight—corresponds with an increasing efficiency in behaviour. There is less chance of damage or death as a result of inadequate reaction to environmental conditions. Thus it is clear that in the struggle for existence those groups of animals were successful in which a more complex central nervous system made possible a higher type of behaviour. In this way the Placentalia everywhere defeated the Marsupialia and other primitive mammalian orders; the Carnivora defeated the Creodonta (with smaller and more primitive brains), the monkeys the Prosimii, and finally man all higher vertebrates.

Furthermore, the levels of central nervous function are especially characteristic of the general advance of the animal kingdom as a whole. Animal evolution not only produced lateral divergence (cladogenesis) but also caused upward progress (anagenesis). Such anagenetic advance is characterized by four factors, all of which are advantageous in the struggle for existence:

1. Increase in complexity.
2. Increase in rationalization and centralization of functions.
3. More autonomous and therefore more plastic behaviour.
4. Approach to the level of organization attained by Man, as the latest dominant type.

During the evolution of central nervous systems greater complexity is already achieved when the number of neurons is increased. This is advantageous because it favours the ability to react to single minor complexes of stimuli (for instance reaction to single components of the retinal image) and because it makes possible a further diversification of function. A rationalization of functions already results from the facilitation of association in a nerve-centre, in which the end-stations of sensory stimuli are lying close together. Increase in the number of end-stations and, above all, the intercalation of pure regions of association produce the histological basis for a more plastic response to stimuli. They favour the non-inherited actions guided by experience and those guided by insight. The behaviour of the animal becomes more rational and at the same time more autonomous. Finally, an approach to the human level of organization is especially favoured by the growing plasticity of nervous and psychic performance. It is in the realm of central nervous functions that anagenesis is especially conspicuous; it must not be confused with "improvement", which is restricted to an increasing adaptation to special environmental conditions. This is merely a specialization and as such is quite different from anagenetic advance, i.e. a general improvement towards a higher level (cf. Rensch, 1947).

It is important to note that the four factors mentioned above are advantageous in the struggle for existence because we can conclude from this that the development and progress of nerve centres was inevitable.

We may perhaps say that the general plans of construction of the Carnivora, differing from those of the Creodonta in specialization only, do not involve any progress. But we cannot say this about their brains, which are not only absolutely and relatively larger but also more complex. The same is true of the differences between the Protungulata, and for *Hyracotherium* (= *Eohippus*) as against recent Ungulata (T. Edinger, 1948); or those between Australopithecini and recent man. Recent birds also have more advanced brains compared with *Archaeopteryx.*

Besides this widespread tendency to anagenetic advance an increase of absolute brain-size also results from the frequently found increase in body-size in the lines of descent. This tendency, known as Cope's rule, is valid among most of the non-flying vertebrates (cf. E. D. Cope, 1896; C. H. Dépérét, 1907; B. Rensch, 1949). Among mammals exceptions to this rule are few. On the contrary, long lineages are known which show a more or less *continuous* increase in body-size through a great part of the Tertiary (horse-line from *Hyracotherium* to *Equus*; dog-line from *Cynodictis* to *Thephrocyon* and finally to *Canis*; whale-line from the Archaeoceti to the recent Cetacea; some elephant lines since the Oligocene; etc.). The absolute increase of body-size is accompanied by a decrease in relative brain-size, but in spite of this the *absolute* size of the brain increases to such a degree that its volume among the last forms of a line of descent may be several times larger than its original volume.

With regard to the general anagenetic advance and to the absolute increase of brain-size in many lines of descent, the question now arises whether a selective advantage is always connected with these facts. In order to answer this we have first to consider whether and to what extent the growing brain mass alters the proportions of single parts and single cytoarchitectonic regions. Further, we have to see whether the morphological alterations of the phyletically growing brain are merely a consequence of the difference of proportions of the growing body which is to be innervated, or whether perhaps the cytoarchitectonic alterations result in functional advantage or disadvantage.

At present we can only give very inadequate answers to these questions. But it may be of interest for future research to summarize the results already obtained.

2. ALTERATIONS OF CENTRAL NERVOUS DIFFERENTIATION IN CONSEQUENCE OF INCREASE OF BODY-SIZE

All the main alterations of body size of animals influence both the absolute and relative size of the central nervous system. Apparently, the rule is valid for the whole animal kingdom that among closely related groups the larger species have absolutely larger, but relatively smaller central nervous systems. A. von Haller (1762) already recognised this fact and later G. Cuvier (1801), A. Brandt (1867) and others confirmed it. H. Goossen (1949) was able to show in our laboratory that the rule is valid for insects. For mammals O. Snell (1891) and later in more detail, E. Dubois (1897) and L. Lapique (1898) established the conception that brain weight shows a fixed relation to body-size. This relation can be calculated as the $\frac{5}{9}$th power (= 0·56) of the body weight, at least when species are compared which are more or less identical except in body-size. These authors held the opinion that the relation, which corresponds with an exponential formula, is the expression of the fact that larger animals have relatively smaller inner and outer surfaces to be innervated and that consequently the central nervous system can be relatively smaller. This assumes that the functions of the brain of related animals differing only in body-size would be the same. But E. Dubois (cf. 1930) was also convinced that there exists a fixed relation concerning the advancing phyletic development of the brain within single mammalian orders. He assumed that from time to time the forebrain reaches a higher level by doubling the number of neurons during embryonic development. His selected examples seemed to prove this, but later the comparison of larger numbers of species gave intermediate values. Therefore R. Brummelkamp (1939) examined the brains of many Rodentia, Ungulata, Amphibia and fishes, and concluded that such jumps in cephalization do exist but that they are smaller. According to his results the exponential formula: Brain volume $= c.$ body-size$^{0\cdot 56}$ is valid where c may have different values corresponding to a geometrical series with the modulus $\sqrt{2}$, that is to say—$(\sqrt{2})^0$–$(\sqrt{2})^1$–$(\sqrt{2})^2$–$(\sqrt{2})^3$, etc., corresponding with the series 1–1·42–2–2·83–4–5·67, etc. He established this by plotting the logarithms of the brain weights and of the body weights on a system of co-ordinates: the values then fall on approximately straight lines, the gradients of which correspond with the $\frac{5}{9}$th power (= 0·56) while the distances between them correspond to the above-mentioned jumps in cephalization. I had already (1947, p. 300) considered this result sceptically because mostly species with rather large differences in body-size were chosen, whereas those of intermediate sizes were not considered. Recently, D. Sholl (1947) has also criticized the conception of Dubois and Brummelkamp on a mathematical basis (with special reference to the $\frac{5}{9}$th power). The fact that among races of the same species a power of only 0·26 (instead of 0·56) is valid, seems to indicate that intermediate values also exist.

Furthermore it is of interest to find out how single parts of the brain alter in relative size when the body-size increases phyletically. The figures published by C. U. Ariens Kapper (1926) and J. Kelers Putnam (1927) seem to indicate that the relative size of the cerebellum does not show much regularity with regard to body-size. Among rodents, monkeys and whales the larger species seem to have a relatively larger cerebellum. Deviations from this rule among ungulates, Carnivora and Insectivora are supposed to be connected with special modes of life. I believe there does exist a more general rule of proportion for the cerebellum, if we confine the comparison to related species with a similar mode of life. When we compare such animals we find that the cerebellum of larger species is apparently smaller in relation to the total brain, but has more folds. My first measurements of some volumes gave the following results: cat 12·2 per cent, lion 11·4 per cent; sheep 10·1 per cent, cow 9·7 per cent; *Cavia cobaya* 14·8 per cent, *Hydrochoerus capybara* 10·9 per cent.

A corresponding difference can be shown if we calculate the percentage of the *brain-stem* (brain without pallium and cerebellum), as I already pointed out in 1947 (p. 215, Fig. 64). In Table 1 (compare Fig. 1) which illustrates these facts the quantitative values were calculated by measuring with a planimeter the corresponding surfaces of the cerebellum, of the brain-stem and the pallium (as far as this is visible) which were obtained by photographing medial sections of the whole brain. We then find that the cerebellum, the brain-stem (medulla oblongata and diencephalon), and also the corpus callosum of the telencephalon are relatively smaller in smaller species as compared with related larger species. This implies that the cortex is relatively larger in larger species. The same may be concluded from the table given by Dubois (1930, p. 257–258). Here we may compare the percentage of the "psychoencephalon" of at least two groups: *Bos* (Ox) 83·7 per cent, *Ovis* (Sheep) 81·9 per cent, *Tragulus* (Goat) 75·7 per cent; *Pteropus* (fruit-bat) 79·4 per cent, *Myotis* (little brown bat) 65·8 per cent. Here too, the "neo-encephalon" of larger species is both

TABLE 1

Differences in proportion of brain-parts of related mammals of different body-size shown by calculating the percentage of the areas of photographed medial sections measured by planimeter. Average values of both hemispheres.

Species	Pallium	Corpus callosum	Cerebellum	Brain-stem
	in % of the whole medial area of the brain			
Hydrochoerus capybara	44·4	8·3	17·7	29·8
Cavia cobaya	26·7—	9·3+	22·0+	42·9+
Lion	56·7	6·0	19·5	24·2
Cat	51·6—	7·9+	23·7+	34·7+
Cow	51·5	8·6	19·7	25·4
Sheep	51·7=	9·5+	22·5+	27·9+

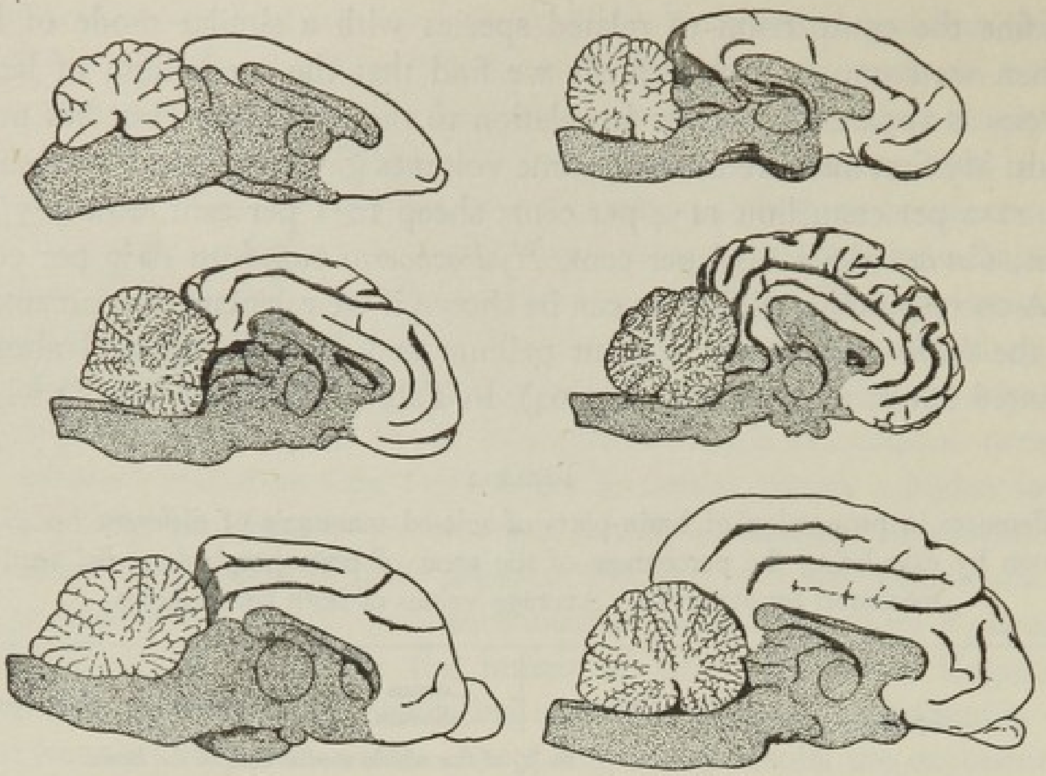

FIG. 1.—Relatively larger size of the cerebellum, of the brain-stem, and of the Corpus callosum (dotted) in smaller species compared with large ones. Medial section, left half of the brain. Above: *Cavia cobaya* (left), *Hydrochoerus capybara* (right); middle: sheep (left), cow (right); below: cat (left), lion (right). Small species enlarged on the scale of the large species.

absolutely and relatively larger. [However *Balaenoptera* (whale) compared with *Delphinus* (dolphin) shows the opposite relation.]

It is possible to examine these relations more precisely by comparing not only the adult brains but also their ontogeny. J. Huxley (1924, 1926, 1932) developed a new theory about the relations between the relative growth-rates of organs or structures, the proportions of parts in the adult, and the absolute size of the body. This theory, based on D'A. W. Thompson's work on growth-gradients (1917) is of great importance for the understanding of ontogeny and phylogeny, for individual variability and speciation and therefore for taxonomy in general. The subsequent work done by Huxley's school and numerous other workers demonstrates the importance of the theory, which is now being applied to physiological problems as well.

I take this opportunity of expressing my deep admiration of Julian Huxley for these fertile ideas.

In most animals, it is important to note, the pre-natal growth of the brain is positively allometric, whereas its post-natal growth is negatively allometric (in man only after the second to third year). Now, among mammals the single parts of the brain develop differently. The embryonic telencephalon is at first relatively small, but then it shows positive allometry and comes increasingly to cover the mesencephalon and metencephalon. This tendency changes from positive to negative just before birth. In man the telencephalon reaches 93·5 per cent of the total brain in the eighth foetal month. At birth the value is 92·7 per cent, in the ninth post-natal month 89·0 per cent and from the second year onwards only 88·0 per cent. The brain-stem, on the other hand, shows a steady negative allometry from soon after the differentiation of the five main brain-parts. Its percentage value falls from 8·3 per cent in the third foetal month to 1·5 per cent at birth and 1·4 per cent in the first year. It then rises a little (up to 1·9 per cent in the 10–20 year of life) (cf. W. M. Krogman, 1941, p. 652). The phyletic changes in adult brains correspond more or less with the pre-natal gradients of the above-mentioned brain-parts. If we compare endocranial casts of fossil skulls of the horse-series from *Hyracotherium* (= *Eohippus*) to *Equus*, as T. Edinger (1948) has done so well, we see that in *Hyracotherium* (Eocene) the brain parts are still situated one behind the other. But from *Mesohippus* (Oligocene) through *Merychippus* (Miocene) to *Pliohippus* (Pliocene) and *Equus* (Pleistocene) they become increasingly covered by the forebrain, which acquires more and more folds (Fig. 2). The same is shown by a comparison of the endocranial casts of the dog ancestor *Thinocyon* with that of the recent *Canis*, or of *Archaeopteryx* with recent birds (T. Edinger, 1950). Here phylogenetic change occurs through an addition to the final stages, an *anaboly* in the sense of N. N. Sewertzow (1931). Recapitulation in these groups is pushed back to the pre-natal phase and is abbreviated. Other changes occur as well; Edinger has rightly emphasized that embryonic stages of the recent horse already have a larger brain than adult fossil species with the same skull-length.

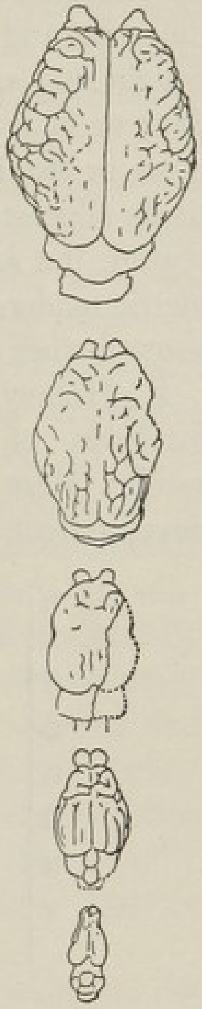

FIG. 2

Endocranial casts of skulls of the horse-line. Reduced on the same scale. (After T. EDINGER.)

But in spite of such deviations we have to consider the fact that during the course of evolution certain growth-gradients were selected with the result that an increase in body-size according to Cope's rule must automatically produce a more progressive type of brain with an increasingly larger forebrain. Thus to some extent the brain structure of more primitive ancestors implicitly contained the progressive structure of their descendants.

More light is thrown on the connections between ontogenetic and phylogenetic brain-development by analysing the growth-gradients of cytoarchitectonic units. To illustrate this K. W. Harde (1949) studied the post-natal growth of the forebrain of the white mouse in our zoological laboratory at Münster. He showed that the cortex does not grow isometrically but that there exist special growth-gradients for single cytoarchitectonic regions, the allometric tendencies of which are often different and sometimes contrary. These tendencies may change at certain stages, especially at birth or when the eyes are opened (thirteenth day) or at maturity. Generally, the phyletically older brain-parts grow more or less isometrically (as does the semicortex) or may be first negatively allometric and then isometric (schizocortex). The most progressive region, the *holocortex 7-stratificatus* has a more or less positively allometric tendency until maturity. In these larger regions some special areas show further differences with regard to their growth-rates.

B. Homeyer (1951) who examined cytoarchitectonic units in the forebrain of *Triturus vulgaris*, in our laboratory obtained similar results. Here also the allometric tendencies change during post-natal development, especially during metamorphosis and in early maturity.

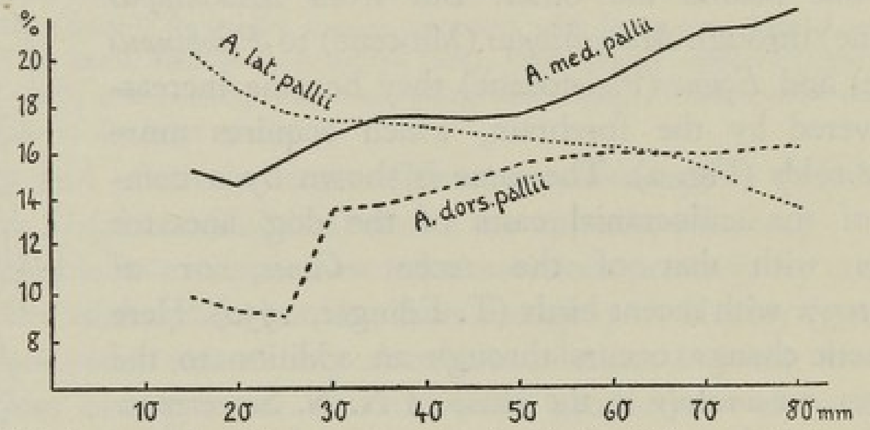

FIG. 3.—Relative growth of three parts of the fore-brain of the newt *Triturus vulgaris*. Abscissa: absolute size of the animals. Ordinate: brain parts in % of the whole forebrain. (After B. HOMEYER.)

The most progressive regions, the area medialis and the a. dorsalis are positively allometric in relation to the whole forebrain, whereas the a. lateralis and the a. striatum are negatively allometric (Fig. 3).

If an animal becomes gradually larger in the course of evolution and the separate growth-gradients of the brain do not change genetically, then the larger brain must automatically acquire new proportions: its positively allometric regions must become relatively larger in the adult animal and the negatively allometric parts relatively smaller. But single growth-gradients may be altered by selection. How far these suppositions are actually verified has recently been shown by C. H. Schulz (1951), who compared the cytoarchitectonic differences between adult mice and rats—(two Murinae of different size) with the ontogenetic tendencies of the mouse. She showed that the general positive allometry of the most progressive region, the *holocortex 7-stratificatus*, was also effective phylogenetically. The corresponding values for the series mouse-rat-rabbit (the latter after K. W. Harde) are 37·2, 39·8, 42·0 per cent of the total forebrain (the differences between these average values were statistically significant). In a similar way the *holocortex bistratificatus*, mostly positively allometric in the mouse, increases in relative size in the series mouse-rat-rabbit (not quite statistically significant). The more or less negative allometry of the semicortex of the mouse corresponds with a marked decrease of the ratio in the above-mentioned series: mouse 18·7 per cent, rat 13·9 per cent, rabbit 9·0 per cent. But the *holocortex 5-stratificatus* shows the contrary effect; this region is only positively allometric until the thirteenth day after birth (when the eyes are open) after which it is negatively allometric. In spite of this fact its relative value increases in the series mouse-rat-rabbit: 12·2 per cent; 13·8 per cent; 17·0 per cent (statistically significant). Similarly, the relative size of other forebrain regions, of single areas within them or of histologically well-defined groups of areas correspond with the ontogenetic growth-tendency, at least in some cases. (In other cases—not all statistically significant—they do not.) For our particular problem it is important that it is especially the most progressive parts, i.e. the 7-layered and 5-layered cortex, which show a relative increase parallel with an absolute increase in body-size. We can perhaps understand the difference between the phyletic and the ontogenetic growth tendencies of functionally distinct brain-regions if we assume that the single gradients may be subjected to special selection.

In any case the cortex does not show isometry in phylogeny and the above-mentioned hypothesis of the doubling of the whole cortex by jumps (Dubois) or of its increase in a geometrical progression with the modulus $\sqrt{2}$ (Brummelkamp) becomes very improbable on the basis of such histological studies.

In conclusion we must remember that, purely *cytologically*, small and large brains in the same related series are not functionally comparable. S. T. Bok and J. Van Erp Taalman Kip (1939) showed by comparing mouse, rat, guinea-pig and rabbit that the normal cell-density in homologous forebrain-regions is more or less inversely proportional to the square root of the linear dimensions of the body. The average "territory" which a ganglion-cell occupies, is directly proportional to the square root of the linear dimensions of the body (though exact comparison is only possible between the nearly-related Murinae rat and mouse). Apparently this relation only results from the fact that in a larger animal there is a larger region to be innervated. Correspondingly, the number of cortex-cells is nearly proportional to the spinal length of adult animals (R. Brummelkamp, 1940). Furthermore, the number of dendritic ramifications is proportional to the length of the dendrites (S. T. Bok, 1936). As species which are considerably larger than related smaller ones mostly have larger neurons, it can be concluded that large species have absolutely more dendritic ramifications. I have proved this by comparing the main processes of the large pyramidal cells in homologous regions of the white rat and the white mouse. In the *regio retrospleniasis granularis* of the mouse the average number is 3·5 (2–6), in the rat 4·5 (2–7); in the *regio temporalis* of the mouse 3·7 (2–5), in the rat 4·2 (3–6) (B. Rensch, 1949). Recently A. Spina Franca Netto (1951) has compared homologous pyramidal cells from central parts of the cortex of the related rodents *Hycrochoerus capybara* (Capybara) and *Cavia cobaya* (Guinea-pig) (ratio of body-weights 107 : 1), but without referring to the above-mentioned paper. He, too, showed that the markedly larger cells of the larger species have many more dendritic ramifications (Fig. 4). Among ganglion cells outside the brain G. Levi (1924) had already shown similar differences.

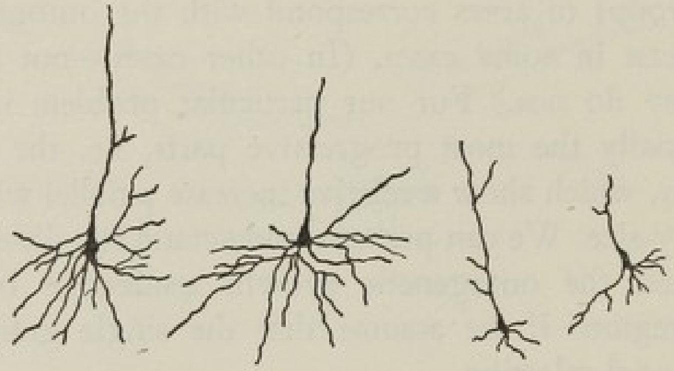

FIG. 4.—Pyramidal neurons of medium size (II layer) of homologous part of the cortex of *Hydrochoerus capybara* (left) and *Cavia cobaya* (right). Same enlargement. (After A. SPINA FRANCA NETTO.)

If we now attempt a provisional generalization we may say that larger species of mammals as compared with related smaller species have:

(1) An absolutely larger brain and an absolutely larger though relatively smaller forebrain.
(2) A relatively larger forebrain in relation to the whole brain.
(3) A relative enlargement of progressive regions of the cortex (7- and 5-layered cortex).
(4) In most cases more and absolutely larger ganglion cells and therefore more dendrites (still to be proved in sensory neurons).

Now we may ask whether all these differences which are the consequence of the different volumes of the bodies innervated (cf. A. Brandt, 1898), may also be advantageous for the larger species, since a relative increase of more complicated regions of the cortex and an absolute increase of the number of ganglion cells and dendrites allow more complicated nervous connections and therefore a more plastic behaviour and an increased utilization of experience. We have also to consider that larger species normally have a greater duration of life (B. Rensch, 1947, p. 141).

3. DEPENDENCE OF CENTRAL NERVOUS (PSYCHIC) PERFORMANCE ON ABSOLUTE BRAIN-SIZE

The conclusions of the preceding chapter led to some experiments in my laboratory, designed to show (1) whether larger species learn more quickly than identically trained related smaller races or species; (2) whether larger species can learn more; (3) whether they can remember longer; (4) whether the type of learning is different. These experiments are still in progress: the results obtained to date only partly confirm my initial assumption that large animals are generally superior. The results were also somewhat heterogeneous; we can nevertheless draw some preliminary general conclusions. Our experiments were made on mouse-strains of different body-size, on rats and mice, on breeds of domestic fowl and on Cyprinodont fish of different size.

The most definite results were obtained by R. Altevogt (1951) in experiments on breeds of domestic fowl of different size (dwarfs, bankivas, italians, leghorns, "hawks", brahmas). The birds were trained to choose one or two different patterns (boxes with pieces of cardboard showing the pattern, one of which the hens had to open in order to obtain a grain of maize). The patterns were: red (+) versus green (—), blue versus yellow, black circular spot versus black triangle, cross versus square, narrow stripes versus broad, white triangle versus white circular spot, vertical wavy line versus vertical bar. The first pair of patterns was learned (i.e. 68 per cent or more right choices) by six dwarfs in two to three days after an average of fifty-four trials, by eight middle-sized italians in three to four days after eighty-nine trials, by eight large brahmas in three to five days after eighty-one trials. Similarly the smaller races learned the following tasks more quickly than the larger races: circle versus triangle (black), blue versus yellow (Table 2), small narrow versus broad stripes were learned equally quickly by all groups. On the other hand, the large hens learned significantly more quickly than the dwarfs in the two tests, square versus cross and triangle versus circle (white); but these two tasks were the most difficult. In the third task the hens had already learned to choose a black circular spot on a white background in preference to a black triangle; now they had to choose the triangle, but both it and the alternative circle were white on a black background. The task, cross versus square, was also relatively difficult too, because in contrast to all other patterns these had no contrasting

Table 2

The speed of learning of races of domestic fowl of different body-size. Successively trained visual tasks. Sixty-eight per cent or more right choices on the average = learnt. Each first-named pattern is the positive one.

Trained animals	Average number of necessary trials					
	Red–green	Circular spot–triangle (black)	Coarse–fine stripes	Blue–yellow	Square-cross	Triangle–circular spot (white)
6 dwarfs ..	54	217	214(5)	39(5)	452(3)	509 (2)
8 italians ..	89	368	283 (7)	53 (7)	410 (7)	250 (7)
8 brahmas ..	81	389	205	49	287	209 (7)

background and were only indicated by outlines (white black-outlined cross and square on white background). Thus, the easier tasks were learned more quickly (on the average) by the smaller (two bankivas gave similar results), the more difficult ones by the larger breeds.

Corresponding with this result the larger breeds also learned more than the smaller ones. As soon as the first four tasks had been learned successively all four tests were given repeatedly (in most cases ten or twenty times) one after the other on the same day. The large and the small races showed approximately the same results. This was no longer the case when the corresponding tests were made with five tasks: the results of the second, third and fifth tasks were now markedly poorer with the dwarfs than with the larger breeds. When six tasks were given the dwarfs failed completely. Only some of the medium-sized italians succeeded when the training was often repeated, whereas the large brahmas still gave good results. The best brahmas even learned to master seven tasks simultaneously, at least for a short time (one to two days).

Since the birds were trained to perform these tasks one after the other, the tests, with multiple tasks, show that the larger breeds retain what they have learned for a longer time than the smaller ones. This was still more marked in a test given after twenty days without training (unpublished). Then three brahmas still succeeded well in six tasks, whereas the dwarfs and the bankivas only remembered three to five tasks, the italians and the "hawks" being intermediate.

Finally, it may be mentioned that during difficult multiple tests experimental "*neuroses*" only appeared among four italians and one bankiva, but not among the large brahmas, which always showed a quieter and more "thoughtful" behaviour.

Together with Dr. K. W. Harde I began similar experiments with giant and dwarf strains of the house-mouse, which Dr. D. S. Falconer

(Edinburgh) kindly supplied to our institute. The larger of these strains (which had been produced by selection by J. W. McArthur, 1949) had three times the body weight of the dwarf strain. In this case we intended to investigate the type of learning; we therefore set them to learn a simple rhythm. In a simple maze of glass painted black on the outside (Fig. 5) the mice had the possibility of running either to the right or to the left. One of the two passages each time ended in an impasse, which could not be seen from where the passage diverged. (Possible traces of smell were removed with alcohol after each run and the component sections of the maze were frequently exchanged.) The mice had to learn to make the following succession of turns at the intersection: right-left; right-left; right-left. In this case also the dwarfs learnt more quickly than the giants. With ten trials a day six dwarfs reached an average of more than 68 per cent of right choices after three days, six giants only after seven days. Between the nineteenth and twenty-ninth day (when the experiment ended) the dwarfs made 95–99 per cent right choices, the giants only 85–93 per cent.

The mice also resembled the breeds of domestic fowl, in that the giants were quieter and less "nervous". But the giants learned the task successively from the beginning to the end, i.e. at first they learned the first turns and only later on the last ones, whereas the dwarfs very quickly learned the entire rhythm, this probably resulted from their quicker running, which was interrupted by fewer pauses. (In other situations the dwarfs were more easily inclined to jump, which we could show quantitatively in other experiments: cf. B. Rensch, in press.)

The dwarfs also remembered better. After ten days without training the dwarfs only made on the average 5 per cent of errors, the giants 7 per cent. After fifteen further days without training the dwarfs made 5 per cent of errors, the giants 16 per cent.

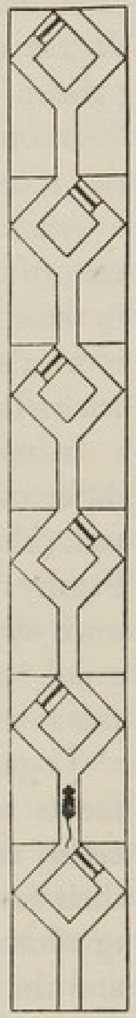

FIG. 5 Diagram of the maze for training a rhythm in mice.

These experiments suggested that related *species* of different size would also show similar differences. Accordingly Miss F. von Boxberger (unpublished) compared the learning ability of white mice and white rats. In a maze she presented two flap-doors with different patterns, as R. Altevogt had used. One flap-door was invisibly locked, the other one could be passed and behind it the animal reached a space where a reward (milk) was provided. In this case the more "nervous" mice learned better than the rats; to about the same extent in all the tasks, except that of the black versus white circular spot which was mastered more quickly by the rats.

As soon as the animals had mastered the single tasks, they were put into a long maze, in which they had to pass flap-doors with the various patterns, one after the other, until they reached the reward. As with the above-mentioned hens, the number of tasks which could be mastered at the same time was six. When the six-task test was performed twenty times, 67 per cent of the mice made 68 per cent or more right choices (a significant result), whereas only 32 per cent of the rats reached this degree of success. These markedly worse results of the rats in comparison with the mice are probably caused by the fact that the more "nervous" mice hesitated more often before choosing, whereas the rats run more steadily, but more "blindly".

After five weeks without training, 30 per cent of the rats and 40 per cent of the mice made on the average more than 68 per cent correct runs in the six-task test (significant). A repetition of this experiment gave even more definite results—rats 40 per cent, mice 80 per cent of successful trials. Retention thus appears to be better in the mice.

In another experiment with new series of nearly mature rats and mice different results were obtained. Here the animals were given only one task (black spot versus white spot). The rats learned a little more quickly. Finally they reached 83 per cent of right choices on the average, the mice 86 per cent. After ten days without training both species still gave good results: rats 78 per cent, mice 76 per cent. Three weeks later the rats could perform their tasks but the mice could no longer do so.

Together with L. Padour and U. Wellensiek I made further experiments with Cyprinodontidae of different size, the large *Xiphophorus helleri* and the small *Lebistes reticulatus*. These fishes were presented with their food (a piece of *Tubifex*) on a fork, its two prongs ending in white quadrangular plates with different patterns. The size of the feeding-forks and the patterns were proportional to the eye-size of the animals. Here the results of different series of experiments were not quite homogeneous. At first the fishes were trained successively to choose a red versus a green circular spot, then a black square versus a black cross, then a blue circular spot versus a yellow spot, and finally broad stripes versus fine stripes (in all cases the patterns were transposed at irregular intervals from one prong to the other). After equal training-time (normally twenty trials per day) the smaller species at last mastered the three tasks, separately reaching 68 per cent or more right choices (choices without food). Then all three tasks were presented successively on the same day. The *Lebistes* succeeded in all these tasks, whereas the *Xiphophorus* only succeeded in the task in which it had been last trained. A similar result was obtained with four tasks. Thus the small species learned more than the large one.

Somewhat different results were obtained when a new series of fishes were trained in a single but a more difficult task. Here the animals had to distinguish between four horizontally arranged and two vertically arranged points. After the same training-time (sixty-four days) four *Xiphophorus* reached 80 per cent right choices (without food). The smaller *Lebistes* (two specimens) learned more slowly in the first half of the experiment, but then more quickly; they eventually reached 95 per cent of right choices. The patterns were then modified. At first, instead of the series of horizontal and vertical points, we offered a horizontal and a vertical stripe of corresponding length and breadth, i.e. the fish had to choose the horizontal stripe corresponding to the horizontally arranged points to which they had been trained. Now the *Xiphophorus* made only 52 per cent "right" choices, showing that they had not recognized the similarity. *Lebistes* on the other hand had made 66 per cent right choices, i.e. their recognition of the similarity almost reached a significant value (68 per cent). A similar difference between the two species was found when the learned patterns (whose effect had been strengthened once again by new training) were modified by being reduced to half their original size. Now the large *Xiphophorus* made 77 per cent right choices, the small *Lebistes* only 62 per cent. When this experiment was repeated five weeks later (after new training) *Xiphophorus* reached 87 per cent, *Lebistes* 81 per cent. However, when only three (instead of four) horizontal and three (instead of two) vertical points were offered, *Lebistes* gave better results (80 per cent), whereas *Xiphophorus* did not recognize the similarity (only 52 per cent right choices). On the other hand *Xiphophorus* was more successful when the pair of patterns was modified by inclining both the horizontal and the vertical series of points by about 30° in the same direction. They reached 87 per cent right choices, *Lebistes* only 71 per cent on the average. Thus in the transposing experiments involving modifications of pattern as a whole the large and the small species gave nearly the same results, sometimes the one being more successful, sometimes the other.

A repetition of the experiments with a new series of fishes gave similar results. Once again the large *Xiphophorus* learned more quickly than the small *Lebistes* in the first half of the experiment, but more slowly in the second half (a third series of fishes gave the same result). After forty-one days of training five *Xiphophorus* mastered the task and swam to the pattern (without food) and reached 90 per cent right choices, one *Lebistes* 100 per cent (four specimens were ill). In two more transposing experiments involving modification of the pattern (horizontal against vertical stripes, and rows of points inclined at an angle of about 30°) *Xiphophorus* reached 53 and 93 per cent right choices on the average, *Lebistes* 80 per cent and 63 per cent, that is to say here, too, both species gave similar results.

But in experiments involving retention of learning, the large species were markedly better. After the experiments involving modification of pattern, they were given the original tasks again for one week. Then, after fourteen days without training, two *Xiphophorus* (three were ill) chose the right pattern in 90 per cent of cases, while four *Lebistes* had forgotten the task (only 40 per cent of right choices). After ten further days without training *Xiphophorus* still made 85 per cent of right choices; *Lebistes* only 31 per cent. In another series of fishes both species finally reached 94 per cent of right choices (after thirty-one days of training); after ten days without training five *Xiphophorus* still made 96 per cent of right choices, but five *Lebistes* only 84 per cent. Experimental "*neuroses*" were often seen in *Lebistes*, but never in *Xiphophorus*.

The Indian elephant which has a brain of absolutely large size is also capable of learning a number of tasks. One animal learnt twelve visual tasks (cross versus circle, triangle versus two spots, etc.) and finally it could perform them all simultaneously when the tasks were changed *ad libitum*. Three months later the animal could still master all the tasks (B. Rensch and R. Altevogt). O. Koehler and his school showed that a raven learnt to count better than jackdaws and large parrots learnt better than the budgerigar (Melopsittacus) (cf. O. Koehler, 1939, 1943; K. Schiemann, 1939; H. Braun, 1952).

Summarizing all hitherto obtained results we may state that closely related races or species differing markedly in body-size show different central nervous performance. Alike among mammals, birds and fishes the smaller animals are more "lively" but also more "nervous", the larger animals quieter and more "thoughtful". The type of learning is also different: small animals learn more quickly if the tasks are relatively easy (domestic fowl), or they are worse in the first part of the experiment (apparently because of "nervousness" and timidity); but outstrip the larger animals in its later course. When learning *rhythmic* turns the dwarf strain of the house-mouse has an advantage because of its method of running (see earlier). Only the smaller animals sometimes show experimental "*neuroses*" (fowl, Cyprinodontidae). It is of interest that all these differences depend more on the *relative* difference in body-size, less on the absolute dimensions. Thus in these respects "large" Cyprinodontidae of a length of 5–6 cm. behave similarly to giant races of domestic fowl.

The hitherto obtained results of these experiments leave the question open, whether, in fish and Murinae, larger animals are generally capable of learning more, or more difficult tasks than related smaller animals.

But the positive results with large breeds of domestic fowl make this conclusion not improbable, as do apparently better performances of large dogs compared with small ones, of large compared with small parrots, and of Corvidae compared with Fringillidae or of ravens compared with jackdaws. It is probable that large forms show better retention of learning than small (fowls, Cyprinodonts, elephant).

As long as these experiments with different groups of animals (which will be published later in more detail) have not been concluded, it is too early to try to give any definitive interpretation or conclusion. I want only to mention that the quicker learning of small races or species is correlated with their fewer and absolutely shorter dendrites. Further, the greater liveliness of smaller animals may have an influence, since smaller animals nearly always have a higher metabolism on account of their relatively larger surface both external and internal. The fact that larger animals are able to retain learned tasks for a longer time may indicate that learning has some physical basis in improved histological connections. The fact that larger animals can learn more, or more difficult tasks (fowl, elephant, raven, parrots) may be due to their having a more complex switch-mechanism (more dendrites) and an absolutely larger brain-mass; K. S. Lashley (1931) and J. D. Layman (1936) found, when brain-mass was operatively reduced learning ability was proportional to the amount of brain removed. Much more experimentation is needed before more can be said on the subject. Nevertheless, my attempts to work out the methods to be employed in such work may have been helpful.

At least we can already state that the evolutionary increase in absolute body-size (Cope's rule), and the consequential changes in absolute brain-size and in the proportions of the parts of the brain and of its cyto-architectonic organization cause essential changes in central nervous functions and "psychic" performance.

4. THE IMPORTANCE OF BRAIN-EVOLUTION FOR HUMAN PHYLOGENY AND FOR THE UNIQUENESS OF MAN

In the first section we saw that the progressive evolution (anagenesis) of some types of organism and Cope's rule of increase of body-size in phyletic lineages, both explicable by selective advantage, caused an inevitable increase of absolute brain-size. In the second and third sections we showed that this involves an alteration in the proportions of the various parts of the brain and in their histological structure which contributes to an improvement of central nervous functions. In man's line of descent we may at least consider the increase of the cortex, the relative increase of "progressive", i.e. more complicated cortex-regions, the absolute increase in the number of neurons and of dendritic ramifications, as such selectively advantageous factors. Thus the trend towards the human level of brain organization may be regarded as inevitable. Another important factor here is the prolongation of the juvenile phase (cf. L. Bolk, 1926) found in many large animals. This could only occur where multiple births, and therefore intra-uterinal selection for rapidity of development, had been eliminated. But once this had taken place, the prolongation of the juvenile phase was favoured by selection, because thereby the period of learning, that is to say the period of gaining experience and of exploration by play, is also extended (K. Lorenz, 1943). Thus the evolution of man, too, was inevitable.

It is interesting that both J. Huxley (1942) and I (B. Rensch, 1947), during a period of disruption of the civilized world by war, independently arrived at the same conclusion. Furthermore, we both independently recognized the unique evolutionary position of man, which is based on the development of a motor speech-centre in the brain. This region of Broca, a positively allometric brain-region, could be used for a new function. Thus true speech originated, and both the transmission of experience by tradition and the acceleration of thought by means of verbal concepts became possible. As Huxley so rightly emphasized, both speech and conceptive thought were acquired as the result of selection. As a consequence a unique development of the human mind could occur which is no longer founded on mutation and selection, but on the non-inherited transmission of experience through tradition. The development of writing and printing permitted this development of tradition forming to be raised to a higher level than single brains can achieve by individual learning. Through books, "extracerebral chains of associations"—as I called them (1947)—were created, with which the human brain can establish connection at any time, and with the aid of which it can achieve super-individual effects. Thus in human civilization, tradition soon became the dominant factor. Customs, laws, methods of administration, periodicals, intellectual movements and lines of thinking attain a degree of persistence in time which is impossible to the individuals involved in them.

Thus the progress of human civilization becomes more and more autonomous in character. In modern man, automatic evolution through natural forces seems to be replaced by a progressive development based on free-will. Man himself is capable of recognizing, defining and promoting the development of human values. He can try to transcend the struggle for existence by love of his fellows; he can further the development of personal liberty, tolerance and other ethical values, he can promote the scientific pursuit of truth, he can develop religious concepts and create aesthetic values.

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P. M. SHEPPARD

Evolution in Bisexually reproducing Organisms

INTRODUCTION

The great advances in understanding the process of evolution, made during the last thirty years, have been a direct result of the mathematical approach to the problem adopted by R. A. Fisher, J. B. S. Haldane, S. Wright, and others. However, mathematical theories give no information on the conditions found in nature, but only show in what circumstances different factors can be of importance in evolution. It is generally agreed that in bisexually reproducing species evolution will proceed more rapidly when they are divided up into a number of isolated and partially isolated breeding communities. But the relative importance of selection and genetic drift, in these circumstances, is a matter of profound disagreement (Fisher and Ford, 1947; Ford, 1949; and Wright, 1948).

Wright (1932) has maintained that fluctuations in gene-frequency, as the result of genetic drift, will be important in the production of harmonious gene-complexes, which will then increase in frequency in the population as the result of selection. He argues that when genes are, on the average, at a disadvantage, but at an advantage in certain combinations, they will never spread in a large population because of counter-selection; but, in small breeding communities their proportions will fluctuate because of sampling errors. Consequently, they will sometimes become sufficiently numerous for the harmonious combinations to be common, thus altering the average disadvantage of the genes to an advantage. They will then increase at the expense of their allelomorphs until the new combinations are characteristic of the population. Wright (1932) also suggested that drift will result, either in a new species being formed, which will then compete with the old one, or in the whole species evolving because of excess emigration from the better adapted colonies. In his earlier papers (1931, 1932) he even suggested that differences as great as those between species and genera might be non-adaptive and the result of drift.

On the other hand, Fisher and Ford (1947, 1950), although agreeing that the division of a species into a large number of colonies is favourable for rapid evolution, because of the diversity of habitats and therefore of the selection pressures to which each group is exposed, maintain that fluctuations in the direction and intensity of selection will be more effective than drift, as their action will not be confined to relatively small populations. This criticism is important, because small populations will not only be more liable to extinction (Dowdeswell, Fisher and Ford, 1949), but also will be able to maintain less variability (Fisher and Ford, 1928; Fisher, 1930).

The mathematical treatment of evolution makes it clear that mutation rates, as low as those found in the laboratory, can only be important in controlling the direction of evolution in exceptional circumstances, but that isolation, population size, genetic drift and natural selection can all be important factors in bisexually reproducing organisms, although their actual importance in nature is a matter of dispute. The controversy will be only resolved by field work and not by mathematical argument. Consequently, the hypotheses derived by mathematicians have given a great impetus to experimental work on the genetics of populations.

THE GENETIC DIFFERENCES BETWEEN SPECIES

Before considering the results of field studies of evolutionary processes, it is necessary to consider very briefly one of the assumptions implicit in all the mathematical models. This assumption is that the evolution of species and higher categories is the result of the accumulation of small differences of the type normally produced by mutation. Goldschmidt (1940) has claimed that although the concept of selection acting on genes is fundamental for an understanding of adaptation to different environments within a species, the differences between species and higher systematic groups are not the same as those between subspecies, and are the consequence of "systemic mutations." The role of selection on these "mutations" is confined to direct acceptance or rejection of the new form. There are a large number of objections to this view, most of which have been adequately considered elsewhere (e.g. Dobzhansky, 1941). However, it is worth while reconsidering two of them:

(1) It has already been shown by Fisher (1930) that the larger the change in an organism the more likely it is to be harmful. Consequently, Goldschmidt's "systemic mutations," which have never

been observed, would have very little chance of surviving even if they did rarely occur.

(2) At least one male and one female of the new "mutant" would have to appear at the same time and in the same breeding community, in a bisexually reproducing organism, for the new type to persist. Moreover, such a small population as a single pair will have little chance of surviving.

Some of the apparent difficulties in evolutionary theory, which Goldschmidt hopes to explain by postulating "systemic mutations," are in fact just the situations which would be expected under the more orthodox hypotheses. Much of his argument in favour of these "mutations" is based on the fact that the differences between species may frequently involve chromosome rearrangements, particularly inversions and translocations. However, it will be shown that these differences are exactly the ones which would be expected if species evolve gradually.

Wright (1940a, 1941, and 1949) has suggested that translocations must usually be established as the result of genetic drift and not by selection, because of their low fertility when heterozygous. But translocations will have more effects in the heterozygote than just those on fertility, and on rare occasions their net selective value may well be advantageous. That translocations do occur intraspecifically in nature was shown by Dobzhansky and Dreyfus (1943), who found one translocation in two individuals of a wild population of *Drosophila ananassae*, but were unable to determine its selective coefficient.

Other chromosome-rearrangements are known to have high selective values, and it is probable that over long periods of time some translocations will arise which are sufficiently advantageous in their other effects to overcome their low fertility when heterozygous. Moreover, because of the lower fertility of the heterozygote, it is likely that the homozygote will be at an advantage to it, so that translocation polymorphism will be rare. Furthermore, even if the conditions in which the heterozygote is at an advantage only last until the translocation is represented in over 50 per cent of the chromosomes in the population, it will still increase in frequency until it is fully established unless it then becomes very disadvantageous. As it comes to be established in a breeding community, a gene-complex adjusting it to the local environment will be selected in the way that Spiess (1950) and Dobzhansky (1950) have shown for inversions. When this gene-complex has been established, any outbreeding to migrants will cause a breakdown of the modifier system which will mean that the heterozygotes may well be at a disadvantage to both homozygotes. In these circumstances the translocation will not spread to adjacent colonies. A similar breakdown of an adjusted gene-complex has been demonstrated for inversions (Dobzhansky, 1950).

In these conditions outcrossing to the rest of the species will lead to selection for sexual isolation on the lines suggested by Dobzhansky (1941) and a new species will evolve. It is of interest to note that Koopman (1950) has shown that sexual isolation can be increased between species by selection.

It has been found (pp. 209–11) that genes controlling certain characters, for example, colour and fertility, may also affect mating behaviour. Consequently, if an isolated population becomes differentiated from other colonies it is likely that one of the characters affected will be sexual isolation. If this evolution proceeds far enough the mating behaviour of the animals in the population may become sufficiently badly adjusted to the behaviour of individuals from other colonies for complete sexual isolation to be established. This view is supported by the fact that several strains of *Drosophila repleta* have been shown to exhibit different degrees of sexual isolation which is not associated with their geographic origin (Wharton, 1942). It follows that sexual isolation can result either from the direct action of selection on the lines suggested by Dobzhansky (1941) or as the by-product of general evolutionary changes.

Data on the genetic differences between species are in agreement with the hypothesis that they are formed as the result of the accumulation of mutants (including chromosome rearrangements) and that most, but not all, of these have small effects. In other words most of the characters distinguishing genera, species and subspecies are under multifactorial control. It is therefore true to say that the difference between the "microevolutionary" changes which can be observed in the field, and the more obvious changes which give rise to species, genera and higher categories, is only one of degree; it is not one of kind as Goldschmidt (1940) has maintained. Consequently, general conclusions on the relative importance of different factors in evolution can be drawn from population studies.

THE IMPORTANCE OF SELECTION IN DETERMINING GENE-FREQUENCIES IN WILD POPULATIONS

As has been pointed out, one of the fundamental problems in the theory of evolution, at the present time, is the relative importance of natural selection and genetic drift. In an attempt to investigate this point Dobzhansky has made extensive observations, over many years, on the frequencies of certain chromosome inversions in several species of *Drosophila*, particularly *D. pseudoobscura* and *D. persimilis*. At first he concluded (1941) that the rearrangements were selectively almost neutral and that the differences in their frequency, between populations, demonstrated the action of genetic drift. However, his later observations (1943, 1948) indicate quite clearly that they have very large selective values and that the heterozygotes are nearly always at an advantage over both homozygotes. Other investigations by Carson and Stalker (1947), Stalker and Carson (1948), Dubinin and Tiniakov (1945, 1946a, 1946b), Spiess (1950) and Dobzhansky, Burla and da Cunha (1950), suggest very strongly that this polymorphism is widespread in *Drosophila*. Investigations by Philip (1942) and Hsu and Liu (1948) show that the same situation is also common in species of *Chironomus*. In fact it may be of frequent occurrence throughout the whole animal kingdom but difficult to detect because of the absence of giant salivary gland chromosomes.

Many other polymorphic situations have been used to illustrate the results of genetic drift, especially in land snails, where striking polymorphism is often found. It has been claimed that the differences between colonies in the genera *Partula* and *Achatinella* are caused by drift. However, the data on the environments of the populations studied by Crampton (1916, 1925, 1932) in *Partula* and by Welch (1938) in *Achatinella mustellina* are not sufficient to draw any such conclusions. Many of the differences between the populations studied concern the proportions of dextral and sinistral shells. Mutants having effects as large as this are not likely to have very small selective values. This view derives support from the fact that in another snail, *Fruticicola lantzi*, which shows variation in the frequency of dextrals and sinistrals between colonies, Gause and Smaragdova (1940) have demonstrated that the physiology of the two types is very different. The sinistrals are much more sensitive to starvation than the dextrals, a character which can hardly be even approximately neutral in survival value in the wild.

Among the other land snails, *Cepaea nemoralis* (L.) has been widely quoted as demonstrating the results of genetic drift. Mayr (1942) has maintained that the various banding patterns on the shell of this animal are selectively neutral. Diver (1929) found that *Cepaea* has been polymorphic since at least the Neolithic period, which indicates that the genes controlling the pattern are not neutral in survival value, but that the polymorphism is stable. However, this does not invalidate his conclusion (1940) that the differences between populations are due to drift, because sampling errors can cause fluctuations in gene-frequency even when selection is too strong to allow the loss of any of the allelomorphs from the population (Wright, 1948).

Cain and Sheppard (1950) carried out an investigation in order to try to determine the relative importance of selection and drift, in controlling gene-frequencies, in colonies of *C. nemoralis*. They took random samples of snails from a large number of colonies and recorded the colour and banding pattern of each shell. It was found that the greener the background on which the snails were living the higher was the proportion of yellow shells in the colony and the more uniform the background the lower the percentage of effectively banded shells (shells with the two upper bands absent can be classified as effectively unbanded for ecological, though not, of course, for genetical purposes). This result as it stands is not conclusive because no quantitative measurement of the greenness or uniformity of the background was recorded. However, the habitats were also grouped according to broad ecological types, which could not readily be misclassified, as for example beechwood, oakwood, mixed deciduous wood and hedgerow. It was at once obvious that samples from similar habitats are more like one another than they are like samples from other ecological situations (Fig. 1). Colonies classified according to their environment form groups on the diagram and the greatest scatter is found in the rough green herbage class in which there is more variation in the nature of the background than in any other type of habitat studied. However, even in this class only three colonies depart markedly from the others. Two of them are on backgrounds which would explain their difference and only in the third do the frequencies of the phenotypes suggest that factors which differ from those affecting other colonies are operating.

The patterns of the shell of *C. nemoralis* are genetically determined (Lang, 1904, 1908, 1911, 1912; Fisher and Diver, 1934). Consequently, the correspondence between populations living in similar habitats can only be explained adequately by natural selection. Cain and Sheppard (1950) suggested that there are two types of selection acting; one physiological, which puts certain gene combinations at an advantage over all others, in this way maintaining the polymorphism, and the other the result of predators hunting by sight, determining the actual ratio of the phenotypes in the colony. Their proportions will depend both on the relative conspicuousness of the different patterns on the particular background and on the intensity of predation.

Although the investigation indicated that predators are one of the agents of selection and although predation was demonstrated, the required differential elimination of phenotypes was not observed. However, during further work this type of selection was proved (Sheppard, 1951a). It was shown that the Song-Thrush *Turdus ericetorum* Turton did kill a higher proportion of yellow shelled snails on a brown background and a higher proportion of pink and brown ones on a green

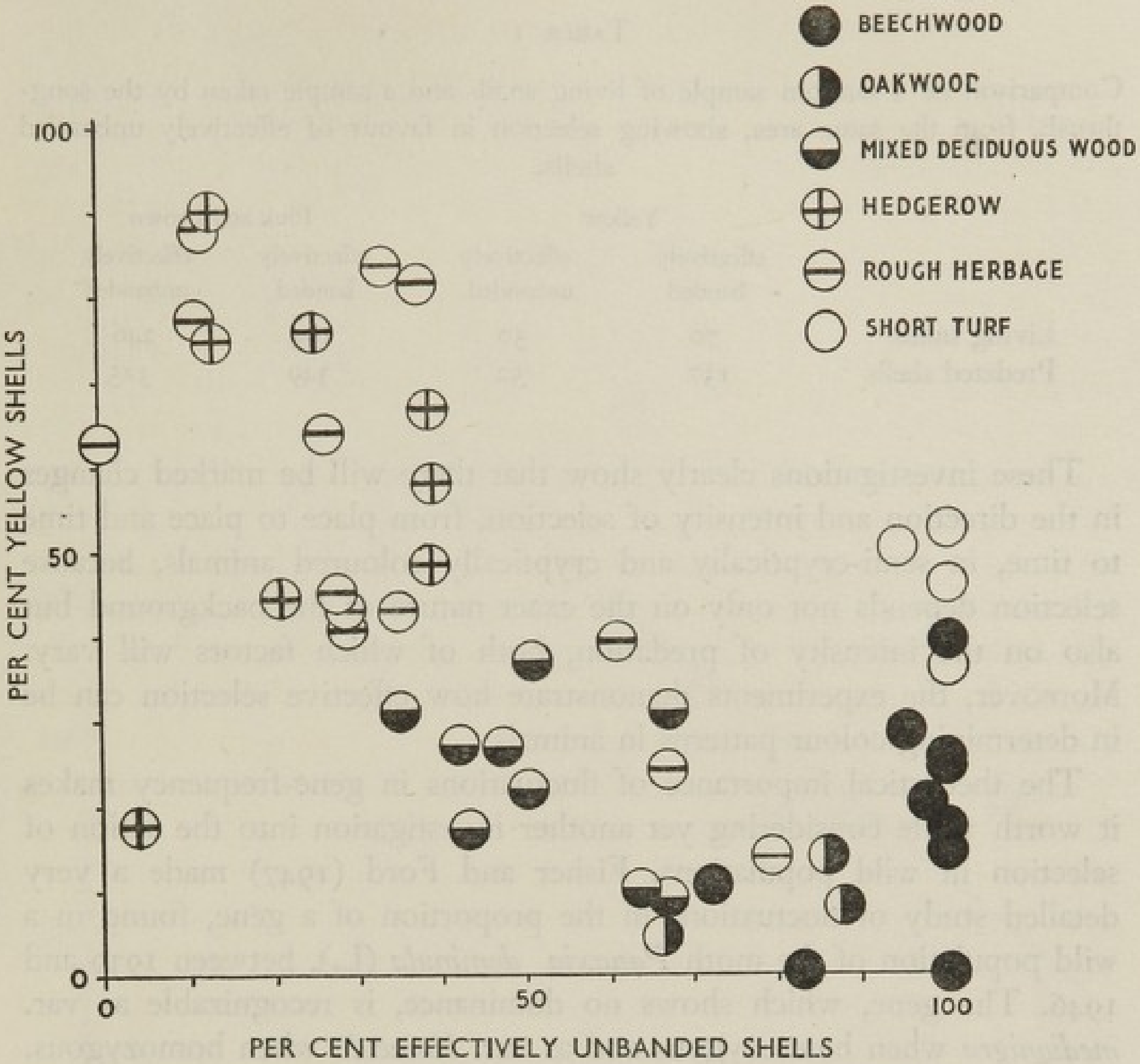

FIG. 1.—The relation between the percentage of yellow shells and the percentage of effectively unbanded shells, in each locality, is given in the diagram. Note that localities classified together because of their ecological similarity tend to group together. Because the rough herbage class includes the most diverse backgrounds it shows the greatest scatter in the diagram.

background. The method employed was to observe the proportions of the different varieties of shells broken on thrush "anvils" in a mixed deciduous wood, between April and June. Not only did the percentage of yellow shells on the "anvils" decrease as the background got greener in the spring but also, from a knowledge of the proportion of yellow shells in the colony, it was possible to show that at some time in early May yellow changed from being disadvantageous to being advantageous. To ensure that the results were not due to thrushes changing their feeding-grounds, marked snails were used in one colony. A later investigation, using almost the same methods (Sheppard, unpublished), showed that in one locality there was selection by thrushes for effectively unbanded shells (Table 1). Lamotte (1950) has also demonstrated selection by thrushes on banding patterns, but there it was in favour of banded individuals.

TABLE I

Comparison of a random sample of living snails and a sample taken by the song-thrush, from the same area, showing selection in favour of effectively unbanded shells.

	Yellow		Pink and Brown	
	effectively banded	effectively unbanded	effectively banded	effectively unbanded
Living snails	70	50	194	246
Predated shells	137	52	349	325

These investigations clearly show that there will be marked changes in the direction and intensity of selection, from place to place and time to time, in semi-cryptically and cryptically coloured animals, because selection depends not only on the exact nature of the background but also on the intensity of predation, both of which factors will vary. Moreover, the experiments demonstrate how effective selection can be in determining colour patterns in animals.

The theoretical importance of fluctuations in gene-frequency makes it worth while considering yet another investigation into the action of selection in wild populations. Fisher and Ford (1947) made a very detailed study of fluctuations in the proportion of a gene, found in a wild population of the moth *Panaxia dominula* (L.), between 1939 and 1946. The gene, which shows no dominance, is recognizable as var. *medionigra* when heterozygous and as var. *bimacula* when homozygous. Except in the vicinity of Oxford it is only found as a great rarity. They estimated the size of the moth population by marking, releasing and recapturing the insects. From a knowledge of the population size they were able to show that the observed fluctuations in the gene-frequency were too great to be ascribed to genetic drift. These conclusions have been criticized by Wright (1948). However, an extension of their work (Sheppard, 1951b) did not substantiate these criticisms, but made it clear that the frequency of the gene is, in fact, controlled by selection. The heterozygotes have been at an average disadvantage of about 10 per cent to the wild type since 1939 and no evidence has been obtained that this value has fluctuated over the period (Fig. 2).

The proportion of individuals in the colony which were carrying the mutant increased remarkably between about 1929 and 1939. It is known from the reports of collectors that the population was not reduced to a very small size between these dates and therefore the selective value of the gene must have changed. The importance of these observations, from the present point of view, is that they demonstrate that alterations in selective values are sometimes sustained for varying lengths of time.

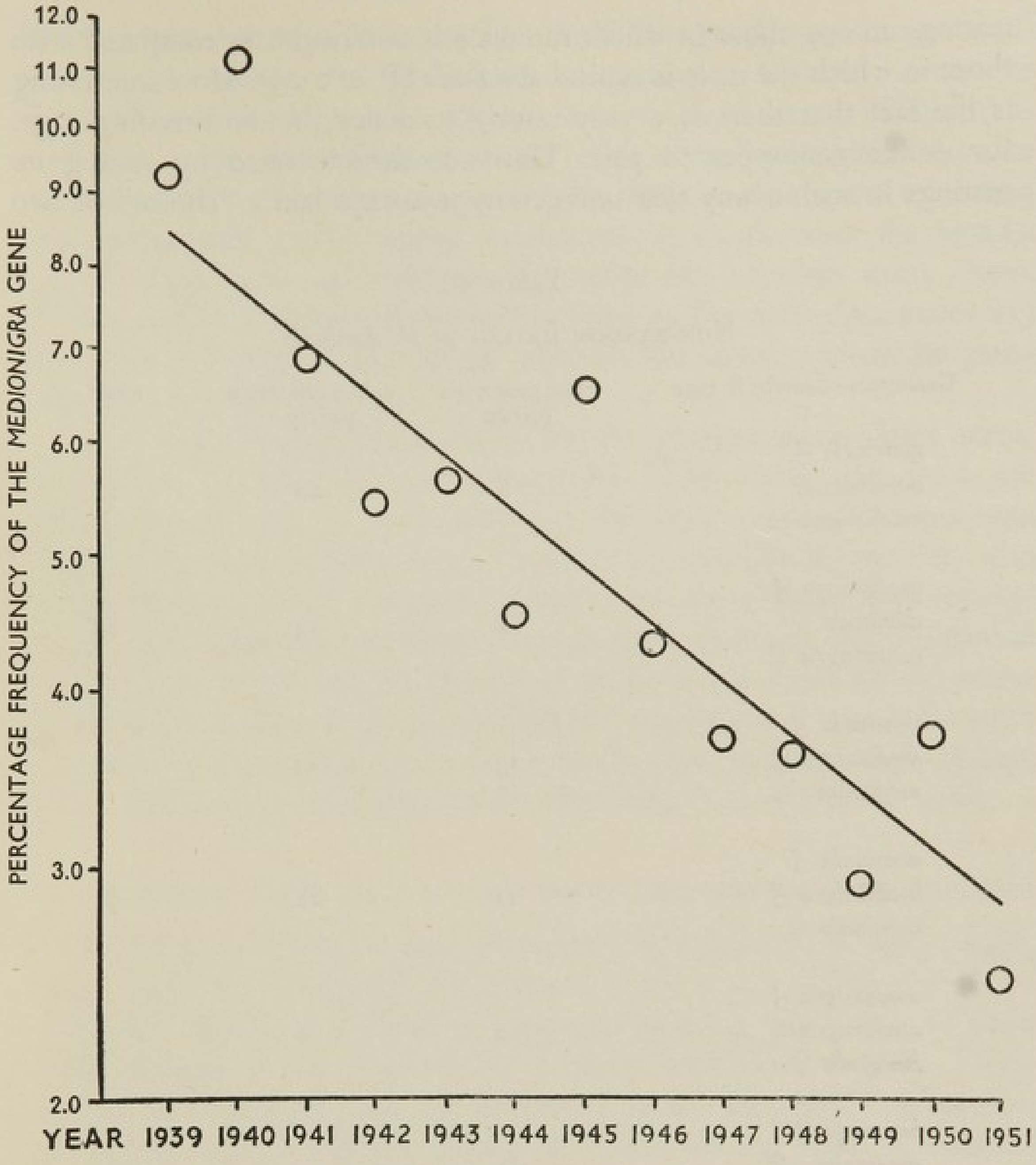

FIG. 2.—In the diagram the regression line has been fitted by assuming constant selective values for the three genotypes. The observed frequency of the *medionigra* gene is plotted on a logarithmic scale.

Secular fluctuations will be more effective than non-secular ones in causing changes in gene-frequency. Wright (1948) investigated the relative importance of drift and non-secular fluctuations in selective value, in causing gene-frequency changes but did not consider the more important agent, namely long-term fluctuations.

THE PLEIOTROPIC EFFECTS OF GENES IN WILD POPULATIONS

Although all the agents controlling the selection on var. *medionigra* and var. *bimacula* are not known, there is evidence from breeding experiments (Sheppard, unpublished) that there is an excess of infertile matings among those in which the male is *medionigra* as compared with those in which the male is typical *dominula* ($P < 0\cdot05$). More interesting is the fact that there is a very strong tendency, in the breeding cage, for unlike genotypes to pair. This was demonstrated by setting up matings in such a way that one genotype always had a "choice" of two

TABLE 2

NON-RANDOM MATING IN *P. dominula*

Genotypes of moths in cage	like genotypes pairing	unlike genotypes pairing	totals
dominula ♂ *dominula* ♀ *medionigra* ♀	8	20	28
medionigra ♂ *dominula* ♀ *medionigra* ♀	12	14	26
dominula ♂ *medionigra* ♂ *medionigra* ♀	13	14	27
dominula ♂ *medionigra* ♂ *dominula* ♀	11	22	33
medionigra ♂ *medionigra* ♀ *bimacula* ♀	2	0	2
bimacula ♂ *medionigra* ♀ *bimacula* ♀	0	1	1
medionigra ♂ *bimacula* ♂ *medionigra* ♀	2	10	12
medionigra ♂ *bimacula* ♂ *bimacula* ♀	3	15	18
dominula ♂ *dominula* ♀ *bimacula* ♀	2	1	3
Totals	53	97	150

mates, only one of which was like itself (Sheppard, 1951b, 1952b). If mating is random, the probability of getting a departure from the expected results as great or greater than those observed (Table 2) is less than 0·001. Since females, in the wild, often "assemble" a number of males before they mate, it is probable that this disassortative mating also takes place under natural conditions. In *P. dominula* the females usually only pair once whereas the males can copulate many times. Consequently, if there is disassortative mating, the *medionigra* males will be at an advantage to the typical males in this respect, when the gene-frequency is low.

The results obtained from studies on *P. dominula* are in direct agreement with similar work on *Drosophila*. They show that there are fluctuations in selective value and that these are not always short-term changes but may involve longer periods of time. Moreover, they also prove that very large selection pressures are sometimes found unassociated with stable polymorphism. The fact that a gene in a wild population often affects more than one character (as in *Cepaea*, *Panaxia* and inversions in *Drosophila*) is also of considerable importance, because the more characters a gene controls the more likely it is that any single change in the environment will alter its selective value (see, e.g. Cain, 1950).

ISOLATION AS THE RESULT OF ECOLOGICAL BARRIERS AND OF DISTANCE

Isolation is a factor of great importance in evolution. Wright (1940a, 1943, 1946) has suggested that distance alone in a uniformly inhabited area may often be a sufficiently important isolating mechanism to allow large changes in the proportions of genes from place to place. Diver (1940) has suggested that the differences in the proportion of varieties in several areas in a single colony of *Cepaea* are the result of isolation by distance and genetic drift. To investigate this point a single colony of *C. nemoralis* which inhabited both beechwood and open grassy downland was studied (Sheppard, 1952a). It was found that the parts of the colony in the five beechwood areas had a low proportion of yellow shells, as in colonies in other beechwood habitats, whereas in the two green downland areas there was a high proportion of yellow shells. Where downland and beechwood joined, the areas which had intermediate gene-frequencies were less than fifty yards wide. The observations confirm Diver's view (1940) that distance is an effective isolating agent in *Cepaea*, but show that differentiation is the result of selection and not drift. Lamotte (1951) states that *C. nemoralis* colonies of not greater than thirty metres radius are panmictic breeding units. His value does not seem to fit the data for this colony very well, but even if migration is much less than that suggested by his result, selection would have to be very intense to cause the observed differentiation.

There are indications that a narrow cart track which crosses the colony at one point is an effective barrier to migration. This marked effect of of a minor ecological barrier, which the animals could easily cross, has previously been found in the two butterflies *Polyommatus icarus* Rott. and *Maniola jurtina* L. by Dowdeswell, Fisher and Ford (1940, 1949). The areas (approximately three hundred yards wide) inhabited by *P. icarus* are almost complete barriers to the interchange of individuals between nearby breeding communities of *M. jurtina* and those occupied by *M. jurtina* are barriers to *P. icarus*.

The data obtained from investigations on *Cepaea*, *Panaxia*, *Drosophila* and many other animals show that species are often divided up into isolated and partially isolated breeding communities giving just the conditions that favour rapid evolution. Moreover, the results also indicate that genes having distinct effects usually have very large selective values in the wild and that these values are not confined to stable polymorphic situations. It is very probable that the frequency of these major genes and chromosome rearrangements, in natural populations, is controlled by selection, except in colonies so small that they can rarely persist for long periods of time. There are of course apparent exceptions many of which are merely uninvestigated (Cain, 1950, 1951). The frequencies of the A, B, and O Blood groups in man are apparently non-adaptive (Wright, 1940b). However, even here there is some evidence that selection is acting (Race and Sanger, 1950). Moreover, the stability of the frequencies over long periods of time, in certain groups of people, indicate that the proportions of the genotypes may be adapted to the gene complexes found in these "races" (Ford, 1945).

THE EVOLUTION OF MULTIFACTORIALLY CONTROLLED CHARACTERS

Although the major genes are the more easily studied, it is the minor factors (polygenes, modifiers, etc.), controlling characters multifactorially, which are probably the most important in evolution (Fisher, 1930; Wright, 1931), with the possible exception of chromosome rearrangements which may be important agents in initiating selection for sexual isolation (see above). It is these polygenes and modifiers which are the most likely of all genes to show drift because each, taken by itself, will have a small effect and therefore a small selective value. Consequently, even when multifactorial characters are stabilized by selection, it is possible that the frequency of the genes controlling them may fluctuate as the result of sampling errors. The effectiveness of selection on multifactorially controlled characters has been well illustrated with regard to size, shape and colour in many animals. It is therefore interesting to consider the effect, on such characters, of the same type of selection by predators which also determines the proportions of the major genes in *C. nemoralis*.

Cain and Sheppard (1952) have examined the mean body shade in nineteen breeding communities of *C. nemoralis*, as well as the exact shade of shells in the pink class. It was found that there was a significant correlation ($P < 0{\cdot}01$) between the percentage of yellow shells in a colony and the mean body shade. The higher the proportion of yellow shells, that is to say the greener the background, the lighter is the mean body shade of the population. Although there is a tendency for yellow unbanded snails to have a paler body ($P < 0{\cdot}05$) this is insufficient to account for the observed correlation. There is good evidence that direct environmental effects (phenotypic variation) play no part in this correlation.

In the breeding communities investigated it was observed that the greener the background the lighter was its shade. It appears that the correlation between the proportion of yellow shells and the mean body shade is due to a correlation between body shade and background shade and is almost certainly the result of natural selection. This hypothesis is further supported by the fact that a highly significant correlation ($P < 0{\cdot}001$) was found between body shade and shade of pink shells. Colonies with a light mean body shade also have a light shell shade in the pink class. This again is not the result of the same genes controlling both characters.

In *C. nemoralis* natural selection, as the result of predators hunting by sight, determines both the frequency of distinct varieties and the expression of characters under multifactorial control. The adaptation of body shade to the background is a good illustration of the delicacy of selection because the body is only exposed to view when the snail is active and even then the colour of the shell is usually a far more conspicuous character. Even in the single colony studied by Sheppard (1952a) the correlation holds when the different areas are compared.

Although it is often possible to show that certain characters are adaptive, particularly those which vary from population to population, it is usually very difficult to show that specific and subspecific characters of taxonomic value are also adaptive. However, some observations of Dr. H. B. D. Kettlewell's, which he has kindly allowed me to quote, are particularly interesting in this respect. He selected, in a stock of *P. dominula*, for at least ten generations, in such a way that the area of black on the hindwings was much reduced, or even absent in extreme examples, and the white areas on the forewings were very much increased. This result was obtained by selecting for four characters, three of which were under multifactorial control and the fourth determined by a single incompletely dominant gene. At the end of the period the population was still variable but, on the average, the wing colour and pattern departed as far from the typical form as do many of the geographical subspecies.

An artificial colony of this stock was made by introducing the correct food plant for the larvae in a suitable locality where *P. dominula* did not occur, and releasing the modified population. After three generations the average ground colour and pattern of the moths in the colony was almost normal and very different from the released stock. It could be shown that the reversion towards the wild type was not due to immigration because the moths still carried the mutant gene although its effect was much reduced. There must have been very heavy selection for the gene-complex producing the colour and pattern which is normal for the species in England. It is of interest that the breeding community was much reduced in size in the first generation but has since increased remarkably. The selection was probably not directly for pattern, but for a balanced gene-complex on the lines suggested by similar work on *D. melanogaster* in the laboratory (Mather and Harrison, 1949). The observations clearly show that the colour pattern, which is a taxonomic character, is indirectly controlled by natural selection.

Selection must be as effective on genes controlling behaviour and physiological characters as it is on morphological ones (see Haldane, 1949, and Timofeeff-Ressovsky, 1940). Consequently, populations, except the smallest, must always be as highly adapted to their environment as changing conditions will allow, a fact which has been well illustrated by the work, quoted above, on *D. pseudoobscura* and *C. nemoralis*.

CONCLUSIONS

Two main points emerge from the present discussion:

(1) Breeding communities are highly adapted to the local environment in which they live, with the possible exception of very small populations and of those living in rapidly changing conditions.

(2) Gene-frequencies will show marked fluctuations as the result of natural selection, quite apart from those resulting from genetic drift.

Data on population size, migration, the effects of ecological barriers and isolation by distance show that species are usually divided up into breeding communities of varying size. Many of these colonies will be of the correct size to allow marked changes as the result of drift, providing that the selective values are sufficiently small. However, recent work indicates that chromosome rearrangements and genes producing easily recognizable characters usually have large selective values. Alterations in their frequency in wild populations will be particularly common because these genes often have multiple effects, so that any single change in the environment is likely to affect the selective value of a large number of them.

Characters under multifactorial control are apparently subject to equally rigorous selection. Consequently, the frequency of the polygenes and modifiers determining them will also alter as the result of selection. This does not preclude the possibility that they will fluctuate through sampling errors. However, it has been shown (Mather and Harrison, 1949; Harrison and Mather, 1950) that such genes are usually aggregated into balanced linkage groups by selection. Drift will then not act on single genes but on groups having very similar effects. But Dobzhansky and Spassky (1944) and others have shown that individuals homozygous for a particular chromosome are normally at a considerable disadvantage to those which have received the two homologous chromosomes from different sources. It is probable that the same situation holds for individual balanced linkage groups, so that many of them will not become frequent through sampling errors because their increase will be opposed by selection. Moreover, any interaction between polygenes will further reduce the effect of drift.

In small and intermediate sized populations selection will normally be more effective than drift in altering the gene frequencies of factors having small effects as well as those with larger ones. In the species or subspecies as a whole it will be even more efficient because random fluctuations will be confined to the smaller populations, which are less variable (Fisher, 1930). The structure of breeding communities in bisexually reproducing organisms ensures that there will be fluctuations in gene-frequency, which Wright (1931, 1932) has shown to be necessary for rapid sustained evolution. However, it now appears that selection is the predominant agent in evolution and that non-adaptive evolution must be rare although it may occasionally be found in very small populations. Thus Wright's concept of drift, though frequently invoked as an important agent in evolution, must be judged of negligible significance as compared with selection.

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Mimicry in Cuckoos' Eggs

PART I.

PRESENT KNOWLEDGE OF CUCKOO PARASITISM

(1) "BROOD PARASITISM" AND ITS ADAPTATIONS

THIS type of parasitism in birds is characterized by the parasite laying in other species' nests, so that its eggs are incubated and its young fed by the foster parents. Several widely distinct groups of birds practise "brood parasitism," but the cuckoos have developed it most. All the forty odd species of the Old World sub-family Cuculinae are parasitic. In this paper the European cuckoo *Cuculus canorus* L. is the main species studied.

Egg mimicry is an adaptation to reduce the contrast between the eggs of parasite and host so that there shall be more chance of acceptance. If a cuckoo species parasitizes a host smaller than itself, its egg is unusually small. In the non-parasitic *Coccyzus americanus* the mean dimensions of the eggs (from 53 measured, Bent 1940) are 30·4 × 23·0 mm.; in *Cuculus canorus* 100 British eggs (Witherby *et al.* 1938) averaged 23·05 × 17·23 mm. Yet the American bird is smaller than the British (wing 138–156 mm. compared with 216–228 mm.). In such circumstances, a further adaptation is the instinct of the newly-hatched cuckoo to eject its nest mates and so secure the whole of the food for itself. On the other hand, cuckoos like *Clamator glandarius*, which parasitize hosts their own size (magpies and crows), lack this instinct and their eggs are not reduced in size.

The most remarkable adaptation is the mimicry of the host's egg in colour and markings. The accuracy of the imitation varies, but at its best it may be difficult for the human eye to distinguish the egg of the parasite from those of the host. This is demonstrated well in Baker's frontispiece (1942).

Newton first (1893) drew the conclusion from this that cuckoo species are divided into groups, each laying a certain type of egg and consistently patronizing the host most suited to it. He called these groups noncommittally "gentes," and about half the species sufficiently studied are so far known or suspected to have such sub-divisions.

Convincing proof of this condition is difficult to obtain, but the following considerations have weight. (i) Chance (1922) studied intensively the movements of a few individual female cuckoos through several seasons and recovered nearly all the eggs they laid. These are now in the British Museum and they demonstrate the astonishing uniformity in shape, colour and markings of the eggs of one bird. If we consider the shell weights of two series of eggs from the same female in adjacent breeding seasons (fresh eggs only included since the weight decreases during incubation), we find the average weights are 196·6 mg. (no. of eggs $= 20$; $\sigma = 9{\cdot}6$) and 198·0 mg. (no. of eggs $= 14$; $\sigma = 5{\cdot}7$). Not only is the spread of these weights round the mean very small, but the means of each season are very close. By contrast Chance quotes a series from a cuckoo of a different gens and here 19 eggs had a mean weight of 247·6 mg.

(ii) Big collections, such as those of Rey and Čapek in Europe and that of Baker in Assam, contain series of eggs remarkable for their uniformity, each of which almost certainly comes from the same female.

(iii) Chance's observations show that a cuckoo pays unremitting attention to the movements and habits of a single foster species and lays in the nests of other species only in an emergency. Out of 61 eggs laid by one bird in four seasons 58 were placed in nests of the meadow pipit *Anthus pratensis*.

(2) DISCRIMINATION BY THE FOSTER PARENTS

If egg mimicry has evolved by natural selection from a range of variations the most likely selective agent is the discrimination of the foster parent.

Experiments by Swynnerton (1918), Rensch (1924) and Salim Ali (1931) have shown that the ability to detect and throw out ill-matching eggs varies not only between species, but also between individuals of the same species. This is reasonable, since parallel selection of the host's powers of discrimination would be a necessary complement to the process. Supporting evidence comes from tabulating the desertions of clutches with cuckoos' eggs: Baker (1942) states that of 1,642 cuckoos' eggs laid in the nests of normal fosterers 8 per cent were found deserted; of 298 in nests of abnormal fosterers 24 per cent were deserted.

Some people (see, e.g., Meise, 1930) have contended that once this double process of selection has been started the result must be "perfect" mimicry and extermination of the host. This idea takes no account of the regional effect of particularly successful cuckoos: Schiermann (1926) gives the following yearly decline in nests of a population of reed warblers *Acrocephalus scirpaceus* together with the increase in victimization, 14 (29 per cent parasitized), 15 (40 per cent), 12 (50 per cent), 11 (73 per cent), 9 (67 per cent), 9 (67 per cent) and 8 (88 per cent). It is more probable that a patchwork of parasite-host oscillations is established with parallel fluctuations in selection pressure. The instance of *Cacomantis merulinus* and its host *Prinia socialis* in Deccan quoted by Baker (1923, 1942) probably illustrates this, but the evidence is not first-hand.

(3) CO-EXISTENCE OF SEVERAL GENTES IN ONE DISTRICT

The specialization implied in the evolution of different gentes means that each can be more efficient by exploiting egg mimicry and that two or more can occupy the same region without competing for hosts, and much intensive work, particularly that of Rey, Čapek and Baker, has shown this to be so. It is more difficult to decide what limits the number of gentes that can live together. On general grounds (i) the host must have roughly the same period of development as the parasite; (ii) it must take suitable food; (iii) it must bring sufficient; (iv) it must breed at the right times and in the right places; and (v) finally it must have an adequate density relative to the female cuckoo's territory (figures quoted vary between 37 and 173 acres). The number of gentes, however, actually found together in one locality never comes anywhere near the limit indicated by the above restrictions. Thus Makatsch (1937) noted 5 cuckoos of 2 gentes together, and Baker (1942) found side by side 4 cuckoos each of a different gens. This discrepancy between potential and actual numbers of host species is reverted to below.

PART II.

THE EVOLUTIONARY PROBLEM OF CUCKOO PARASITISM

(4) THE NATURE OF CUCKOO GENTES

In this section the aim is only to state the possible interpretations of cuckoo gentes. A discussion of evidence follows in sections 5 and 6.

First, the gentes may be considered as biological, or more precisely, micro-geographical races. If so, they must be reproductively isolated and form separate populations. They must also have evolved in isolation.

If this is so, the crucial point is how crossing is prevented in an area containing several gentes. The female cuckoo may have a small territory, but males range farther. Čapek (1896) and Chance (1922) both cite birds with recognizably queer calls and the widest diameters of their ranges were 3·1 and 3·0 miles respectively. Over such tracts the opportunities for crossing seem considerable.

Even if by some means crossing can be prevented, there is a further difficulty. Such reproductive isolation would promote the accumulation of genetic differences in characters other than egg-colour unless opposed by selection, and none has ever been recorded. On the contrary the distribution of gentes cuts right across that of geographical races in *C. canorus*. It is conceivable that nobody has used fine enough methods to detect divergences of this kind yet, but this is an unlikely explanation.

Secondly, the gentes may be polymorphs. In truly polymorphic species the different types or phases form a single interbreeding population; they are usually sharply distinct from one another; and their mode of inheritance is often simple, even unifactorial. The nature of polymorphism, its probable origin from rare mutants maintained at a low frequency by mutation versus adverse selection, and its establishment by a balance of selective agencies have been discussed fully by Ford (1945).

There are striking resemblances between cuckoo mimicry and Batesian mimicry, and both Poulton (1926) and Cott (1940) have assumed that they are controlled in the same way. In both mimicries the phases may be distributed singly or side by side and their relative frequencies regulated by the availability of their "models" (in Batesian mimicry the edible mimic must not become too common relative to the distasteful model, since predators learn the taste by experience).

The similarities, however, are only superficial. In cuckoo mimicry there is another important requirement; the cuckoo's egg must not only mimic the egg of a particular host, but it must be placed in that host's nest. If the young cuckoo forms a life attachment to its host species while in the nest (section 6 contains the evidence for this), then this attachment will be passed on from mother to daughter. But the type of egg laid by the daughter is partly controlled by the father, so that a bird might be produced which consistently laid in the "wrong" nest as far as egg matching was concerned. Such continuous mis-layings would entail far more waste than a random distribution.

Apart from this, intermediate types of egg are found abundantly in some regions and, more important still, just in these regions there is least topographical isolation between the gentes. In other words, the standard of mimicry is correlated with the degree of isolation. The evidence for this is given in sections 7 and 8.

Cuckoo gentes, therefore, show some of the characteristics of polymorphs and some of biological races. To "sit on the fence" in this way may not be unprofitable to cuckoos. Gentes which are highly specialized in mimicry will sacrifice plasticity and with it the ability to turn to new hosts. Discrimination by the hosts obviously varies widely in time and place and cuckoos which retain a reservoir of variation will benefit accordingly.

(5) THE ORIGIN OF CUCKOO GENTES

Before considering the crucial question of how several gentes are maintained in one area, it is worth examining some evidence from present distribution of gentes to discern how they may have arisen. The origins of polymorphism are discussed in Ford (1945) and Dobzhansky (1937). Three main points emerge. (i) Polymorphic phases are usually found as rare varieties in other parts of a species' range so that their original spread must have been due to a geographically limited selective advantage. (ii) If the spread has been from a limited point, the frequency may decline centrifugally from this point. (iii) The distribution of polymorph ratios may follow the geographical differentiation of a species, but the phases will always potentially belong to the same population.

Consider an illustration from Ford (1945). In the African mimetic butterfly *Papilio dardanus* a group of subspecies is distributed along a cline from South Africa up the east coast (race *cenea*), through east Central Africa (race *tibullus* followed by a wide transitional area) to west Central and West Africa (race *dardanus*). The distribution of four mimetic female forms along this cline is as follows: *hippocoonides* is at first rare, increases to over 50 per cent in the transitional zone, then to nearly 100 per cent in the west where it is adjusted to copy another race of its model and is known as *hippocoon*; *planemoides* is rare at each end of the cline, but rises to some 20 per cent in the middle; *cenea* behaves in the reverse way to *hippocoonides*; and finally *trophonius* occurs at a small frequency throughout.

This distribution suggests that the first three forms arose where their abundance is greatest, but, once started, they may spread throughout the range and perhaps in this way the geographical origin of *trophonius* may have been obscured.

Cuckoo gentes in Finland have a parallel distribution (Wasenius, 1936). Three main types of egg are found. The commonest, blue and unspotted, is found in nests of the redstart *Phoenicurus phoenicurus* and occurs mainly in the south of Finland except along the coastal strip. A second type of egg mimics very closely those of the brambling *Fringilla montifringilla*, which have a pale-blue background and heavy reddish spots, and is found chiefly in the north and east-central parts of the country. A third type with a white background almost obscured by fine grey markings is laid in nests of the wagtail *Motacilla alba* whose eggs it matches quite well and, although it is mainly restricted to the Gulf of Finland archipelago, there are sporadic records from all parts. Again these focal points in the distribution suggest points of origin, but since there is no information from Russia, the picture is incomplete.

The Swedish distribution (Rosenius, 1929) extends the above in an intriguing manner. Three of the gentes are the same, namely those parasitizing the brambling (North Sweden), the redstart (Central Sweden) and the wagtail (South Sweden). In addition to these there is a gens attached to the meadow pipit, which is distributed thinly all over the country. Finally there are two gentes confined to the south, parasitizing the whitethroat *Sylvia communis* and the garden warbler *S. borin*. Since these two are common hosts in Germany, they probably followed the retreat of the ice-cap into South Sweden, bringing their cuckoos with them. If we neglect these last, the original four gentes show an even more striking parallel to *Papilio dardanus* in their distribution than the Finnish gentes. Taking both countries together we may infer from the pattern that the basic number of gentes was small, and that they arose in different broad areas (with the possible exception of the meadow-pipit gens which is more evenly distributed). So far the similarity to normal polymorphism is obvious, and even the intrusion of new gentes from the south into Sweden agrees with the hypothesis favoured by Ford (1945) and Mayr (1947) that polymorphic phases may arise in restricted regions and spread from them.

If this is so, then we can see why the number of gentes living side by side falls short of the possible hosts. Frequently one finds abundant species, which are unparasitized in some parts of their range, but parasitized in others. If the necessary adapted egg is absent in some areas, it is probably impossible for it to evolve in the presence of other gentes.

Cuckoo gentes, therefore, may well have arisen in the same way as polymorphic phases; how they are maintained is a more difficult question and is next discussed.

(6) THE MAINTENANCE OF CUCKOO GENTES

If the frequency of gentes in an area is maintained on a polymorphic basis, there should be no difficulty in preventing "mixed" eggs from appearing. The real problem is not how a mimetic egg type maintains itself in the presence of other types, but how it can get into the right nests.

Attachment to the host species probably arises while a young cuckoo is in the nest. Consider the following evidence. (i) Modern work on ethology has shown that behaviour patterns, which are innate or learned very young, are released by specific visual or auditory "signals." The surroundings of the nest in which the young bird is reared, the type of habitat and the plumage and calls of the foster species are far the most likely signals to release the subsequent parasitic behaviour. (ii) Accidental layings (i.e. eggs laid in the nearest available nest when the one marked down by the cuckoo has been destroyed), which now and again succeed, may produce cuckoos permanently attached to the wrong host: Chance (1922) studied one cuckoo which laid nine eggs in the nests of the spotted flycatcher *Muscicapa striata*, and another which foisted 14 eggs on the yellow bunting *Emberiza citrinella*, both uncommon hosts in Britain. (iii) Some cuckoo hosts are themselves polymorphic in egg colour: if the cuckoo mimics more than one of the colour phases, its eggs are laid at random with either type of the host (in spite of the fact that discrimination by the hosts might obscure this). Baker (1942) cites *Cacomantis merulinus* and its hosts of the genera *Cisticola*, *Orthotomus* and *Prinia* in Assam, and De Chavigny and Le Du (1938) give similar evidence for *C. canorus* and *Diplootocus moussieri* in Morocco. We should expect this result, when there is no plumage, voice or habitat difference to guide the parasite.

If this is how attachment to the host arises, how is it that crosses do not occur to produce females permanently attached to the wrong host?

From searching the abundant and uncritical literature on the subject I am satisfied that such cuckoos *are* produced, though not nearly in the numbers that might be expected. Čapek (1896) gives the clearest evidence. Of 8 cuckoos watched by him, all attached to the redstart, 6 laid series of pale-blue eggs adapted to those of the host: of the other two, though, one laid 19 eggs which were "chocolate-grey" in ground colour clouded with brown, the other laid 5 eggs of a greenish-brown spotted type. These are in startling contrast with the pale-blue eggs of the host.

Cuckoo gentes, therefore, cannot be maintained on the basis of a normal polymorphism. Some measure of isolation must exist between gentes in the same region and the more complete this isolation the fewer will be wrong layings and the higher the standard of mimicry.

Such isolation will most likely come from micro-geographical or habitat divergencies. The inference that the cuckoo is attached to its host by recognizing its plumage or surroundings strengthens this likelihood. Restriction by this method is easy to envisage for the female cuckoo with its relatively small territory. The male covers a larger area, admittedly, but it is reasonable to suppose that in country divided into blocks of well-differentiated habitats, heathland, reed-beds, pine forests, etc., he will tend to consort with females of the same gens by recognizing the habitat and foster species among which he was reared. When these habitat blocks become small enough then the degree of isolation will be reduced and cross mating will occur between the gentes. The next two sections examine the relation between the standard of mimicry and the degree to which the gentes are isolated by habitat. Fortunately two well-worked areas offer evidence.

(7) DISTRIBUTION OF CUCKOO GENTES IN THE KHASIA HILLS, ASSAM

Baker (1942) distinguishes six types of *C. canorus* eggs here. (i) Background white, fine red markings; host, the fantail warbler *Cisticola juncidis*. (ii) Background white, abundant red markings; hosts, the hill warblers, *Prinia polychroa criniger* and *P. atrogularis*. (iii) Background salmon, blotched and clouded with brown; hosts, verditer flycatcher *Muscicapa thalassina*, niltava flycatcher *Niltava sundara* and white-tailed blue robin *Myiomela leucoura*. (iv) Similar to (ii), but markings heavy and blotchy; host, brown bush warbler *Bradypterus luteoventris*. (v) Background blue, sometimes faint markings; hosts, Pekin robin *Liothrix lutea* and silver-eared mesia *L. argentauris*. (vi) Variable, usually heavily blotched with brown or red; hosts, Indian pipit *Anthus richardi rufulus* and Blyth's pipit *A. r. godlewskii*.

From the distribution and habitat preferences of the hosts given in Baker's *Fauna of British India* (1922–30) the following table, giving a rough measure of isolation by habitat, emerges.

TABLE 1

Distribution of Baker's cuckoo egg-types i to vi in Assam.

Height above sea level (ft.)	Open ground			Woodland ravines	Forest	
	Marsh and green grass	Dry grass	Scrub		Deciduous or evergreen	Conifer
3,000–	6	6, 1			5	5
3,500–	6	6, 1, 2	2	3	5	5
5,000–		2	2	3	5	5, 4
6,000–		6, 2	2	3	5	5, 4
6,500–				3	5	5, 4
7,500–9,000				3		

Isolation by habitat clearly occurs between most of the egg types. There is, however, overlap between types i, ii and vi on dry grassland. In his book (1942) Baker states that type vi is variable and eggs approaching type i are often laid in pipits' nests. Furthermore in the *Fauna* he states that eggs intermediate between types i and ii are common. The other notable overlap is between types iv and v in conifer forest, but in an earlier paper (1907) Baker throws light on this. Of the two hosts to which type v is adapted only the Pekin robin will overlap with the bush warbler (type iv), since the mesia prefers evergreen forest. But the Pekin robin is "only a straggler in the Khasia hills," whereas the brown bush warbler is plentiful in Assam only in this locality. This overlap, therefore, is more apparent than real.

We can conclude from this that precisely in the places where Table 1 reveals overlapping does confusion occur and the standard of mimicry decline. Elsewhere the gentes may remain isolated by habitat and so maintain the distinct nature of their egg types.

(8) DISTRIBUTION OF CUCKOO GENTES IN WESTERN EUROPE

Information here is very muddled and its trustworthiness often dubious, but approximately it indicates the pattern of distribution shown in Fig. 1. Here is a desperate tangle, and a tangle that is matched by the overall low standard of mimicry. Records reveal only two well-adapted egg types. One is the pale blue redstart type (already mentioned in Finland and Sweden), which occurs in parts of Czechoslovakia and Saxony; the other densely clouded and freckled with greyish-green matches closely the eggs of the great reed-warbler *Acrocephalus arundinaceus*, which abounds in Hungary's vast tracts of reed-bed and marsh. Otherwise, though eggs may show some rudiments of mimicry, the situation is summed up in the following observation of Rey (1892). Of 139 cuckoos' eggs found in nests of the red-backed shrike *Lanius collurio* only 12 resembled those of the host. Of the others he describes 25 as most like those of the garden warbler, 62 as "mixed" and 35 as "independent" types.

Thus in west Central Europe good mimicry only occurs in large tracts of homogeneous habitat (the Hungarian reed-beds), or in localities which are the remains of a once much more extensive habitat (the Czechoslovakian forests). Now this part of Europe has obviously been the most intensively cultivated and the breaking up of large homogeneous areas has probably brought about this low standard of mimicry by decreasing the reproductive isolation between gentes. We may reasonably suppose that, should the gentes cross, the expression of the genes for egg colour, even with a simple switch method of inheritance, will be modified by experience of fresh internal environments. If discrimination by the hosts is neither vigorous nor lasting, such modifications (like Rey's "mixed" and "independent" types) will not be frequently enough rejected.

From examining these two regions in the range of *C. canorus* we may conclude that the standard of egg mimicry and the amount of habitat isolation between the gentes are undoubtedly associated. Cuckoo gentes may evolve in restricted areas similarly to polymorphic phases, but, when they come together, they need to retain their identity (i.e. to remain separate populations) to some extent or their efficiency will be impaired. This may mean that other genetic differences can accumulate between the gentes, though compared with a geographical subspecies a cuckoo gens is probably much less durable.

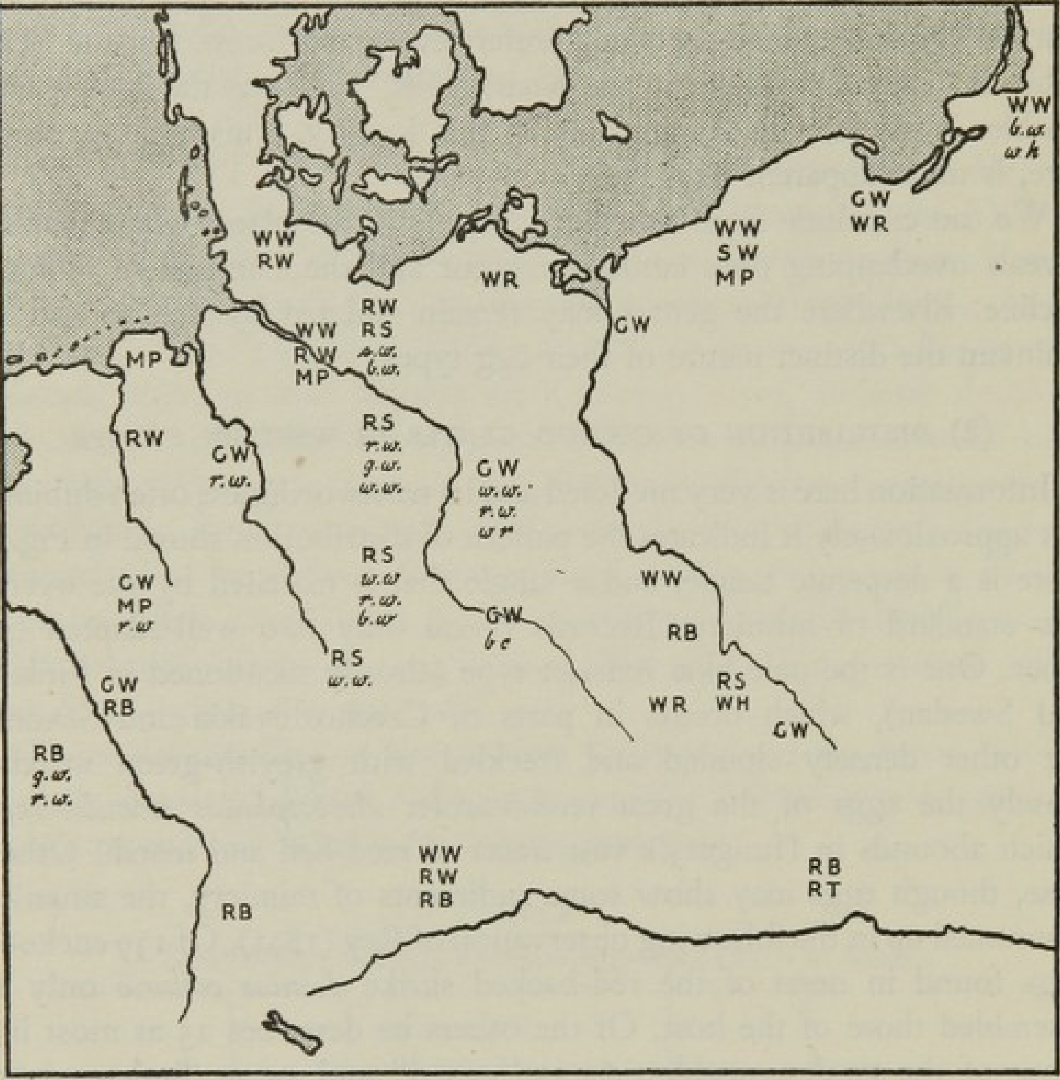

FIG. 1.—Map of Central Europe showing the distribution of host preference in the common cuckoo. Data from Rey (1892), Makatsch (1937) and Groebells (1937) have been used. The key to the symbols for the host species is as below.

BC	blackcap *Sylvia atricapilla*	RT	redstart *Phoenicurus phoenicurus*
BW	barred warbler *S. nisoria*	RW	reed warbler *Acrocephalus scirpaceus*
GW	garden warbler *S. borin*	SW	sedge warbler *A. schoenobaenus*
MP	meadow pipit *Anthus pratensis*	WH	whitethroat *Sylvia communis*
RB	redbreast *Erithacus rubecula*	WR	wren *Troglodytes troglodytes*
RS	red-backed shrike *Lanius collurio*	WW	white wagtail *Motacilla alba*

N.B.—Capital letters indicate a principal, small letters a subsidiary host.

(9) THE PART PLAYED BY CUCKOO GENTES IN EVOLUTION

The different groups of birds exhibiting "brood parasitism" can be arranged progressively according to the complexities of their adaptations. The cuckoos have obviously reached a stage at which they have lost much of their adaptability. The only group which has specialized further is the parasitic weaver birds (*Ploceidae*), for in these each parasitic species has its own host species to which it is permanently attached and a very complicated form of mimicry has arisen involving the recognition pattern of the chicks' mouth markings.

Of course, increase in adaptation does not of itself lead to speciation: it is possible, however, that cuckoo species by splitting into gentes may establish themselves side by side without competing for hosts. Consider the Himalayan cuckoo *C. saturatus*, whose range (Central and Eastern Asia down into Burma) falls entirely within that of *C. canorus*. The two species are closely related, but in the Himalayas at any rate *C. saturatus* parasitizes only leaf warblers (*Phylloscopus spp.*), which *C. canorus* avoids. Two cuckoos, each subdivided into several gentes, might easily settle down together and produce a situation like this merely by "cancelling" the overlapping gentes.

Consider further the competitive inter-relations of a whole group of cuckoos in one region. Baker's work in Assam reveals in this one place a nexus of fifteen species, nearly half of which belong to the genus *Cuculus*.

If we examine Table 2, we see that most of the closely related cuckoos, at any rate, avoid competing with each other by patronizing different hosts or by breeding at different times. Apparent overlapping could probably be explained, if we had more facts. For example, Mr. Salim Ali has kindly informed me (*in lit.*) that *Clamator jacobinus* usually haunts more open country than *C. coromandus* and therefore concentrates more on the babblers as hosts than on the laughing thrushes.

(10) CONCLUSIONS AND SUMMARY

We may conclude that if cuckoo species split into separate gentes and if these gentes are not particularly stable, but fluctuate with the availability of hosts and with change in the barriers between habitats, then two closely related species may come together and stay together without competing for the same hosts. This implies that the origin of species in cuckoos has arisen by the methods normal in birds, namely by differentiating in geographical isolation and then meeting as separate populations. We must then regard gentes as intermediate between polymorphs and geographical races. Instead of the normal polymorphic condition in which the phases interbreed indiscriminately and remain distinct through

TABLE 2

Competition between different cuckoos in Assam.

Species	Altitudinal range	Habitat	Main fosterers	Breeds
Cuculus canorus Common cuckoo	up to 9,000 ft.	mainly forest	1. *Cisticola juncidis* 2. *Prinia spp.*	May and June
C. saturatus Himalayan cuckoo	5–10,000 ft.	forest	leaf warblers (*Phylloscopus spp.*)	May and June
C. poliocephalus Small cuckoo	4,500–10,000 ft. (rare)	ravines in evergreen forest	bush warblers (*Cettia spp.*) *Phylloscopus spp.*	end May to end July
C. micropterus Indian cuckoo	most common below 5,000 ft.	forest	1. laughing thrushes and chats. 2. *Dicrurus*, *Oriolus* and *Terpsiphone*	mid-May to end June
C. sparverioides Large hawk-cuckoo	3–9,000 ft.	forest	1. laughing thrushes 2. *Arachnothera magna*	mid-June to end July
C. varius Common hawk-cuckoo	up to 3,000 ft.	forest	laughing thrushes	May and June
C. fugax Hodgson's hawk-cuckoo	2–6,000 ft.	ravines in evergreen and pine forest	flycatchers and babbler *Brachypteryx*	end May to August
Cacomantis merulinus Plaintive cuckoo	up to 6,000 ft.	open country	1. *Cisticola*, *Prinia* 2. *Orthotomus*, *Prinia*	July to October
Penthoceryx sonneratii Banded bay cuckoo	up to 8,000 ft.	light forest	quaker babbler, *Alcippe*	May and June
Chalchites xanthorhynchus Violet cuckoo	to 5,000 ft. rarer on low ground (rare)	broken land and forest	1. *Arachnothera longirostris* 2. sunbirds, *Aethopyga*	? as next sp.
C. maculatus Emerald cuckoo	to 5,000 ft. rarer on high ground	dense forest	1. sunbirds, *Aethopyga* 2. *A. longirostris*	April to July
Surniculus lugubris Drongo cuckoo	?	scrub and light forest	?	?
Clamator jacobinus Pied Crested cuckoo	up to 6,000 ft.	scrub and light forest	laughing thrushes	May and June
C. coromandus Red-winged crested cuckoo	up to 6,000 ft.	scrub and light forest	laughing thrushes	May and June
Eudynamys scolopacea Koel	up to 2,500 ft.	open ground near villages	crows	June-July

a simple genetic control, there must be a condition with some degree of isolation between gentes so that mimetic egg types can be produced and maintained. This isolation is not usually complete or enduring enough for cuckoo gentes to be classified simply as biological races. The standard of mimicry in egg colour and pattern improves with the amount of isolation that a particular gens enjoys, but selection pressure with a wide range of intensities enables the gentes to establish themselves relatively quickly from an evolutionary point of view; and, of course, to vanish with equal speed.

In conclusion it is hardly necessary to emphasize how tentative are these conclusions. We need much more of critical observation and experiment and, despite the fact that much of it seems difficult or impossible to carry out, the example of Chance's work shows that the difficulties can be overcome by perseverance and ingenuity.

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The Origin and Evolution of Courtship and Threat Display

INTRODUCTORY

It is now generally recognized that display serves a function. Building upon the foundations laid by Selous (1901, 1905, 1906–7, 1933), Huxley (1914, 1923, 1934a, b), and others, Lorenz (1935, 1939, 1941, 1943), drawing from an unrivalled amount of observational data, has given the most comprehensive description of the function of display. According to his hypothesis, which has since been confirmed in several cases (see Tinbergen, 1948), display serves to release a response in other individuals. Sometimes this response is immediate and stereotyped. In other cases it may appear only after repeated stimulation. Often it is not one stereotyped reaction, but a reaction of a higher integrative level, viz. an increase of the readiness to perform one of a group of (causally and functionally) related activities. In such cases other variables determine which of these activities will be performed. Movements or organs serving this function were called by Lorenz (1935) releasers. Functionally, therefore, display consists of releasers. The most comprehensive review of releasers has been given by Baerends (1950). Their function may be (*a*) interspecific, and if so, they may be (1) one-sided, and be useful to the displaying species only. This is the case in warning displays, particularly false warning displays (Huxley, 1934a), and in cases such as the lure display of the Angler Fish (Wilson, 1937). Many interspecific displays are (2) symbiotic; they serve both species involved. The colours of flowers attracting and guiding pollinators belong in this category. When display has (*b*) an intraspecific function, it serves social co-operation and inter-individual threat. These two functions are just as dependent on the correct functioning of releasers as co-operation, and

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* I am indebted to Dr. A. J. Cain for critically reading this article in MS.

interaction between the organs of an individual are dependent on the correct functioning of hormones and the nervous system. Just as the functioning of hormones and the nervous system implies not only the sending out of signals but also a specific responsiveness in the reacting organ, so the releaser system involves a specific responsiveness to particular releasers in the reacting individual as well as a specific tendency to send out the signals in the initiator. The releaser system ties individuals into units of a super-individual order and renders these higher units subject to natural selection.

In this essay I will discuss two types of intraspecific display: threat and courtship.

COURTSHIP

Functions

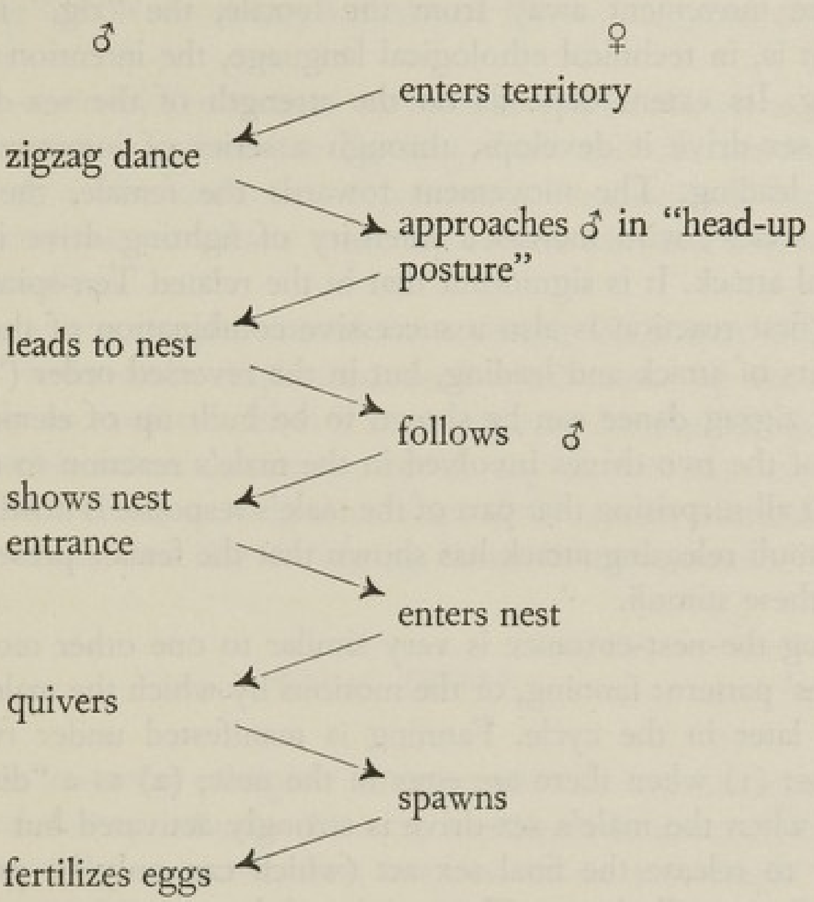
There are at least four different aspects of the functions of courtship. Firstly, the mating activities of male and female have to be synchronized. Whereas a gross synchronization is attained by "somatic" reactions to outside stimuli, such as day-lengthening in many animals of the northern temperate zone (Rowan, 1938; Burger, 1949), the more exact timing of responses is effected by releasers. This timing is done in two stages: display may synchronize the gonadal cycles of the two partners (Craig, 1913); once this has been effected, it synchronizes to a fraction of a second their reciprocal mating activities. Secondly, display serves orientation; song, for instance, and song flights, attract females; also, special ceremonies may guide the partner to the nest-site (Tinbergen, 1935, 1952a). Further, some releasers, such as the brightly coloured patches of skin seen round the genital aperture of female Baboons and Chimpanzees, probably guide the male to the female's copulatory organs. Thirdly, courtship serves to suppress non-sexual responses in the partner. The male usually has to overcome escape tendencies in the female, released by stimuli from the male which it has in common with predators. The female on her part usually releases attack in the male; she has therefore to appease him. In spiders, the male must suppress the female's feeding responses. Fourthly, courtship must be specific, so as to reduce the chance of interspecific mating; its specificity serves reproductive isolation.

These are the reasons why courtship display, in spite of its conspicuousness which may endanger the individuals' lives, is not on balance disadvantageous; on the contrary, it has definite adaptive value, serving the species through its function of co-ordinating mating responses of sex partners.

Causation

The causation of courtship displays has been worked out in the Three-spined Stickleback (Tinbergen, 1951; Tinbergen and Van Iersel, unpublished work). More fragmentary evidence on other species suggests that some of the general conclusions reached are valid, at least for vertebrates.

The sequence of mating activities in the Three-spined Stickleback is the following:



The male reacts to a pregnant female entering the territory by performing its zigzag dance, which is a series of quick leaps, each leap consisting of a movement away from the female and towards the nest, and of a subsequent movement towards the female. When the latter responds to him by swimming towards him in the head-up posture, he turns round and swims to the nest ("leading"). She follows, and when they reach the nest, the male "shows-the-nest-entrance." Hereupon the female enters the nest. The male then touches her tail-base with his snout in a series of rhythmic thrusts ("quivering"), which causes the female to spawn. Stimuli from the eggs then cause the male to enter the nest and to ejaculate sperm. Experiments with models have shown that each response in this sequence is a reaction to stimuli provided by the partner's preceding activity.

Of the male's five movements, two can be recognized as parts of the mating behaviour. Leading to the nest is the appetitive behaviour (Lorenz, 1937; for an elaboration of ethological concepts and terms used in the present paper, see Tinbergen, 1951a) preceding the consummatory act of sperm ejaculation. The three other elements, however: zigzag dance, showing the nest entrance, and quivering, cannot be immediately recognized as sexual movements.

Analysis showed that each zigzag, as its name implies, consists of two parts. The movement away from the female, the "zig," is incipient leading; it is, in technical ethological language, the intention movement of leading. Its extent depends on the strength of the sex-drive; with growing sex-drive it develops, through a series of intermediates, into complete leading. The movement towards the female, the "zag," is incipient attack; with increased intensity of fighting drive it develops into actual attack. It is significant that in the related Ten-spined Stickleback the first reaction is also a successive combination of the intention movements of attack and leading, but in the reversed order ("zag-zig"). Thus the zigzag dance can be shown to be built up of elements of the patterns of the two drives involved in the male's reaction to the female. It is not at all surprising that part of the male's response is hostile; analysis of the stimuli releasing attack has shown that the female presents at least some of these stimuli.

Showing-the-nest-entrance is very similar to one other movement of the species' pattern: fanning, or the motions by which the male ventilates the eggs later in the cycle. Fanning is manifested under two sets of conditions: (1) when there are eggs in the nest; (2) as a "displacement activity" when the male's sex-drive is strongly activated but the stimuli necessary to release the final sex act (which can only be provided by fresh eggs) are still absent. Close study of the movements of showing-the-entrance shows that they are almost identical to fanning. The situation is one in which displacement activities are known to occur in other animals as well: the sex-drive is strong but thwarted. Such a thwarted drive then finds an outlet through an "allochthonous" or displacement activity, a movement normally belonging to the motor pattern of another instinct. When an activity is caused by its "own" drive, it is called autochthonous, a term which I will have to use farther on. Showing-the-nest-entrance, although very similar to autochthonous fanning, is not caused by the parental drive as autochthonous fanning is, but by the sex drive. It also differs from autochthonous fanning in two respects. Firstly, the male raises his dorsal spines and turns his back towards the female. This can be recognized as an element of aggressive behaviour; no doubt the close proximity of the female is responsible for this. Secondly, the male, instead of standing free in the water as it does while fanning autochthonously, thrusts his snout into the nest entrance. As we will see later, this latter difference has nothing to do with elements of any other drive; it is the result of a secondary evolutionary process.

Quivering is also very similar to fanning, and again the situation is such as to expect a displacement activity caused by a strong but not satisfied sex-drive; again the male has to wait until the female lays eggs. Quivering differs from autochthonous fanning in that the fish again is not standing free in the water, but thrusts his snout against the tail-base of the female.

Thus the series of five distinct movements can be shown to be caused by two underlying drives: the fighting drive and the sex-drive. The zigzag dance is the outcome of balanced, "ambivalent" motivation; showing-the-nest-entrance and quivering are the outcome of a strong but thwarted sex-drive.

Similarly, many components of the courtship behaviour of birds and fish can be shown to be displacement activities, caused by the thwarting of a strongly aroused sex-drive. Thwarting may be due to the absence of indispensable releasing stimuli, but it may also be due to a conflict with the attack drive, or with the escape drive. Other elements of bird and fish courtship can, like the zigzag dance, be recognized as intention movements.

SEXUAL THREAT

Functions

The great majority of fights between animals are intraspecific and form part of the reproductive behaviour pattern. Reproductive fighting is always spatially restricted, it is confined to an area round a (topographical or mobile) centre of interest. This centre is always some object or situation which is indispensable for reproduction. It is often the sex partner, and in many cases includes a territory as well. Another aspect of fighting is that it is directed at individuals of the same species and (usually) of the same sex. Since most individuals withdraw at once when they are attacked or threatened, and even those that do not retreat can be fought off by actual attack; because, further, fighting is stronger the nearer the intruder comes to the centre of interest (Huxley, 1934b), sexual fighting effects a certain degree of spacing-out of individuals. The significance of spacing-out differs from one species to another; it may be found in the prevention of too many individuals sharing one territory or one female, while other territories or other females remain unutilized. In some species it is a corollary of the cryptic coloration of the brood: the dispersal of camouflaged animals prevents predators from specializing on them (Tinbergen, 1951b).

Hostile encounters only rarely develop into actual fighting; more often threat display is involved. This presents an evolutionary problem to which I will presently return.

Causation

The Herring-gull shows a variety of types of aggressive behaviour. Apart from walking or flying towards the opponent and actual attack—which represent the appetitive behaviour and the consummatory act of the attack drive—several threat movements can be observed. Two of these, the upright threat posture and grass-pulling, have been analysed: for a detailed discussion see Tinbergen 1952b.

The upright threat posture is characterized by a stretching of the neck, a lifting of the wings, and a downward pointing of the bill. All intermediates between this posture and actual attack can be observed; the posture clearly is a preliminary to attack, in which the weapons—wings and bill—are kept in readiness. However, when the opponent is very near, the position of the neck changes; it is withdrawn, as a preparation to general withdrawal. In this posture, therefore, two components can be distinguished: one is the intention movement of attack, the other that of escape or withdrawal, and the upright threat posture can thus be understood as an ambivalent intention movement, the outcome of the simultaneous arousal of two antagonistic drives.

Grass-pulling is very similar to the movements of collecting nest material, an element of the nest-building pattern. It is a displacement activity, and is also due to the simultaneous activation of attack and escape (Tinbergen, 1952b). It appears when both are more strongly activated than when the upright threat posture appears; obviously mere intention movements, which do not use up much nervous excitation, are not sufficient as outlets when the activation of the drives is very strong and the higher intensity movements of these drives are physically incompatible. There are certain differences between the autochthonous collecting of nest material and grass-pulling; a grass-pulling gull pecks violently at the material and pulls at it; both elements can be recognized as parts of the fighting pattern which are superimposed upon the displacement activity serving as an outlet.

Aggressive behaviour of the Herring-gull, therefore, contains, apart from the appetitive behaviour and the consummatory act of the fighting pattern, at least two elements which are "derived" movements; the appearance of both of them is due to the interaction of two conflicting drives.

This conclusion applies to the threat behaviour of other species as well. The Three-spined Stickleback shows threat behaviour which is composed of the intention movements of both drives, the so-called "duels," in which each fish alternately attacks and withdraws. Another threat posture is displacement sand-digging, a nest-building movement. Displacement-preening, displacement-eating, displacement-sleep and various other displacement activities are elements of threat in a number of bird species. This does not mean that all displacement activities of these types have threat function in all species; they may often be outlets of other drives, such as the sex-drive.

Thus it is clear that many threat "ceremonies" are "derived movements." Part of them are combinations of intention movements of the instincts involved; they are autochthonous. Others are movements "displaced" or "borrowed" from instincts which themselves are not activated at the moment. Both serve as outlets for the drives involved. The use of "borrowed" movements has been recognized by various authors (Selous, 1933; Huxley, 1914, 1923; Makkink, 1936; Kirkman, 1937; Kortlandt, 1940; Tinbergen, 1939, 1940; Lorenz, 1941).

THE EVOLUTION OF RELEASERS

The origin of the releaser function

We have seen that many types of display originated as mere outlets of excitation. The outlets are different from one type of excitation to another. The study of their causation has revealed the type of the underlying motivation. In order to act as releasers it is necessary that these outlets shall be "understood" by the reacting individual, that is, are responded to adequately. For instance, displacement nest-building of a Herring-gull as an outlet of aggressiveness must not release nest-building, but withdrawal or attack, according to the circumstances. How has this been brought about?

Two circumstances may have led to the establishment of the proper type of responsiveness. Firstly, the threat behaviour alternates with autochthonous aggressive behaviour. Secondly, the threat movement itself is, as we have seen, usually a composite movement: the displacement movement may be mixed with elements of attack. Therefore, the special responsiveness to threat or to sexual releasers may have been facilitated by their being mingled with autochthonous movements, and this responsiveness may therefore be but a special case of responsiveness to aggressive or sexual behaviour, and this again is but a special instance of responsiveness to outside stimuli in general. The origin of this responsiveness is not known, but we can at least state that the problem of the responsiveness to releasers can be reduced to the general problem of the origin of responsiveness to outside stimuli.

Ritualization

As already suggested by Huxley (1923), derived movements form, in many cases, the "raw material" from which have evolved the specialized types of display as we know them to-day. This discovery has been made through comparisons of three types. Firstly, the specialized movements have been compared with the movements from which they are obviously derived. A displacement activity differs in certain respects from its autochthonous "example." It is usually incomplete. This is supposed to be due to the fact that the impulses which find an outlet through a displacement activity meet with a certain resistance in the central nervous system; only when the underlying drive is exceptionally strong does a complete displacement activity ever occur. Further, displacement activities are often integrated with elements of the activated drive itself: the grass-pulling of Herring-gulls, and the displacement sand-digging of sticklebacks show elements of attack. In general terms: autochthonous elements are superimposed upon the displacement activity.

Secondly, when derived activities which have no releaser function are compared with those that have, it is generally found that the releasers differ more strongly from their example than those derived activities which merely serve as outlets without releasing responses in other individuals. This is particularly clear in displacement fanning of sticklebacks. When a female in a glass tube is presented to a male (which allows her to show herself in the territory but prevents her from following him) the male, after a series of zigzags, swims to the nest and performs a sequence of displacement fanning, which can scarcely be distinguished from autochthonous fannings. However, both showing-the-nest-entrance and quivering, though recognizable as displacement fanning, differ in certain respects from autochthonous fanning. These differences, as we have seen, are partly due to superposition of new autochthonous elements; thus in showing-the-nest-entrance the male raises his dorsal spines, a sign of aggressiveness. Other differences, however, cannot be explained in this way; as I mentioned above, the male also pushes his snout into the nest. Experiments with models have proved that this type of displacement fanning has a releaser function: it guides the female to the nest entrance. This kind of comparison therefore suggests that some differences are connected with the signal function, that this function has been secondarily acquired in evolution, and that it is responsible for evolutionary changes in the form of the movement. Movements which were originally mere outlets of surplus excitation have acquired a releaser function, and this, it seems, has made them subject to a secondary evolutionary adaptation to this new function.

Thirdly, the differences between derived activities with releaser function and the originals from which they have been derived can be compared in closely related species. It will then be seen that these differences vary quantitatively and qualitatively from one species to another. In view of what is known of the function of releasers, this can only be interpreted as adaptive radiation. The adaptive divergence is often remarkably extensive, in fact often more so than in other functions in the same group. This suggests that the evolutionary divergence of releasers has been relatively rapid, which again is understandable in view of the fact that in closely related species, particularly in those that overlap with each other, there is a premium on reproductive isolation. This does not only apply to courtship display, but to threat as well, for threat display, as much as any other type of conspicuousness, renders individuals vulnerable to attack by predators, and it is therefore of selective advantage to limit threat and fighting to occasions when they are needed. By specificity of threat display the chances of interspecific reactions are reduced.

Comparisons of this type enable us to describe the kind of changes which must have occurred when a derived movement, by adaptive evolution, has developed into a highly specialized releaser. In other words, it enables us to describe the course of ritualization. In this process, several principles can be detected which obviously have operated repeatedly. Before enumerating these principles I should stress the fragmentary nature of the evidence. Much more detailed work will have to be done to strengthen the as yet tentative generalizations. Such work must involve detailed description of the movements, analysis of their function, analysis of their origin, and comparison of homologous sets of derived movements together with their originals in a number of closely related species. I should add that it is only possible to establish homologies if the causation is understood as well.

The principles of ritualization have been worked out mainly by Lorenz (1941) and by Daanje (1950). Daanje found them in intention movements; later, it was recognized that several of the principles could be found in displacement activities as well (Tinbergen, 1952b). This in itself is not surprising; in fact it might be expected since ritualization has nothing to do with the movements' origin but only with their subsequent adaptation to the releaser function.

Principles of ritualization

Development of conspicuous structures.—Most observers agree that when brightly coloured structures occur in a species, they are used in display. We are not concerned here with the cases in which they are purely aposematic, nor with the aposematic function in case they serve both this and the releaser function.

Many examples have been given by Huxley (1923), Lorenz (1935), Heinroth (1911), Tinbergen (1948) and others. In such cases, movement and structure are directively correlated in such a way that the movement displays the structure to the other individual. Good examples are found in ducks (Lorenz, 1941). Throughout the group, displacement-preening is part of the courtship. This movement therefore can readily be assumed to be homologous in the various species. Slight differences between species are correlated with differences in the structures which are displayed by the preening movement. These structures are not homologous in the various species. Two extreme cases are the Mandarin Duck and the Garganey. Whereas most ducks pass the bill along the inside of the wing, touching a series of secondaries, the Mandarin touches just one particular secondary. This one is strikingly different from the others; its vane is very much enlarged and is orange, instead of dark green like the others. The Garganey touches the hand coverts on the outside of the wing, which form a light greyish-blue field. It has been concluded in such cases that of the two components, movement and structure, the first is primary in this sense that the structure has developed its conspicuousness only after the movement had acquired signal function. I think now that we should not call either primary, since movement and structure must have been there before the releaser function was acquired; what developed after that was the conspicuousness of the releaser, and this is a matter of subsequent development in both.

Further correlation of the movement with the morphological structures involved.—The example of the Mandarin and the Garganey shows that the development of conspicuous structures has coincided with a change in the movement itself. This change is adaptive and can only be characterized as an increase in the efficiency of the display. Numerous examples of this principle are known. For instance, erection of the gill-covers, a component of frontal threat widely spread among fishes, is sometimes supported by conspicuous colour—or enhanced patches on the gill-covers. Two Cichlid species, *Hemichromis bimaculatus* and *Cichlasoma meeki*, have a gold-rimmed, pitch-black patch on the gill covers. In the first species, this patch is located much more dorsally than in the other. In correlation with these facts, the dorsal part of the gill-cover is spread more fully in *H. bimaculatus*, and the ventral part is displayed in *C. meeki* (Baerends and Baerends, 1950).

It is less well known that some display movements can only be understood as having been ritualized with a view of avoiding stimulation rather than providing it. An obvious case is the "head-flagging" of Black-headed Gulls (Tinbergen and Moynihan, 1951). When mates or prospective mates meet, they often turn their heads emphatically away from each other. If this is understood as serving to display the occiput and the dorsal surface of the neck, it would be rather out of line with other examples of display, for the white neck cannot be considered to be particularly conspicuous. However, the function of the movement is appeasement, and it can be understood when it is realized that it is just the opposite of the threat posture. In the threat posture the bird faces the opponent, pointing its bill forward, and this gesture is made more conspicuous by the brown face, which forms a regular brown disc round the bill. The demand for appeasement has prompted the development of a movement—of as yet obscure origin—into "head-flagging," the only function of which seems to be to turn the weapon and its supporting releaser away from the partner. The origin of the movement—which strictly speaking does not at present concern us—may be found to be any movement which involves a turning of the head. It is possible, though by no means proved, that the frequent displacement-preening, which can be observed during such encounters, and in which the head is indeed turned away, has been the raw material which has been ritualized into head flagging. A study of related species might allow verification of this.

A similar example is found in the Coot. A threatening Coot points its bill at an opponent. This gesture is emphasized by the white frontal plate. Friendly birds bend the head to such an extent that the frontal plate is parallel to the water surface, and hidden from view. A similar gesture is found in the Waterhen during copulation.

The adaptive evolution of this type of display seems to have been dependent on a reverse evolution of the threat gesture. It could be called an instance of "further correlation of the movement with the morphological structures involved," but of a peculiar type, for instead of enhancing the showing-off of the structure it avoids displaying it. It is the same process, but with a negative sign.

Schematization of the movement for its own sake.—Many species have specialized on the further development of the movement itself, often without any support by conspicuous coloration. This is clearly the type of ritualization to be expected in those species in which the need of cryptic coloration is all-important. Such further development is characterized by (1) an increase in the extent of some elements of the movement, and (2) the abolition of other elements. Various courtship movements of ducks are derived from the intention movement of jumping, probably betraying the tendency to mount the female. This movement, as Daanje (1950) has shown, involves a withdrawal of the neck, a shortening-up of the body, and a lifting of the tail. These movements have been ritualized in many different ways. In the Garganey and in the Chilean Teal, for instance, the withdrawal of the neck is very much exaggerated, and the tail movement is absent. In many species such changes may be so great that the movement as a whole can scarcely be recognized. The result of the changes is that the movement becomes both simpler and more conspicuous.

Another change in the movement, which is found both in those displaying brightly coloured structures and those that dispense with them, affects its onset and its end: both become more abrupt. This not only helps in making the bright structure appear more suddenly, but is also seen in movements such as the head-flagging of the Black-headed Gull. It is a means of making the movement more striking; it is calling attention to the change, either that from non-conspicuous to very conspicuous appearance, or the reverse.

In patterned movements of the type with which we are concerned here there is a rigid co-ordination between the movements of the parts involved. Neck-movements, for instance, may be synchronized with tail- and wing-movements. Von Holst (1937) has analysed this co-ordination, and thus enabled us to see that the result of ritualization is sometimes a breakdown of co-ordination, the parts becoming independent in both rhythm and extent.

It is possible, and even probable, that the principles mentioned do not exhaust the possibilities. However, even at the present stage it is already possible to see one general trend in all these types of ritualization: in all cases, ritualization tends to make the movement both simpler and more conspicuous.

Recent studies of the sign-stimuli that normally release innate behaviour have made us understand the significance of this process. The reactions shown to the various types of display, both courtship and threat, are as a rule innate. We know that innate behaviour is usually released by stimuli of a special type. Many of the external changes which can be received by the sense-organs have been shown to take no part at all in the release of a particular response. The mechanism responsible for the release is highly selective: it responds to only a few "sign-stimuli." Accordingly, the schematization of movements and structures involved in display can be understood as an adaptation to their function of releasing innate responses.

"*Emancipation*"

The result of ritualization is that the original movements are altered. This means that the central nervous structures responsible for them must have altered. In this way the movement becomes "emancipated"; from a mere derived movement it becomes, through gradual change, a "new" and more or less independent movement. The displacement-preening of ducks, for instance, could be considered, before ritualization began, part of the preening pattern, which was used as an outlet of the thwarted sex-drive. Ritualization made it different from the original displacement-preening, and at the same time incorporated it into the pattern of the sex-drive. Thus a study of ritualization is not only important from the sociological point of view, but beyond that it shows us how behaviour can change during evolution. The analysis of the principles of adaptive change reveals that "new" movements may arise through addition of small quantitative changes. The effect of producing something "qualitatively new" is caused by quantitative changes in the component elements.

It is difficult to decide whether the two types of movements mentioned, intention movements and displacement activities, are really the only types of raw material of display. The reason of this uncertainty is obvious: ritualization has altered display movements to such an extent that many of them are now independent movements, very different from what they once were. The only way to discover their origin is by the comparison of closely related species. In groups with few species, or in groups of which only one or two species have been studied, or in groups where the study of display has been superficial, the origin of many movements is still obscure. Only continued study will enable us to test the validity of our as yet tentative generalizations.

Variation and selection

We have seen that the comparative study of display leads us to recognize ritualization as a type of adaptive evolution. In order to complete our task of reducing the problem to the general problem of adaptive evolution we will have to consider whether there is innate individual variation, both in the form of displays and in the innate responsiveness to them, and whether these variations are subject to selection.

Although it is obvious that there is much individual variation in display, and although it is probable that much of this has an innate basis, I do not know, in vertebrates at least, of any systematic study providing direct proof. My own experience has convinced me that not only is there much variation, but that the amplitude of variation is often considerable. In both the Herring-gull and the Three-spined Stickleback, the species which I know best, there are consistent individual differences in the strength of drives, in the tendency to display, and in the form of the display. An extreme example was one individual male Three-spined

Stickleback which consistently, in showing-the-nest-entrance, failed to turn its back towards the female. Instead of turning on its side, it stayed in normal balanced position with the back upward. Although in this, and other cases, actual proof of the innate character of this deviation is lacking, our knowledge of the learning processes which influence the sticklebacks' behaviour does not leave much room for doubt that such deviations must be innate.

In judging the selective value of individual differences in courtship we must, as Huxley has repeatedly stressed, consider more than female choice alone. This is true in two respects. Firstly, many types of courtship displays function only after the pair has been formed. Secondly, a definite selection, resulting in one male being responsible for more offspring than another male, is rarely dependent on female choice in the "psychological" or anthropomorphic sense of the term. In sticklebacks I have observed again and again that a female enters a series of territories in succession. Whether she will spawn or not depends on whether a male can arouse her sufficiently to bring her over the threshold of spawning. All kinds of intensities of female response can be observed, from a mere turning towards the male, through partial following, following but failing to enter the nest, entering the nest but failing to spawn, to the complete chain of activities, culminating in spawning. It is not at all rare to see a female enter a territory, respond only weakly to the male's courtship, and leave again only to enter the next territory where a more intensely courting male at once releases her complete chain of sexual activities. Everything we know about the importance of the intensity of external stimulation for the release of innate responses points to the conclusion that differences in the intensity of display are correlated with differences in the intensity of the responses to it. The innate responsiveness to the display fits the display exactly in most cases; that is to say, the natural display provides the optimal stimulus. The zigzag dance, the red colour, the motion of leading to the nest, that of showing-the-nest-entrance, and the quivering of the male stickleback have all been shown experimentally to be essential for the release of the female's responses.

It seems that in some cases the responsiveness is, so to speak, running ahead of the development of the releaser. In some cases "supernormal" stimuli have been discovered, that is stimuli more effective than those given in the natural situation (Tinbergen, 1951a). This would tend to promote the further development of the releaser. It is probable that in cases where such responsiveness to supernormal stimuli is well pronounced, other requirements have prevented the further development of the releasers. This is particularly obvious in the reactions of some birds to eggs. Oyster-catchers, when given the choice, prefer clutches of five to normal clutches, and prefer eggs of double or more than double the normal dimensions to eggs of normal size. Obviously, adverse selection-pressure in relation to other factors has prevented the development of larger clutches or larger eggs.

Concluding this section, it must be stressed that although all incidental evidence suggests that there is enough innate variability and sufficient selective pressure acting upon this variation, systematic studies of this problem are greatly needed.

THE BALANCE OF DRIVES

In the discussion of the function of fighting and threat I pointed out that they result in spacing-out, and that spacing-out is of great advantage to the species. However, since threat involving conspicuous displays is a distinct disadvantage to the individual (though less harmful than actual fighting), and since, as we have seen, threat is the outcome of a balanced activation of fighting and escape, the question arises: why has not selection favoured the development of individuals with a fighting drive which is so strong that it overrides the escape drive? Since we know that outright, uninhibited attack intimidates the opponent and causes it to withdraw immediately, would not such variants be at a tremendous advantage?

Our analysis of the causation of courtship display provides the answer. A courting individual is really under the influence of more than the sex-drive only. The first reaction of males to females is usually a mixture of sexual responses and aggressive, or sometimes escape responses. The female releases attack because, being a member of the same species, she cannot help showing some of the sign-stimuli which release the male's attack. She may release the escape drive because her approach cannot but provide stimuli typical of a predator. Because of the arousal of the attack drive in the male, while it is true that a variant male with an exceptionally strong fighting drive would be highly successful in driving other males off, it would undoubtedly be at a disadvantage in its relations with females, for it would attack them, and females would be less able to switch it into purely sexual behaviour. Such events have actually been observed in song-birds in captivity (Braun, 1915).

There would be still another possible way of producing a "relentless fighter," viz. by lowering the escape drive. A similar argument can be applied to this: an individual with a lowered escape drive would probably be more vulnerable to attack by predators than normal individuals.

Considering courtship, a similar problem arises. Since courtship display doubtless endangers the individual, one would expect that it would be beneficial both to the species and to the individual, if mating could be effected without it, just by immediate performance of appetitive behaviour and consummatory act. Again, a consideration of the requirements in other spheres of life provides the solution. Instincts mutually suppress each other, and an increase in the strength of the sex-drive would suppress both the fighting drive and the escape drive, which again would endanger the individual. Also, it would suppress the parental drive, which would endanger the individual's offspring.

It seems, therefore, that the present situation, in which each drive is not so strong as to override other drives, nor so weak as to endanger the individual in other situations, has evolved by the influence of selection on the individuals as wholes. As Huxley stressed in 1923, all the individual's functions have to be considered, and selection has produced a state of balance, or compromise.

CONCLUSION

Three types of approach have led to an understanding of the origin and evolution of courtship and threat display: (1) a study of the causation of display, (2) a study of its function, and (3) comparison of related species.

Displays are primarily caused either by low, or by ambivalent, or by strong but thwarted motivation. In courtship, aggressive and escape tendencies are combined with sexual tendencies; in threat, both aggressive and escape tendencies play a part. The two sources of display recognized so far are intention movements and their derivatives, and displacement activities. Their causation can be understood in terms of specific drives, dependent on internal (motivational) factors and external releasing stimuli.

Displays have various functions. Some of these are concerned with the co-ordination of the activities of the individuals involved, some with reproductive isolation.

Comparison shows that the various activities which form the evolutionary raw material of display, while in themselves originally mere outlets of surplus excitation, have been subject to adaptive evolution as releasers. This adaptive evolution has caused radiation within each group, as a consequence of the need of (1) avoiding inadequate intraspecific responses, and (2) avoiding interspecific responses. This type of evolution, or ritualization, follows the same general lines throughout: it increases the efficiency of the displays in their function of providing sign-stimuli. Ritualization may lead, through quantitative change of components, to the development of behaviour patterns which at first glance appear to be qualitatively new.

The development of displays, against selective pressure tending to abolish them because they render the individual more liable to attack by predators, can be understood from a study of the requirements of the individual and the super-individual unit as wholes; a certain balance of drives has evolved as a compromise which satisfied the needs of both individuals and species.

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T. S. WESTOLL

Mountain Revolutions and Organic Evolution

THE understanding of large-scale earth-movements grew essentially from the observations of Hall and James Hutton in the south of Scotland about one hundred and fifty years ago. An unconformity, where a series of strata is found lying on the eroded and truncated edges of older rocks which had been tilted or folded prior to the erosion, received at that time a satisfactory explanation that opened a new field in geology. Since then it has been a fundamental part of geological theory and practice that the rocks—and especially the fossiliferous rocks—of the earth's crust record not only the history of living beings, but the history of the deformation of the crust, of changing conditions of erosion and deposition, of movement of shore-lines, of the birth, rise and destruction of mountain ranges. The paleontologist and the structural geologist have necessarily been partners in the elucidation of this vast and tattered history, because in general the sequence of events is "dated" (geologically speaking) on fossil evidence.

Even the development of physical means of dating events (e.g. the radioactive clock method, which was first essayed just fifty years ago) has not essentially changed the picture. Assays of uranium, thorium, etc., and of the radiogenic lead and helium produced from formerly-existing atoms of such elements, could of course be made from any suitable sample of rock and a "radioactive age" for that rock determined. But unless that sample can be shown to belong to a rock mass with determinable and significant structural relations to other rock-masses whose geological age is known from stratigraphical and paleontological evidence, the determination of "radioactive age" will not contribute seriously to our understanding of earth-history.

There have been, therefore, three main ways of determining the ages of rock-masses—the first primarily geological, involving the superposition of newer strata upon older; the second paleontological, based upon observed successions of fossils in clearly superposed strata and greatly extended by detailed evolutionary studies once the key sequences have been found reliable; and the third primarily physical, such as the "radioactive clock" method. The two first give excellent agreement, except in areas where the apparent superposition is misleading as a result of overfolding or dislocation by faulting, but they give only an order of succession and position in the succession ("geological age"), not duration or dates. The radioactive clock method, applied to igneous or other rocks whose geological age is well established and closely defined, has given on the whole a remarkably good confirmation of the geological succession; however, many older determinations, especially those involving the helium-ratio, are quite unreliable, so that a new chapter of investigation is now opening. But we have now a skeleton time-scale in years, allowing a more or less quantitative analysis of geological processes.

Many of the earlier stratigraphers accepted a more or less catastrophic view of the geological implications of unconformity. Widespread extinction of faunas and floras were regarded as natural phenomena, in spite of the growth of a uniformitarian philosophy of geological processes after the publication of Lyell's *Principles of Geology*. The existence of richly fossiliferous bands seemed to attest the mass killing of great numbers of organisms—one recalls Hugh Miller's "platforms of death" where the fish-bearing limestone nodules occur in bands in the Middle Old Red Sandstone of the north of Scotland. More recent investigations show that populations were but rarely, and only locally, overwhelmed and buried in this fashion. More often than not such a fossil-bed represents a brief moment in geological history when conditions were unusually favourable to the preservation of cadavers, and merely throws into relief the far more normal process of rapid putrefaction and nearly complete disintegration of dead animals and plants. There are certainly no fossil-beds known at this time that can, by any stretch of the normal imagination, be regarded as the vast cemeteries of a world-wide catastrophe.

One long-continued effect of the influence of unconformities (and of the less blatant disconformities, where newer rocks rest on an essentially undeformed and only slightly eroded surface of older rocks, without angular discordance) has been in the selection of series of strata as type-developments of geological systems. Frequently, in the early heroic days of far-travelling, long-walking and quick-sighted pioneer stratigraphers, an unconformity was taken as the "natural" dividing line between geological systems. Because an unconformity (or disconformity) represents a lapse of time unrecorded in the area concerned, the fossil faunas and floras on the two sides of an unconformity may be profoundly different. But as exploration has extended our knowledge, lacunae in time have been largely filled in by the sedimentary record in other places. We are now, indeed, in an interesting phase of development in stratigraphy and bio-stratigraphy, in that more or less complete bridges are known between many adjacent geological systems, so that defining the beginning and ending of, say, the Devonian or Carboniferous systems has become a matter for arbitration.

At the same time as biostratigraphers have been filling some of the gaps in the succession in this way, they have become more and more impressed by the deficiencies of the geological record, and by the very great importance of facies-differences in strata of similar age.

It is certainly true that most of the extended successions of sedimentary rocks, no matter how simply homogeneous they may appear at first sight, were not deposited continuously at the same rate. Comparison of fossiliferous successions of Jurassic marine sediments in England, for example, led S. S. Buckman to the view that "non-sequences" are surprisingly widespread. Some non-sequences were suspected first of all from the succession of ammonite-faunas collected at close intervals. A particular section often lacks elements represented elsewhere; for example locality 1 may show a succession ABCDEFG . . . and locality 2 may show ABEFXYG . . .; the implication being that no sediments are preserved in locality 1 representing the interval of time represented by the XY faunas, or in locality 2 of the interval of CD. In some cases subsequent examination of the succession in the field revealed evidence proving such contentions, such as thin beds of rolled and phosphatized lumps occasionally including remanié fossils washed out of the older sediments. There can be little doubt that Buckman and some of his followers sometimes went too far and asserted the presence of non-sequences on insufficient grounds, but the trend of recent work has been to emphasize that a thickness of apparently conformable fossiliferous strata does not necessarily represent a continuous and uniform record. The geological results of work of this kind are important. It can often be demonstrated, on both fossil evidence and the results of detailed mapping and lithological study, that a group of strata such as the Jurassic system or parts of the Carboniferous system in Britain and adjoining parts of Western Europe, which earlier generations would have regarded as fairly simple cases of nearly continuous sedimentation, are full of non-sequences, disconformities, minor unconformities and even more serious breaks, which in turn throw light on the broad problem of deformation of the earth's crust. In this conclusion we are supported mainly by facts derived from the more richly fossiliferous of our deposits.

It is probable that equally striking results would emerge from other less favourable deposits if we could obtain more fossil evidence. Fossils are commonest and most varied in type in certain shallow-water marine (neritic) deposits, and it is shallow seas that most clearly mirror, in their bottom sediments and their contained organic remains, any disturbance of the earth's crust or of sea-level. Even in somewhat deeper (though not necessarily very deep) seas, such as that in which the Chalk of England and France was laid down, there may be less obvious but no less important evidence of changes in conditions; but here it is not so easy to relate evolutionary change and the effects of earth movement.

The paleontologist has a major contribution to make towards another aspect of the study of earth-movement. In shallow water marine environments, for example, quite small changes in sea-level, minor crustal warping, or alteration in the volume and kind of sediment poured in by the rivers (which may relate to changes in climate or in relief of the lands), may result in noticeable differences in the kind of sediment on the sea-floor and in the nature of the animals living there. A period of moderately deep-water and relatively widespread similar sediments may be followed by one of shallower water and diversified sediments and fossil contents. This differentiation of contemporaneous facies is at the base of most problems of detailed stratigraphy; and where a world-view is necessary we must take into account a great variety of terrestrial, fresh water, brackish water and marine facies. The determination of the age-relationships of strata of markedly different facies is not easy, and can very rarely be precise; but stray elements of one facies-assemblage may be found in others (e.g. land plants and vertebrates washed out to sea) and occasionally one has the good fortune to find an interfingering succession of different facies so that a more or less detailed partial correlation may be made. It may be said at once that the remarkably detailed picture which we now have of, say, the British development of the Jurassic system and its history of minor crustal unrest would not have been possible without the concept of facies-differentiation and facies-correlation.

It is not too much of an exaggeration to say that geological *formations* (such as the Wenlock Limestone, the Oxford Clay, the Upper Greensand) are differentiated from those above and below, even where there is no apparent unconformity, by change of lithological facies. This may be gradual or relatively abrupt, and the more abrupt it is, the more suspicious will the field-geologist be that a non-sequence or disconformity may be present, even though of trifling extent in geological time. Such changes are usually accompanied by changes in fossil content, and of course give the sequence of fossil faunas in any local stratigraphical column an episodic character. If our knowledge were confined to one small region we might be forced to accept a direct relationship between the factors governing lithological facies (including earth-movements) and the record of organic life. But as our field-studies are extended we find that a single formation (of one or more than one "member" in the sense of a lenticle or stratum of a kind easily differentiated from those above or below) is not of indefinite extent or of uniform thickness; and in many cases, its deposition can be shown to have begun or ended at somewhat different times in different places. Only in extreme cases can such heterochroneity be established on purely lithological grounds; this is a field in which paleontology plays a vital part. As studies of this kind are continued the apparently episodic nature of the sequence of faunas is greatly modified; instead we can more readily view the record as one of the colonization of new environments, by such organisms as are fitted for them, as the conditions change. A particular change of conditions, beginning in a restricted area, will thus come to have its special faunal facies, and if the new conditions spread so will the whole facies, sedimentary and biological. In certain cases it may even be possible to demonstrate an evolutionary sequence in some elements of the "new" fauna and to prove heterochroneity more or less directly.

In all such cases two correlated questions at once arise; what happened to the descendants of the replaced facies fauna, and where did the new facies fauna come from? The vast majority of cases, because of the limited exposures of geological formations, allow no certain *detailed* answer to be given, but in shallow-water marine deposits there is not much doubt that comparatively simple and well understood ecological factors are involved. Any area of sea-floor (using the term in distinction to the floor of the deep oceans, since true oceanic deposits are so rarely found in the accessible geological record on the present-day land-masses as to be negligible) is in direct and indirect communication with many other such areas, and mobile adults, free-swimming larvae and essentially planktonic young stages may move into, or be swept into, the area from outside. Only those adapted to the local conditions will thrive and have a chance of contributing to the fossil record; and if the local conditions should change it would be odd indeed if there were no inflow of individuals or their larval offspring from another region which could live in the new conditions. If the new facies is very different from the old and isolated from comparable ecological regions, it may be some time before it is fully exploited and colonized, and the facies-fauna may show numerous effects of isolation or be highly specialized when studied in detail. But generally there will be some part of a broad region which will carry a suitable facies-fauna for each of the most frequent types of sedimentary facies,* so that the colonization is probably usually rapid. Similarly when a particular sedimentary facies comes to an end in one part of a broad region its particular facies-fauna will die or migrate; but there will usually be, at no very great distance, a similar but not necessarily identical faunal assemblage which can act as a reservoir ready to contribute its share to the recolonization of the old sedimentary facies if it should return.

The most remarkable examples of such changes are surely those provided in the cyclothems, the so-called "rhythmic" or "cyclic" sedimentary sequences, which are now known to have a long scattered spread in geological time and to occur in many continents. In cyclothem sedimentation a sequence of lithologically distinct members is repeated several times in the same order. Some typical cyclothems have been fully described elsewhere† and only two kinds need be mentioned here. One is very widespread in the upper Carboniferous (Pennsylvanian) and lower Permian deposits of the United States west of the Appalachians, and in the upper part of the "lower Carboniferous" (including some Namurian equivalents) of the North of England. In this type of cyclothem (details based on the English "Yoredale type") a marine limestone lies above a coal-seam, often immediately above it, implying a great change in conditions. The limestone passes up into calcareous shale with marine fossils, which is succeeded by ferruginous, then by sandy shales, often passing up into micaceous flaggy-bedded sandstones. Coarser gritty sandstones with typical deltaic foreset bedding often conspicuous, overlie these, and often rest on a channelled surface. The top of the sandstone may be overlain by a fireclay or seat-earth bearing a coal-seam, after which the limestone of the next cyclothem is typically developed.

A second kind of cyclothem succession, this time without any known marine bands, is characteristic of parts of the Middle Old Red Sandstone of Caithness and Orkney. A "limestone" with fishes, or sometimes a remarkable bed of clots and pebbles of deformed and (when formed) partly hardened sediments, lies on a series of micaceous shales and mudstones. The limestone or "nodule-bed" is followed by calcareous flagstone or flaggy siltstone, which becomes less calcareous and more sandy upwards, and passes up into the topmost member, a thick micaceous shale or mudstone with ripple-marks, rain-drop imprints and deep desiccation-cracks. The next cycle follows.

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* By this term we imply here not only the gross physical nature of the accumulating sediments, but such other factors as depth of water, nature of currents, temperature, salinity, oxygenation and other chemical properties, many of which have a direct bearing on the nature of the rock produced.

† Eg. T. Robertson (1948), and papers in *Internat. Geol. Congr.*, Rept. of 18th Session (Great Britain, 1948); Part IV, "Rhythm in Sedimentation," 1950.

In both cases a relatively "deep-water" limestone (but certainly not very deep-water—a matter of a few tens or scores of feet) directly succeeds sediments or rocks (coal-peat or mudstone) which were largely exposed at the surface when formed. The succeeding strata may perhaps be regarded as "filling in" the body of water, and in both cases more coarse-grained sandy sediments appear about midway up the sequence. The most obvious paleontological interest lies in the sequence of different ecological facies-faunas and floras in any cyclothem, and the reappearance of similar (but not necessarily identical) faunas in corresponding strata in cyclothems above and below. There can be little doubt that the marine faunas of the "Yoredale" limestones entered the area from some region outside the area of "Yoredale" rhythmic sedimentation at the beginning of each cyclothem as defined above, but it is not yet possible to show with certainty where this area lay. It is possible, too, that the extensive shallow seas in which the "Yoredale" limestones were deposited were ecologically rather distinct from the faunal-reservoir region, so that some time would be taken for full exploitation of the new ecological opportunity. It is perhaps not to be expected that successive limestones should yield faunas showing nicely graduated evolutionary change in all groups of species; some will doubtless do so, others will contain intermittent ecological and geographical races of species evolving more or less continuously in the somewhat different conditions of the faunal reservoir-areas. This represents a very interesting field for detailed studies.

In the same way we must regard the plants and other "terrestrial" fossils of the higher sandstones and coals as being able to spread out over the delta-flats from a continuously-occupied reservoir-area towards the land.

The significance of cyclothems to our main theme is that they have frequently been interpreted as consequences of tectonic movement (e.g. of periodic sharp local falls in relative level of the land). Other explanations have been offered, but do not seem fully satisfactory. In any case, the paleontologist should beware of regarding any sequence of clearly related species from similar members of successive cyclothems as a truly evolutionary sequence. It seems most reasonable to regard each successive marine episode as providing a new, widespread, ecologically distinctive habitat which was colonized from the appropriate reservoir areas; the faunas that succeeded in becoming established did so because of opportunism rather than by destiny.

Earth-movements of the kind just discussed are, of course, very minor. The broader field of large-scale mountain-building and its consequences has attracted more attention as possibly related to the rise to dominance, or the decline and fall, of biological empires. In little more than sixty years an imposing volume of work has been published on this general topic. We may note briefly the growth of the idea of the geosyncline (J. S. Dana in 1873, developing earlier views), of the contrast between epeirogensis and orogenesis (due to G. K. Gilbert in 1890), of the recognition of short periods of intensive orogenesis (e.g. by Stille since 1924), and of attempts (e.g. by Joly in 1925, by A. Holmes since about 1930 and by Umbgrove in 1942) to show a general periodicity of such orogenetic movements. Many geologists to-day would accept the following as a broad and necessarily superficial summary of an "orogenic cycle." The cycle begins by the formation of a depression, often arcuate and elongated, in a section of the earth's crust; this is for long periods occupied by the sea. Such a depression, a geosyncline, receives great quantities of debris from the rapid erosion of the adjoining lands, which may show compensatory uplift. The processes of sinking of the floor and filling with sediment continue more or less irregularly, sometimes punctuated by general slight uplift, more often by slight crumpling movements of greater or less intensity. The sedimentary prism may accumulate to depths of perhaps 15–20 km., and then seems to be in an unstable condition. It is subjected to great compressive forces across the axis of folding, and suffers severe crumpling, dislocation along surfaces of shear and slip, and metamorphism, while a variety of igneous rocks, gneisses and granites may be added to, incorporated into, intruded into, or produced within, the pile. This phase is conveniently separable as the structogenic phase (Stille); at the same time, and for some time after, the thickened prism rises to produce a young mountain range, often with accompanying igneous activity. Such a change involves a broader regional uplift, so that a time of essentially continental sedimentation and rapid erosion ensues. After a long interval the general relief is lowered sufficiently to admit shallow marine transgressions; marine planation and surface erosion may ultimately destroy great parts of the chain.

It was Gilbert's view that the violent but localized movements associated with the climax of such a process (the *orogenetic* type, involving what is termed above the structogenic phase and the immediately following uplift) must be distinguished from the *epeirogenetic* type of earth-movements involving apparently simpler rise or fall in the relative position of land-level to the seas, some of which are suspected to be world-wide, but also including broad gentle warping and faulting of the earth's crust. Later workers suggested further generalizations—for example, that orogenies were of short duration and widely separated in time, with essentially epeirogenetic movements between them (e.g. Joly). Such a view is now known to be too simple, but it has undoubtedly had a great influence on some evolutionary theorists, who would relate the extinction of some groups and the rise of others to particular orogenetic periods.

It does, however, remain broadly true that in any one continent we have the traces of only a few important periods of folded-mountain formation since Pre-Cambrian times, and that the worn-down remains of each set of these mountains may form sub-parallel belts of complex structure with more or less arcuate or swinging plan. In Europe, for instance, a mid-Paleozoic series of fold mountains (the Caledonides) can be traced in Britain and Scandinavia; a complex series of arcuate worn-down mountains of late Paleozoic Age (the Variscides or Hercynides) in Cornwall, France, the Rhineland and across Central Europe; and a still more complex series (the Alpides) of essentially early and middle Cainozoic age across Southern Europe and the Mediterranean region. It is also true that between the second and third of these periods, for example, most of Europe was in a state of relative quiescence.

But on a broader world view, and on closer examination of local detail, this simple picture is seen to be a caricature. It is certainly not true that all continents show important mountain-building at the same general period as Europe—in other words the Caledonian orogenesis as formerly defined (late Silurian and early Devonian folding) is not world-wide, and important periods of orogeny in western North America, for example the Nevadan and Rocky Mountains crumplings, had little effect in Europe. On the other hand, detailed investigations of many groups of fold-mountains has revealed a great complexity; for example, the North-Western European "Caledonides" have been shown to be in all probability not a single range but a complex of sub-parallel ranges, some of which had histories of sedimentation and folding quite separate both in space and time from others. And instead of a single climactic compression followed by uplift, almost any unit of such a series of chains shows a record of several episodes of folding and other tectonic activity, some of which are admittedly minor.

It is from such a position that Stille has developed a new theory of orogenetic phases, short in duration and wide in effect, but very much more numerous, separated by long anorogenetic periods. The distribution of these orogenetic phases is not strictly rhythmic (in contrast to Joly's view), and between 1924 and 1940 Stille increased the number of Cambrian and later phases from 34 to 42. Stille's synthesis has had a profound effect on many stratigraphers, and has been both seriously criticized and stoutly defended. (Stille, 1924, 1936, 1940; Gilluly, 1949; Rutten, 1949; Umbgrove, 1942, 1950.) Some important points must be made. The geological age of a period of folding is always between limits—it cannot be older than the youngest event of clearly pre-folding date (e.g. the youngest strata involved) or younger than the oldest event that clearly post-dates the folding (e.g. the oldest strata resting unconformably on the folded rocks). In many cases those limits are not very close, and the period of folding is widely indeterminate; only in a few cases can reasonably close limits be set. And here let us remember that an interval of half a million years is only about 1 per cent of Carboniferous time, and would represent close dating, but is about half of Pleistocene time, and would be too coarse to distinguish between events of the Pasadenan folding in California and the present day. If Stille is correct, an orogenetic phase, limited in its area of maximum effect, will be recognizable over much wider areas by "synorogenetic" effects in epeirogenic regions outside, and of course such effects will be useful horizon-markers. But this is a large assumption, and is not now widely accepted. Nevertheless it has one implication that must act as a warning; certain stratigraphers use minor tectonic events as time-markers, which may be useful in a limited area but is a terrible trap if used for distant correlation. The writer does not know whether differences in rapidly-evolving stocks above nearly contemporary minor unconformities have been used to suggest source-areas and directions of migration of the fossils concerned, rather than as evidence of heterochroneity, on the basis that the events are synchronous because a single very short orogenetic pulse is involved; but such would be a logical way of dealing with the observed facts if one followed Stille closely.

This does not mean that the whole of Stille's work is worthless; far from it. We can now be assured that earth-movement of a fairly violent kind has been frequent here and there over the world during its long history, and we can no longer accept a simplified model of few long-separated orogenetic phases. Indeed, it is now becoming the fashion to use the term "Caledonian epochs of folding" to cover events from late pre-Cambrian to late Devonian inclusive; "Variscian epochs" from late Devonian to the end of the Triassic, and so on, so that there is even an overlap in time. Such an extension of usage may be going too far, but at least the evolutionist should now know that to talk of the extinction of the graptolites and the origin of land-floras and tetrapods as "results of the Caledonian mountain-building" is rather empty verbiage. This conclusion is probably rather widely acceptable; nevertheless there is, and must be, some rather direct connection between earth-movement and evolution. At the present day some 5 per cent of the earth's surface is occupied by shallow seas (the margin of the "continental shelf" being the conventional limit). In these shallow seas live the densest marine populations. At times in the geological past these seas may have spread far more widely over the lands, at others they may have been much more restricted. Reliable measures of these variations cannot now be given, and may never be made, but one may guess that the maximum extent of shallow seas may well have been some ten times the minimum. Fluctuation of this kind may provide alternating severe selection-pressure and broad new conquests for the populations. Furthermore, the rise of new mountain chains and the ensuing regional elevations provide new territory for animals and plants favourably placed to exploit them. The successes of some groups in taking advantage of such new opportunities are liable to result in adaptive radiations; the restrictions imposed by the other extremes are likely to intensify competition and to reduce the numbers of those less successful in adaptation. But one cannot say that a particular orogenesis "caused" the rise of land vertebrates and a land flora; it happened that organisms with suitable structures and physiological capacity existed in sufficient numbers to take advantage of the situation. Nor can one blame the filling in and crumpling of the Silurian geosynclinal seas for the extinction of the graptolites, for example, or some wide transgressions and regressions of the Cretaceous seas for the fate of the great Mesozoic marine reptiles and the ammonites. Such changes helped, no doubt; but it seems altogether wiser to suppose that they were not in themselves enough. All these groups had survived, with local and perhaps important losses, various movements of the same kind, but as they grew in length of lineage they also became more and more specialized along divergent lines. In the end few were able to survive, and they only briefly, not because of direct effects of earth-movement, but almost certainly because of the greater potentialities of some upstart competitors for a dwindling ecological *Lebensraum*. In this respect it is particularly interesting to consider some Mesozoic cephalopods. Already in the late Triassic period, for some reasons unknown but probably involving changes such as we have discussed, both the ammonites and (as my friend Dr. Bernhard Kummel has shown me) the nautiloids were drastically reduced in number and variety. The survivors were able to recolonize their hereditary environments by a great radiation during the Jurassic. Near the end of the Cretaceous Period they were again in trouble, and only the nautiloids survived, in small variety, to have only a modest radiation in Cainozoic times. The opportunity was doubtless there for ammonites; perhaps they lacked the qualities to benefit by opportunism. But even here we cannot suppose that earth-movements were the only factor; perhaps they were not even crucial—the problem of extinction is certainly a very complex one. "The truth is never pure, and rarely simple."

The possibility that evolutionary "bursts" within the history of a group may be related to earth-movement has been much canvassed. Such "bursts" have been (often loosely) defined in two main ways—(*a*) as phases of unusually rapid change in a lineage or closely-defined group (e.g. the tachytelic phase in the sense of Simpson (1944), and (*b*) as relatively short periods of rapid differentiation of genera in a group (as in adaptive radiations, etc.). The second type is probably in many cases a summation of several tachytelic offsets.

A recent discussion (Symposium, 1952) is a valuable contribution to this latter study, though some valuable work is not directly listed in the references therein (e.g. Bulman, 1933). In this symposium the various major contributors and those entering the discussion show considerable differences of opinion on the relation of evolutionary "explosions" to earth-movements. Some, for example, rely heavily on theories involving pulsating-earth-movements (including a curious carry-over of a form of theory that regards geological systems as bounded "naturally" by such pulsation, and including a lower transgressive, a middle, and an upper regressive division—which is certainly a caricature of facts). Others show what, to this writer, is a healthy iconoclasm in this matter. It is particularly instructive to read the paper in the symposium by Cooper and Williams on the history of brachiopods; among other good services they have distinguished a serious artefact of evolutionary patterns as a "monographic burst," due to the existence of exhaustive monographs on selected faunas; some of these are also marked by an extreme degree of generic and specific "splitting," but their effects are often not too easy to assess and discount. There are, of course, many stratigraphical paleontologists who would sturdily defend a more or less direct control of evolutionary pattern by earth-movements. But it seems more reasonable to regard at least most evolutionary "bursts" (of both the real kinds noted above) as evidence of the irrepressibly opportunistic nature of evolution; and no doubt in great part those considerable extinctions we have noted may be the converse of the picture. There is a dynamic interplay between living organisms and their environments, so much is certain. But crustal unrest of itself is not enough; what matters is specific changes in specific environments which are either fully occupied by, or become available to, forms of life suitably fitted to inhabit them. It may well be that restriction of an environment may lead to great extinctions; but it is rarely possible to take into account all (or even most of) the factors involved in such extinctions (cf. Arambourg, 1950). Great evolutionary developments almost inevitably involve successful exploitation of new opportunities; similar *conditions* may well have occurred many times, but creatures fitted for such an adventure may rarely be available to break in and deploy widely.

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Colour Vision and its Evolution in the Vertebrates

Colour plays such an integral part in our own daily lives that it comes as somewhat of a shock to most of us to learn that there is no certain evidence that it has any existence for the placental mammals other than the primates. Indeed it seems that the proverbial red rag is probably very little more effective as a visual stimulus to a bull than a dark cloth flapping in the moonlight would be to us, since experiments have shown that the red rag owes its peculiar excitatory quality to its movement rather than to its hue. On the other hand, there is good evidence for a sense of colour among birds, some reptiles, and in some groups of fishes; a colour sense may also be present in some amphibia. There is no doubt, however, that so far as reliable data are available, the occurrence of colour vision among the vertebrates as a whole is by no means universal. In making these generalizations it is perhaps necessary to emphasize that we are considering colour vision to be present only in those animals where there is well-substantiated evidence for its presence. This means that it has been clearly established by objective tests that such animals can distinguish objects by means of wave-length differences and not simply by brightness or shape. Unless these tests have actually been made, the data on the presence or absence of colour vision are for the most part valueless. Many of the animals which are capable of being trained, and many others which react by characteristic behaviour to the stimulus of light, have been examined for the presence of colour vision, and, as already indicated, the occurrence of this faculty is confined to certain groups. When it does occur, it appears in a somewhat similar form; and roughly the same wave-bands comprise the visible spectrum as in many animals which have no colour vision. There is, however, insufficient evidence in most cases to say whether the systems are always trichromatic and so may be presumed to depend on three independent pathways from eye to brain, each pathway having a different spectral sensitivity, as is the case in the normal man, or whether they may resemble some forms of human colour-blindness and depend on two pathways only. It is unlikely, owing to the manner in which nerve impulses are conducted, that any sort of colour vision can arise from stimulation of a retina possessing only one type of pathway to the brain. With two or more receptors, however, there are several possible variations.

How and why then has the process of evolution succeeded in producing colour vision in only certain particular groups of animals, and why are the vast majority of mammals apparently condemned to live in a world of greyness? These are questions for which a study of the physiology of vision linked with a study of the evolutionary process may help to provide the answers. In making the attempt it will be convenient to begin by a discussion of some of the salient points in the physiology of human colour vision in order to try to establish its probable structural basis.

In the normal human eye there are four distinct, though not rigidly separated, regions of the retina. The boundaries of these regions are neither sharp nor permanent and they differ to a certain extent according to the state of adaptation of the eye and to the size of the visual field used in their investigation. Nevertheless these four broad regions can be distinguished and they are found to differ both in structure and function; their properties are best described by reference to Table 1.

From this table it is evident that the human retina is uniform neither in structure nor behaviour, and it is therefore pertinent to inquire how far the observed structural differences may be responsible for the differences in function. By elucidating this problem, in which assistance may be obtained by comparisons with the eyes of other vertebrates, a more complete picture of the mechanism and evolution of colour vision as a whole may be obtainable.

The human eye, like that of nearly all vertebrates, is provided with two main classes of receptors, namely the rods and the cones. The rods, in man as in many species, are specialized for reception of light at low intensities and their neural connections are also involved in this specialization. There is, however, no logical reason why the possession of this property should necessarily eliminate them as possible participants in vision at ordinary levels of illumination. It is quite probable that their high sensitivity is, at least in part, achieved by summation effects occurring in the bipolar and ganglion-cell layers of the retina as well as by the increased sensitivity of the rods themselves. There is evidence to suggest that a human rod may itself be able to respond to a single quantum of light and that it is thus about as sensitive as it is possible

TABLE I

	Foveal centre 0′–30′	Macula lutea 30′–5°	Near periphery 5°–65°	Far periphery 65°–90°
Low-threshold rods	none	few	very numerous	numerous
High-threshold rods	?	?	?	probably numerous
Cones	very numerous 2 μ diameter 80 μ long	numerous	frequent	frequent 10 μ diameter 30 μ long
"Dark" cones	numerous	more numerous	scarce	very scarce
Midget bipolars	numerous*	numerous	a few	a few
Flat bipolars	numerous*	numerous	numerous	numerous
Mop bipolars	none	few	numerous	numerous
Large ganglion cells	none (?)	very few	frequent	very few
Small ganglion cells	numerous*	numerous	few	very few
Pigmentation	xanthophyll	xanthophyll	none	none
Max. scotopic sensitivity	555 mμ	507 mμ	507 mμ	507 mμ (?)
Dominant subjective colours in light adaptation	orange-red, blue-green			blue, yellow
in dark adaptation	violet, red	far red	far red	far red
Neutral point	575 mμ	none	none	500 mμ
Acuity	high	moderate	low	very low
Colour vision	dichromatic tritanopic	trichromatic	trichromatic	dichromatic deuteranopic

* These are all displaced laterally from the area which they serve.

for it to be. Several rods probably have to discharge simultaneously or respond within a given time and in a given area of retina before the ganglion cell with which they are connected receives a stimulus sufficiently great to make it discharge. In other words these ganglion cells rely on spatial summation. Similar calculations have been made from measurements of threshold energies for the fovea, where the receptors are at least predominantly, if not entirely cones, and where the threshold for white light is many times higher than it is more peripherally where rods preponderate. These calculations have indicated that individual cones may be almost if not quite as sensitive as individual rods. Because, however, rods are linked in large numbers to a single ganglion cell, which may allow their individual effects to be summated, their ability to transmit nerve impulses in the optic nerve may be considerably greater than that of the cones, for these connect up to ganglion cells on a much more individualistic basis which allows of far less spatial summation. That rods need not necessarily be only concerned with great sensitivity is shown by experiments on the eyes of guinea-pigs and cats which have made it clear that some ganglion cells connected only to rods, i.e. to elements activated by visual purple, have thresholds as high as that usually associated with cones. There is evidence also from entirely colour-blind men that similar "high threshold" rods may also be present in the human retina.

A large body of evidence indicates that rods and cones, or more accurately the cells which give rise to them, are two rather distinct and probably mutually antagonistic types of cells which are, at least potentially, always present in the retinae of vertebrates, and although rods are usually considered to be the more sensitive elements and are associated with night vision, this property may well depend just as much on the neural connections which rods make as on the high level of photosensitivity of the receptors themselves.

On the other hand, we nearly always find that it is the cones which are concentrated in those areas of the retina, e.g. the fovea in both man and birds, in which high visual acuity is found, and this correlation may again relate to the fact that cone connections seem always to approach the ideal of one ganglion cell to each cone. The respective neural connections, diffuse for rods and precise for cones, seem to be as characteristic of the two races of cells as are the connections of the two main subdivisions of the autonomic nervous system, wherein those of the sympathetic nervous system are ill-localized, while those of the para-sympathetic system are much more punctate.

However this may be, the eyes of both the most primitive and of the highest living vertebrates, show the presence of both rods and cones as distinct structural elements. There can thus be very little doubt that there must be fundamental differences between the two types of cells which produce these structures and that the particular outgrowth of the neural tube of the vertebrate embryo which is known as the optic vesicle, and from which the eyes of all vertebrates are derived, must contain cells which readily differentiate into two camps, namely rod-producers and cone-producers. This ability to divide into two opposing camps is also a property of other and, embryologically speaking, closely related neural tissues; neuroblasts may become cholinergic or non-cholinergic, or they may become member cells of the sympathetic or of the parasympathetic nervous systems.

Now, since the spectral sensitivity of rods is different from that of cones, there is already present in the eye of the most primitive vertebrate, as in that of man, a potential receptor mechanism for distinguishing wave-length differences as well as differences in light intensity. Such a mechanism by itself would indeed be imperfect and dichromatic, since it could only have two independently sensitive pathways. Colour confusions would inevitably arise in such eyes which would be of much the same kind as those which arise in the majority of human colour-blind subjects or when vision is confined to the dichromatic regions of the normal eye, i.e. the central fovea and the far periphery. Nevertheless it is theoretically possible for some degree of colour discrimination to be achieved by such a system. This is not meant to imply that all eyes which possess rods and cones must have colour vision, but merely that if other necessary developments occurred, both in the retina and in its central connections, it is at least possible for them to possess it.

Now it might with some force be argued that the extreme periphery of the human eye is its least specialized part, and therefore that its performance may give valuable clues as to the potentialities of other unspecialized or more primitive eyes. In the far periphery, rods and cones are demonstrably different from each other and, so far as visible structure is concerned, all members of each group appear to be identical. Both are present in large numbers but, in spite of this, visual acuity is very low, probably as a result of the poor development of the bipolar cell layer and of the very limited numbers of ganglion cells capable of providing separate fibres in the optic nerve, to say nothing of the central neural connections. Neither the rod system nor the cone system of the far periphery is so sensitive (as judged by the thresholds for red and blue) as it may become elsewhere in the retina and this relative insensitivity and low acuity combined with the presence of well-developed receptors suggests that the primitiveness lies mainly in the neural connections and in the central analytical system. The structural aspects of the extreme peripheral regions of the human retina are in many ways closely similar to those of the eyes of the selachians and of others of the more primitive fish. The retinae in these groups tend to have well-developed receptors but only limited numbers of cells in the other two retinal layers. In some ways therefore the evolution of eyes and of their performance among the vertebrates appears to centre more on the evolution of the neural mechanism than on the receptors themselves. In interpreting the behaviour of the far periphery of the human eye as a guide to that of eyes of more primitive animals like the fish mentioned, we must bear in mind that we have an unfair advantage over the animals possessing only the primitive retinal pattern, in that we are able to compare peripheral vision with that arising from the more efficient mechanisms located nearer the centre of the eye. Thus, by virtue of these comparisons and, of course because of our greater development of the integrating nervous system, our peripheral vision may be interpreted very differently from the way in which vision in a primitive eye with similar structure might be interpreted by its possessor. On the other hand, it might be considered that, since the far periphery of the human eye is a hangover from the past, its performance may also represent the primitive form of vision.

Whatever significance we may attach to its structure, the periphery of the human eye, under photopic conditions, is at least partially colour-blind and interprets colours in terms of yellows and blues with a neutral or white point in the blue-green region of the spectrum. This is precisely the sort of vision which one might expect from a mechanism having two types of receptor, e.g. rods and cones, if there were some device for recording whether, in general, rods were responding more than cones and thus perhaps giving a sensation of blue, or equally with cones and yielding no colour, or less than cones and giving a sensation of yellow. Now as the far periphery of the human eye becomes dark-adapted in dim light the rod mechanism becomes more sensitive; the blues and greens desaturate, so that eventually yellow and all colours on the blue side of it appear white, while those on the other side now give rise to a sensation of red. Although the actual mechanism which could produce these sensory changes is difficult to visualize and is almost certainly not as simple as the one indicated here, the changes themselves are not inconsistent with the idea that the relative performances of rods and cones may be playing the major role in the colour vision of the far periphery, and that it is essentially the interaction between these two groups of receptors which determines the hue. Thus it may be presumed that an eye built on the same general pattern as that found in the far periphery of the human eye, e.g. the eyes of primitive fishes, may well have the necessary mechanism in the retina whereby wave-length differences could be discriminated to an extent comparable with that attained by the human periphery. Once again this does not mean that the possessors of such primitive eyes do actually distinguish hues, for this must depend both on the presence of some neural elements capable of determining the differences between the responses of the rod and cone mechanisms and on the development of some central interpreting machinery. There are indications, from the behaviour of the human eye, that the rods or at any rate those pathways which originate in rods and which are responsible for the very high scotopic sensitivity are inhibited by cones, and that simultaneously with this inhibition they become capable of giving rise to a blue sensation. The following experiment illustrates this point. When an area of the dark-adapted retina is illuminated with light of any wave-length between violet and yellow and the intensity is such that only the rods and their high-sensitivity pathways are stimulated, the colour is interpreted as grey; but if an adjacent field is illuminated with light of any wave-length between yellow and red of such intensity that the colour is perceptible, i.e. so that cones are probably involved, then the first field darkens and a sensation of blue is aroused from it. The darkening suggests inhibition of the rod pathway and the development of hue suggests activation of a mechanism which measures the difference between the responses occurring in the two fields, i.e. between rods and cones, since the blue only appears when both fields are illuminated.

If we may judge anything about primitive eyes from the behaviour of the periphery of the human retina it would seem likely that a primitive eye built on the same general plan might at least attain to this same level of distinguishing between the wave-lengths at the two ends of the spectrum; furthermore, in the evolution of human colour vision the separation of blue from yellow, or "cold" colours from "warm" colours is perhaps the most primitive of psychological colour distinctions and it is the one which the far periphery can achieve. It is also the distinction made by the majority of the congenital colour-blind subjects. The sensation of white, which might equally be described as the fundamental sensation of light, may be presumed to arise under all those conditions when the eye is, for structural or functional reasons, unable to detect differences in responses among its receptors, i.e. in white light the responses from the two pathways may, for convenience, be regarded as equal since the eye cannot detect the difference between them.

Now, as compared with the extreme periphery, the central regions of the human eye have specialized in two main directions and parallel specializations can be inferred in many other animals. The foveal centre has specialized for high acuity and precision of form vision. It has a relatively high threshold, and those elements which elsewhere are responsible for great sensitivity are missing. The near periphery (say 2°–40° from the optic axis) on the other hand specializes in high sensitivity and sacrifices acuity. It is therefore interesting to see what effects these specializations may have on colour vision.

At the foveal centre (less than 1° from the optic axis) where acuity is highest and dark adaptation least, colour vision, during fixation at least, is relatively imperfect and dichromatic, as it is in the far periphery. This area differs from the far periphery in that it is relatively insensitive to blue, and certain well established colour confusions are made by it.

These differ from those made by the far periphery but are the same as those which have been described as characteristic of the rare form of colour-blindness known as tritanopia, an abnormality often associated with pathological changes in the peripheral retina and involving rods. In photopic conditions when the test field is surrounded by a light field, all colours are interpreted subjectively as some shade of either blue-green or orange-red (the common signal lights). In this way the foveal centre differs sharply from the far periphery which sees colours in terms of blue and yellow. Under scotopic conditions, the only colours which are seen by the central fovea at threshold level are violet and red. Intermediate spectral colours appear grey at the threshold. The foveal centre thus behaves as though it possessed only two independent pathways. Similar behaviour may also be found in other parts of the retina, though with less ease, and only if the fields are small enough and fixation so perfect that scanning movements are prevented. This probably indicates that whatever is responsible for the trichromatic character of normal vision requires conditions which stimulate receptors over a comparatively large field. In the fovea and elsewhere, when the fields are large enough, or when movement is allowed, vision becomes trichromatic under photopic conditions. As scotopic conditions are approached, hue discrimination diminishes and eventually when only the rods remain above threshold, vision becomes monochromatic, and only a sense of light remains.

It is safe to conclude therefore that at the foveal centre itself there are for all practical purposes only two types of elements activating different pathways and differing in spectral sensitivity. The third pathway contributes nothing, provided that fixation is maintained and it probably occurs far less frequently in the foveal centre than anywhere else. This conclusion is supported by observations on the eyes of dichromats who are deuteranopic or protanopic, i.e. subjects who are colour-blind and cannot distinguish readily between certain greens and reds. In at least some deuteranopes, i.e. in some so-called green-blinds, only one type of element is functional in the central fovea, and it is of interest to note that for such subjects all wave-lengths appear colourless when fixation is maintained. These elements have their maximum sensitivity at about 575 mμ, i.e. in the yellow region of the spectrum. There is also evidence that in protanopic (so-called red-blind) observers the foveal centre again behaves as an area of total colour-blindness, and in their case the maximum sensitivity lies at about 540 mμ, i.e. in the green. Structurally, the photosensitive elements in both cases are probably cones, but the possibility of the incorporation of rods in the receptor mechanism of the protanope is not excluded with certainty. No definite visibly distinct groups have so far been defined among the central elements of the normal fovea, nor is there any specific information about the histological structure of the foveal centre of such colour-blind subjects. The problem therefore lies in determining what are the elements which are responsible for foveal centres whose maximum sensitivities lie at 575 mμ and at 540 mμ, for there is quite good evidence that these two types of receptor are the same as those which are present together in the normal foveal centre, whose maximum sensitivity lies at about 555 mμ.

There are many species of animals which have good daylight vision and in whose eyes cones very heavily preponderate. In these animals maximum sensitivity appears to lie between 565mμ and of 575 mμ, and it is interesting to notice that a photosensitive pigment, iodopsin, has been extracted from such an eye (the chicken's eye) and found to have its maximum sensitivity in this region. There is thus no difficulty in believing that the deuteranope who has his maximum in the same region may rely on the same pigment, which may indeed be the cone pigment. Whether this will in the end turn out to be so is of course uncertain, but the evidence is at least suggestive. On the other hand no similar pigment, with maximum at 540 mμ, has as yet been isolated so that the sensitivity of the foveal centre of the protanope is not so easily explained. It may depend on an as yet unidentified pigment for there are several known photosensitive pigments, which seem to be variants on the parent substance, visual purple or rhodopsin, and which have been extracted from the retinae of various vertebrates, and there may well be more still to be unearthed. Alternatively it may depend on some mixture of known pigments, or conceivably on the combination of rods and cones on to a single pathway, though the evidence from certain experiments in differential adaptation is against this.

In a nutshell, human colour vision appears, at present, to be dependent on two pathways with maximum sensitivities at 540 mμ and 575 mμ, and on a third pathway which requires the stimulation of a larger area of retina than that required by the others and which makes its major contribution in the perception of blue. Cones are certainly involved and the evidence is suggestive that rods may be also.

In some birds there is no doubt that a definite subdivision has occurred among the cones, for often the cones can be seen to possess oil globules through which the light would have to pass in order to reach the sensitive segment and these globules may be coloured red, orange or yellow, while green ones have also been suspected in some species. Thus these species of birds could, with suitable neural connections, base a colour system either on rods and cones or they could use only the cones and still have three or even more pathways.

In man there is no evidence for such oil globules, but it is true that certain staining methods do show some cones, particularly in the central parts of the eye, to be somewhat different from the majority of their neighbours in their staining reactions and relationships with the pigment epithelium. In fact, in these preparations it is possible to separate the cones into two somewhat arbitrary groups on their staining characteristics, but there is no evidence as yet which will allow us to connect this tinctorial distinction with distinction of function.

The position is made more complicated than it might otherwise be because the sensitivity curves of the known photosensitive pigments, visual purple (rhodopsin), porphyropsin, iodopsin and the newly described visual red are all closely similar in shape though displaced by different distances along the spectrum, so that under some conditions it might be difficult to decide whether a neural pathway depends on a receptor with mixed pigments or on two receptors with different pigments.

The majority of animals seem to possess rods activated by visual purple (max. 507 mμ) and cones depending on a pigment (or pigments) with a maximum absorption at about 575 mμ. Some fish and perhaps a few other animals have porphyropsin (max. 530 mμ) in their rods, and also a cone pigment with maximum sensitivity at about 600 mμ. As already indicated, it is not inconceivable that the 540 mμ pathway in man might be the result of a rod, or visual purple receptor, and a cone (max. 575 mμ) both transmitting their effects on to flat bipolar cells which have been described as making contact with both rods and cones over most of the retina in the normal eye. As a possible support for this view it is interesting to note that in many teleost fishes, especially the more diurnal, in which colour vision has frequently been shown to be present, there exist the so-called double cones which seem to be combinations of two types of receptor and which may thus provide intermediate types of sensitivity.

Three different hypotheses could account for the basis of human colour vision as it is at present understood and these may be briefly considered:

1. Colour vision could be mediated by three types of cones, of which one pair would be effective in the foveal centre, and another pair in the far periphery. There is no histological evidence which speaks unequivocally in favour of this hypothesis.

2. Colour vision may have evolved as the result of the adaptation of the eye for other visual purposes. If we may regard the extreme periphery of the human eye as being still in a relatively primitive and undifferentiated form, the retinal connections there are such as to provide

a generalized light sense mediated by the combined efforts of rods and cones. From this a high-sensitivity pathway activated by rods, and perhaps partly inhibited under photopic conditions by cones, has begun to separate. If both function together in daylight conditions then the high sensitivity path and the mixed rod and cone path could provide the sort of vision which characterizes the far periphery in much the same way as was indicated on p. 269 where it was supposed that the effective paths might be mediated by rods or cones respectively. Nearer the centre of the eye the high-sensitivity pathway at first becomes more important, but in the very centre it entirely gives way to a specialization on the part of the cones towards greater visual acuity so that numerous pure cone pathways become established. In this region many of the cones discharge by way of the midget bipolar cells which appear themselves to have developed from the flat or cone bipolar cells, probably as a means of reducing the area of retina relaying on to each optic nerve fibre and thus of increasing visual acuity. These midget bipolar cells activated by cones only could thus, if certain other conditions were fulfilled, provide a pathway which would have a different spectral sensitivity from either the primitive mixed rod and cone pathway, or from the partially inhibited high-sensitivity rod pathway with its characteristic accumulation of visual purple or perhaps, under photopic conditions, of its breakdown products formed by the action of light.

3. The extreme periphery may show what can be achieved with regard to colour vision by the interaction of rods and cones only. Since this arrangement, depending as it would on two receptors only, could not provide a higher degree of colour sense than that found in dichromats, the cones in the rest of the retina may have further differentiated into two groups (perhaps those separable by staining) with spectral sensitivities differing because of some as yet unknown cause, so that three types of receptor emerge, two types of cones and the rods.

This analysis of the position and possibilities in man may now be used to assist in considering the problem of the occurrence of colour vision in the vertebrates as a whole where the same possibilities must necessarily prevail. How have the rod and cone systems, which seem to be the fundamental ingredients of the vertebrate retina, been used in different animals to provide a colour sense and why has this developed only in certain groups? On the basis of the analysis of the human mechanism, a trichromatic colour sense could result if the receptor layer of the retina provided one of the following combinations of receptors: (1) three types of cone, (2) two types of cones and one type of rod, and (3) one type of cone and two types of rods. There is as yet no evidence that colour vision ever occurs in the complete absence of cones, so that the fourth possibility of three types of rod can be eliminated, but any of the other three methods may be considered as possible, and there is evidence among birds alone that the first two have been used. Moreover among the amphibia the retina of the frog can be seen to contain two types of rods and two types of cones, and thus a potential basis for tetrachromatic vision, so long as their spectral sensitivities are different.

Now, as already stressed, the vertebrate eye always differentiates from the same modification of neural tube tissue, and the rods and cones develop from the layer corresponding to the ependymal layer of the neural tube so that their potentialities must be limited to those of this particular layer. In following the development of eyes in different species and groups, it is clear that within this framework the eye in each case becomes suited as best it can to the needs of the animal; and looking in the other direction, the limitations set in the way of modifications of the eye may determine the character of life that an animal may lead, e.g. the performance of its eye may well determine whether a given species hunts by day or night, or whether it preys on coloured butterflies or on minute high-flying diptera and the like.

In the most primitive vertebrates the eye is already structurally very well developed, as compared with many photosensitive structures in the invertebrates, but there is evidence that its performance may not be of a very high order as compared with that achieved among the birds or mammals. In primitive eyes the full sensitivity of the receptors themselves may not have developed. The manner in which the receptors and neural elements are linked together may not have sorted itself out as efficiently as in higher forms, and the number and central connections of the optic nerve fibres may limit performance. If we are permitted to judge from our own visual mechanism and its nervous connections the destination of the optic nerve fibres in many of the lower vertebrates is such that the eye may assist in orientating the animal and directing its movements without providing much in the way of a subjective image of the animal's environment. On the other hand, in those birds which hunt butterflies in districts where mimicry occurs among the butterflies it is difficult to believe that there is no subjective picture of the prey which they are hunting. It is also tempting to believe that hawks, in which visual acuity can be shown to reach a very high order of perfection, must have some very real appreciation of the retinal image as a whole. We can of course only speculate on such matters. The fact remains, however, that high visual acuity, a colour sense, the rapid appreciation of movement and even extreme sensitivity all demand complex neural mechanisms behind the necessary modifications of the receptors themselves, to which they must presumably be secondary, for it is unlikely that the central mechanisms for trichromatic colour vision, for example, could develop as such, before there was any suitable differentiation into three groups among the receptor cells themselves.

In considering these specializations for particular ways of life, two general principles must be recognized. First, where visual acuity is high it is nearly always the cone receptors which are specialized. Secondly, where sensitivity is high then the rods preponderate. There are, however, exceptions to both these principles, which is perhaps further proof, if such were needed, that rod and cone cells differ more fundamentally than in simply possessing different thresholds and pigments. Moreover, the cause of this bias of the receptors to their particular functions lies probably in the nature of the connections which the two groups of cells make with their corresponding optic nerve fibres. Animals with nocturnal or crepuscular habits are probably more assisted by possessing eyes with which they can distinguish vague shapes in the darkness than they would be by eyes which, though quite effective in daylight, allowed their prey to escape unobserved in the night. Those of us who walked about in the black-out during the war learnt to realize the value of high sensitivity even though acuity was bad. If the retina is to be packed with highly sensitive rods, the cones may have to be eliminated or greatly reduced, and this to all intents and purposes has occurred in many nocturnal species. At the other extreme, the development of high acuity over a wide field of view, and the development of two foveae, as in some birds, may lead to an almost complete monopoly of the available space in the retina by cones and thus make the eye relatively useless at night and send the owner to roost at sundown. The eye of man, like several others of his features, must be seen as a compromise, since it has good, though, by comparison with hawks, not the best visual acuity at its centre, and also high, though, again by comparison with cats, not the highest sensitivity in the periphery.

In considering the factors which have determined whether an animal should or should not possess colour vision, it is clear that "Nature" must have weighed up the value which the possession of a colour sense or of the ability to discriminate between the different wave-lengths would have as compared with increased visual acuity, increased sensitivity and other possible specializations of the visual mechanism. Colour vision would presumably only have survival value if it gave the animal which developed it some advantage over its fellows in finding food or mate, or in combating adverse conditions, or in the procreation or the rearing of young. Moreover any such advantage might well be offset by sacrifice of acuity or form vision or of sensitivity to low intensities of light.

Finally, colour vision is unlikely to be very advantageous unless combined with reasonably high visual acuity, which of course entails not only suitable retinal structure, but also a well developed mechanism of accommodation and image formation.

We do not know the exact manner in which birds distinguish colours but both the pigeon and the hawks can do so, and there are certain differences in their retinal structure which may illustrate the comparative values to be attached to colour vision and to other retinal functions. In pigeons the retinal receptors consist of four types. There are three types of cones, possessing respectively red, orange or yellow oil globules; and in spite of the fact that the bird rarely remains active at night there are a number of rods. The various receptors are fairly evenly distributed over the whole retina with only a poorly developed fovea in which rods are present. Assuming that their neural connections are adequate, these receptors could thus provide excellent colour vision over an extended field of view. The proportions of the cones with different coloured globules differ in different parts of the retina and this may lead to slightly different colour sensitivity in the different parts of the visual field. A somewhat similar arrangement is found in the crow. In view of the manner of life of the pigeon and the crow and the nature of their food this type of vision may well be better suited to their needs than very great visual acuity would be. On the other hand for swallows the catching of insects in mid-air, or for the buzzard and other members of the hawk tribe the spotting of small animals in open fields or the chasing of small birds through the air, would demand high acuity and a very keen perception of movement. It is therefore interesting to find that these birds have developed two foveae in each eye, one "looking" forward and by combining with that of the opposite eye giving stereoscopic vision, the other, lying on the optic axis of the eye and therefore "looking" out from the side of the head. Now in the foveae of the buzzard and the hawks the cones are apparently all of one kind. They are uniformly thin, and closely packed, and they all contain yellow oil globules. There are no rods in the fovea itself, but these make their appearance immediately extrafoveally even though, once again, the birds are not habitually nocturnal; further out towards the periphery, a third type of element appears in the form of cones with red oil globules. A possible interpretation of this arrangement may lie in the fact that the highest degree of acuity can be achieved in an area in which all the receptors have the same spectral sensitivity because then every difference in the response between receptors can be interpreted as a difference in form of the object observed. It is particularly true when there is also a device, in this case the yellow oil globules, which tends to eliminate the blurring effects of the uncorrected chromatic aberration of the eye. With two or three type of receptors in the fovea, each with a different spectral sensitivity, differences in response would depend partly on intensity differences and partly on wave-length differences, and this, especially if accompanied by an imperfect cerebral mechanism for hue analysis, would complicate the interpretation of the retinal image and might well act to the detriment of the bird in question. It is possible therefore that the buzzard sacrifices colour vision in its fovea in order to concentrate on form vision, and it contents itself with seeing colour only with large field or with peripheral vision. A close parallel to this is of course seen in the normal human eye where the fovea centralis has practically eliminated the "blue" receptor. Once again man has made a compromise, this time between hue discrimination and acuity since two types of receptor are retained, as they are in the parafoveal areas of the buzzard. These two types of receptor in the human fovea, however, have special properties. When working independently of the rest of the eye they cannot distinguish yellow from white and this, together with many other pieces of evidence strongly suggests that they each have the same sensitivity to yellow. Now it is normally the yellow rays from an average scene which are brought to a focus on the photoreceptor layer so that the receptors are all equally sensitive to the main stimulus which they receive. Virtually therefore the human foveal centre is an area in which under most ordinary conditions the receptors behave as a fairly uniform population and yet the area can also diagnose colour to such an extent that an occasional reference to slightly more peripheral receptors can produce complete colour discrimination. Thus the human eye is definitely an eye for all purposes and has not become extremely specialized in any one direction. At first sight it would appear that this hypothesis about visual acuity and a uniform population of receptors could be put to the test by reference to those colour-blind subjects in whom the fovea is monochromatic and in whom it has been shown that this area possesses but one type of receptor. It is thus disappointing to find that, in so far as they have been tested, these subjects actually have a somewhat lower visual acuity than do normal observers. However, until something more is known about the distribution and connections of the receptors which are present in the foveal centres of red-green-blind observers as compared with those in normal eyes this apparent contradiction must lose most of its force as an argument against the view that acuity may be better served by a uniform population of receptors. If the hypothesis is correct it means that, for the buzzard at least, colour discrimination is subsidiary to form discrimination and does not assist the animal to survive as much as does the ability to discern with accuracy the form and movement of external objects. A colour system can only develop and evolve if it gives definite advantages to its owner, or can, under certain limiting conditions, become a deciding factor between destruction or survival. Compared with its form, the colour of any given object varies so much from time to time with the nature of the light, etc., that perception of form must often be far more important than perception of hue. Moreover our own colour sense is so extremely fickle when subjected to abnormal situations, that, unless other systems are far better, too great a reliance on colour alone, without accompanying high acuity, would inevitably lead to serious errors of judgment. Furthermore, to such animals as the herbivora living on abundant vegetation, the senses of taste and smell, together with a keen sense of hearing and good night vision to detect the approach of possible enemies, are probably far more important than very sharp daylight vision, and the penalty for poorly developed sight is less likely to be starvation than in the case of those animals which have become accustomed to hunt small animals and insects. It is not surprising therefore that these animals have no colour vision, though they have good night vision. In those birds which prey on butterflies, an acute colour sense may well assist in separating the good from the bad, and this may also apply to the insect-eating lizards whose colour vision appears to depend entirely on cones, since rods seem to have been lost by most members of this group. In the case of hawks, on the other hand, seeking small relatively grey birds and mammals against a background of earth, we have seen that form vision may well be of more importance than colour and so force the colour sense into a subsidiary position. The other side to this picture is of course equally important, namely that particular trends in the development of eyes may determine which niche the animal shall occupy in its environment.

Another interesting facet of the colour vision problem in relation to evolution reflects the frequency with which the possession of colour vision by an animal is accompanied by elaborate courtship behaviour and very often by coloration differences between the sexes. It would almost appear that such behaviour, either by raising sexual activity and hence productivity, or for some other reason, puts a premium on colour vision. In some of the gaily coloured teleost fishes and in the more brightly coloured birds, sexual display reaches its highest levels. Moreover, in the more soberly coloured *Homo sapiens*, it would be unwise to deny that brightly coloured dresses and painted lips have no emotional significance. Is this connection between colour vision and sexual behaviour perhaps some refinement of the well established and more general connection between the amount of light falling on an animal and its sexual activity?

The process of the evolution of colour vision therefore, as seen among the vertebrates, depends first on the evolution of its essential structural basis; this means that it must always have been developed from essentially the same elements, namely those which can be derived from the optic vesicle. Thus, only certain types of mechanism are initially possible. Probably only certain pigments can be used, i.e. those which can be formed or accumulated by the cells of the optic vesicle. Within this framework there seem to be only a limited number of possible colour mechanisms available and all must have somewhat similar though not identical properties. The evidence is not yet adequate to decide whether all these possibilities have in fact been realized, but the variation in structure between the cones of different species and the presence of coloured oil droplets in some species which have colour vision and not in others suggest that colour vision does not always rest on exactly the same basis and so has probably been separately evolved several times; whenever it appears it is probably, owing to its necessary subordination to form vision, based on mechanisms which were first evolved for other purposes as, for example, for increased acuity or raised sensitivity. Sexual selection and the influence of colour on sexual behaviour may sometimes have been an important element in the evocation of a colour mechanism.

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Memory, Heredity and Information

The problems of biology are difficult because they mostly involve consideration of the influence on any situation of many events, including some that occurred a long time ago. Other branches of science have been able to obtain precise results by simplifying the situations they deal with so that the events of the more remote past can be neglected. A chemist can forecast the properties of his materials without, in general, troubling himself with their full history. In biology only limited success can be achieved by investigations of the reactions of organisms or their parts unless the more remote history is considered. This is obviously especially true in the study of evolution, of heredity and of learning processes. These three subjects are usually considered by completely different investigators, using different methods, but they have it in common that they deal with the influence of series of past events upon the present. They may therefore have something to gain from the methods used for the study of transfer and storage of information by engineers, who have devised methods for examining situations in which series of past events control present ones. These methods are based essentially upon statistical techniques of forecasting, but they deal with the subject in a way that is especially convenient for problems of human communication and perhaps also for biology.

In spite of much discussion of the application of information theory in biology there is still a considerable uncertainty about the status of the analogy and about its usefulness. Such doubts perhaps arise partly because the comparisons have often been made with insufficient examination of the premises and purposes of the engineer. The application of the analogy has therefore been vague, giving a method with little exactness or power. This is perhaps inevitable at first; the most useful ways of using a new analogy can be found only with practice. Already this analogy seems to provide effective ways of speaking about some of the most difficult biological problems, which have otherwise eluded solution. The numerous detailed facts that have been accumulated by such studies as those of genetics, biochemistry and neurology still fail to give us a general method by which we can speak about the control of living organization. Communication theory deals with the problem of transmission of control and there is therefore some reason to hope that it may be helpful in providing methods for studying the system of control that ensures homeostasis in living organisms. In fields such as the study of heredity and of memory we need a hypothesis to show us which facts and correlations are likely to be significant for study of the maintenance of organization. At present attention is directed to individual entities such as proteins, chromosomes, genes and neurons. It may be that through the use of information theory we can arrive at some means of exact treatment of the system of organization of which these units are but the parts.

Mathematicians and engineers of course themselves approach communication problems in various ways, not all necessarily of equal value for the biologist. In order to discover which if any of their techniques may be useful we may first examine the procedures used, trying to find what are the essential features of the situations for which they are appropriate. In most treatments communication theory deals with an entity called "information," which has the property of being "transmissible." The characteristics of information are variously defined. The original sources of the system of words are clearly to be found in the way in which we describe our relations with each other. "Communication is the transmission of information from mind to mind" (Gabor, 1950). "The fundamental problem of communication is that of reproducing at one point either exactly or approximately a message selected at another point" (Shannon, 1948). Clearly before we can usefully apply the techniques used by communication engineers we must investigate what is implied by such words as "information" and "message."

Shannon analyses a communication system as consisting of five parts, (1) "an information source which produces a message or sequence of messages to be transmitted to the receiving terminal," (2) "a transmitter which operates on the message in some way to produce a signal suitable for transmission over the channel," (3) "the channel . . . the medium used to transmit the signal from transmitter to receiver," (4) "the receiver ordinarily performs the inverse operation of that done by the transmitter, reconstructing the message from the signal," (5) "the destination is the person (or thing) for whom the message is intended." The problem for the biologist anxious to use the methods of communication theory is to identify analogues of these five elements in living systems.

In its most general form communication theory is concerned with the influence of the past and its transmission to the present, in fact with that process of forecasting which is the fundamental activity of all science. This type of treatment therefore merges with the general methods for the study of probability and forecasting. These are of course of great value in biology, but if we are to make full use of the specific methods of communication engineering we must keep before us their particular characteristics. Indeed the special interest of the method for the biologist is that it deals with the way one process influences another by remote control rather than directly. The first process (information source) sets up some change in the activity of a transmitter and hence in a transmission line. This change, arriving at the other end, after receipt, influences the process at the destination and changes its course. The change in the activity in the line therefore as it were represents the change in the source. This may be expressed in other words by saying that the events in the line represent a coded version of the original change, and that they are decoded by the receiver. We cannot investigate here the interesting question of what kind of similarity between the processes is implied in such a communication system. The nature of the processes in the transmitter and transmission line evidently governs the exactness with which events in the source determine events in the destination.

The information in a system may be defined as that feature of it which remains invariant under re-coding (Shannon). In practice the possibilities of re-coding from one system of transmission to another are limited. Different transmission systems have different possibilities as transmitters of information. The ways in which the actions of source and destination are related are obviously influenced by the nature of the transmission system available between them. Thus among different human races the language system provides codes whose differences determine the different patterns of social behaviour. The nature of the transmission line and its code thus has a powerful influence on the information that is conveyed.

We are concerned with finding ways in which the information conveyed along the line can be measured. In the treatment suggested by Shannon it will be observed that the information source "produces a message . . . to be transmitted. . . ." The treatment depends upon the concept of selecting one message from a set of possible messages. Any given information source is regarded as having a given set or number of messages among which one is chosen. The feature of any given system that is regarded as supplying information is thus its capacity to generate a message. Evidently the measure must be in terms of behaviour at the receiving end of the line. The only events in the line we can identify as conveying "information" are those that produce changes in the receiver. The general method of dealing with the problem is therefore to study the pattern of events in the receiving end of the system, and to correlate it with that in the channel.

In order to give the word "information" a precise meaning and to enable a measure of information to be defined, the message is regarded as one selected from a set of possible messages. If we want to measure the amount of information being produced by a process, it can be shown (Shannon) that a suitable measure can be defined that is a simple function of the probabilities of the different events taking place.

The study of the flow of information thus involves investigation of the variation in the frequency of the events that influence the transmitter and hence the channel. It is these variations that, by their influence on the receiver, provide the information that controls the responses. Variations occurring through irregular disturbances constitute the "noise," which disturbs the transmission of signals along any channel.

If we are to apply these methods in biology it is clear that we must use them approximately in the same way as the engineer does, or at least recognize when we are departing from his use. If we are to speak about transmission of information in any biological system we must make it clear what are the sources and destinations and what is the transmission line. Only if we do this shall we be able to use the analogy of coding and to speak of the amount of information in a system in satisfactory terms by investigating the correlation between the events in the sending, transmitting and receiving systems.

It is characteristic of populations of living organisms that they are complicated open systems that maintain a high level of organized activity. They resist the tendency to dissipate into their surroundings. The chief problem of general biology is to specify the means by which organisms thus remain alive. Applying the language of communication theory we may say that they do it by virtue of the property they have of receiving, storing and acting upon large amounts of information. They have the property of acquiring continually more and more information, suitably coded, and as evolution has proceeded the accumulated store enables the higher organisms to survive in more and more "improbable" conditions. The difference between organism and environment becomes greater and greater or, as it has been put before, the organisms enter more and more difficult environments (Young, 1938). The information collected provides the control that makes homeostasis possible. The value of this concept is that it enables us to specify, in principle quantitatively, the various sources that contribute to the homeostatic control, thus bringing together the facts of genetics, biochemistry and physiology.

The organism remains intact by its ability to follow changes in the environment, which may be regarded as the source of information. We may consider each individual as a machine that receives these changes, translates them into a coded version and transmits them through its system to effector agents. These decode the message and produce an appropriate action upon the environment, which is thus the destination. This transmission line is of course especially obvious in higher animals with their receptors, nervous systems and effectors, but simpler animals and plants do not differ in principle. The problem for biology is to specify the control system that enables the living machine to react in this way. We may do this by saying that the organism acts not as a simple transmission line but as a computor. In devising the appropriate reaction to each environmental change it calls upon what we may compare with a "memory" or "set of instructions" as to how it shall operate. This memory provides information from two sources, (1) that which has been transmitted to the organism from its ancestors, (2) that which has been acquired and stored during its lifetime.

We have therefore to study the flux of events in each sort of organism, to discover how they are related to change in the environment and how they produce changes in the latter. Certain features of this flux of change constitute the information that controls the performance of the whole. Since the "machine" is self-maintaining the special problem is how its instructions ensure correct responses. The problem obviously resolves itself largely into the study of the nature of these instructions stored in the memory of the organism. In a higher animal they are to be found partly in the genetic mechanism, partly in the memory of the nervous system.

We may regard the flow of events in the world around organisms as constituting a series of messages that are the instructions determining the course of the future. The organism selects certain among these messages and transmits them in code to its computing system. Here, with the aid of the stored information, forecasts are made of the probable course of events and the organism then makes appropriate actions anticipating the environmental changes. The individual organisms and populations that survive are those that make correct forecasts.

The value of this method of approach is that it shows the similarity between the system of computation employed in the memory of the individual and of the species. The mechanisms of natural selection and of the brain may each be said to compute the probability that a given set of circumstances has occurred before. The method of doing this is to take a large number of individuals, each carrying the coded record of a slightly different set of circumstances. It is then arranged that of this great number only those survive in which the set they have experienced is repeated. This process, sufficiently often repeated, provides the forecasting device that is required. Individual organisms that have experienced a variety of situations will exist and in any given situation the aggregate of individuals whose experience corresponds most closely with the present set of circumstances will survive. Similarly in the nervous system, there will be sets of nerve cells that have become associated as a result of previous situations and which will provide appropriate forecasts when these situations recur (Hebb, 1950; Hayek, 1952; Ashby, 1951). Sholl and Uttley (1953) have shown the requirements for machines that will compute the conditional probability of occurrence of sets of events in this way. It is possible therefore that we shall find ways of dealing with the fundamental general problem by a re-examination of the old comparison between heredity and memory, with the aid of the techniques of information theory. It is not to be expected that really powerful new methods will emerge until the technique can be applied by someone with a fully adequate knowledge of all the fields involved. All that we can do at present is to point out some of the characteristics of the systems of transmission of information used by the hereditary mechanism and by the nervous system. The comparison at least focuses attention on the necessity for devising means of speaking about the organization of the processes involved. By suggesting methods by which the information content of the processes could be measured it provides hypotheses for investigation.

We may say, then, that every population of organisms operates at each moment under the influence of three sources of information, controlling the course of future behaviour.

(1) There is the information provided by the events in the world around.
(2) There is the information received from ancestors.
(3) There is the information that each organism has acquired and stored during its lifetime.

To make this concept precise we must find how to measure the amount of information that is available from each source to different organisms.

INFORMATION RECEIVED FROM THE ENVIRONMENT

The capacity of the organism to receive information from the events occurring around it depends upon its ability to "react" to these changes. Such reactions are in the first place physical and chemical changes produced generally in the organism. Any environmental change may produce change in the organism, but the information of heredity ensures that certain especially reactive points are provided. For example plants have chlorophyll, which is activated by light, and animals have respiratory pigments. The organism thus selects the message to be transmitted.

The amount of information acquired from the environment could be measured if we could estimate the number of points at which external events influence the direction of change of metabolic processes. This would give a measure of the degree of responsiveness of the organism as the number of units of information received per second. The activities proceeding in the organism thus constitute a transmission line. They are influenced by changes in the environment and their variations produce changes in the "effector" agents, which in turn act upon the environment. No means have yet been devised for measuring the amount of information passing through an organism, but Haldane (1953) provides a general discussion of the problem. The principle of the method that might be used is to assess the number of alternative actions that the organism might perform in unit time. Such an assessment must ultimately be made in terms of the physical and chemical interchanges with the environment. Recognition of appropriate units throughout the body may not be so difficult as it might appear. They may be differently chosen for different purposes, bearing in mind that the purpose of isolating them is to allow correlation of changes within the organism that constitute the transmission line with environmental changes acting as a source.

A practical difficulty that immediately presents itself is the large number of transmission lines involved. This is characteristic of biological systems and seems to present a severe difficulty in the application of classical information theory, which has dealt mostly with transmission along relatively few lines. It is not yet clear exactly what form of treatment will allow us to make useful statements about the organization of events in a large number of parallel and interacting lines, such as are provided by the transmission system of the brain or the hereditary mechanism. However there is no reason to think that the problem could not be solved by appropriate extension of existing methods. The difficulty is to find ways of simplifying the situation sufficiently to allow of an exact treatment that shall yet describe the essential characteristics of the organization.

ADAPTATION AS STORAGE OF INFORMATION

The physico-chemical reactions between environment and organism leave a more or less permanent impression on the activities of the latter, and this constitutes a coded record or memory of the information received. As a result of this familiar "adaptation" every organism carries a memory of its immediate past, which serves as it were to forecast the future. If a plant has received relatively little water or an animal little oxygen it will be provided with relatively long roots or more haemoglobin.

THE INFORMATION RECEIVED BY HEREDITY

Events occur around populations of organisms and are received and coded by their influence upon genetic mechanisms. Selection ensures that the genes of a population include those items that have produced survival under the set of conditions (events) that the population has experienced. In this sense the genes are a code, which "stands for" certain features of environment. The hereditary message is the instruction to the various metabolic processes to proceed in such a manner as to ensure homeostasis. It is transmited along a large number of channels and in bisexual organisms the information in two lines comes together and interacts in each generation. We may say that the hereditary information is decoded in each generation by the process that goes on in development and throughout the life of the individual. The influence of heredity is felt of course not only during embryological development, but throughout every day of life, by control of the specific processes of synthesis and metabolism as they proceed.

In order to measure the amount of information that an organism receives by heredity we should have to estimate the number of events that are influenced to proceed in one way rather than another by the action of the inherited germ plasm. This is of course a very large number, it includes among other things all the acts of synthesis in which the composition of the inherited nucleo-proteins influences the direction of action. However, this number is in principle knowable. We could estimate the frequencies of events occurring in the inherited material and correlate these with changes going on in the various molecular species of the organism. This would provide a measure of the amount of hereditary information passing through the system. Discussion of the possibility of performing such a feat of measurement would lead us too far. Its difficulty should not be a deterrent. Some such calculation must be made if an exact general biochemistry is to emerge.

Estimation of the amount of hereditary information in this way is of course related to estimation of the number of genes. A "single gene difference" is the hereditary entity that produces a difference between two phenotypes. But "phenotype" is a concept that requires careful definition if it is to represent a metabolizing organism adequately. The total of gene differences among the individuals of a population includes all those inherited differences that determine distinct metabolic processes and this number can only be determined when we have an estimate of the latter. It is possible that current estimates of the "number of genes" in an individual (for example 14,000 in Drosophila) are considerably too low. However, a single difference in the inherited material often influences a number of different processes in the adult. It may be possible to use information theory in the development of genetics for study of the nature of the events in the transmission line provided by the chromosomes and cytoplasm (Kalmus, 1949). At present, in spite of all the advances of genetical science we know little of the code in which hereditary information is conveyed. Study of nucleo-protein metabolism begins to tell us about the rate of synthesis of particular features of the molecules of the nuclear material, and hence of what may be compared with the frequency characteristics and noise level of the transmission line.

For the purpose of comparison between the information of heredity and of neural memory we may notice some features of the control system of the evolutionary machine. The instruction is carried in a large number of separate channels. The activity differs slightly in each channel. At intervals the activity in the lines is allowed to interact and thus produces a new pattern of instruction. After decoding (development) this provides a new means of transmitting the information from the environment through the organism. Only if this transmission system is effective can it survive. Thus natural selection acts as a "filter," which destroys those signals in which the instruction provided by heredity is incongruous with that coming from the environment. The environment ensures that only those organisms which meet all its requirements regenerate the instruction. The essential features of the process seem to be, (1) A large number of channels containing similar but not identical instructions. (2) Combination from time to time of the information in two channels. (3) Interaction of the combined information with that provided by a transmitting source, the environment. (4) Regeneration of the information only in those channels where it is suitably congruous with that coming from the source.

By this means populations of organisms maintain a stable pattern of activity as long as the information provided by the environment remains constant. Change in the type may be produced either by change in the environment itself or, perhaps, by change in the sensitivity to environmental information on the part of the organism. The extent of change in this responsiveness produced by a given change in the environmental condition would give an estimate of the amount of information that is stored by "adaptive change."

INFORMATION PROVIDED BY THE NERVOUS SYSTEM

The nervous system constitutes a part of the body provided by heredity that is especially sensitive to environmental change. The results of its responses play a particularly important part, in higher animals, in regulating the pattern of action in such a way that the organism remains alive. We can analyse its activities by measuring the amount of information that it receives and transmits along its channels to other parts of the body. The transmission takes place by translating the change in the surrounding world into a code of nerve impulses, of whose characteristics something is known.

In simple nervous systems the method of receipt and coding is mainly determined by the instruction from heredity. The morphogenetic processes produce a simple pattern of neurons and nervous activities, so that a given environmental change always produces the same action. The receptor thus acts as a coder, converting the external event (say, a chemical or photic change) into impulses in a few or even in one nerve fibre, producing (say) avoidance responses by the animal. It is characteristic of the simpler nervous systems that they employ few and often rapidly conducting units. For example, in some tubiculous polychaete worms (*Myxicola*) the receptors of the tentacles send impulses mainly into a single vast syncytial nerve fibre, whose processes reach to all the longitudinal muscles (Nicol and Young, 1946, Nicol, 1948). To any environmental change there is a high probability that *Myxicola* will perform the single action of withdrawing into its tube. The encoding system, fixed by heredity, is able to receive and transmit only very little information. A wide variety of changes in the environment all produce the same message, namely a short sequence of nerve impulses in the giant nerve fibre. The animal can do few things, the probability of its giving the retraction response to any environmental change is high. Its nervous system transmits little information; on the other hand the noise level of the channel is low. Of course *Myxicola* can also perform some other actions besides retraction, but these need not concern us here.

The "reflex" systems of higher animals, for example those of the spinal cord, have similar characteristics. They are operated by relatively few fibres, and these are large. Thus the largest fibres in the mammalian nervous system are those concerned with the proprioceptor reflexes. The total amount of information conveyed by such systems is small. Under given conditions stretch of a muscle will produce a response that can be forecasted with a high degree of probability. The large size of the fibres provides the advantage of high conduction velocity. Each afferent fibre of reflex systems probably makes connection with a fixed and rather small number of internuncial and efferent neurons. The pathways are laid down largely as a result of heredity. Histologically this is reflected in the fact that synaptic contacts are made by means of definite terminal buttons. The probability that impulses in any one afferent fibre will produce a particular result is high; the pathways are correspondingly definite and the areas of particular synaptic contact are large. An extreme case of this is seen in the stellate ganglion of the squid (Young, 1939), where two pre-synaptic fibres control each post-synaptic one, and the areas of contact involved are very large. Bullock (1948) has shown that stimulation of the larger pre-synaptic fibre always produces a post-synaptic impulse. Unfortunately details of the effects of interplay between the two pre-synaptic fibres are not yet known. This provides a clear example of a low information channel, with limited variability of response, composed of few large fibres, with large areas of synaptic contact.

MEMORY IN THE NERVOUS SYSTEM

The nervous system of higher animals shows to a greater extent than any other part of the body the capacity for storing information that passes through it, by the process of "adaptation" that we call "learning." In spite of the specialization of the memory of the nervous system there is no reason to think that it differs fundamentally from the adaptive hypertrophy of other tissues (p. 287). This perhaps provides us with a first clue as to the nature of nervous memory—it is a persistent change in the metabolic activity of the nervous system, produced under the influence of the environment. Knowledge about the nature of nervous memory is at present very limited. It is not known whether the change involved in learning is of the nature of a change in the anatomical connections within the system or of the activity of the circuits present. The weakness of our methods for dealing with the subject is undoubtedly due largely to the difficulty of finding appropriate models that shall provide a language with which we can speak about these complicated processes. This weakness can only be overcome by attempting new comparisons in order to discover a language that will suggest fruitful hypothesis and observation.

The comparison of memory with heredity and of both with the storage and transmission of information by machines provides a useful way of approaching the problem. All memory systems may be said to depend on maintaining a particular state that can be made to influence transmission along a communication channel. The relationship between changes at the transmitting and receiving ends is influenced by the information stored in the channel. In the case of heredity the effect of the environment upon the living system is dependent upon the pattern of activity transmitted to the system by the genes. This pattern is maintained by transmission along many interacting channels. Similarly in the nervous system the nature of the response to a given "stimulus situation" depends upon the memory carried within the system, and the maintenance of this memory involves the presence of a very large number of channels. The parts of the nervous system that show power to learn have similar features in such different animals as insects, cephalopods and mammals. They all contain a large number of small nerve fibres. No method has been discovered for description of the complicated inter-relationship between the fibres in these higher nervous networks, but they seem to be arranged so as to allow for the impulses set up in any one pathway to interact with those in others (Young, 1951). The synaptic mechanisms involved, for example in the cerebral cortex, are less understood than those of the spinal cord, but they are probably such as to allow for a great amount of interaction between impulses in various pathways. They do not show specific patterns of connections and terminal buttons have not yet been found throughout them. Histologists are modestly inclined to believe that this is because their methods have been inadequate; it may be that definite synaptic terminal points will be ultimately revealed throughout the nervous system. We already know many cases, however, where nerve fibres influence other nerve cells by passing close to them or to their dendrites without ending (Young, 1952). It is possible, therefore, that in higher nerve centres whatever "endings" may be found they do not produce always and only response of a particular cell. Such synaptic systems do not involve large areas of close contact between single input fibres and the cells. Moreover the input fibres are connected with the cells at random. This is very clear in the superior frontal and vertical lobes of *Octopus*, where the ingoing bundles break up in such a way that two neighbouring fibres may be distributed to widely separated parts of the lobes. The cerebral cortex contains essentially similar arrangements. Sholl and Uttley (1953) have shown how with random connection of input channels and suitable identical units it is possible to design a machine for computing conditional probabilities.

A part of the nervous system in which learning occurs is therefore not one containing channels of high probability, fixed by heredity. It is characteristic of the reactions mediated by such systems that they are not forecastable with high probability for all members of a species, as are, for example, the withdrawal responses of *Myxicola* or a tendon reflex in man. We may express this by saying that the system of "coding" by which external changes set up internal ones is fixed not by heredity, as in lower parts of the nervous system, but as a result of the past history of the individual. The problem of the study of memory and the learning process is thus to investigate this code. We have seen that this is done by communication engineers by studying the variations in the events in the source, transmitting, conducting and receiving systems and then seeking for correlations between them.

We can begin in a very elementary way to do the same for the nervous system, although at present the attempt can be little more than an exercise. A considerable difficulty is introduced in the case of most higher organisms by the fact that the great number of effector agents makes it possible for the organism to perform a large number of different actions. We need not, however, deal with all of these actions. With suitably controlled experimental conditions we can limit ourselves to considering only the question of forecasting whether or not a particular action will be performed. In experiments with the octopus this can conveniently be done by investigating whether the animal leaves its home and makes an attack on presentation of a particular stimulus situation, say a crab or a white square at one metre distance (Boycott and Young, 1950).

It is characteristic of these animals that on first placing them in this situation no accurate forecast of their response is possible. Some octopuses will immediately attack either a crab or a large or small white square. Others will not attack any of these objects. Some will attack a crab or a small square but not a larger one. What the animal will do is determined by its particular past history, which of course we do not know.

Suppose, however, that the octopus has attacked when either a small (4 $cm.^2$) or large (8 $cm.^2$) plate has been shown, and is given food after the former, but a shock after the latter attack. We shall find that on subsequent presentation it will attack the smaller but not the larger square. Over the first few trials the probability of attack on the smaller square may not be very high and conversely there may be a number of attacks on the larger square. However, as the process of "training" proceeds the probability of "correct" reactions rapidly increases. The animal now has a pattern of behaviour in these situations, determined by the history of its immediate past. Since we know this we can forecast the behaviour. The information provided by the environment is now coded in such a way as to produce a positive response to one square but not to the other. The problem to be solved is how to correlate changes in the activity of the nervous system with these changes in the behaviour of the animal. The difference between the state of the nervous system of the untrained and the trained octopus constitutes the engram whose setting up and maintenance we wish to study. The method available is to look for other fields in which a similar change of state is known to occur, in order to see whether we can identify the significant features in the nervous system. It may be that although we cannot find any other sort of memory exactly analogous to the nervous one yet there are features of others that will give us hints.

Storage of information for subsequent transmission to other human beings is often ensured by the leaving of some coded deposit, as in a photograph, map or book. The essence of these is that the information transmitted by the source is stored by setting up a two-dimensioned display in space. The idea that the engram left by experience is some physical deposit in the brain has an attractive simplicity and is partly true, but it raises many difficulties. In its literal form it is contrary to all our knowledge of the dynamic nature of living activities. Even the memory of heredity is carried by cellular components that are in continual metabolic activity. However the adaptive changes that take place in tissues other than those of the nervous system involve a change in the physical composition of the reacting system. When a muscle contracts the processes that lead to the synthesis of muscle proteins are stimulated and the muscle fibre becomes larger. There is considerable reason to believe that conduction of impulses along nervous pathways also involves long-lasting changes of metabolism (see Young, 1952). These may be considered to be processes of growth and they may well produce changes of size of fibres and dendrites, and hence of degree of influence of one neuron upon another. These changes, even if they were very small, would alter the probability of conduction along particular pathways in the higher nervous centres, if synaptic contacts there are less definite than are those of, say, an anterior horn cell.

It is therefore not unreasonable to expect to find some change in the spatial dimensions of the reacting material correlated with the change in behaviour during learning. No such change has hitherto been detected, or indeed looked for seriously and further discussion is fruitless at present.

In an alternative type of storage, involved in many calculating machines, the information is carried by specific variations in a time series. The high speed computing machines use systems whereby large series of events are coded so that they are represented by their positions in a time series that is repeatedly scanned at short intervals. This is the basis of memory systems composed of conduction along columns of mercury. It is very unlikely that the memory system of an animal such as an octopus involves coding of the information provided by, say, a 4 cm.^{2} plate exactly in this way and we have no information as to the existence of a scanning device such as would be necessary. Octopuses make eye-movements, but there is no evidence that these take place at the necessary speed. Eye movements are not necessary for the recognition of shapes by man (Barlow, 1952). The whole conception of carrying a large amount of information in a single channel is alien to the working of the nervous system, where each unit operates with a low degree of precision. Instead we find that where behaviour is controlled by past history, that is to say where large amounts of information are stored, the nervous system makes use of a large number of channels and moreover there is provision for interaction between these.

This suggests that an essential feature of the memory system is a display in space with an increase in the number of dimensions used in the representation and with the time dimension possibly of less importance. In this sense the analogy of the photograph, printed book or map has value. In looking for the coded version of the change transmitted from the outside world we may well look for characteristic states distributed in space within the nervous system. This does not mean of course that we need neglect altogether the analogy of a self-re-exciting system such as that provided by memories depending on a display in time. The parts of the nervous system involved often have the possibility of the setting up of self-re-exciting circuits, for example in the cerebral cortex or in the vertical lobe system of cephalopods. Pringle (1951) has discussed the possibility that learning consists in the setting up of patterns of synchronization within a population of linked oscillators. Overlapping fields of input axons and dendrites are a feature of the cerebral cortex and the octopus learning system. There are abundant circuits that could provide closed loops, with shared neurons as the means of synchronization.

The analogies so far examined have suggested that we should look for changes in the transmission through the nervous system to correlate with learning by looking for (1) structural differences between different parts; (2) changes in metabolism; (3) changes in dimension; (4) perhaps by looking for a change in some system of self-re-excitation and regeneration. The difficulty is that so far we have not been able to find an example of an instruction of comparable complexity conveyed in any of these ways. We may perhaps find an answer by combining these analogies with that of the memory system of heredity. Here also an instruction is preserved by transmission through many interacting channels, with regeneration at intervals after passing through a filter provided by comparison with the environment (p. 289).

Unfortunately we do not know what different processes are set up in the optic lobes of an octopus by white plates of different sizes. Taking our clues from what has been said already we may suppose that they involve anatomically different sets of neurons, in fact that there are different displays in space corresponding to each plate (see Hebb, 1949;

Hayek, 1952). A plausible hypothesis would be that the larger plate excites activity of the optic lobe to a greater depth than the smaller one, but it is not necessary that the different "cell assemblies" (in Hebb's term) be thus crudely separated in space, each could consist of cells widely scattered through the optic lobe system. Suppose that any stimulus so alters the balance of activity within the nervous system as to initiate an attack. If the attack provides food, the probability that it will be repeated is increased; if it provides a shock, that probability will be decreased. Assuming that partly different sets of cells are involved, how are we to try to identify the change that has made them produce different effects? The clues available are not many, but they provide something to work on. The optic lobes have self-re-exciting connections with the superior frontal and vertical lobes and removal of the latter produces erasure of the memory (Boycott and Young, 1950). It may reasonably be assumed then that the process which has become different in the two sets of cells is some form of self-re-excitation. It has often been objected that specific memories cannot depend on such activities since they are not abolished by anesthesia. This is also the case in octopus, whose memory is disturbed but not abolished by urethane. However, there are many rhythmic processes that are profoundly modified by anesthesia and yet recover. For example, when urethane is administered to an octopus the heart beat is greatly modified and nearly stops, but not quite. Ten minutes later the circulation is normal; is it surprising that the memory circulation is also restored? There are endless similar examples of the modifications that metabolism undergoes and yet recovers its "normal" pattern. We should expect that a memory depending on cyclical activity would only be wholly erased by anesthetic or other action so prolonged that the animal is killed. It may be said that this implies that the memory consists of some other (metabolic or structural) features and not essentially of self-re-exciting chains, and we have already considered it highly probable that such metabolic changes exist. The change involved in memory is a change of the activity of a complicated system and it is hard to say whether its characteristics lie in its "composition" or in its "activity." The answer will be found only when we succeed in finding variations in the nervous system that correlate with those in behaviour and can thus be identified as providing the code in which the memory is carried.

A further line of evidence about the nature of the different processes that provide the information of neural memory comes from the study of the conditions of their survival and of the process of forgetting. If an octopus is shown squares of 4 and 8 cm., receiving food when it attacks the former, but a shock from the latter it will thereafter continue to attack the smaller square but remain at home when the larger is shown. For some hours after receiving a shock the probability of attack on the large plate is low. But if this plate is shown later it will ultimately be attacked, usually after about three days. By a series of experiments we can estimate the probability of such an attack at a given time after the shock has been received. The "memory" of the previous shock thus becomes erased; whatever difference there was between the processes aroused by exhibition of the two plates has now disappeared. Further experiments show that, as in our own familiar memories, the duration depends on the frequency of presentation, *whether or not the positive or negative reward is given.* Thus an octopus that has not seen for four days a white plate and crab from which it had received a shock is likely to attack it. But by showing the plate and crab together every day the memory can be prolonged for eleven days or more.

If comparison with the environmental situation thus sharpens the memory engram it may well be that the process of retention itself consists of a continual re-comparison of a process presented in a self-re-exciting system. Here the analogy of the memory of heredity may again help us, although it is difficult to produce a precise picture. We have supposed the information provided by, say, an 8 $cm.^2$ plate and a shock to be coded by the production of a particular form of activity in a set of cells in the optic lobes. These perhaps excite a wide range of cells in the superior frontal and vertical system, which again fire back into the optic lobe. The impulses may reach to all parts of the latter, but only when they reach the previously excited region do they have any effect. Here they find the remains of the previous process and re-generate it and the whole cycle proceeds over again.

This is almost as far as we can go in suggesting a means of examining the change that constitutes neural memory. But it may be helpful to press a little further the comparison with the process of heredity. In both cases the environment produces changes in the actions of a population—of nerve cells in the one case, of whole organisms in the other. Those processes which "fit" the changes in the environment survive and it is they which propagate and regenerate further activity. This does not yet enable us to identify the processes in detail in the nervous system, but it does suggest that the methods used for study of survival among populations might be useful (Pringle, 1951).

Our problem is to find those processes in the nervous system the variation of whose activity constitutes the instruction to behave in one way rather than another. Evidence suggests that the significant variables are likely to be distributed in space through the nervous system. They may involve changes of metabolism of long-lasting nature, but these are probably maintained by cycles of nervous activity. Most difficult of all to grasp is the fact that the specific features reside in the behaviour of populations of transmission lines and in their interaction.

It may seem that such vague statements about the processes do not warrant any great optimism that the methods of communication theory will solve the problems of neural memory. The applications are admittedly inexact at present. They do, however, seem to allow at least some grasp of a problem that has certainly not yielded to other methods. Most important of all, they provide a language that allows correlation of the behavioural changes of learning with changes in the nervous system. The absence of such correlation is an outstanding lack in current physiological and psychological treatments. A precisely parallel lack is felt when trying to speak exactly about the alterations in living organization that take place during evolution, and when seeking to correlate the changes in the pattern of activity of the organism with the changes in the genotype of the population which controls them. Information theory provides a technique that enables just this sort of correlation to be made. By using the analogy of transmission along communication lines we may find means of assessing in one system of language all the influences that go to the maintenance of homeostasis. By treating all these influences as sources of "information" we can bring together the knowledge derived from many different fields of biology. We can say that the organism is instructed by the information it receives from heredity, from its environment and from whatever memory store it has built up during its lifetime. We can express our knowledge about events in any part of the organism in terms of the probability that they will happen. By applying the analogy of transmission of information along channels we can then study the correlations between different processes and hence make forecasts about one from knowledge about another. If the analogies of information theory are a help towards doing this they assist in building a general science of biology that shall show exactly how each population maintains its balance and evolves.

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S. ZUCKERMAN

Correlation of Change in the Evolution of Higher Primates

INTRODUCTION

All students of human evolution believe that man belongs to the mammalian order of Primates, and that he evolved from some group of non-human Primates. Most would also affirm that he is an Old World or catarrhine Primate, and that his descent was either from the stock from which all the Old World monkeys and apes sprang, or from the one which gave rise to the extant (and extinct) apes. Even the few who would not concede this measure of common origin, and who contend that the *Hominidae* began evolving independently of other catarrhine Primates, from the very base of the Primate stem, would subscribe to the view that while man possesses a number of specialized characteristics, of the kind regarded by Wood Jones (1948) as unique "hallmarks of mankind," there is a remarkable range of anatomical resemblances between all Old World Primates that can be due only to parallel evolution.

Since there is this wide area of agreement, based on a considerable body of anatomical and palaeontological knowledge, and since no serious student believes that man is derived from any of the existing apes or monkeys, or from any of their immediate phylogenetic forbears, it is of interest to ask what more is likely to be discovered about man's descent. Two developments seem possible. In the first place, we might expect to be able to retrace the actual morphological steps taken by man in his evolution—by, for example, the discovery of an indisputable series of "missing links" in a fossil lineage. Secondly, we might one day succeed in elucidating the circumstances in which man's evolution actually occurred. Unfortunately, both of these issues are to-day clouded by great uncertainty. And because we know little about the genetic changes and selective forces to which man was subjected in his prehistoric past, the second is almost limited to inferences derived from general evolutionary doctrine. The problem that is most alive at the moment in discussions of human evolution is therefore the first.

To describe it as alive is not, however, to imply that it shows many signs of co-ordinated growth. On the positive side we have the fact that the number of fragments of fossil hominoid bones that have been described, although relatively small, has increased fairly rapidly in the past thirty years. Against this we have to reckon that the evaluation of most of these remains has been embroiled in much controversy. Here the fundamental difficulty has been that in the great majority of cases the descriptions of the specimens that have been provided by their discoverers have been so turned as to indicate that the fossils in question have some special place or significance in the line of direct human descent, as opposed to that of the family of apes. It is so unlikely that they could all enjoy this distinction that, in the circumstances, an outside observer might well imagine that an enterprising anatomist would find little difficulty in substantiating a claim that an artificially fossilized skeletal fragment of any one of the living great apes had a greater relevance to the story of Man's evolution than to that of the skeleton of which it was a part.

Over and above this, it has to be admitted that in spite of the increase in the number of fossils available for study, there is a surprising lack of novelty about the conclusions regarding human origins to which their investigation leads. Broadly speaking, almost all the material discovered in the past thirty years has been used to illustrate the thesis that the *Hominidae*, as represented by Man; the *Ponginae*, comprising the existing apes; and the fossil hominoids assigned to the *Dryopithecinae* and the *Australopithecinae* (both of which in Simpson's (1945) scheme are subfamilies, with the *Ponginae*, of the family *Pongidae*), are part of some common hominoid stock, and that the human line sprang from a part of it in which the so-called "brachiating" specializations of the modern arboreal and semi-arboreal great apes had not yet developed, or had not fully developed. Some students have gone further and do not find the fossil evidence incompatible with the thesis that man evolved from a stock of simians which had already become specialized as brachiators, i.e. animals which were able to swing from branch to branch in the trees (e.g. Gregory, 1949; Washburn, 1951).

All this, however, was said about human evolution many years ago, before there had been any serious discussion about, for instance, the evolutionary status of the *Australopithecinae*. And as Straus (1949) has shown, most of this picture of evolution can be deduced from comparisons of the anatomy of existing Primates, and without referring at all to the palaeontological evidence. Moreover, none of the more recent fossil material provides any specific information about the time at which the independent evolution of the *Hominidae* began. Thirty years ago it was reasonable to infer from the available evidence that man had separated from the main hominoid stream, and had begun his independent evolution, as far back as the Oligocene (Osborn, 1927; Zuckerman, 1933). The picture hardly seems to be changed by the much larger amount of fossil evidence that is now available (see Straus, 1949).

Diagnostic hominid features

It will no doubt be argued that while these general observations are valid, the fact remains that the discovery in recent years of fossil Primate material now assigned to the *Australopithecinae* and *Dryopithecinae* provides them with far greater substance than could be extracted from the previous anatomical, physiological and palaeontological evidence. From the point of view of scientific method and logic, it is questionable whether this is so.

Views on phylogeny are never more than inferences, drawn in the light of the geological time-scale, that are based on an assessment of the resemblances and differences between organisms, living and extinct. In the case of primate evolution the inferences are sometimes very insecurely based because of inadequacies of the evidence—as must have been the case, for example, when a fossil tooth now recognized as that of a peccary was assigned to a Primate genus of its own called *Hesperopithecus*, which was supposed to resemble the human type more than any known ape (Gregory and Hellman, 1923). But whatever the inferences, in the final analysis it is the anatomical evidence which counts, whether it relates to existing or extinct types. No single part of it is given greater factual substance, merely by the frequent repetition of some phylogenetic idea which it is held to support.

The lack of accepted criteria by which to judge the hominid nature, or otherwise, of "borderline" features in bones makes the whole position very difficult. For this reason it is every bit as justifiable for Wood Jones to emphasize the lack of a premaxillary suture in man, and its presence in the *Australopithecinae*, as implying the absence of a close evolutionary connection between the two, as it is for others to illustrate an opposite view by reference to certain Australopithecine dental features. And if one turns from isolated characters to what Le Gros Clark (1950) calls a "total morphological pattern which is presented by an assemblage of features in a particular combination," it is almost always possible to derive from the same anatomical material patterns pointing to different conclusions—for example, one set of characters in a fossil bone suggestive of a hominid, and another of a pongid affinity. The simple fact is that there should be no trouble in diagnosing what bones are manifestly human and what are clearly ape; whereas considerable difficulties arise when efforts are made to define hominid characters, and to assess their phyletic significance, in fossil fragments which, in the bulk of their features, are otherwise simian. As matters rest at present, no fossil Primates which would be universally regarded as belonging to the Hominidae have been found earlier than the middle Pleistocene—the period of the Swanscombe skull in England (Marston, 1950) and of the genus *Pithecanthropus* in the Far East (according to Hooijer (1951) Pekin Man and early Java Man are "neither lowermost nor late Pleistocene"). At the same time, fossils which are manifestly simian occur in all geological formations as far back as the early Miocene. The apparent hiatus in man's evolutionary history between the early Miocene and the earlier part of the middle Pleistocene has so far been filled, not by the hard facts one would prefer, but mainly by speculation.

Nevertheless, there is no difficulty about defining the major overt features in which man differs from all other Old World or catarrhine Primates. Man is a big-brained Primate with the power of articulate speech. He walks erect and uses his hands—emancipated from the task of carrying his body—to work with artificially-fashioned tools. His teeth, and correspondingly his face, are small relative to those of the apes, and he is omnivorous as opposed to being predominantly frugivorous. These are the essential physical qualities which distinguish him from the ape, whose capacity for speech is confined to the utterance of sounds the connotation of which is purely emotive, and whose very limited ability to use "permanent" tools, as demonstrated in experimental studies, is probably never manifested in the wild.

If material signs of these essential evolutionary changes were to be sought in fossil remains, attention would have to be directed to (1) the development of a brain of human shape and proportions; (2) a decrease in the size of the teeth and of the face, with the associated changes in the curvature of the dental arcade; (3) evidences of an upright posture, with the appropriate dimensional relations of limbs and trunk. This three-fold pattern of physical change is necessarily presupposed by the belief that man is descended from a non-human Primate—however many other specifically hominid features of a less obvious kind may also have evolved in the process.

In this article I propose to examine some of the evidence that has been put forward to support the proposition that the tripartite pattern of major change, or a significant piece of it, is manifested by the fossil Primates now assigned to the *Australopithecinae*. My discussion will deliberately be kept to general issues only, and will focus predominantly on the question of the relevance of cranial features to the assessment of changes in the posture of the body.

THE BRAIN

If a fossil skull were discovered which provided an endocranial cast of the size and shape similar to those obtained from known human skulls, it would be justifiable to infer that the specimen had once enclosed a hominid brain. Such a possibility does not seem to arise in the case of any of the Australopithecine remains described so far.

Those specimens which permit of reasonably accurate estimates of endocranial volume do not depart from the range of size met with in the great apes. This had been clearly demonstrated by Ashton (1950) who, in a comparison of published figures for four specimens of *Plesianthropus transvaalensis*, and for one specimen assigned to each of the species *Paranthropus robustus*, *Australopithecus africanus*, and *Australopithecus prometheus*, found that whereas the endocranial volumes of most of these extinct animals fall easily into the range for the gorilla, all are significantly smaller than the endocranial volume in the extinct hominid genus *Pithecanthropus*. Suggestions have been put forward by Broom and Robinson (1950a) that some specimens, particularly from the Swartkrans deposit, had cranial capacities of the order of 800 to 1,000 cc., and that they had brains as large as those "found in some other creatures which have exhibited typically human behaviour" (Robinson, 1950). These estimates appear, however, to be almost in the nature of guesses, as are also suggestions that the Australopithecines may have had higher relative brain-weights than, say, chimpanzees. They cannot be properly evaluated until they have been substantiated, and until some justification is provided for assuming that because the relatively large-brained Pekin man, *Pithecanthropus pekinensis*, made fires and used crude tools, so too did the individual assigned to the Javanese hominid species *Pithecanthropus erectus*, and whom we know only from a fragment of calvarium whose endocranial capacity is estimated to have been about 750 cc.

In their general shape the endocranial casts of the *Australopithecinae* also do not appear to diverge in any material way from existing apes, nor do their surface markings provide any reason for supposing that there were any differences from the apes in the fissural pattern of the brains of these creatures—regardless of claims to the contrary by Broom and Schepers (1946) and by Broom, Robinson and Schepers (1950). This view is securely based on the results of several studies, all of which have shown that that there is very little correlation between the fissures and gyri of the brain and the markings on related endocranial casts (e.g. man:

Symington, 1916; Packer, 1949; Hirschler, 1942; Connolly, 1950; Apes: Le Gros Clark, Cooper and Zuckerman, 1936; Weidenreich, 1936; Connolly, 1950). Connolly (1950), who is the last to have written on the subject, and who has studied both human and ape material, sums up the situation, with respect to the human brain, in words which should discourage all but the most imaginative from attempts to find the mark of the human mind in the impressions of an endocast. "Information," he puts it very simply, "may occasionally be gleaned from endocranial casts with regard to the fissures of the brain." His studies showed that the surface markings of the human brain are most likely to be reproduced on an endocranial cast in young individuals between the ages of 12 and 17 years, and that in the adult the vault and much of the rest of the cast is as a rule smooth. In his studies of apes he found that only in the gibbon did the markings of the endocast follow at all closely the convolutionary pattern of the brain. Correspondence between the two was very much less in the orang-utan, and very slight in the gorilla and chimpanzee.

In spite of this discouraging background, Schepers (Broom and Schepers, 1946; Broom, Robinson and Schepers, 1950), has used the casts to derive cyto-architectural maps of the actual brains of the fossils —forgetting the well-known observation that the relation of sulci to cortical areas is very variable between one brain and the next. And overlooking the fact that the functional relations of different cyto-architectural features of the greater part of the brain surface are little, if at all, understood, he has also speculated without restraint about the human character of the brains, and about the mental life of the *Australopithecinae*.

Weidenreich (1948) has underlined the tenuous nature of these claims (as also has Connolly). He quotes Scheper's statement that the area around the sylvian fissure, which in man forms "the neural basis for vocal and manual dexterity alike," is well developed in *Australopithecus*. From this Schepers infers that the Australopithecines "must have been virtually true human beings, no matter how simian their external appearance may have remained." Here, as Weidenreich indicates, we have the complete *reductio ad absurdum*. The *Australopithecinae* must have been hominids even if their morphology reveals them as apes.

Like Dart (1949a), in his turn, Schepers is, however, well advised to seek for signs—whatever their nature—that the *Australopithecinae* both used speech and fashioned tools. Man's evolution has not been solely endosomatic. It has also been exosomatic, to use terms coined by Lotka to differentiate between the evolution (*a*) of organs which are material parts of the individual, and (*b*) of extensions of the individual in the form of artificially-fashioned instruments or tools. The distinction between these two kinds of evolution is well worth emphasizing because, as Medawar (1951) rightly points out, it helps to correct "the belief that man's fine brain is *sufficient* cause and evidence of his superlative biological status." What has conferred fitness in the long selective process through which man has evolved has been largely the uses to which he has put his brain in fashioning tools and in altering his environment. Once we leave the field of speculation, however, there is no reason to believe that the *Australopithecinae* did possess human brains, or that they used them to determine a human exosomatic evolution. As scientists, therefore, we have to dismiss as groundless such arguments about the hominid status of these creatures as have been based upon the internal conformation of the cranial cavity. The cytoarchitectural maps of the Australopithecines could well be allowed to fade into the limbo already haunted by the ghost of the "hippocampus minor" with which Owen, nearly one hundred years ago, endowed the human brain as a unique possession, ignorant, alas, of the fact that it was already possessed by all mammals (Elliot Smith, 1927).

THE JAWS AND FACE

The fact that the *Australopithecinae* had the brains of apes, which is the safest inference we can make from the facts now available, does not, however, preclude the possibility that they are "missing links" in our own evolutionary lineage, or, as Le Gros Clark (1949) has suggested, the "little modified survivors of such an ancestral stock." For as students of human evolution have always realized—even if only as speculation—man may not have evolved in an orderly way, all bodily features becoming less monkey- or ape-like, and more human, in a regular gradation. The big brain may have come after the upright attitude, or it may have been the other way round. On the same plane of speculation, we may equally suppose that the changes in different bodily systems may not only have been out of phase with one another, but also very gradual, so that at one evolutionary stage the "proto-men" may have been more like apes than human beings. There is, in fact, only one condition that we must insist on when attempting to unravel man's evolution—namely, that at all stages of his emergence "man" was adapted, or was able to adapt, to his environment, whatever it happened to be. If we suppose otherwise, we deny ourselves any opportunity we might otherwise have of explaining human survival within the framework of evolutionary doctrine.

It is unnecessary here to enter into any detail about the relative size of the teeth and face of the *Australopithecinae*. For whatever qualitative differences there may be between certain of their dental features and the corresponding ones of existing apes, it is a fact that with the exception of their incisors and canines, the size and general shape of the jaws and teeth of these animals were very much more like those of the living apes than like acknowledged members of the *Hominidae*, either living or extinct (Ashton and Zuckerman, 1952a; Zuckerman, 1952). There is, indeed, no question which the Australopithecine skull resembles when placed side by side with specimens of human and living ape skulls. It is the ape—so much so that only detailed and close scrutiny can reveal any differences between them. In saying this, no more is being stated here than has been admitted by Le Gros Clark (1950) and Gregory (1949), both staunch adherents of the view that the *Australopithecinae* are phylogenetically more closely related to man than the apes, and both of whom describe the jaws of these animals as massive and projecting (see Figs. 1 and 2).

The jaws and face of the *Australopithecinae*, like the brain, thus provide no obvious sign of the major changes in the evolutionary transformation of some monkey-like creature to manhood. What then of the beast's posture?

POSTURE

Here we are on ground that is covered both by conflicting statement and uncertain argument. To appreciate the position, we need to retrace our steps.

The first Australopithecine fossil to be discovered was the Taungs skull, of which Dart gave a preliminary description in 1925, and which he assigned to the genus *Australopithecus*. It was followed in 1936 by part of another skull, which was afterwards referred to a new genus *Plesianthropus* (Broom, 1936), to which has since been relegated a rich array of other specimens; and then by other remains, for which a third genus *Paranthropus* was defined. In 1938 the lower end of a humerus and a fragment of ulna, both referred to the genus *Paranthropus*, and of the lower end of a femur, which was assigned to *Plesianthropus*, were described by Broom (1938a), and since then many post-cranial fragments, including specimens of three innominate bones, have been discovered. Of the three innominate bones so far described, one has been referred to the genus *Australopithecus*, one to *Plesianthropus* and one to *Paranthropus*.

It has been argued by many writers that the *Australopithecinae* were creatures which walked erect like man—in Le Gros Clark's words (1949): "that these fossil creatures were equipped with limbs rather similar to those of Man, and quite distinct from those characteristic of modern apes" . . . and that they "were capable of standing and walking approximately in human fashion." This contention was first put forward

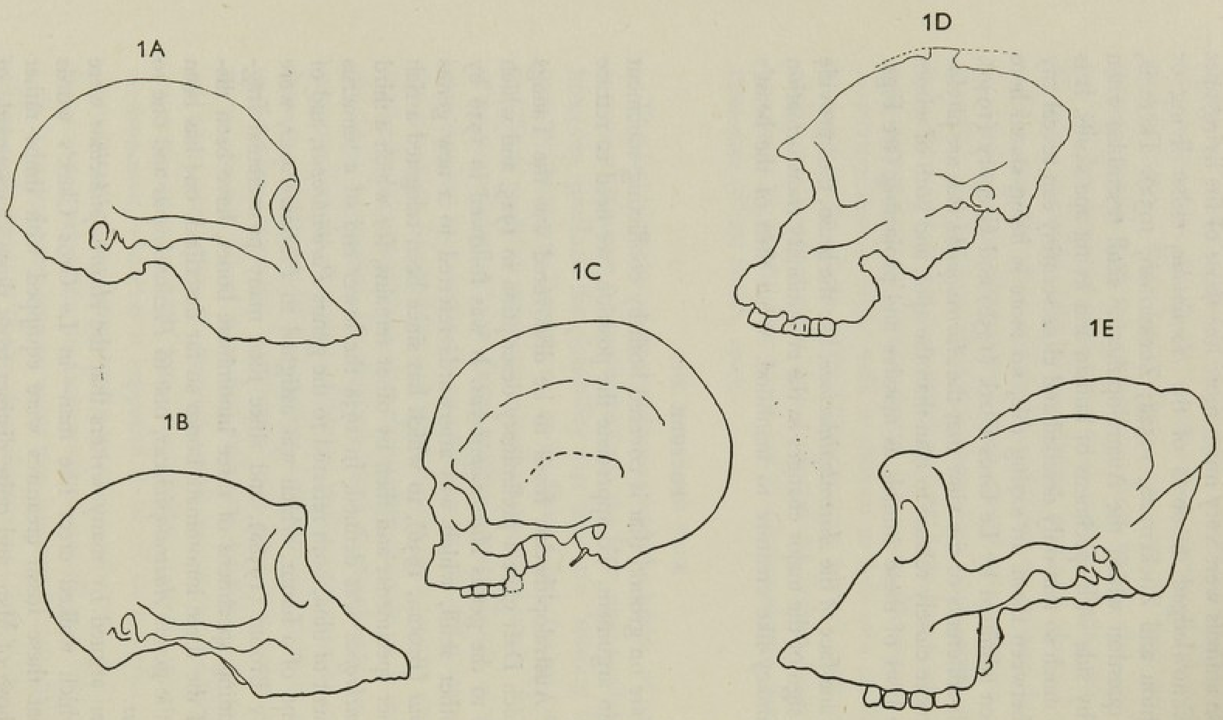

FIG. 1.—Lateral Outlines of Various Skulls.

Approximately quarter natural size.

(*a*) *Plesianthropus transvaalensis*, skull V. Traced from Plate I, Broom, Robinson and Schepers (1950).

(*b*) Adult female chimpanzee skull (taken at random).

(*c*) Australian aboriginal.

(*d*) *Paranthropus crassidens*. Traced from Plate 4, Broom and Robinson (1952).

(*e*) Adult male gorilla skull (taken at random).

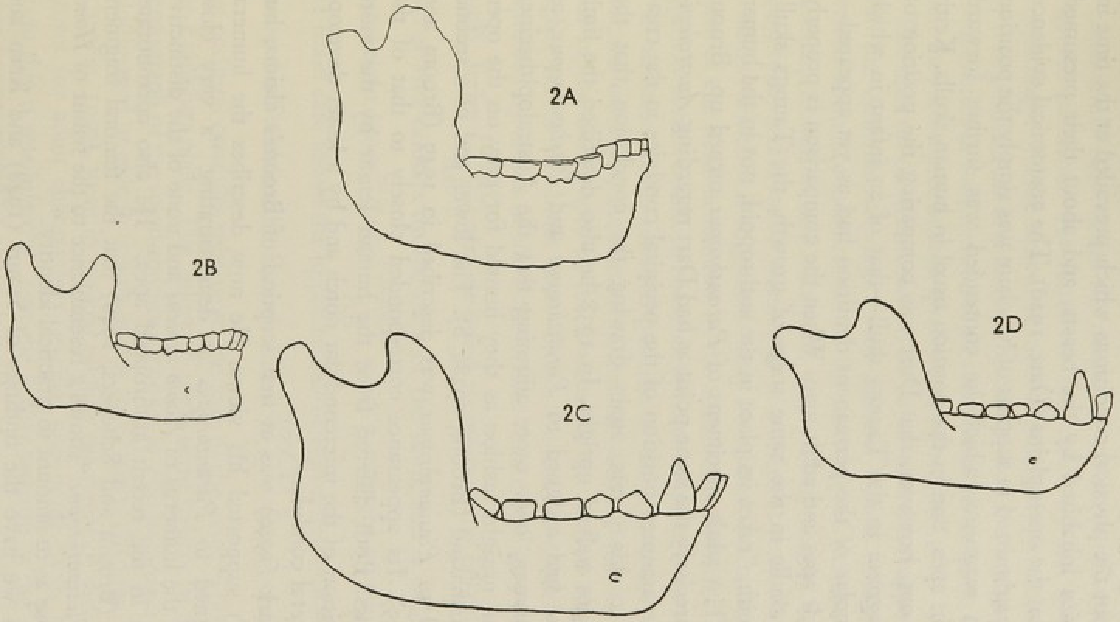

Fig. 2.—Lateral Outlines of Mandible.
Approximately one-third natural size.

(*a*) *Paranthropus crassidens*. Traced from Plate 1, Broom and Robinson (1952).
(*b*) Mandible of South African native.
(*c*) Mandible of adult female gorilla (taken at random).
(*d*) Mandible of adult male chimpanzee (taken at random).

by Dart (1925) on the basis of what Keith (1931) has described as "geological, geographical and anatomical" evidence. I shall not refer here to the geological or geographical evidence, since it consists essentially of speculations about the physical conditions which prevailed at the time in the part of Africa inhabited by the beasts, and about their presumed hunting habits on the open plains (Dart, 1926). The anatomical evidence which Dart first submitted in support of his claim was simply the position of the foramen magnum, which he contended was further forward relatively than in apes, and in the position usual in human skulls. Keith (1931) pointed out, however, that Dart was comparing the position of the foramen magnum in the Taungs skull—that of an infant in which only the first molar of the permanent dentition had as yet appeared—with that in adult apes and adult man. When the comparison is properly made between skulls in the same stage of growth, the Taungs skull, according to Keith, "takes its place in the anthropoid, not in the human series. . . ." When adult specimens of *Paranthropus* turned up, Broom (1938b) made precisely the same point as had Dart regarding *Australopithecus* about the assumed position of the occipital condyles in the creatures assigned to this genus, again drawing the conclusion that the Australopithecines walked upright. In 1938 he also described the limb bones which he had assigned to *Paranthropus* and *Plesianthropus*, as being nearly human, once more affirming that the Australopithecines proceeded in an upright fashion as they hunted for prey on the open plains of Bechuanaland (Broom, 1938a, b). The lower end of a second femur assigned to *Plesianthropus* was described in 1949 (Broom and Robinson, 1949). Its appearance corresponded closely to that of the earlier fragments. Both differed from the human femur by the more forward disposition of the intercondylar notch and by a lesser development of the lateral condyle.

Le Gros Clark (1940) was at first sceptical of Broom's claims, but later (1947a, b) supported his views. He now describes the humeral fragment assigned to *Paranthropus* as demonstrating "a very close resemblance to the humerus of *Homo sapiens* and none of the distinctive features found in the recent anthropoid apes." He also corroborates Broom's view (Broom and Schepers, 1946) that the femoral fragment attributed to *Plesianthropus* "shows a resemblance to the femur of *Homo* which is so close as to amount to practical identity."

Against this we have the findings of Straus (1948) and Kern and Straus (1949), who submitted the data to a somewhat more detailed analysis than was published either by Broom or Le Gros Clark. Straus's study suggests that the humerus is no more hominid than anthropoid . . . "In both absolute dimensions and proportions it bears a particularly close resemblance to both man and the chimpanzee. Regarding its proportions, however, it is in general more like the average chimpanzee than like the average man, but this should probably not be stressed since it consistently falls within the ranges of variation of both species." The fragment of femur was found to be "definitely not great-ape," in its morphology. "At the same time it is not peculiarly or exclusively hominid, for it resembles man and cercopithecid monkey in about equal degree. . . . Its characters *in toto*, therefore, no more betoken an erect, bipedal posture than they do a pronograde quadrupedal posture."

The next set of considerations to be advanced in support of the thesis that the Australopithecines were animals which walked upright was derived from a consideration of the anatomy of the innominate bones (Broom, Robinson and Schepers, 1950; Dart, 1949b; Le Gros Clark, 1949, 1950) and from an assessment of a series of cranial indices, referred to below, which it is suggested "may be related to a common factor, the poise of the head in relation to the vertebral column" (Le Gros Clark, 1950). It is convenient to consider the cranial indices first.

In addition to the forward position of the foramen magnum and the occipital condyles, the Australopithecine skull is believed to differ from that of the living apes in the lowness of the nuchal ridges and in the higher set of the brain case. These features have been quantitatively expressed by means of the three indices shown in Fig. 3 (Le Gros Clark, 1950). Index $\frac{100AG}{AB}$ was designed to indicate the height to which the nuchal area extends up the back of the skull, and is called "the nuchal area height index." Index $\frac{100FB}{AB}$ gives a measure of the proportion of the brain case above the upper orbital margin relative to the total height above the Frankfurt horizontal. Index $\frac{100CD}{CE}$ describes the position of the occipital condyles relative to the base of the skull, when orientated in the Frankfurt plane. The values of these three indices as derived from a photograph of the fossil specimen known as *Plesianthropus* 5, a presumed middle-aged or elderly female of this fossil genus (Broom, Robinson and Schepers, 1950), were in general outside the range of the corresponding figures for adult chimpanzees, gorillas and orang-utans of both sexes. From this it was inferred "that the bodily posture of the Australopithecinae approximated in some degree to that characteristic of the Hominidae" (Le Gros Clark, 1950). Before considering either this conclusion, or the view that the three indices are correlated, in the sense that they reflect a common factor, it is useful to refer briefly to the evidence about posture which is provided by the innominate bones.

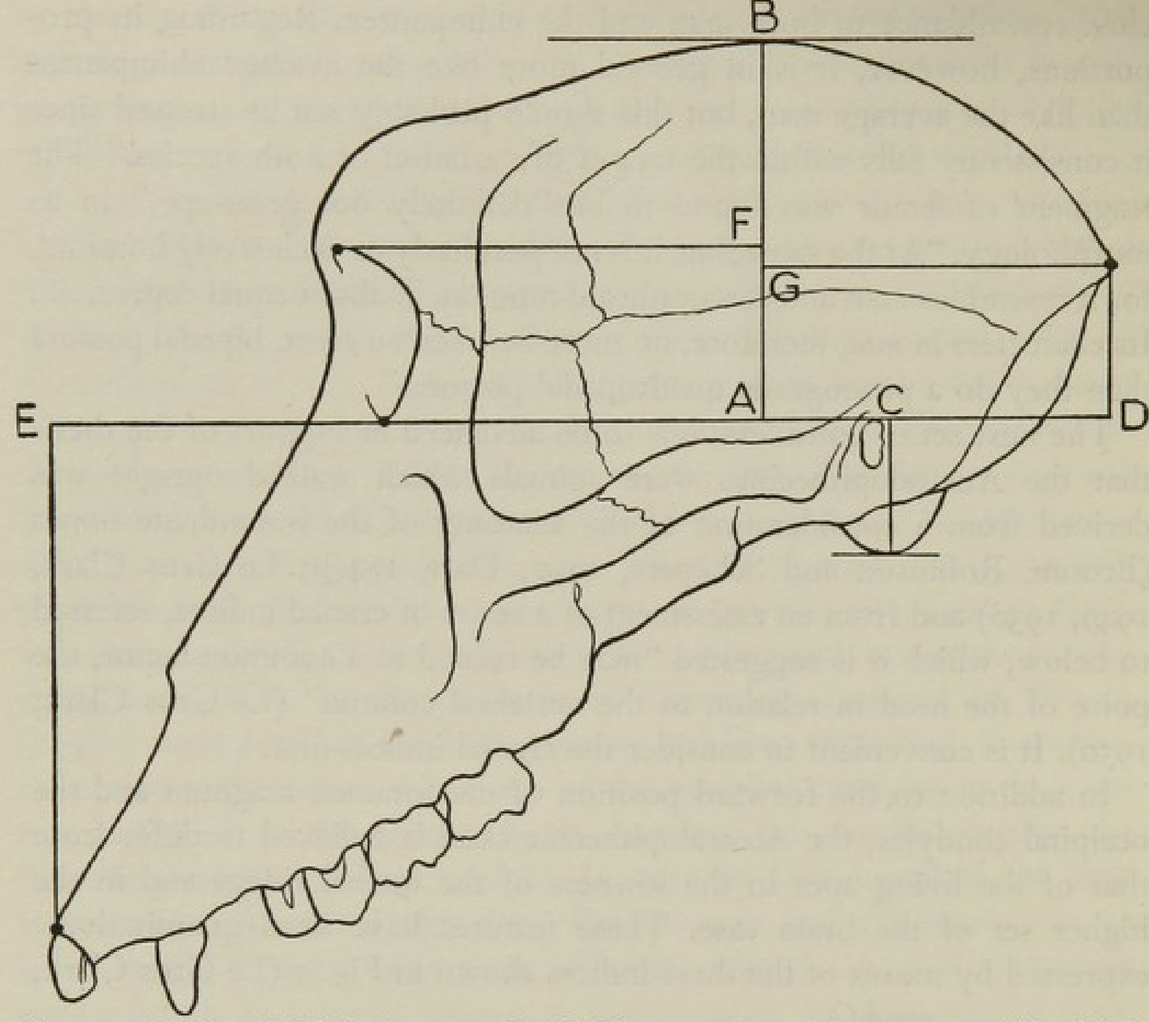

FIG. 3.—Profile of skull of mature female baboon orientated on ear-eye (Frankfurt) horizontal.

E A C D = Frankurt plane (= horizontal).
A B = Height of vault above Frankfurt plane.
A G = Height of nuchal musculature above Frankfurt plane.
F B = Height of vault above upper orbital margin.
C = Position of lowest point of occipital condyle relative to E D, maximum projection of skull in Frankfurt plane.

At first sight this evidence, which depends mainly on the shape of the ilium, appears impressive (Dart, 1949b; Broom, Robinson and Schepers, 1950; Le Gros Clark, 1950; and Robinson, 1950). The human ilium is broader and more flattened than that of the ape. This difference is usually regarded as being related to the particular form of the human gluteal muscles, and in some way—not very clearly specified—to the maintenance of the erect posture. The gluteus maximus in man is the most powerful extensor and lateral rotator of the thigh. The gluteus medius and minimus, whose area of origin covers by far the greater part of the blade of the innominate bone, are abductors and rotators, and also take an active part in the movements of the pelvis which are associated with walking. The long lip of the broader human ilium also provides a more extensive area for attachment of the abdominal muscles.

The main feature in which the Australopithecine ilium resembles the human rather than the ape bone is in its breadth and shortness. This is taken to imply a significantly different gluteal musculature than is found in apes, which in turn is taken to mean that the animals walked upright. Robinson (1950), however, points to two features in which the Australopithecine innominate differs from the human innominate bone. They are "the relatively long border from the inferior to the superior iliac spine, due to the projection of the superior spine and the relatively great distance between the acetabular rim and the region for muscular attachment on the ischium." In these characters, he observes, the Australopithecine innominate resembles that of the ape, but he suggests that these features "may simply indicate incomplete adaption to an erect gait." Other features in which the human and Australopithecine innominate differ are described by Broom, Robinson and Schepers (1950) who, in concluding their account of the orientation of the *Plesianthropus* bone, wrote that in this respect the ilium is "almost that of man, but that the pubis and ischium resemble more those of the chimpanzee."

It has become customary to treat the different kinds of evidence that have been adduced in support of the view that the Australopithecines walked upright as interdependent, and to counter-balance any deficiencies in one by reference to the indications provided by another. So it is that Robinson (1950) can say that even though the distance between the inferior and superior iliac spines, and between the acetabular rim and the muscular attachments of the ischium, suggest that the innominate bone of the Australopithecines is ape-like, reference to the structure of the base of the skull, i.e. to the relative position of the occipital condyles, indicates that we are nevertheless dealing with a creature that walked upright. The correlated picture which is described for us is of animals (*a*) whose forelimb bones do not reveal the powerful muscular markings observed in modern brachiating apes, (*b*) whose ilium was not dissimilar from the human ilium, (*c*) whose femur (if we disregard the views of Kern and Straus) was hominid in character, (*d*) whose talus showed certain hominid characteristics, at the same time as it did not preclude free movements of the toes, as occur in the great apes, and (*e*) whose occipital condyles and the area of attachment of the nuchal musculature indicated that the head was carried on the vertebral column as in bipedal animals such as ourselves. The degree to which all these features are regarded as correlated is well indicated by Le Gros Clark (1950) who has written: "The hominid construction of the pelvis is also in entire conformity with (and, indeed, might have been predicted from) the hominid characters of the skulls and other limb bones and with the predominantly hominid character of the dentition."

Without at this stage affirming any contrary view about the posture of the Australopithecines, it is interesting to consider whether or not this degree of correlation in fact exists, and whether it is justifiable to sustain deficient anatomical evidence in one region of the body by reference to features displayed by another part of the skeleton. As I have already remarked when considering the repercussions of phylogenetic views on anatomical interpretations, in the final analysis it is the anatomical evidence which counts, and no single part of it is given greater factual substance by the mere repetition of some phylogenetic idea which it is held to support. Similarly, there are limits to the extent that one can make good the deficiencies in our detailed information about one anatomical area by reference to another. Cuvier's (1813) belief that "commencing our investigation by a careful survey of any one bone itself, a person who is sufficiently master of the laws of organic structure, may, as it were, reconstruct the whole animal to which that bone had belonged" has unfortunately too often proved fallacious, as the fate of *Hesperopithecus*, to take a single example from the Primates, shows only too well. The laws of organic structure are, alas, not quite as clear as Cuvier may have supposed, brilliant though his generalization was.

Indices of cranial balance

Dr. Ashton and I have assembled numerical values for the three cranial indices referred to above, not only for the great apes but also for man and for various species of monkeys (Ashton and Zuckerman, 1951). In addition to the skulls of the three great apes, three series of human skulls, and the skulls of gibbons and of five species of Old and New World monkeys were measured. The results of this enquiry are shown in Fig. 4. They confirm that the "nuchal area height index" is significantly smaller in *Plesianthropus* 5 than in the great apes, and that it agrees with the human value. They also show that the supra-orbital height index of the *Plesianthropus* skull agrees in magnitude with that of man, and that it surpasses the range of variability in the sub-human Primates studied, except in the case of the gorilla, where the comparison may be misleading because of the presence in this ape of a sagittal crest.* On the other hand, our findings also indicate plainly that the condylar-

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* The fact that both FB and AG, in the first two of these indices, are highly correlated with AB limits the amount of useful information the indices FB/AB and AG/AB actually provide about the expansion of the cranial vault and about the height to which the nuchal musculature reaches. CD, in the index CD/CE, on the other hand, is not necessarily correlated with CE, and does not therefore suffer from a corresponding shortcoming.

position index in *Plesianthropus* 5 is very much closer to the range for the sub-human Primates than for the three human types studied. This result is important in view of Schultz' (1942) experimental observation that the ratio of the pre- and post-condylar segments of the skull makes it possible to predict "with very considerable accuracy the ratio between the weights needed to balance the head at the corresponding landmarks. . . ." Vallois (1926) also provides interesting comparative data for man and the apes about the counter-weight which has to be applied to the occipital region in order to prevent the skull, when balanced on the occipital condyles, from tipping forwards. The obvious conclusion from all the evidence is that if *Plesianthropus* did stand upright, its head was balanced as in apes rather than as in man.

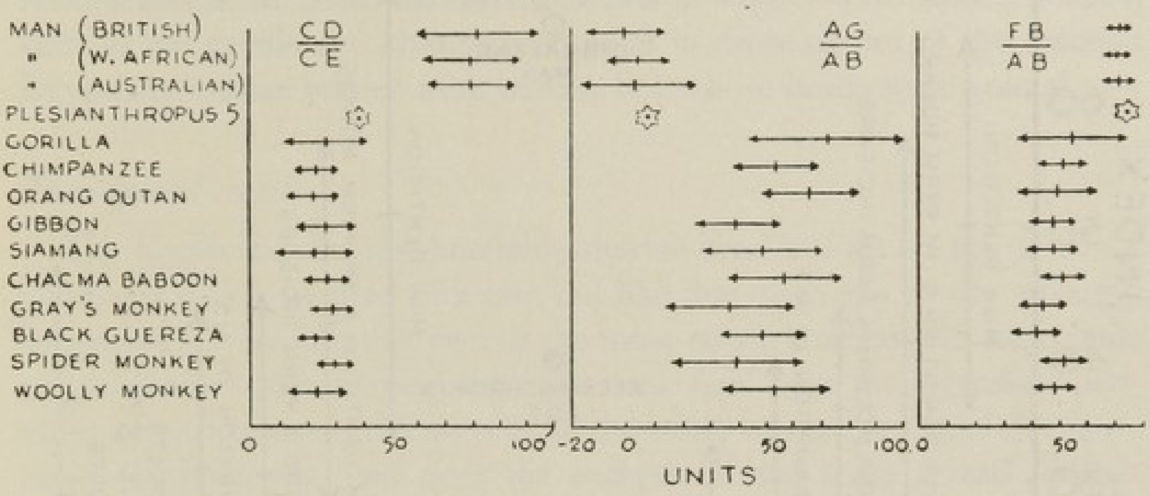

FIG. 4.—The condylar position index (CD/CE), the nuchal height index (AG/AB), and the supra-orbital height index (FB/AB) in man, *Plesianthropus*, apes and monkeys. The position of the mean values is shown by the small vertical bar on the horizontal line which indicates the 98 per cent fiducial limits on either side of the mean.

We next attempted to find out whether the three indices are correlated, as would be expected if they are related to a common factor—the poise of the head in relation to the vertebral column. The results were in general negative. This finding, taken together with the observation that the three indices in *Plesianthropus* 5 do not diverge from the great apes and monkeys on the one hand, and from man on the other, either in the same direction or to the same relative extent, suggests that if one, or even possibly two, of the indices are in some way influenced by the way the head is poised on the vertebral column, all three do not—contrary to what has been suggested—have this significance.

The closer approximation of the position of the occipital condyles in Plesianthropus to that in apes, as opposed to men, either living or extinct, is also apparent when the comparison is made with ape skulls in which the inion is not prolonged backwards as in adult gorillas (Ashton and

Zuckerman, 1952b). Moreover, the age differences in the value of the index are fairly considerable (Fig. 5), in spite of the fact that there are no clear-cut, or indeed obvious, differences in the gait of young and adult great apes, or in the way they carry their heads. In view of this, it is doubtful if the index does provide an exact measure of the way the head is carried in the living animal. If *Plesianthropus* did in fact walk upright, the conclusion that its skull was balanced on the vertebral column as in

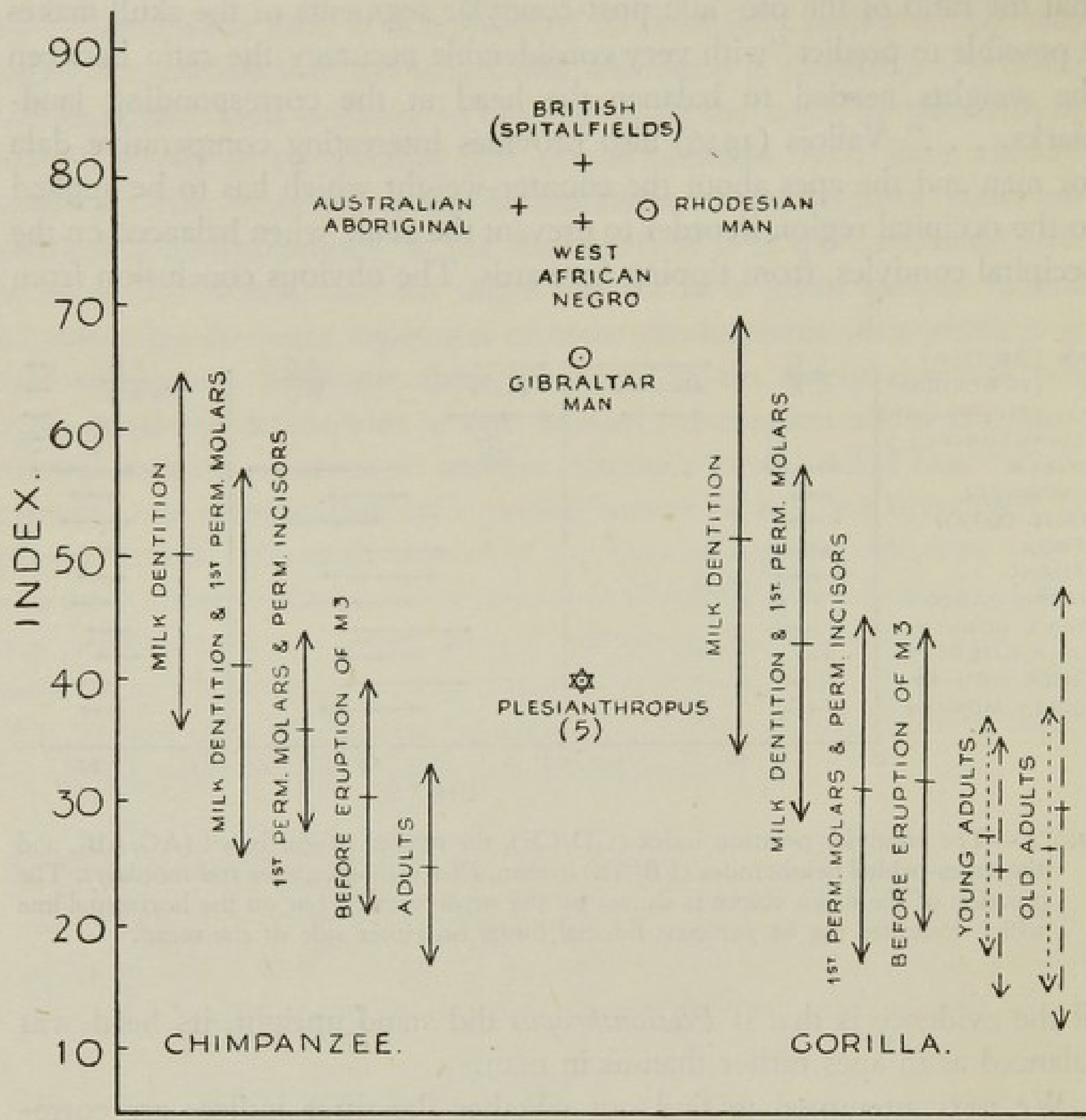

FIG. 5.—The value of the condylar-position index in various hominids and in apes of different ages.

Mean values for the gorilla and chimpanzee are represented by short transverse bars, the 98 per cent fiducial limits being indicated by arrows.

+ indicates average values for three types of modern man.

⊙ indicates values for singles specimens of fossil man.

✡ indicates the value for the Australopithecine specimen *Plesianthropus* 5.

———— Both sexes
-------- Female
— — — — Male

apes, rather than as in man, cannot therefore stand on the basis of this evidence alone. Postural features of this kind need to be established on the basis of the nature of the nuchal musculature, on the curvature of the spinal column, and on the carriage of the trunk on the hind limbs.

Whatever anatomical significance the so-called head-balancing indices may therefore have, their precise values in the Australopithecine skull *Plesianthropus* 5 hardly supports the inferences about posture that have been drawn from the nature of the innominate bones. On the contrary, given, as is suggested, that the abdomen and pelvis were supported on the hind-limbs in an erect posture, they actually suggest that the Australopithecine head was carried as it is in a quasi-quadrupedal animal, such as the gorilla and chimpanzee, or as in those deities of the Ancient Egyptians, whose bodies were human but whose heads were animal.

The sagittal crests

The likelihood that the Australopithecine head was set on the vertebral column not like the head of a man but like that of an ape is very strongly supported by the fact that two of the most recent Australopithecine finds are of skulls which possess sagittal crests. And here the argument provides a much more secure exercise in the study of the correlated development of characters than does the analysis of the three cranial indices referred to above.

These skulls were first described by Broom and Robinson in the latter part of 1950 (a, b) and have been assigned to the species *Paranthropus crassidens*. Both specimens are regarded as female, and in one the sagittal crest is present for a distance of 140 mm. and reaches a height of 12 mm. above the level of the brain case. Unfortunately the occipital region of both skulls is lacking. Because a crest was not obvious on the occiput of an adolescent skull, also assigned to *Paranthropus*, Broom and Robinson assumed that the sagittal crest in their two adult specimens did not extend backwards to a confluence of sagittal and occipital crests. This particular inference is, however, hardly justifiable, for an immature skull would not be expected to be furnished with such a crest.

The interesting anatomical puzzle which these two specimens pose is what, in fact, was the nature of the occipital region?

The Growth of the Primate Skull

Nowhere is the orderly and correlated development of the body better illustrated than in the skull. It consists of a cranium or brain-box, and a face consisting of eyes, nose and jaws. The size and shape of the endocranial cavity are correlated with the size and shape of the brain. The size and shape of the face are mainly conditioned by the character and size of the permanent teeth. The development of the jaws in turn affects the brain-box, in so far as the growth of the muscles of mastication is associated with their spread over the cranium. As a result the latter becomes remoulded by the development of an external bony film, which in a creature like the gorilla may be several millimetres thick. An understanding of the dynamics of skull growth thus depends on a clear appreciation of the developmental interaction of cranium and face.

This problem has been the subject of several investigations (e.g. Keith, 1910; Zuckerman, 1926; Huxley, 1932; Krogman, 1930, 1931a, b, c), from which certain clear-cut generalizations may be readily derived. The outstanding one is that the process of growth is associated with an enormous change in the relative proportions of the cranial and facial skeletons (Fig. 6). This is due to the fact that the main development of the jaws, and the eruption of the permanent teeth, occur after the brain has completed the better part of its growth. To take the example of man, the brain of the average individual almost certainly reaches at least 90 per cent of its final volume by the seventh year, when the first tooth of the permanent dentition—either the first molar or the central incisor—starts erupting (e.g. Scammon and Dunn, 1922). The position is little different in the chimpanzee (Zuckerman, 1928; Schultz, 1940), or in the rhesus monkey (Zuckerman and Fisher, 1938), in which no significant growth occurs after the permanent incisors and second molars are in place—in spite of the fact that the sutures of the cranial vault may remain open till well after the eruption of the third permanent molars.

Since the growth of the face is associated with the eruption of the permanent teeth, changes in the shape and size of the brain, which for all practical purposes may be regarded as having ceased growing before the jaws assume their mature proportions, cannot be regarded as responsible for the major developmental transformations of the skull. These Keith (1910) attributed to three main factors: (1) eruption of the teeth and increase of the jaws to accommodate the increased dentition, (2) the growth of the muscles of mastication, and especially of the area of origin from the cranium, and (3) the modification of the nuchal area of the skull.

Krogman (1930, 1931a, b, c) considers that the growth of the anthropoid skull is compounded of two major elements—"proportional increase and readjustment." "Proportional increase," which is allometric in nature (Huxley, 1932), occurs until shortly before the eruption of the first permanent molars, and involves "a uniform, relatively rapid, progressive change in proportion," in the course of which the skull attains its definitive form. "The factor of readjustment" begins with the eruption of the second permanent molar, and manifests itself in the upward and backward migration of the foramen magnum, and in a forward and downward swing of the face from the pterionic region. Most of the growth of the skull occurs anterior to the external auditory meatus.

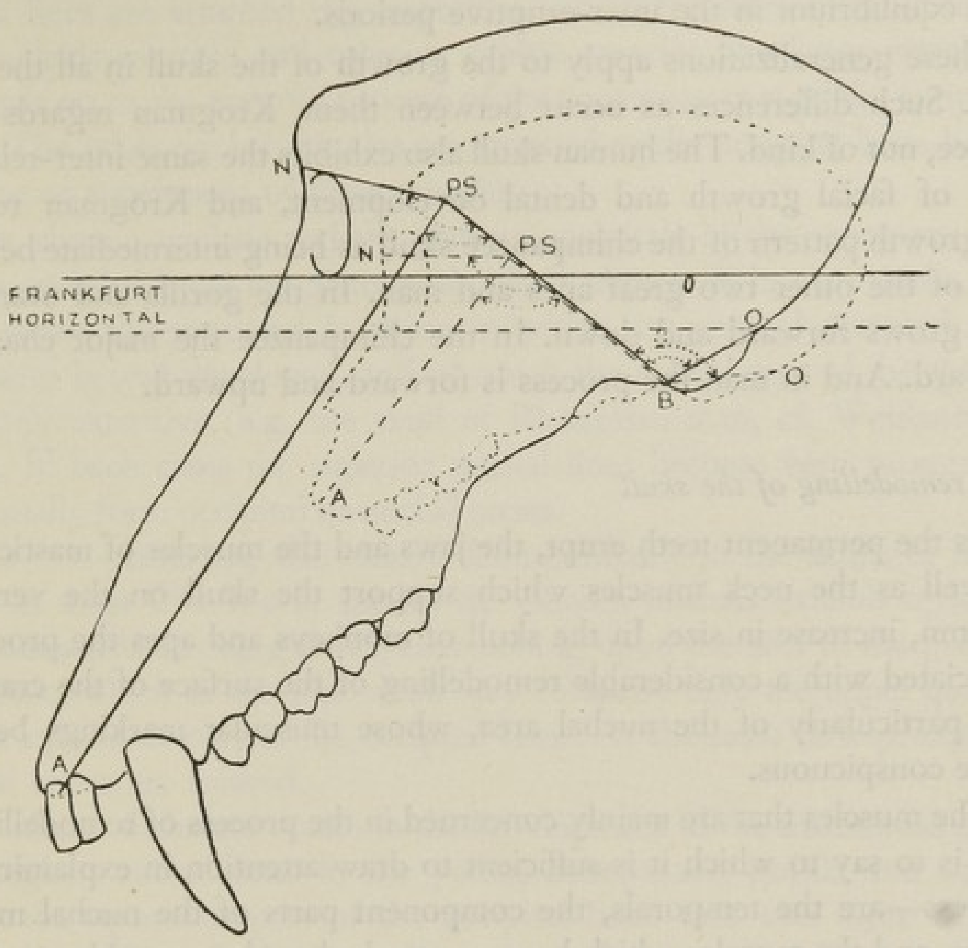

Fig. 6.—Profiles of skulls of an infant and an adult male baboon orientated on Frankfurt horizontal, and showing changes in the basicranial axis.

B = Basion.
P.S. = Prosphenion.
O = Opisthion.
N = Nasion.
A = Alveolar Point or Prosthion.
Angle B–PS–N = spheno-ethmoidal angle, which is more open in the adult specimen.
Angle PS–B–O = Foraminobasal angle, which is less open in the adult specimen.
Angle B–PS–A = Sphenomaxillary angle, which is little different in the two specimens.

"The parieto-temporal, and fronto-spheno-temporal areas, considered as the 'sphenoid complex,' are those of growth and expansion; the occipital area, with the possible exception of the masto-occipital region, is very early stabilized and presents little opportunity for expansion." In spite of this stabilization, a backward and upward swing of the foramen magnum occurs about the time of eruption of the third molar, due to the superior part of the occiput being pulled forward and upwards, the inferior part moving in harmony backwards and upward.

According to Krogman, the face grows in height before the eruption of each permanent tooth, and in length during and just after eruption. It is in equilibrium in the inter-eruptive periods.

These generalizations apply to the growth of the skull in all the great apes. Such differences as occur between them, Krogman regards as of degree, not of kind. The human skull also exhibits the same inter-relationship of facial growth and dental development, and Krogman regards the growth pattern of the chimpanzee skull as being intermediate between that of the other two great apes and man. In the gorilla and orang the face grows forward and down. In the chimpanzee the major change is forward. And in man the process is forward and upward.

The remodelling of the skull

As the permanent teeth erupt, the jaws and the muscles of mastication, as well as the neck muscles which support the skull on the vertebral column, increase in size. In the skull of monkeys and apes the process is associated with a considerable remodelling of the surface of the cranium, and particularly of the nuchal area, whose muscular markings become more conspicuous.

The muscles that are mainly concerned in the process of remodelling—that is to say to which it is sufficient to draw attention in explaining the process—are the temporals, the component parts of the nuchal musculature, and the muscles which become attached to the mastoid part of the squamous temporal bone (the sterno-cleido-mastoid, the splenius capitis and the longissimus capitis). All but the temporal muscle, which arises from the side of the skull in a fan-shaped arrangement, are flat and strap-like muscles of varying width. The temporal has a tendinous insertion into the coronoid process and anterior margin of the ascending ramus of the mandible.

The attachments of the muscles are clearly marked on the surface of the skull, the margins of the temporal muscles being defined by the temporal lines. These, which also give attachment to the epicranial aponeurosis and the temporal fascia, begin anteriorly at the zygomatic process of the frontal bone, and, in the young monkey or ape skull (as in mature human skulls), join the supra-mastoid crest posteriorly. This crest is on the same level, and may be continuous with the superior nuchal line.

The curved superior nuchal lines, which subdivide the occipital bone into a lower planum nuchale and an upper planum occipitale, meet in the mid-line in the external occipital protuberance or inion (Fig. 7). A short distance above the superior nuchal line is a fainter line, the highest or supreme nuchal line, which gives attachment to the subcutaneous occipito-frontalis muscle. To the external occipital protuberance and superior nuchal lines are attached the trapezius; and to the lines themselves the sterno-cleido-mastoid and splenius capitis muscles, the latter extending forwards on to the mastoid process of the squamous part of the temporal bone. The other nuchal muscles are attached to the occipital bone below the line of attachment of these muscles.

The planum nuchale and the planum occipitale of the squamous part of the occipital bone are distinguishable in almost all human skulls, and are sharply differentiated in those in which an external occipital protuberance is well developed, and in which the nuchal area of the skull is relatively extensive (e.g. the skull of Rhodesian man, cf. Weidenreich, 1940). In such cases the superior nuchal lines become very prominent, and usually form occipital or nuchal crests.

The two planes are also clearly distinguishable in the skulls of monkeys. In most Old World species the planum nuchale extends upwards and backwards during growth, encroaching upon the area of the planum occipitale, which in the adult skull may comprise only the upper quarter of the squamous part of the occipital bone. At the same time prominent nuchal crests are formed.

An identical change occurs in the development of the anthropoid skull. The highest nuchal lines in the young chimpanzee, gorilla and orang, divide the squamous part of the occipital bone into two more or less equal parts (Fig. 7). During the course of eruption of the permanent teeth, the superior lines move upwards as a nuchal crest, and encroach upon the planum occipitale. Except when a sagittal crest forms (see below) a small part of the planum occipitale always remains.

Weidenreich (1940, 1943) has made a detailed study of the development of the nuchal crests, to which he refers as the "torus occipitalis transversus." The crests of each side meet in the mid-line in the external occipital protuberance, or inion, and here they also meet the medial extremities of the highest or supreme nuchal lines, which cross the planum occipitale, and to which the epicranial aponeurosis and the occipito-frontalis muscles are attached. These lines, although far less distinct than the superior nuchal lines, sometimes give the appearance of playing a greater part in the formation of the inion.

Laterally the torus runs across the lambdoid suture on to the mastoid part of the squamous temporal, either becoming the crista mastoidea or supra-mastoid crest, or becoming lost in the mastoid process itself. Weidenreich regards the occipital torus as "the hindmost portion of a ring system of protuberances beginning at the level of the articulary tubercle of the temporal bone and extending almost continuously to include the whole post-otic region of the skull." Its purpose is to serve "as reinforcement for the base of the cranial framework." The whole ring is present in the great apes and primitive hominid skulls, but only the posterior part may persist in modern man. Weidenreich does not regard the torus as being due to the extension of the surface of attachment of the nuchal muscles, although he emphasizes that its prominence varies directly with the massiveness of the cervical and temporal muscles. McCown and Keith (1939), on the other hand, regard the torus occippitalis as a cranial feature that results from a "wave" of bone-growth which precedes the expanding insertion of the semispinalis capitis, and to a lesser extent, the trapezius. For present purposes either view is sufficient, since both correctly imply that the prominence of the crests varies directly with that of the muscles attached to them.

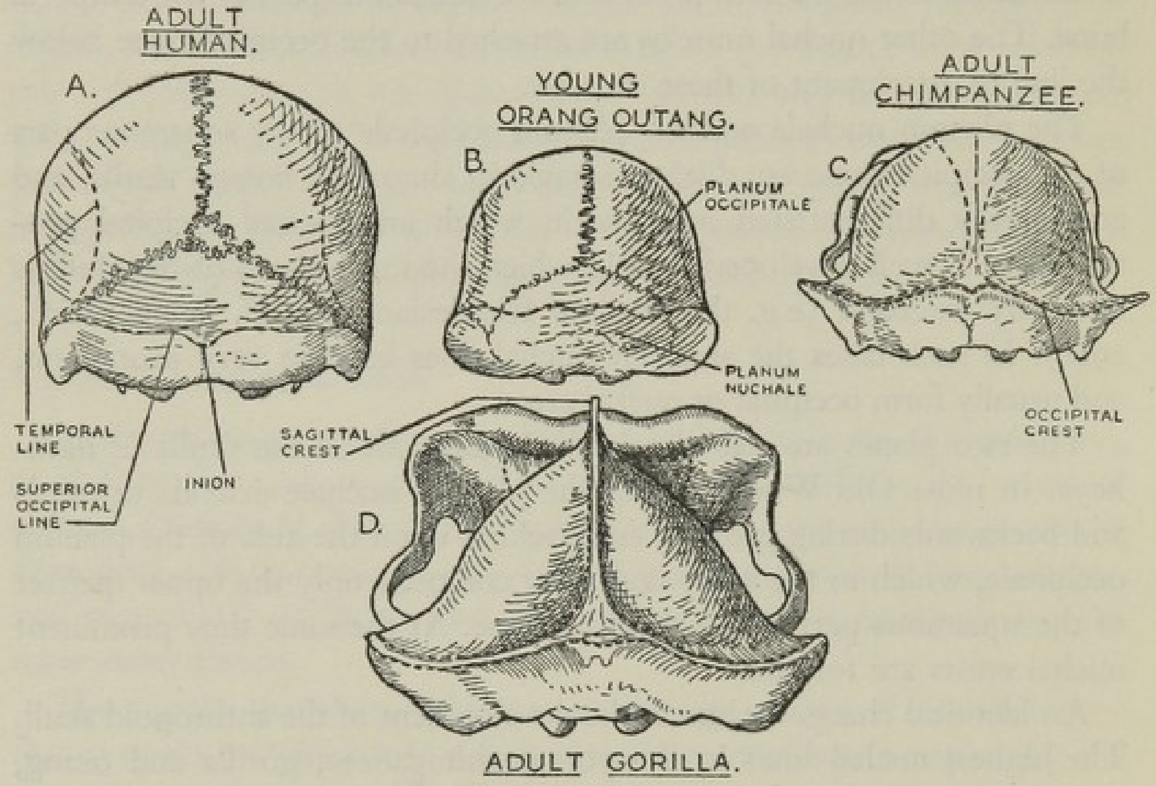

FIG. 7.—The formation of the sagittal and occipital crests.

As the area of attachment of the temporal muscles increases, in keeping with the development of the jaws, the temporal lines move peripherally as the edge of a thin film of new bone. The posterior horizontal and oblique fibres of the fan-shaped muscle appear to grow more rapidly than the anterior and vertical fibres, and the primary meeting-point of the sagittal lines of the two sides is usually just in front of the external occipital protuberance (Fig. 7). Well before they meet, the temporal lines have already fused postero-laterally with the occipital crests, thus helping to form a shelf-like occipital torus. As the temporal and nuchal muscles continue to grow, this plate of bone, which usually begins laterally, extends backwards to form a complete bony shelf round the back of the skull (Figs. 7 and 8).

Simultaneously, the zone of contact of the two temporal lines extends forwards, the lines meeting each other as two waves of growing bone. These fuse into an essentially bilaminar crest of varying height, the highest point almost invariably being just in front of the external occipital protuberance (Fig. 8). The posterior extension of the crest obliterates that part of the planum occipitale which can be recognized above the inion in skulls in which a sagittal crest does not form. In some skulls the crest may extend forward to cover all but the anterior one-third of the cranial vault (Fig. 8).

While a nuchal crest or occipital torus develops in, it is believed, every species of Old World ape and monkey, a sagittal crest develops only in certain species, and then as a rule far more frequently, and more prominently in the male than the female. It is never present in immature skulls, and it continues to develop after all the permanent teeth are in place. It often forms before the sagittal suture is fused, and it becomes most conspicuous in those animals, such as gorillas, which have very powerful jaws.

In the great apes a sagittal crest has never been reported in the female chimpanzee, and it occurs in only about 10 per cent to 20 per cent of adult males of this species (Zuckerman, 1928; Ashton and Zuckerman, unpublished). A crest usually develops in the male orang-utan after the completion of the permanent dentition, but it rarely develops to the same extent as in the male gorilla (Schultz (1941) observed a crest in only 3 of 47 adult female orang skulls). Fusion of the temporal lines to form a crest occurs more frequently in the female gorilla (according to our observations in about 50 per cent of cases), and is almost constant in the male, although the size of the crest varies considerably from animal to animal.

The process of development of the occipital torus and of the sagittal crests (or of the temporal lines) appears to be the same in all Old World monkeys and apes, and represents the same morphogenetic process—an osseous response to the increase in the size of the masticatory muscles and of the nuchal musculature supporting the skull on the vertebral column. The development of these two crests goes hand in hand with a widening of the zygomatic arches, and in most species with the development of a supra-orbital torus—which forms a buttress against which the

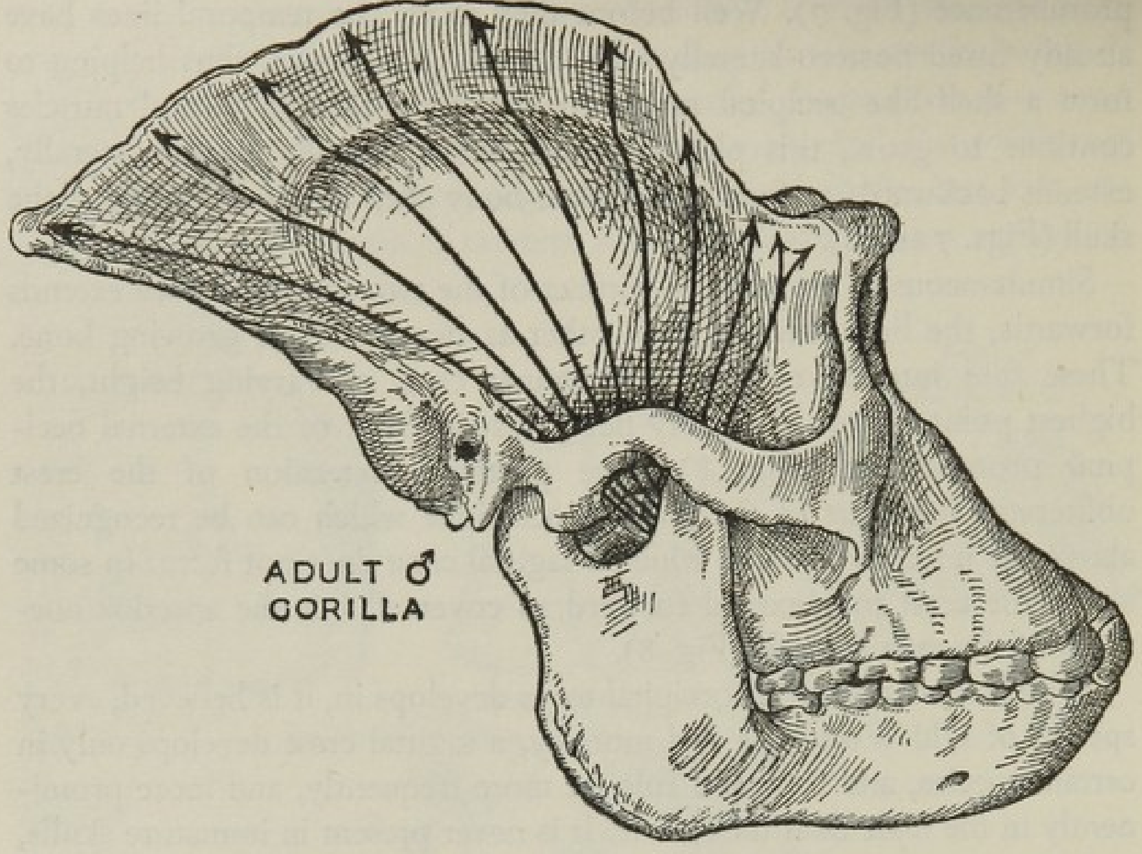

FIG. 8.—The direction of pull of the temporal muscle in the adult male gorilla.

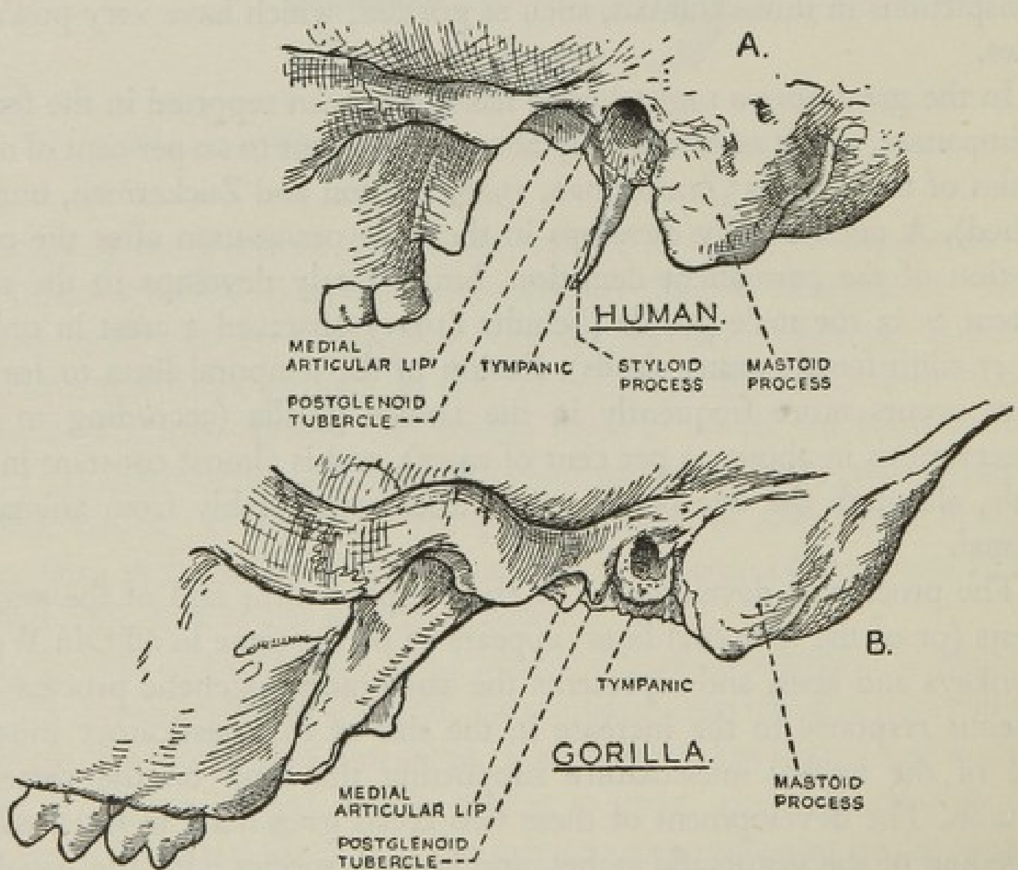

FIG. 9.—The mastoid process in man and the gorilla.

anterior part of the temporal muscle pulls (Fig. 8). The upward extension of the nuchal area, which reflects the increasing mass of the nuchal musculature and of the trapezius and sterno-cleido-mastoid muscles, is also reflected in an increase in the bimastoid diameter of the skull, i.e. in the breadth of the base of the skull, and in the development of a mastoid process, which is usual in the gorilla and frequent in the chimpanzee (Fig. 9, Ashton and Zuckerman, 1952c).

The inference, derived from comparative osteological studies, that the development of the crests is the manifestation of a single morphogenetic process is completely borne out by the results of an experimental study carried out by Washburn (1947). By removing the temporal muscles and severing the nuchal muscles in young rats, he was able to show that the presence of temporal lines and nuchal crests is determined entirely by mechanical factors. In the absence of the muscles, the bony ridges do not develop. Similarly, the coronoid process of the mandible does not grow —in fact it is completely resorbed—when the temporal muscle is removed, a finding which can be related to the observation that the process is greatly reduced in edentulous people. Other experimental and clinical observations which lead to similar conclusions are summarized by Schweitzer (1951).

Changes in the basicranial axis

Before considering the bearing these observations have on the evaluation of the two specimens of *Paranthropus crassidens* which have sagittal crests, it is necessary to refer briefly to the changes which occur in the basicranial axis of the skull as the jaws and the associated masticatory and nuchal muscles develop.

T. H. Huxley (1867) defined the basicranial axis as "a line drawn through the middle vertical plane of the *basioccipital*, *basisphenoid* and *presphenoid*, from the hinder extremity of the former bone to the anterior extremity of the last, at the upper end of the ethmo-presphenoid suture" (Fig. 10). The angle between this line and one continued from the presphenoid to the nasion is called the spheno-ethmoidal angle. It provides a crude and relative measure of the development of the front part of the brain, in the purely descriptive sense that the smaller the angle, the more the floor of the anterior cranial fossa has been "pressed" down by the growth of the frontal lobes. The angle between the basicranial axis and the plane of the foramen magnum is called the foramino-basal angle. It provides an indication of the way the skull is balanced on the vertebral column. In the well-known illustration to his essay "On the Relations of Man to the Lower Animals," in which sagittal sections of various primate skulls are shown, T. H. Huxley (1863) drew attention to the forward position of the occipital condyles in man, and to the fact that the plane of the foramen magnum is much more horizontal in man than in the lemur.

According to the descriptions of Keith (1910) and Duckworth (1915) the growth-changes in the basicranial axis of the gorilla are as follows: (1) After birth and until the brain-case ceases to enlarge, the tendency is for the anterior limb of the basicranial axis—the plane of the cribriform plate—to be depressed. The spheno-ethmoidal angle (angle between prosphenion-nasion and prosphenion-basion lines) thus decreases in size. (2) Growth of the brain in the posterior aspect of the skull opens out the foramino-basal angle (angle between the basion-opisthion and basion-prosphenion lines). (3) A process of "correction," by which the plane of the foramen magnum is altered and the foramino-basal angle becomes smaller, sets in with the eruption of the permanent teeth and the growth of the masticatory muscles. This "correction" is due to (*a*) the growth of the basilar plate pushing the face forwards relative to the occipital condyles (or the condyles backwards relative to the face), and to (*b*) the displacement of the opisthion, or posterior point of the foramen magnum, as a result of the extension and upward growth of the nuchal area.

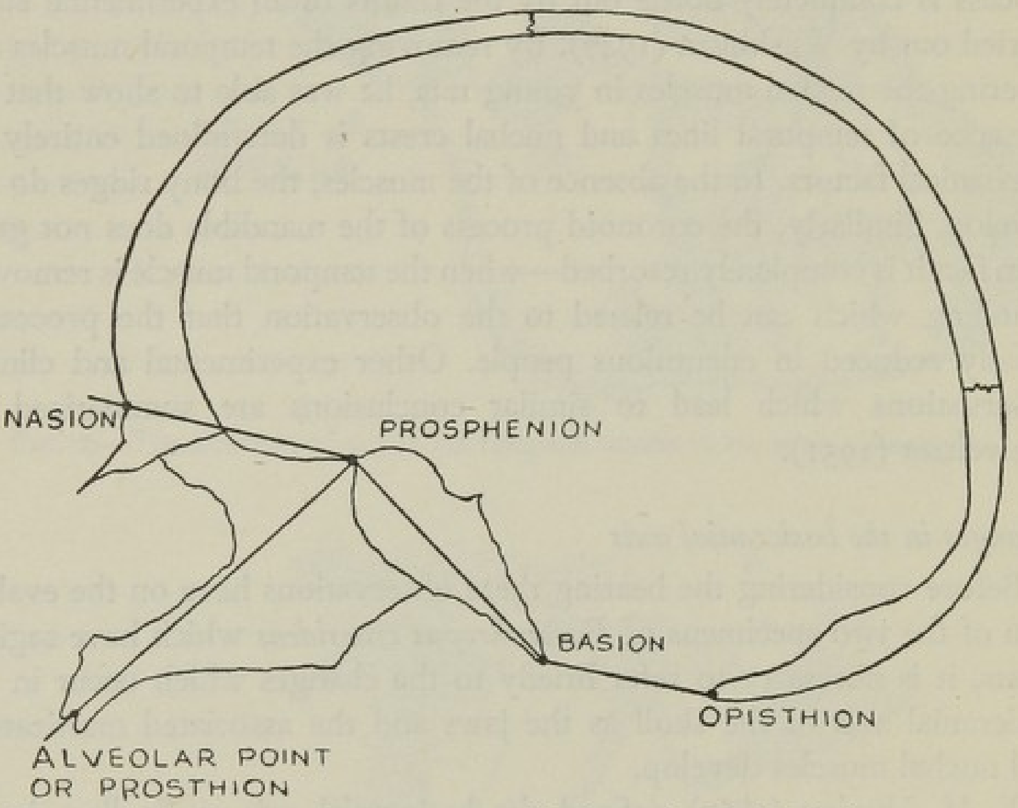

FIG. 10.—The basicranial axis, as originally shown by T. H. Huxley in 1867.

A study of the baboon (Zuckerman, 1926) showed that in this species, as in the gorilla, a backward migration of the occipital condyles, and a consequent decrease in the foramino-basal angle, takes place during the process of "correction" (see Fig. 6). I know of no detailed study of the growth changes in this angle in man. Observations on fifteen sectioned skulls in my own laboratory are suggestive of a slight decrease in the angle with age. A further series of observations indicates that in man the plane of the foramen always faces slightly forwards when the skull is orientated in the Frankfurt horizontal, and that it becomes almost horizontal as maturity is reached. On the other hand, in male and female gorillas and chimpanzees, the plane of the foramen always faces slightly backwards, the angle to the Frankfurt horizontal increasing from about 5° to 20° or 30° during the process of growth.

It should be emphasized that the occipital condyles and the anterior margin of the foramen magnum, to which the anterior arch of the atlas and the odontoid process of the second cervical vertebra are anchored by ligaments, do not alter their position on the vertebral column during growth. The changes which take place in the plane of the foramen magnum are due to the displacement of its posterior margin (the opisthion) as a result of the remoulding of the planum nuchale of the occipital bone in response to the growth of the temporal and neck muscles. Given this muscular development, and the associated changes in the slope of the planum nuchale and the occipital torus, it would seem axiomatic to expect a concomitant alteration in the plane of the foramen.

This is not to say that the occipital condyles do not alter with growth. Very distinct changes do occur in their shape, and appear to assist in the firmer support of the skull. But they can hardly have any effect on the relative position of the foramen.

The significance of sagittal crests in Paranthropus

The sagittal crests of the two presumed female specimens of *Paranthropus crassidens* are similar in all respects to the crests that occur in the great apes. They are quite unlike the kind of sagittal "crest" which occurs in *Pithecanthropus*, Rhodesian man, and occasionally modern man. For as Weidenreich (1940, 1943) has shown, the human sagittal crest is due to a thickening of the sagittal margins of the parietal bones and has "no connection whatsoever with the temporal muscles, the upper limit of which remains in each case considerably below the midline." The apelike sagittal crest of *Paranthropus crassidens* is also associated with a powerful supraorbital torus. The question is, is it conceivable that it was not associated with an occipital torus of the kind possessed by the gorilla, and with the powerful neck muscles of this ape? *A priori* the answer is no.

The detailed description of the developmental changes which result in the formation of these bony crests make it quite plain that in any existing monkey or ape the presence of a sagittal crest would presuppose that of a shelf-like occipital torus, and of an ape-like planum nuchale. To make assurance doubly certain I extended this study to non-Primate mammalian skulls, without encountering a single specimen in which a sagittal crest is not associated with a nuchal crest. Mr. R. J. S. Savage then examined the question systematically, and studied all the Primate skulls in the British Museum of Natural History; he also made a careful examination of Insectivora, Cheiroptera, and Dermoptera, as well as a survey of Carnivora and Marsupialia. He, too, found that the development of a sagittal crest is for all practical purposes invariably associated with a nuchal crest. And he also confirmed that the sagittal crest usually begins to form posteriorly where the temporal lines come together in the region of the inion, but that occasionally, e.g. Cheiroptera, fusion of the temporal lines begins anteriorly. If one of the two crests is missing, it is almost invariably the sagittal crest that is lacking. The only two cases in which Mr. Savage has observed a well-developed sagittal crest and a poorly developed nuchal crest are (1) a specimen of *Nycticebus*, and (2) some skulls of *Nycterus*, the hollow-faced bat, in which the sagittal crest is formed from the highly raised orbital region of the frontal bone. Neither I nor Mr. Savage has ever observed this manner of formation of the crest in a monkey or ape.

Unless *Paranthropus crassidens* is the one exception to a morphogenetic process common to all known Primates, it follows that its possession of a high sagittal crest presupposes the presence of a powerful and shelf-like occipital torus. Moreover, if Broom and Robinson are correct in diagnosing the two specimens as females, the males of the species must have had truly enormous crests—at least as big as those in gorillas.

If, on the other hand, it is assumed that *Paranthropus crassidens* did constitute an exception to a general rule, it would follow that its temporal muscle, and the movements of its jaws, were also exceptional. The likelihood of this being so can be readily tested.

The mechanism of the mandible

The mandible and maxilla of adult Australopithecines are massive. No descriptions have been published of the condylar process in *Plesianthropus*. A photograph of one specimen of *Paranthropus crassidens* shows a condylar process that is much more massive than the usual human condyle, and in which the fovea for the attachment of the lateral pterygoid muscle is not hollowed out as it usually is in man. More detailed descriptions of the condylar process in a presumed large male *Paranthropus crassidens* and a presumed female *Paranthropus crassidens* have recently appeared (Broom and Robinson, 1952). The textual descriptions, text figures (see Fig. 2) and plate indicate that the main features and dimensions of the process in these animals are ape-like. The presumed male specimen is described in the following words: "The condyle is larger than in any known ape or man except the gorilla. It is nearly as broad as that of the gorilla, but not so thick." Other features referred to can be matched in the gorilla. The female specimen is described as follows: "The condyle differs in a number of characters from that in the male jaw. On the outer side, instead of forming a sharp point, it ends bluntly, the outer side of the jaw running about straight up, and in this it can be more easily matched in the chimpanzee than in man, though the same condition is quite frequent in man. The inner side of the condyle has the articular surface turning slightly downwards, and there is a very marked tuberculum pterygoidea superius. Its greatest width is 24.3 mm., and the antero-posterior breadth of the articular surface is 11 mm. The back of the ascending ramus runs up in a line, which is nearly at right-angles to the line of the teeth."

There are several descriptions of the Australopithecine glenoid cavity, which appears to vary somewhat. The glenoid cavity in a skull of *Plesianthropus*, whose reference number is not given (Broom and Schepers, 1946, p. 51), is said to be far more human than ape-like. Specifically it is said to have a small postglenoid process (cf. Fig. 9), and a better developed "lower anterior part of the temporal bone . . . than in man." In their later monograph Broom, Robinson and Schepers (1950) describe *Plesianthropus* 5, the most perfect skull of the species yet described, as having a well marked articular eminence and a "rather large postglenoid process." Fig. 1, Pl. 1 of their monograph is a photograph of the left side of the skull, and it reveals as big a postglenoid process as one encounters in adult chimpanzees. This photograph shows the process as excluding the lateral part of the tympanic from the posterior wall of the glenoid cavity. In *Plesianthropus* 8, also described in the second monograph, there is a postglenoid process, the size of which is not stated, and the tympanic bone is said to form half the posterior wall of the glenoid cavity, the other half being formed by the squamous temporal (cf. Fig. 9). The illustrations suggest a somewhat shallower articular fossa than is usual in man, and one more similar to that of the anthropoid ape. Broom, however, describes this glenoid cavity as typically human.

In the type specimen of *Paranthropus robustus*, described in Broom's first monograph, the glenoid cavity is said to be very large, and to have a well-developed postglenoid process "about two-thirds as long as the transverse concavity" (presumably the articular fossa). It is said to differ from the glenoid cavity of the gorilla by the poor development in the latter of an articular eminence (the "transverse convexity") and of an articular concavity.

All the descriptions that have so far been provided of the glenoid cavity of the Australopithecines emphasize its hominid character first, by reference to the presence of an articular fossa and eminence as contrasted with their presumed absence in the great apes; and second, by emphasis of the small size of the postglenoid process, and the fact that the anterior face of the tympanic bone forms, or helps to form, the posterior wall of the glenoid cavity, as contrasted with a large postglenoid process and no participation of the tympanic bone in the formation of the fossa in apes. Broom has also stated that another distinguishing feature in the gorilla is the presence of a "huge process developed as an inner wall to the fossa," and has implied its absence in *Paranthropus*.

In addition to the presumed hominid nature of the articulation of the mandible, emphasis has been placed on the character of the wear of the teeth of the Australopithecines as indicative of their human, as opposed to ape-like affinities. Thus Le Gros Clark (1947a, b) regards "the type of wear shown in all the premolar and molar teeth" as implying "that the temporo-mandibular joint was constructed on the human pattern." He also observes (1949) that the crowns of the molar teeth "became quickly ground down to an almost flat surface as they are in Man, indicating that the movements of the jaws in chewing were similar to those of the human jaw."* Robinson (1950) emphasizes the same points, and ascribes the assumed differences between dental wear in man and the apes to the restriction of lateral movements of the ape mandible by the interlocking of the large canines—teeth which he believes wear mainly at the side and little at the tip.

Essentially therefore what is believed is that man is able to grind his teeth by rotatory movements of the jaw, whereas in the ape, movement is practically restricted to the vertical plane, and to antero-posterior movement, because of the locking action of the large canines.

The anatomy of the mandibular region of apes

The belief that the glenoid cavity of apes differs from that of man by lacking a fossa and an articular eminence is very widespread. Unfortunately the problem does not seem to have received much systematic study, and the facts appear to be different from those usually quoted.

Before considering the articular fossa and eminence, it is convenient to

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* Marston (1952) from an analysis of skulls, believes "flat" wear to be characteristic of apes; Le Gros Clark believes it to be only an "occasional" finding in old apes, and characteristic of man.

deal with the flange-like plate of bone which, as Broom noted, may form a medial wall to the glenoid cavity of the gorilla. The process is very variably developed, and corresponds to the medial wall of the articular fossa in man. Sicher (1951), in his description of the human glenoid cavity, refers to it as the medial articular lip, and states that it is sometimes elevated into a triangular process, the temporal spine. When it occurs in the gorilla, it is simply an exaggerated downward development of the medial part of the squamous temporal (Fig. 9). From the point of view of the present comparisons the important point is that the medial articular lip in chimpanzees is often no better developed than it is in man.

In both man and apes the glenoid cavity is formed by the squamous temporal and the tympanic bone, which meet each other in the roof of the cavity in the squamo-tympanic fissure (more medially the fissure may be petro-tympanic due to the projection into the fissure of a process of the petrous-temporal). When the postglenoid process is well developed, the lateral part of the squamo-temporal fissure is not in the roof of the glenoid cavity but on its posterior wall, at the lower margin of the process. When the latter is as prominent as it is in adult gorillas, the fissure lies behind the posterior face of the process and, strictly speaking, is completely excluded from the glenoid cavity.

The articular fossa lies immediately in front of the fissure and postglenoid process. The posterior wall of the fibrous capsule of the joint is attached to the fissure and to the lower margin of the postglenoid process. Sicher (1951) points out that in the human skull the posterior part of the articular fossa, which is the posterior margin of the inferior part of the squamous temporal, is elevated into a ridge, called the posterior articular lip. In most individuals the posterior articular lip is higher and thicker at its lateral end, and thus appears in profile as a cone-shaped process between the articular fossa and the tympanic bone. This thicker lateral part is the postglenoid tubercle or process. According to Sicher "whether the posterior articular lip is reinforced to a postglenoid process or is of uniform thickness in its entire extent is not of practical significance."

The fossa, together with the articular eminence, is part of the squamous temporal alone. The main structural difference between the articular fossa of man and the apes lies in the fact that the human fossa is usually deeper and narrower, and therefore better defined, than that of the ape, in keeping with the more antero-posteriorly compressed and slenderer condyloid process of its mandible. This conclusion emerges from a study (Ashton and Zuckerman, unpublished) in which the position of the roof of the fossa relative to the articular eminence, postglenoid process, and other adjacent features was measured in seven hundred ape and human skulls.

There appear to be no significant differences between the condylar processes of adult human and ape mandibles except (1) that the human condyle is slenderer and more compressed from back to front; (2) that the human coronoid notch is bigger relative to the size of the whole ramus of the mandible, the condylar process itself consequently appearing bigger, and (3) that in keeping with the antero-posterior compression of the process, the area of attachment of the external pterygoid muscle to the neck of the process is more of a pit in the human than in the ape mandible, the neck of the human process thus appearing more slender. The orientation of the transverse axis of the articular head appears to be the same in apes as in man, and in both the articular surface usually extends slightly more on to the anterior than the posterior surface of the head of the mandible. In both, too, the form of the condylar process and of the articular surface may show fairly considerable individual variations (see Anthony, 1942; Schweitzer, 1951).

So, too, does the articular fossa, which in man, to quote Anthony (1942), varies in shape "with different nationalities, with different individuals, at different ages in a given individual, and sometimes on both sides of the same individual." Pronounced variations in the depth and contour of the fossa, and in the prominence and shape of the articular eminence have been demonstrated by many workers. But they are no greater than those that occur in the great apes, in which an articular fossa proper, and an articular eminence, which as in Man represents the anterior root of the zygomatic process, is the rule rather than the exception. The eminence can be recognized in very young human and ape skulls, and the view that the articular eminence in man does not begin its main development until the age of 10 or 11 (Humphreys, 1932) depends entirely on the interpretation that is placed on the term "main development." As Humphreys observes, and as Schweitzer (1951) shows in greater detail, both the shape of the articular head of the mandible and of the articular eminence are very plastic, and vary both with age and in accordance with certain clinical conditions which affect the mechanical functioning of the jaws, their form being modelled and remodelled through the absorption and deposition of bone.

In an occasional modern human skull the postglenoid process is as well developed as it is in some adult chimpanzees, although as a rule the process is very much more strongly developed in the great apes, and particularly in the gorilla. It is usually better developed in older gorillas than in young mature specimens. In the gorilla, too, a well-developed process almost always forms the lateral part of the posterior wall of the glenoid cavity, and thus shuts out the tympanic bone, which then only forms the medial part of the wall (Fig. 9). On the other hand the tympanic bone seems always to project below the human postglenoid process, when the latter is present, and thus takes part in the formation of the whole posterior wall of the cavity (Fig. 9). This it also does in the skulls of young apes. Occasionally one encounters a mature chimpanzee or gorilla skull in which this juvenile condition persists. On the other hand, in the gorilla skull the postglenoid process may be so well developed as to exclude the tympanic bone completely from the posterior wall of the glenoid cavity. The differences in this osseous relationship between man and the apes are partly due to the greater absolute prominence of the postglenoid process in the latter, and partly to the fact that the external auditory meatus in these creatures is relatively much smaller and less funnelled than it is in man.

Whether there is any anatomical justification for differentiating between a prominent and a slight articular eminence, or what Weidenreich (1943) calls a "planum preglenoidale," is doubtful. The planum and a well-defined eminence appear to be extremes of the same anatomical conformation. This actually emerges from Weidenreich's belief that infantile anthropoids "have a real (articular) fossa which vanishes as their age increases," i.e. as the head of the condylar process thickens with the increase in the size of the jaw. Weidenreich also draws attention to the fact that "the deep hominid (articular) fossa is without any functional value, since the articular disc levels the differences in height between fossa and tuberculum or planum preglenoidale; the thicker the fossa portion of the disc the deeper the fossa and vice versa. In the anthropoids the disc is thin and its fossa and tubercular portions are of the same thickness."

Nothing in the internal arrangement of the mandibular joint in man and the great apes thus leads one to suppose that there should be any difference in the way the joint works. Nor is there any indication of such difference when one considers the muscles, of which the main ones are the temporal, the masseter, and the medial and lateral pterygoids, on which the movement of the mandible depends.

Their arrangement in the gorilla has recently been described by Raven (1950). An acount of their disposition in the orang is provided by Boyer (1939), and in the rhesus monkey by Howell and Straus (1933). In no single particular, other than that of size, do the descriptions of the muscles in these sub-human Primates differ from the corresponding ones for man.

In man two basic movements of the mandible are recognized (see Sicher, 1951): (*a*) a rotatory or hinge movement around a horizontal frontal axis passing through the centres of the condyles, and (*b*) a forward sliding movement of the head of the mandible and the overlying articular disc along the temporal bone. Movement may be symmetrical or asymmetrical. The rotatory component takes place between the head of the mandible and the disc, and the sliding or translatory movement between the disc and the temporal bone.*

When the jaw opens naturally, at the beginning of rotation, the head of the mandible and the disc slide forward on to the articular eminence or plane. Opening of the mouth is usually said to be due to the action of the supra- and infra-hyoid muscles and platysma, aided by gravity, and to the relaxation of the temporal and other masticatory muscles. For the jaw to open naturally, however, the condylar process has to slide forwards. This movement depends on the contraction of the lateral pterygoid muscle, which is attached both to the joint capsule and to the neck of the condylar process. In a recent electromyographic study, McDougall and Andrew (1953) have obtained suggestive evidence that the masseter directly aids the lateral pterygoid in this action, as well as having a synergic action. Closure of the jaw is effected by the contraction of the masseter, the temporal muscle, and the medial pterygoid. The posterior and almost horizontally disposed fibres of the temporal muscles play a very important part in the process, in so far as they pull the head of the mandible back from the articular eminence or plane into the articular fossa. The more massive the mandible, the stronger are these fibres, as in, for example, the adult gorilla (Fig. 8).

According to a classical description, when the two pterygoid muscles on one side are in action, the corresponding side of the mandible is drawn forwards, while the head of the mandible on the opposite side remains comparatively fixed. The alternate action of the muscles of the two sides is responsible for the side-to-side movement which takes place during chewing. It is also believed that the chewing movements demand the co-ordinated alternate action of the right lateral pterygoid with the elevators of the left (that is to say the temporal muscle, the masseter, and the medial pterygoid). Wheeler (1950) emphasizes the fact that lateral chewing or grinding movements are possible because the two temporo-mandibular joints can act independently of each other. The movement is initiated by both lateral pterygoids pulling the condyles forward. The medial pterygoids then work in alternation. Thus, the left medial pterygoid pulls the left condyle forwards and inwards in a

* According to one standard anatomical text, the horizontal axis of the jaw does not pass through the centres of the condyles but through the mandibular foramina. It is now recognized, however, that the mandible does not constitute—as was once commonly taught—a lever of the third class, but that its fulcrum shifts because of the flexibility of the bilateral joints, and because of the independent action of all the muscles involved (Wheeler, 1950).

circular path with the right condyle as the pivotal point. The mandible then moves to the right. In the return movement the condyles retrace their path mainly through the action of the posterior fibres of the left temporal muscle, and the mandible may either return to the rest position, or the teeth may approximate, mainly through the action of the mandibular elevators, in what is called the masticatory thrust. The extent to which the jaw opens and shuts from side to side in grinding movements depends upon the amount of food in the mouth.

It is usual to explain the forward sliding movement of the human mandible as an action which is made necessary because of the restriction of free space behind the moving mandible, due to the development of a mastoid process. To the extent that such an explanation applies in man, it must also do so in apes in whom, if anything, the greater development of a postglenoid process intensifies the restriction.

The arrangement of the muscles and of the mandibular joint in the great apes thus provide no reason to suppose that they do not use their jaws in the way man does. It becomes necessary, therefore, to examine the proposition that a different use of the temporo-mandibular joint leads to a different type of wear of the teeth.

Wear of the teeth

In the great apes, and in catarrhine monkeys, the occlusal surfaces of the upper molar and premolar teeth incline inwards as well as downwards, and those of the lower teeth upwards and outwards (Fig. 11). In conformity with this orientation, the lingual cusps of the mandibular teeth are relatively more prominent than the buccal, the reverse condition holding in the upper teeth. In normal occlusion the upper teeth also "overhang" the lower, the buccal cusps of the lower molars fitting into the depressions between the buccal and lingual cusps of the upper teeth, and the lingual cusps of the upper molars being received in the corresponding depressions of the lower teeth. This "overhang" is partly related to the greater width of the upper teeth, and partly to the greater breadth of the upper alveolar margin.

The enamel of the teeth gets worn away as a result of the attrition of the frictional surfaces of the teeth, and the dentine becomes exposed at the points of greatest contact. Wear will consequently be most marked on the inner cusps of the upper teeth, and on the outer cusps of the lower molar teeth, since the opposite cusps, which are less in contact with the opposing teeth, are relatively more protected from attrition. It also follows that wear will begin to show itself sooner on the outer than the inner cusps of the lower teeth, and on the inner rather than the outer cusps of the upper. Thus wear of the teeth in the great apes tends to

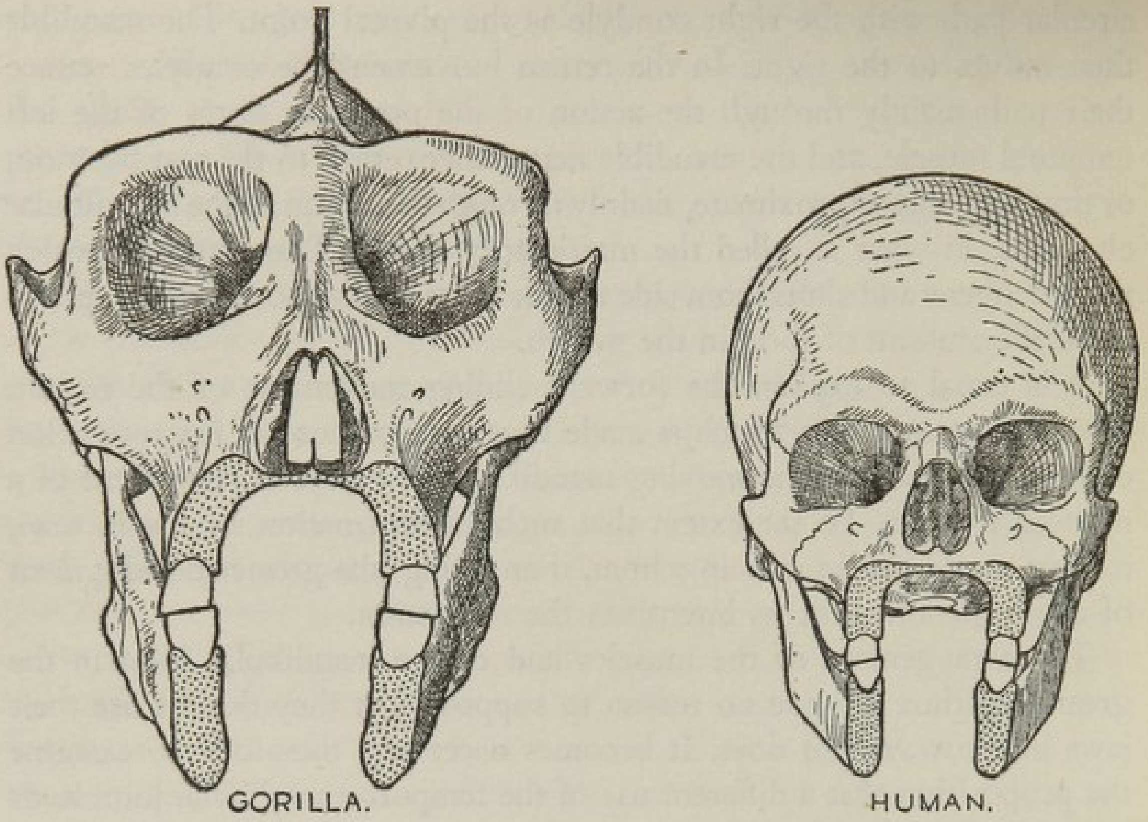

FIG. 11.—The plane of wear of the molar teeth.

emphasize the initial obliquity of the two occlusal planes of the grinding teeth.

The orientation of the occlusal surfaces of the molar and premolar teeth is in general the same in Man as in the apes, although the inclination of the occlusal surface of the upper grinding teeth is usually described as being directed outwards rather then inwards (e.g. Humphreys, 1921; in many skulls the premolars and first molars appear to be directed inwards). The arrangement of the upper and lower cusps relative to each other is also the same as in the apes and monkeys, and as in these animals, attrition begins to show itself first on the inner cusps of the upper molars and on the outer cusps of the lower—that is to say, on the less prominent but more "vulnerable" cusps (Fig. 12, see Hirschfeld, 1926; Schweitzer, 1951). In consequence of the continuing process of wear, the occlusal plane of the flattened upper human molars and premolars becomes directed downwards and inwards, as in the great apes, and that of the lower teeth upwards and outwards (Fig. 11; see Ritchie, 1923; Hirschfeld, 1926; Schweitzer, 1951). These changes are much more obvious in the teeth of primitive peoples (e.g. in the skulls of Australian aborigines, Eskimos, early British) than in those of modern city dwellers.

Almost all statements that contrast the manner of dental attrition in man and apes have been based upon theoretical appreciations of the movements of which the mandibles are capable in dried skulls (e.g.

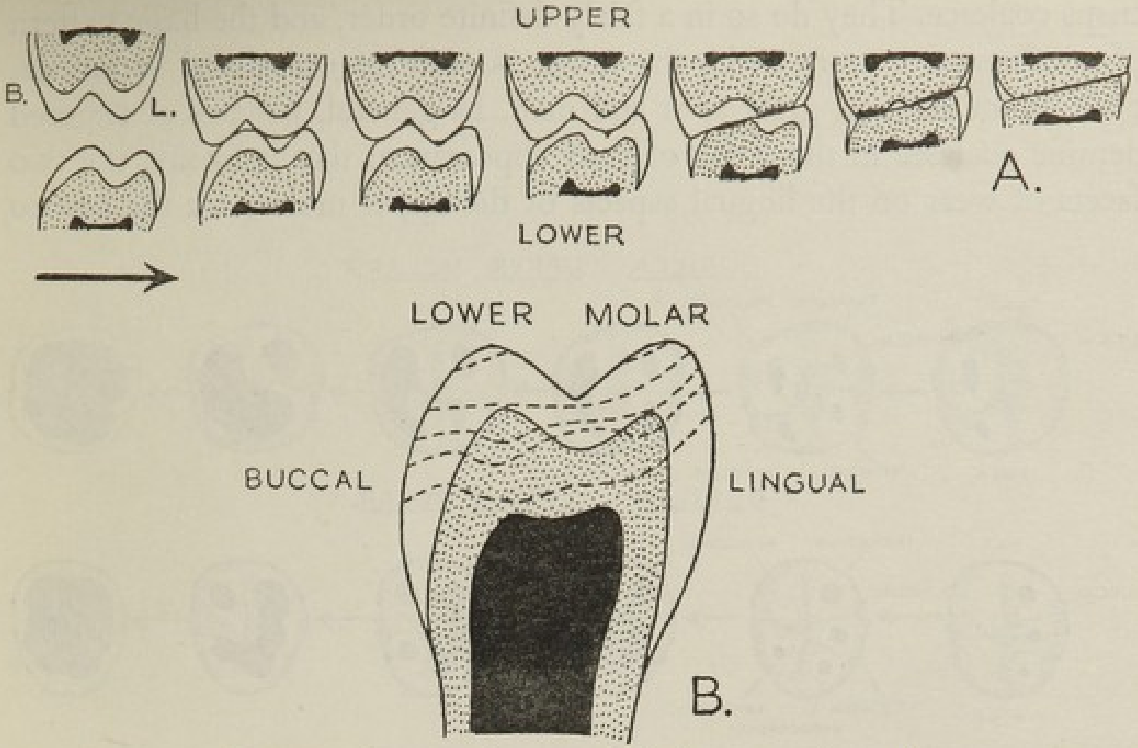

FIG. 12.—Stages in the wear of the human molar teeth (A) after Stein; (B) after Hirschfield.

Marston, 1952). In order to see whether there are any differences in the order and way the teeth wear, an analysis (Ashton and Zuckerman, unpublished) has been made of the order of appearance of the facets of wear on all the teeth in the skulls of about 500 gorillas, chimpanzees and human skulls. Each skull was examined, and the position and relative size of every facet of wear was marked on a schematic proforma. The preliminary results of this study are as follows: *Molar teeth*: The order of appearance of foci of wear is identical in man, the gorilla and chimpanzee, although deviations from the usual pattern may occasionally be observed (Figs. 12 to 14). Wear first begins on the protocone (the antero-lingual cusp) of the upper first molar, and the protoconid, the antero-buccal cusp of the lower first molar. Facets of wear then appear on the other lingual and buccal cusps of these two teeth respectively, and then begin to show themselves on the upper buccal and lower lingual cusps. By the time attrition facets have appeared on two or three cusps of the first molar, they begin to appear in the same order on the second molars, and in turn on the third. The detailed order of appearance on the lower molar is as follows: protoconid, hypoconid, hypoconulid, metaconid, entoconid, the entoconid and metaconid alternating in the order of appearance of wear. On the upper molars the order is as follows: protocone, hypocone, paracone, metacone, with considerable variation in the paracone, the antero-buccal cusp, and the metacone, the postero-buccal cusp.

As the process of attrition continues, the areas of wear on the different cusps coalesce. They do so in a fairly definite order, and the basic pattern of confluence appears to be the same, in spite of occasional variations, both in the African great apes and man. In general, patches of exposed dentine coalesce in the order of their appearance: that is to say, the two facets of wear on the lingual aspects of the upper molars are the first to unite, in the same way as are the three facets of wear on the buccal aspect of the lower first molar. The exposed dentine on the buccal and lingual aspects of the molar teeth unite in variable fashion, the first union sometimes occurring between the worn posterior cusps of the upper teeth, or occasionally on the antero-lingual and postero-buccal cusps (protocone and metacone). The last two patches of exposed dentine to coalesce are those on the two buccal cusps of the upper molars.

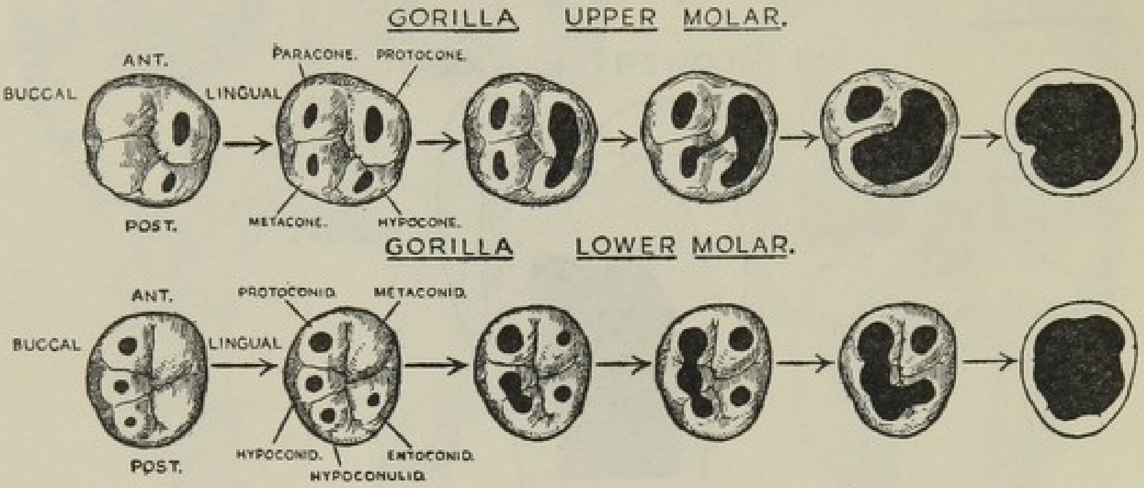

FIG. 13.—Wear in the molar teeth of the gorilla.

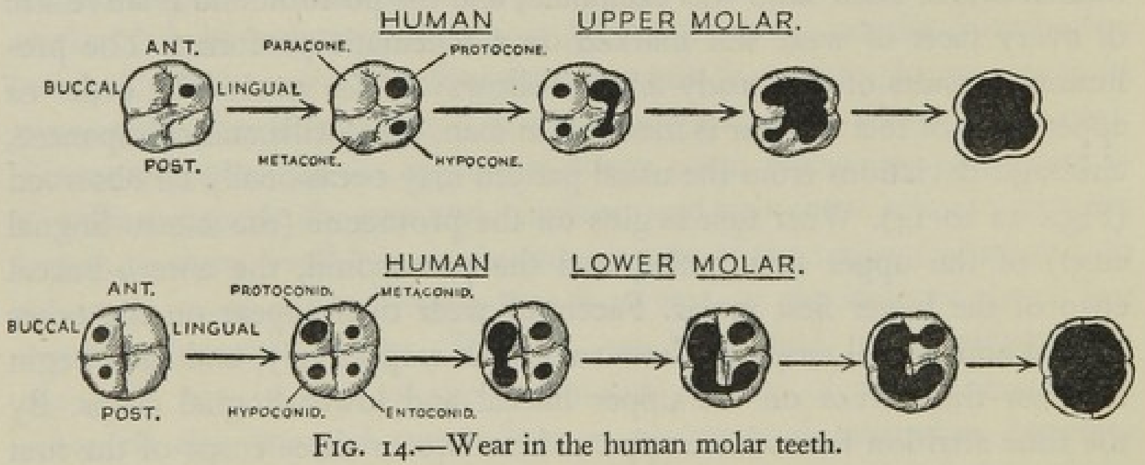

FIG. 14.—Wear in the human molar teeth.

The process of coalescence of patches of exposed dentine in the lower molars is the mirror image of what occurs in the upper, coalescence beginning between the exposed dentine on the outer cusps, and ending with the coalescence of the exposed dentine of the front inner and back inner cusps (see Figs. 13 and 14).

Both in the great apes and man wear of the premolars usually shows itself somewhat earlier than wear in the second molars (Figs. 15 and 16). Wear in the upper first premolar may begin either on the inner or outer cusps, but as the process proceeds, more dentine becomes exposed on the inner cusps. The process of wear on the lower second premolar is the mirror image of that of the corresponding upper tooth.

The first premolar of the great apes is "sectorial" in form, and has to be considered on its own. As a result of the development of its buccal cusp it becomes elongated, and its sloping antero-buccal surface forms, as it were, a whetstone for the lingual surface of the upper canines. In the up and down movements of the jaws, the postero-lingual surface of the upper canines play against the antero-buccal surface of the lower first premolar, so that wear occurs on both surfaces, and particularly on the posterior cutting edge of the canines and on the apical part of antero-buccal surface of the first lower premolar. At the same time wear, due to occlusion with the upper first premolar, begins on the posterior surface of the main (buccal) cusp of the first lower premolar, and extends on to the tip as a triangular facet (Fig. 16). Simultaneously, the rubbing of the postero-lingual surface of the lower canine against the anterior aspect of the upper canine causes wear on the two corresponding surfaces (Fig. 18). Wear then begins on the tip, the process starting in a small even area, and extending gradually, the process being a natural and not a traumatic one. Ultimately, as a result of the three types of wear, the canine

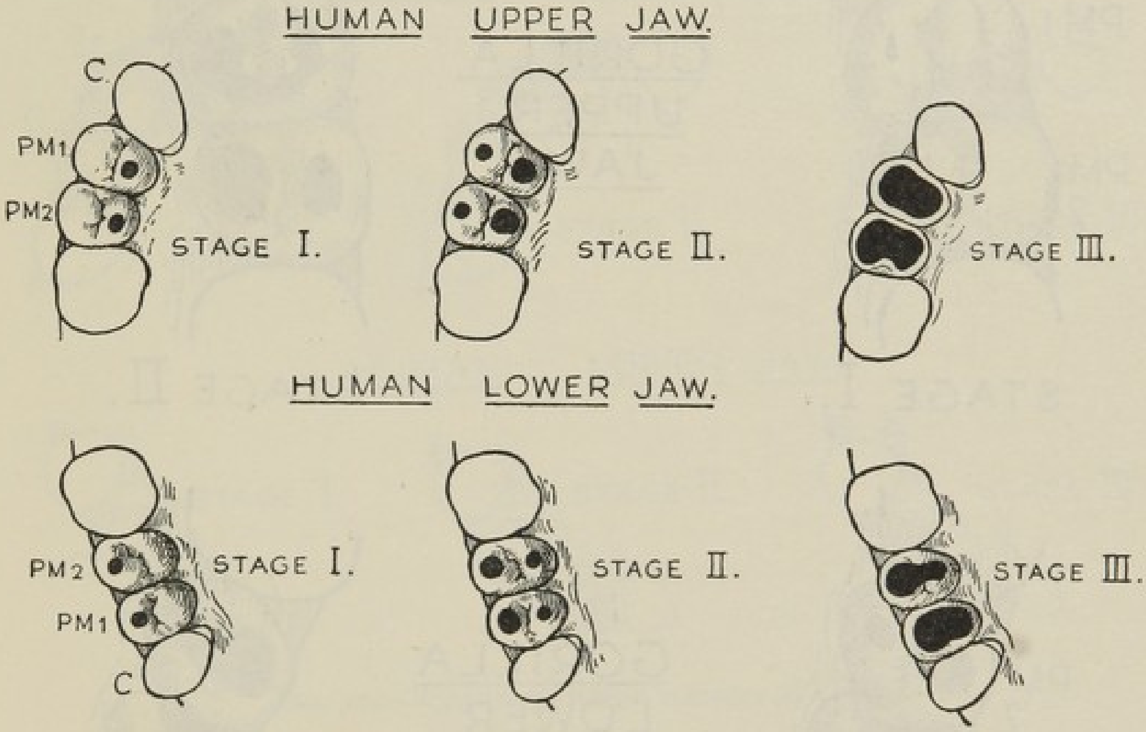

FIG. 15.—Wear in the human premolar teeth.

becomes worn down, until in old animals, it may become a simple flat peg-like structure with an exposed pulp cavity. Even at this stage, however, it is still often possible to identify the three facets of wear.

The manner of wear of the lower canine is complementary to these changes in the upper canine, with the additional factor of the abrasion of the antero-lingual surface of the lower canine against the lateral aspect of the upper lateral incisors (Fig. 18). The lower canine also gets worn down from the tip.

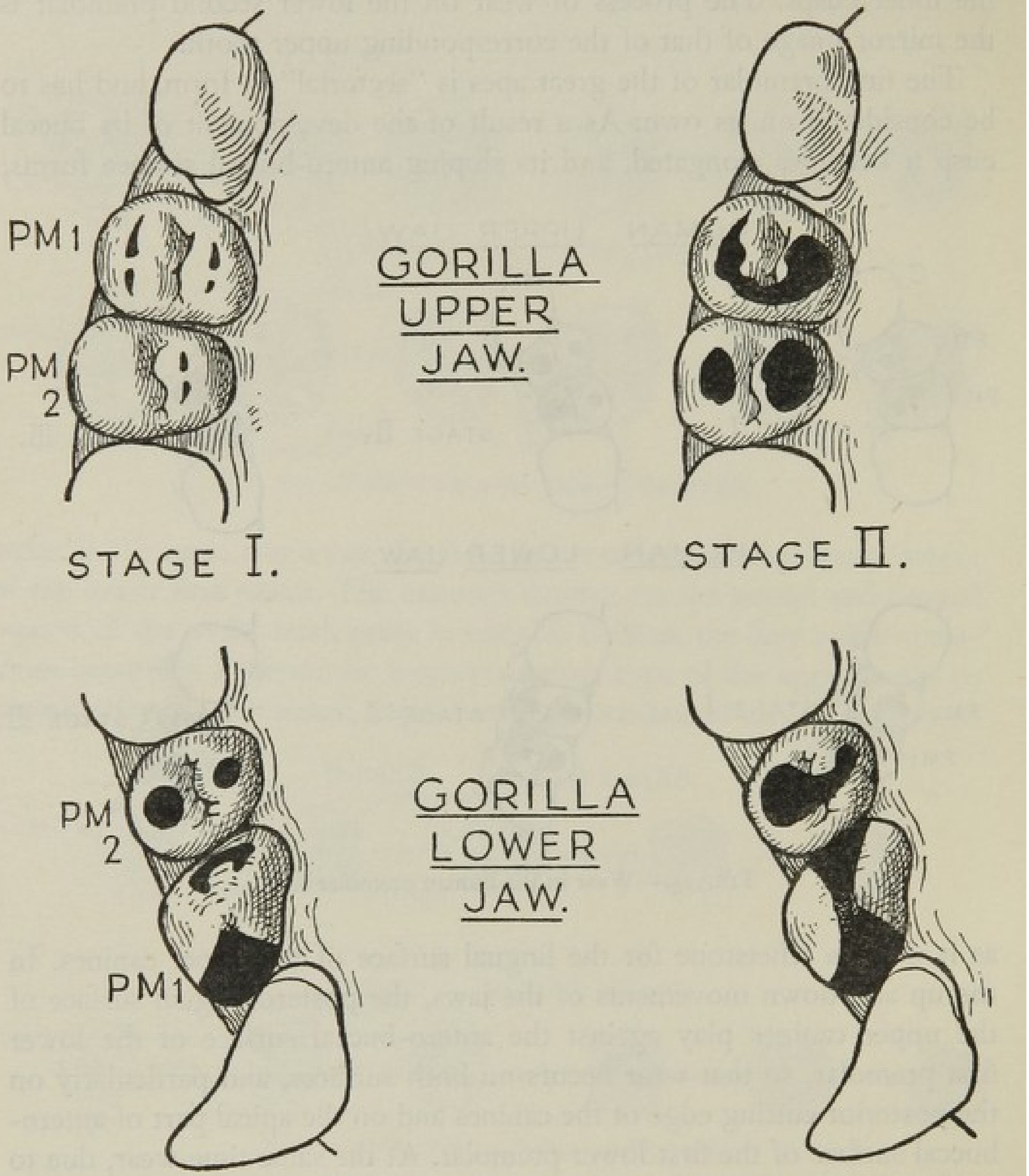

Fig. 16.—Wear in the premolar teeth of the gorilla.

The human canine invariably wears down from the tip alone, and not, as in the ape, from the sides as well (Fig. 17).

In both the upper and lower incisors of the anthropoid skull, wear starts at the cutting or morsal edge, and extends rapidly along the sloping lingual surface, the enamel becoming rapidly worn (Fig. 18). The fact that wear occurs on the lingual surface of the lower incisors is of great significance, since in the normal occlusion of a mandible and skull, the degree of "overbite," by which is meant the projection of the upper incisors over the lower, may be as marked as it is in the human skull. Overbite reflects itself in wear that occurs on the biting edge, and which may extend on to the anterior surface of the lower incisors. The fact that wear also occurs on the posterior or lingual surface can only mean that apes can freely protrude their lower jaws, presumably as a result of the contraction of the lateral pterygoids, and that in this position the lingual surface of the lower teeth becomes vulnerable to the opposing action of the upper teeth. A similar process of attrition is not uncommon in human beings, as can be seen from an examination of skulls from old burials. It also occurs in some modern skulls (Fig. 17). As a result of wear of this kind the incisors can be worn down, both in man and apes, until they are no more than blunt pegs capped by flat surfaces.

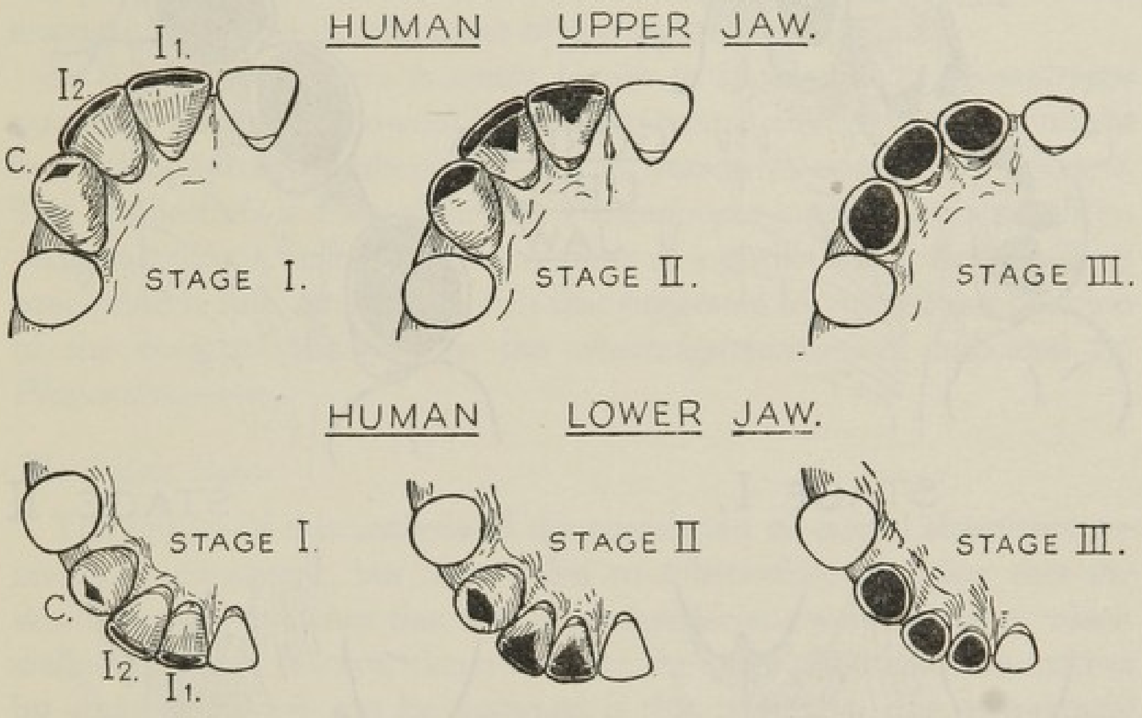

FIG. 17.—Wear in the human canines and incisors.

The remarkable similarity in the order of appearance and coalescence of facets of wear in the teeth of apes and man, and in the final results of the process of attrition, can only mean that if wear in man is due to a capacity to "grind" the premolar and molar teeth, then the ape is able to do the same. This conclusion will not be surprising to those who have studied living apes, for it is a matter of simple observation that chimpanzees, gorillas and orang-outangs chew their food in the same way that we do. In fact, what one normally observes in the great apes are rotary and grinding movements of the jaws, not up and down cutting movements. In turn this means that the presence of large canines does not preclude

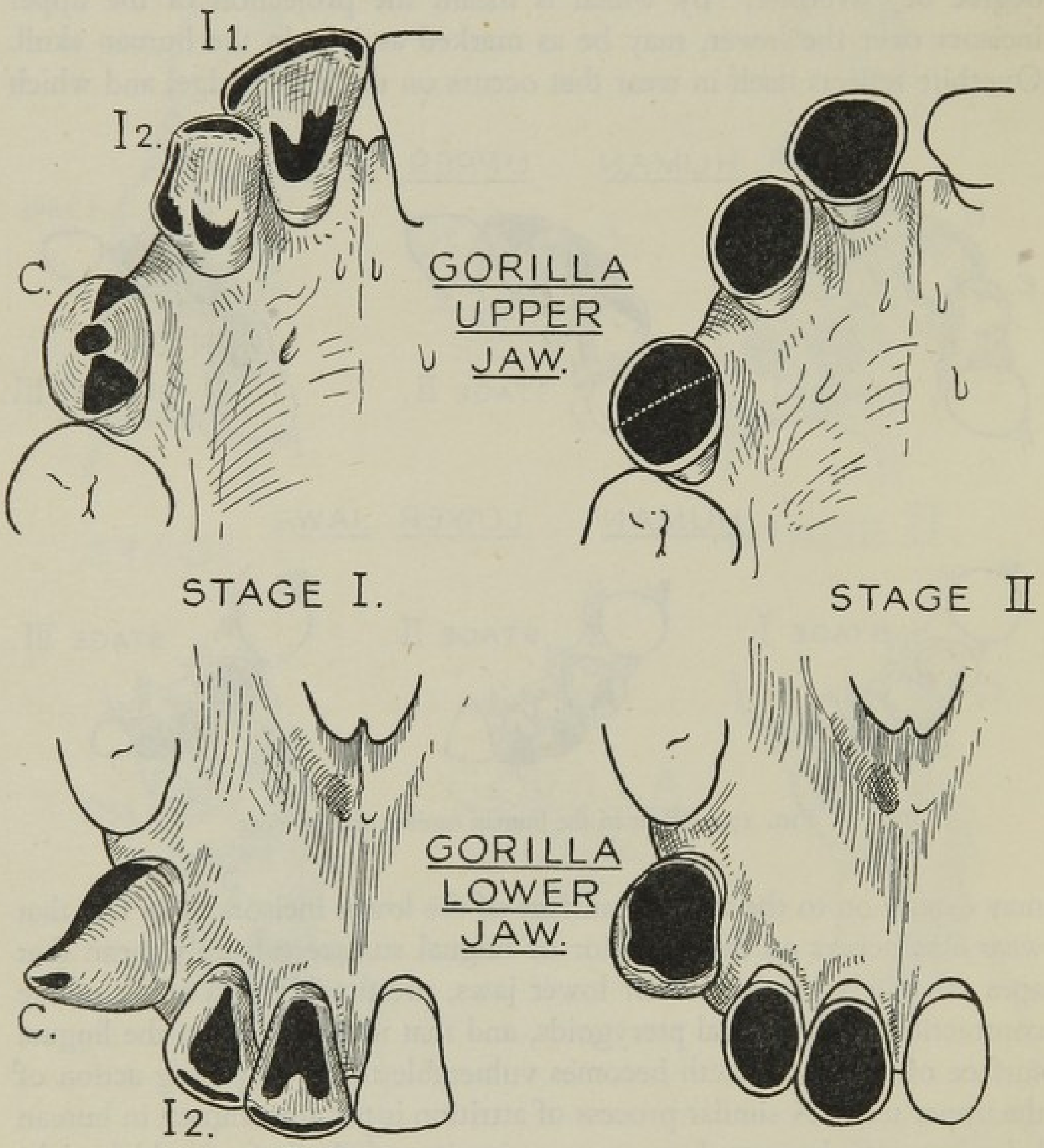

FIG. 18.—Wear in the canines and incisors of the gorilla.

the ape from moving his mandible in the lateral plane, and that protrusion of the mandible neutralizes any "locking" of the movements of the jaw which might otherwise result from the presence of large canines. The contrary impression which has been derived from an examination of the cranium and mandible relates only to such an anatomical preparation.

It follows from all this that if the teeth of *Paranthropus crassidens*, or of any other member of the *Australopithecinae*, became worn in human fashion, they, *ipso facto*, also became worn in the same way as an ape's teeth. It is, therefore, impossible to avoid the conclusion that *Paranthropus* possessed temporal muscles built on the same plan as those of apes—unless we now make the assumption that the Australopithecines used their jaws differently from both man and the apes. If we reject this possibility as altogether unreasonable, we have to suppose that the posterior horizontal component of the temporal muscle in *Paranthropus* was proportionately as well developed as the vertical fibres which were responsible for the development of the sagittal crests.

In other words, there is every reason to suppose that *Paranthropus crassidens* possessed powerful occipital crests, and a very prominent external occipital protuberance—and no reason to oppose such a view. The implication is thus clear that *Paranthropus* carried its head on its vertebral column far more in the manner of a gorilla than of a man. This conclusion is fully in keeping with that suggested by the relative position of the occipital condyles in the *Australopithecinae*, as indicated by *Plesianthropus* 5.

The Pelvic Bones

The results of this analysis of the correlation of cranial characters are internally consistent, but have failed to substantiate the view that the skull provides evidence that the *Australopithecinae* were creatures which walked erect. It follows, therefore, that the only published information by which this view can be sustained is that relating to the post-cranial skeleton. No purpose would be served by referring again to the inconclusive and ambiguous evidence provided by the limb-bones (see p. 310 above). Any categorical statement that the Australopithecines were creatures which stood, walked, and ran upright must for the present rest on the characters of the pelvis.

I have already noted that because of its short and broad ilium, and its well-developed sciatic notch and anterior inferior spine, the Australopithecine innominate gives an immediate impression of being hominid in character. It does so in spite of displaying, as Broom points out (Broom, Robinson and Schepers, 1950), an ape-like ischium which, as in the great apes, is "well removed from the margin of the acetabulum," as well as several other ape-like or intermediate characters (e.g. a more forward anterior superior iliac spine; a flat anterior part of the ilium; a different orientation of the iliac blade relative to the ischio-pubic part of the bone; and a small articular surface for the sacrum). From the presumedly non-ape-like features of the bones, the following main inferences have been derived by Broom and others: that the broad iliac blade of the Australopithecine innominate connoted muscles adapted to the erect attitude; that the short distance between the auricular surface and the acetabulum implies a better arrangement for balancing the pelvis on the heads of the femora; and that the well-developed anterior inferior iliac spine implies a powerful ilio-femoral ligament, which was necessary to prevent hyper-extension of the hip-joint in the erect attitude.

While the first two of these deductions appear convincing, it is doubtful what significance should be properly attached to the presence of a well-developed anterior inferior iliac spine. Such a spine may imply a ligament whose development is normally associated with the maintenance of the erect posture. On the other hand the spine is also well developed in many quadrupedal mammals, e.g. the menotyphlous insectivores, and many carnivores and rodents (Straus, 1929). More important than this, however, are the additional questions that are suggested by the non-hominid features of the bones. Probably the most interesting is the significance which should be attached to the fact, emphasized by Broom, that the sacral articular and iliac tuberous surfaces are very much smaller in the Australopithecine bones than in man.

Because of these unanswered questions, Mr. J. Williams, working in my Department, undertook a comparative study (using the methods of quantitative and qualitative description) of the innominate bones of fifty-four gorillas, chimpanzees and orang-utans, and of thirty-five human beings (seventeenth-century English)—the largest number of specimens which at the time could be conveniently assembled. His biometric technique was designed to yield data which were comparable, as far as possible, with those published by Dart and Broom. Additional measurements were also taken, with the bone always orientated in a specially designed apparatus so that the anterior superior spine, the posterior superior spine (defined here as the point on the iliac crest which lies farthest from the anterior superior spine), and the acetabular point (defined as the closest point on the internal margin of the facies lunata of the acetabulum to the anterior superior spine) were always in the same vertical plane. In this way thirty-three main dimensions of the innominate bone, including the areas of the gluteal, iliac and sacral surfaces, and angles of twist, were measured on each bone. From certain of these figures an iliac-height index, an iliac-expansion index, a sacral index, an obturator index and a pubic index were computed.

The detailed results of this study will be published in due course, and only certain of the main conclusions need be mentioned here. At the outset, however, it is necessary to emphasize that we fully recognize that thirty-three measurements are only a small fraction of an infinite number that could be made of a bone with the shape of the innominate, and that though their purpose was to define the shape of the bone, some dimensions may unwittingly have been excluded which could have materially assisted in this aim. Further, we are fully aware that many of the thirty-three dimensions that were taken may have been correlated with each other, and that no specific weight can be attached to a simple summation of differences or resemblances. With these qualifications, however, the results of the study are highly interesting, and indicate the urgent need for further study of the Australopithecine pelvic bones.

The comparisons were made only with the innominate bones of *Australopithecus* and *Plesianthropus*, since at the time no description of the *Paranthropus* bone was available. They showed clearly that in the bulk of their biometric characters, the Australopithecine bones resemble those of the ape, and particularly the orang, far more than they do the human. Thus in the total height of the ilium the two Australopithecine bones were significantly smaller than both the human and ape bones, whereas in their maximum iliac breadth they were smaller than man, but of the size usual in apes. Nevertheless the relationship of the height of the ilium to its greatest breadth was hominid, and not pongid, in nature. In both fossils, however, the extent of the gluteal areas was significantly smaller than in the chimpanzee and man, but of the size found in the gorilla, and in the case of the innominate bone of *Australopithecus*, in the orang. A precisely similar result emerged in the comparison of the sacral area. The size of the auricular surface, the area with which the sacrum articulates, was significantly smaller than in man, but similar to that in the apes. Further, the ilium "fanned" as in apes, and not as in man.

When the width of the ilium is expressed as a percentage of its height, the index (H) obtained is invariably more than 100 in man, and varies from 50 to 100 for the apes (including the 54 specimens used by Williams in his study and 25 reported on by Schultz, 1930). From this point of view the Australopithecine innominate is hominid. When the least breadth of the ilium is expressed as a percentage of the greatest breadth for the 54 specimens used by Williams (Schultz provides no figures for this index), the value of the index for the apes ranges from 25 per cent to 37 per cent and for man from 38 per cent to 50 per cent. Here the fossils are pongid.

How all this is to be interpreted from the phyletic point of view would seem to be largely a matter of taste. But there seems to be somewhat more justification for regarding the Australopithecine pelvic bones as revealing predominantly ape-like than there is for assuming that they show significant hominid affinities. The most important of the latter, in the sense that it has been most stressed, is undoubtedly the broad iliac blade. Whether the greater relative breadth of the ilium is indicative of the development of hominid gluteal muscles, and of the upright attitude is, however, open to question—for, as pointed out by Schultz (1930), the human ilium, relative to the length of the ischium, is not broader than that of the great apes. As he puts it, "the ilium of man has not really become broader than that of the gorilla but has only become very much shorter." This does not imply a greater development of the human gluteal musculature, even though the latter may in fact be relatively more powerful than in apes.

But whatever lesson one draws from the relatively broad ilium of the Australopithecines, the implications of the auricular surface and iliac tuberosity, which Broom describes as very much smaller than the human, are every bit as arresting, and they point in a completely opposite direction. Schultz (1930) has shown that the great relative size of these two areas in man is related to the erect attitude, and to the transmission of the weight of the trunk, head, and upper limbs on the sacroiliac articulations. Their smaller size in the great apes can be related to the more quadrupedal posture and gait of these animals.

In view of their equally small size in the fossil specimens, it is difficult not to believe that the Australopithecines walked in the same way as do apes. In short, the evidence for an erect posture, as derived from a study of the innominate bones, seems anything but certain.

CONCLUSION

The conclusions to which the present analysis points are clear. In the first place, our safest inference from the available facts is that the brains of the fossil *Australopithecinae* did not differ in size or conformation from those of such modern apes as the gorilla. In the second, we may conclude that the fossils provide no significant evidence of the major decrease in size of jaws and teeth which is presupposed by the thesis that the *Hominidae* evolved from non-human primate forms. And thirdly, the evidence is also clear that the skull of the *Australopithecinae* was balanced on the vertebral column as in apes rather than as in man, whereas it is far from certain that the innominate bones that are associated with these fossils betoken an upright gait of the kind characteristic of the *Hominidae*. This view about the poise of the head is based (*a*) on the position of the occipital condyles in *Plesianthropus* 5; and (*b*) on the fact that two specimens assigned to the species *Paranthropus crassidens* possess sagittal crests. The correlation that exists between the relevant cranial features makes it plain that the presence of these crests presupposes prominent nuchal crests and a nuchal shelf, and correspondingly, the presence of neck muscles as powerful as those which we find in modern great apes. This conclusion is inescapable unless we suppose that in the *Australopithecinae* the temporal muscle was not disposed as it is in all other Old World Primates, including man, and that the mechanism of the mandible in these animals was equally unique. This possibility would seem to be precluded by a number of considerations which I have put forward, and particularly by the facts about dental attrition to which I have drawn attention.

If the Australopithecine innominate bone is regarded as indicating an upright attitude, the considerations which I have advanced thus dispose of the idea that the anatomical features of the cranial and post-cranial skeleton are correlated in the sense, as has been suggested, that they jointly lead to the conclusion that the Australopithecines were bipedal creatures like man. Indeed, if they are correlated anatomical features, it would be in a sense opposite to what has been suggested, for there seems somewhat more justification for regarding the Australopithecine pelvic bones as revealing significantly ape-like than hominid affinities.

If we combine these various conclusions, the safest overall inference that can be drawn from the facts which have been discussed here is that the *Australopithecinae* were predominantly ape-like, and not man-like creatures. While the specimens assigned to this sub-family add considerably to our information about Primate fossil history, they provide no clear indication of the major anatomical changes one would expect in the transformation of a non-human Primate into a big-brained bipedal animal possessing articulate speech, and the capacity to use his hands to work with artificially-fashioned tools. The answer to the question put on page 303, whether the characteristics of the *Australopithecinae* conform either with the whole or a large part of the pattern of change that must have occurred during the transformation to manhood of a non-human Primate is thus, in general, negative.

Such a view is far more conservative than that stated by, for example, Washburn (1951), who believes that the evidence provided by the Australopithecine fossils shows clearly that men were bipeds first, and that "the brain is a recent and extreme adaptation." On the basis of this belief Washburn erects a superstructure of theory about the morphogenetic changes involved in the derivation of the hind-limbs of a bipedal ape-man from that of an ordinary ape. All this would be reasonable speculation if it were certain, as he suggests, that "the critical primary" evolutionary change in the emergence of man was a bending of the ilium which altered the disposition of the gluteal muscles in relation to the hip-joint. Other changes may also have been both critical and primary.

But the general idea, which Washburn supports, that one or more parts of the body may have evolved in a hominid direction while others lagged behind is certainly *a priori* plausible, and to the best of my knowledge has never been denied. It could be regarded as supported by the results of the present analysis, in so far as it shows that the Australopithecine head was carried like an ape's even if, as some contend, the pelvis was balanced on the femora as in man. A lack of morphological correlation of this kind, given that it in fact exists, would imply different rates, and even trends, of development in different part of the body. This is known to have occurred in other mammalian groups. As Simpson (1950) writes: "the same parts may evolve in different directions in different related lines, and different parts may evolve at different rates within the same line."

If we turn from the morphological issues discussed in this paper to those few anatomical features in which the *Australopithecinae* appear to resemble man rather than the apes (e.g. the possession of a single infra-orbital foramen; a reduction in the size of the canines), we encounter the same kind of difficulty in assessing the phyletic significance of the resemblances as we do when we try to decide the evolutionary significance of, say, the possession by the orang-utan of a pterion which follows the human as opposed to the African ape pattern. Moreover, the problem of determining the phylogenetic status of the South African fossils is not made any easier by the fact that no one knows the geological age of the limestone deposits from which they were recovered. As Simpson (1950) puts it, here we lack "the most essential historical datum" by which to judge the matter—"the age of the forms relative to other known hominoids." Rogers (1926), then Director of the South African Geological Survey, was of the opinion that there was little probability that the age of the deposits will ever be determined. Broom was inclined to argue that the *Australopithecinae* may have belonged to the Middle or Upper Pliocene, while Robinson (1951), who provides a more recent estimate from Broom's laboratory, suggests that the ages of the deposits "lie on and around the Plio-Pleistocene junction." As observed on p. 303 true *Hominidae* are known from the mid-Pleistocene.

The likelihood that the *Australopithecinae* belong to the Pleistocene is, of course, in itself no argument that they do not represent "the little modified descendants" of some creatures which stood in the direct line of our own descent. What argues against, rather than for, such a view is the anatomical evidence now available. If the view is to be sustained, we need a great deal more fossil material, not only in order to trace the *Australopithecinae* into Tertiary geological formations, but also for dispassionate anatomical study.

We can safely conclude from the fossil hominoid material now available that in the history of the globe there have been many more species of great ape than just the three which exist to-day. Asia, Africa and Europe were the home of apes of various kinds in the Miocene, Pliocene and Pleistocene. For all that is known about the extent to which the living great apes have diverged from their Miocene forbears, and particularly the extent to which they may have diverged in features of the post-cranial skeleton, it is every bit as likely that some of the Australopithecines represent the forerunners of the modern gorilla and chimpanzee, as that they were the ancestors of some group of protohominids; and far more likely than that, as has been claimed, they were themselves protohominids.

. . . . .

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