PRESIDENTIAL ADDRESS.

Homoplasmy or Convergent Development in Evolution.

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(Presented at the meeting of December 6, 1923.)

This meeting brings to an end the nineteenth year of our society, during which time we have held 216 meetings, thus only twelve meetings have been missed. This is a very good record for so small a society. The observations, captures, records, and descriptions, published in the twenty publications of nearly 2000 pages issued by our society, rank next to the Fauna Hawaiiensis in importance as contributions towards the knowledge of our insect fauna, and in regards to habits, life histories, and food plants, they are the chief storehouse of our knowledge. If our society had not been in existence during these nineteen years, few of these observations would have been placed on permanent record, and the loss to our science would have been great. The complete indices made for each of the four volumes so far completed have made the miscellaneous information scattered through our Proceedings easily accessible to future workers. Our small membership makes it impossible for us to publish our Proceedings upon the subscriptions and sales of our Proceedings, and the trustees of the Hawaiian Sugar Planters' Association have come to our assistance in a very generous manner. We all fully appreciate this help and trust that the good cause that they assist eventually comes back to them through the economic work which is made more possible with every increase in our knowledge of the fauna of the Islands. In no other group of tropical islands is the insect fauna so well known, the endemic insects so distinctly recognized from the later introductions, or the records of the later natural and artificial insect immigrants so fully observed and recorded, and in no other such group of islands has such knowledge been used to better advantage in the control of such insects as affect our economic plants.

To those of us who have been carrying on economic work along the lines of biological control, the following extract from a letter of the great French naturalist, Philibert Commerson, written 150 years ago from Mauritius, is of deep interest, for not only did he foresee the possible economic use that could be made of introducing birds and other animals into Mauritius, but he also clearly recognized the principle of the balance of nature or the struggle for existence.

"It is a misfortune that we have not here any of those birds which destroy insect life. It is only this island that affords the spectacle of great forests without a single woodpecker. That is the great enemy of white ants, other ants, large and small caterpillars. What a service one would render the colony if one could but introduce robins, flycatchers, magpies, shrikes . . . and other insectivorous birds which never touch grain.

"Small hawks, owls, etc., could be imported to keep check on the multiplication of the smaller grain-eating birds; as well as snakes of a non-poisonous kind to destroy the rats. It would even be useful to bring frogs to purify the fresh-water pools, etc., of the swarming multitude of gnat-larvae which abound in them." *

This is a remarkable passage, and opens up a lot of interesting reflections as to where Commerson would have ended had he not died a comparatively young man, a martyr to his zeal for scientific research.

But it is not upon these subjects, interesting as they are, that I wish to speak today, but upon the very different one of:

HOMOPLASMY** OR CONVERGENT DEVELOPMENT IN EVOLUTION.

This subject has formed the theme of many works, but I shall not touch upon its historic or bibliographic side, but I shall simply bring before your notice a few examples to show its universality in the animal world and suggest some of its bearings upon evolution.

In both the Protozoa and the Metazoa we find the same fundamental types of symmetry, i. e., radial, bilateral, spiral, leiotropic, dexiotropic, and modifications of these.† There are

* Life of Philibert Commerson, Pasfield Oliver (1909).

** Webster defines this word as: Resemblance between different plants and animals, in external shape, in general habits, or in particular organs, which is not due to descent from a common ancestor, but to similar surrounding circumstances.

† Kofoid, Nature, August 13, 1923, p. 253.

good reasons to believe that the Porifera or sponges (Parazoa) had a different origin from the Metazoa, the former from the Choanoflagellata and the latter from the Ciliata. Thus, it follows that multicellular animal organisms, with their attendant sexual method of reproduction, and the formation of ova and spermatozoa, has arisen at least twice independently of one another. The production of multicellular organisms was the most momentous step in animal evolution, and the fact that it occurred more than once in the animal world is of supreme significance.

In each great phylum illustrations of homoplasmy, or convergent or parallel development, can be found. The simplicity of the organization of Protozoa is not favorable to the recognition of such development, but students of those organisms could cite good examples.

Stephenson's * paper on Indian Oligochaeta is of great value from our standpoint, as he shows how parallel and convergent development has gone on in a number of genera, and he gives convincing evidence for polyphyly in some of them. I have contended for this in certain genera of Homoptera. This important paper should be consulted by all interested in this subject.

Many cases of homoplasmy could be cited from the Mollusca, but I will confine myself to those cases in which branchiae or gills are replaced by a lung or lung cavity. The animals included in the order Pulmonata all have a pulmonary sac. They are placed in two sub-orders, and are considered by many as having two distinct origins—the Basommatophora, originating from the Opisthobranchiata, sub-order Tectibranchiata, and the Stylommatophora from the sub-order Nudibranchiata. Most of the Prosobranchiata possess branchiae, but some possess pulmonary sacs; of the latter, some families (Cyclophoridae, Cyclostomatidae, Aciculidae) are placed in the sub-order Monotocardia, while others Helicinidae, Hydrocenidae, Proserpinidae are placed in the sub-order Diotocardia. Here we have four groups in which the branchiae have been replaced by lung cavities all having independent origin. Even if we disagree with the above

* Pro. Zoo. Soc. Lond. 1921, pp. 103-142.

classification, we have to admit two origins, viz.: Operculata and Pulmonata, and then within each of these we have to admit convergence of characters upon which the above classification is based. Thus, if we consider the genera of Prosobranchiata, which have pulmonary sacs as forming a monophylogenetic group, we have to admit that they have acquired the one or two auricles independently. The reduction of the shell has taken place independently within the Pulmonata and the Opisthobranchiata, and in each case is accompanied by, and may be the direct result of, the reflected epipodia, which gives protection to the visceral mass.

In another class of Mollusca, the Cephalopoda, we find a very complex eye which, in certain important points, parallels the eye of mammals.

As example of homoplasmy among Crustacea, I cite the Monstrillidae, belonging to the order Copepoda and the Rhizocephala, belonging to the order Cirripedia. Here we have some of the most extraordinary cases of metamorphoses, due to parasitism, in the animal kingdom, and certain of the most remarkable features being paralleled in these two orders. Parasitism has taken place in many of the large groups of animals and has led to reduction of organs and simplification of organism, and numerous cases of homoplasmy can be found among them. Hermaphroditism is found in the Cirripedia, Isopoda, and Epicarida, and have been derived independently from dioecious ancestors. This condition has arisen sporadically in many groups of animals.

Among insects many instances could be cited. The Honorable N. C. Rothschild, in his presidential address to the Entomological Society of London in 1917, pointed out the marvelous cases of homoplasmy among insect ectoparasites. In these we find the development of ctenidia, the form flattened horizontally, the legs situated far apart and spreading, the claws often of peculiar form, their femora with pseudojoints, all in insects so far apart as Diptera, Coleoptera, Heteroptera, and Hemimeridae (Orthoptera sens lat.). His concluding remarks are interesting:

"From the various examples of resemblance I have mentioned, it is evident that the medium in which a species exists, exercises a most powerful influence on its evolution. If that is the case of Epizoic insects, we are not far wrong in assuming that the similarities, often slight in themselves, which sympatric insects (i. e., insects living in the same district) exhibit, are due in the first instance to similarity in the surrounding primary conditions of life." *

Among the Hymenoptera we have some most extraordinary examples of homoplasmy in wasps which inhabit figs. The true fig-wasps, or Agaonides, are wonderfully constructed for the life they lead, especially the male, which never leaves the fig, and passes its life among the forest of fig flowers; it is wingless, or nearly so, flattened horizontally, in many cases the middle legs are reduced or rudimentary, and the mandibles are large for gnawing open the galls containing the females; in fact, their whole morphology has been modified to adapt the insect to its activities within the fig. Other fig-inhabiting wasps belonging to quite different groups of genera, not taking any part in the polinization of the flowers, have males modified along similar lines. A thorough study of the fig-inhabiting wasps, their relationship and homoplasmy, would well repay a number of years' close study. If any of the figs bearing open fruit have gall wasps attached to them, their study should be included, as they should throw light upon the origin of the relationship of insect to fruit.

Wheeler, discussing certain ants, remarks:

"We have here some very interesting cases of convergence, or parallel development, since the underground habit has caused the workers, which rarely or never leave their burrows, to lose their deep pigmentation and become yellow or light brown and to become nearly or quite blind."

Among the Arthropods we find many that breathe by tracheae, i. e., Prototracheata, Myriapoda, Insecta, Arachnida, and perhaps even Isopoda. If the tubes in Isopoda are really tracheae, then these organs had at least two distinct origins, and even leaving these out of account it is highly probable that among the four other groups tracheae arose at least twice independently. Gills have arisen quite independently in many groups, and several times in a single class, such as insects, and even more than once in the same order.

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*Pro. Ent. Soc. Lond. for 1916. September, 1917, cxli, clvi, and figs.

Among the Amphibia the Apoda, or limbless Amphibia, give an example of homoplasmy. Writing of these, Gadow remarks that:

"About forty species are known, these have been placed in seventeen genera, mostly on comparatively slight grounds, and several of these genera are probably unnatural, the distinctive characters having undoubtedly been developed independently in various countries." **

Among the lizards we find five families without limbs which have evidently lost them quite independently of one another. The burrowing snakes have a number of characters in common, but they have more than one origin.

According to many authorities, the birds are not descendants of the Dinosaurs, in spite of the many characters common to both. However striking these characters are, "they are instances of convergent analogies, the upright walk, which has been assumed and improved upon independently by members of both Theropoda and Orthopoda, has produced the same, or nearly the same modifications in them as in birds." *

Among the mammals we find the Metatheria or Marsupials and the Eutheria developing along independent lines, but reaching a number of very similar results. As an example, I quote the Marsupial mole (*Notoryctes*) and the Eutherian mole (*Talpa*) and its allies.

The Cetacea or whales, the Sirenia and the Carnivora Pinnipedia have traveled along the same lines of development independently, and the fossil reptile *Ichthyosaurus* has also traveled along the same lines, which is similar to the normal form of fishes, and apparently is the best adapted to life in the water. In these cases there are innumerable characters in morphology and anatomy which had to be modified to convert these land, or at most amphibious, animals into complete or nearly complete aquatic animals. Some birds have also taken to aquatic life and have been independently modified along lines to fit them for that element. Many insects belonging to different families have also been modified along lines adapting them for a life in the water.

** Camb. Nat. Hist. VIII, Amphibia and Reptiles, p. 89 (1901).

* Gadow, Camb. Nat. Hist. VIII, p. 416 (1901).

Flight, or the power of moving through the air for some considerable distance, has been acquired by animals in different classes, such as fishes, lizards, birds, and mammals. In the case of birds and bats, although the details differ, yet the conversion of the front limbs into organs of flight have been paralleled.

Nearly all the examples cited above are functional homoplasmy, or adaptations of certain organs for certain uses, and it is of great interest to note that the great majority of the most conspicuous cases of homoplasmy are of that nature, for it shows very forcibly the direct or indirect influence of the environment upon the organism.

But there are innumerable cases of homoplasmy in which it is difficult to connect any functional use. Such are well known to any systematist who has worked at a large group and has attempted to draw conclusions as to their relationship. Every entomologist could cite innumerable examples, so I will only refer to a few of those which I find in the group which I have paid most attention to, and recently published upon, namely, the fulgorid Homoptera.

In fulgorids we find a vein in the fore-wing, which is generally considered as the costa. In many forms, including what I consider to be the most primitive, we find this vein coincident with the costal margin, but in others it is some distance from the margin and thus forms a precostal cell or "costal area" which is often crossed by a number of veins. This condition has arisen at least twice among the fulgorids and most likely several times. The amalgamation of the basal portion of the veins has taken place many times quite independently, even within a single family; the commonest is the amalgamation of the subcosta and radius, but the radius and media have also amalgamated together; and also the subcosta, radius, and media. The clavus is normally closed, but in more than one family (i. e., Derbidae, Flatidae, and Fulgoridae) it is found to be open in some genera. Among the Flatidae there are some genera in which the claval veins do not form a fork, a condition peculiar to the Cicadoidea. The arrangements of the branching of the veins and the conditions of the cross-veins are paralleled many times in the superfamily. The reduction of wings in the superfamily has taken place many times quite independently. Another character used in classifying these insects is the condition of the carinae on the frons, whether there be one simple carina, or if it be forked, or if there be two. These conditions are found quite independent of one another in different families and in groups in the same family. The condition of the antennae is also used in some families, and here again there is no phylogenetic connection between those having large, flattened antennae, as they are found in more than one group of a single family (i. e., Delphacidae). In the Derbidae we find the sub-antennal process and shoulder keels developing quite independently, and the latter forming a large antennal chamber in widely separated genera. It may be objected that the present classification of these families is not "natural," and hence the apparent homoplasmy, but in whatever sequence or order these genera may be placed, cases of homoplasmy will be found.

This condition is not peculiar to the fulgorids, but is found in every group of insects of moderate size which one studies. Timberlake, in discussing a single family of Hymenoptera, the Encyrtidae, remarks:

> "The bewildering plasticity of the group whereby the same character may have been developed independently in different genera (as, for instance, the fascicle of hairs at the apex of the scutellum in *Encyrtus*, *Cheiloneurus*, and *Chrysoplatycerus*.)" *

These few cases of homoplasmy, out of vast numbers which could be cited, have not been brought to your notice out of idle curiosity, but because I believe that they are important evidence in the one great problem which should be at the back of all zoological studies, viz., evolution.

Although I appreciate and admire the vast amount of experimental zoology that has been done within recent time, yet, when it is all considered, it does not give direct or indirect evidence enough to base a belief in evolution upon. This belief is based upon nature's own experiments, upon our studies of development, comparative morphology and anatomy of living and fossil animals, upon the geographic distribution in past and present time, and the time sequence as shown by fossils. Most of this information is the direct result of systematic zoology. If all

* Timberlake, Proc. Ent. Soc. Wash. 25 (3), p. 58 (1923).

this evidence was wiped out, the evidence founded upon experimental zoology would not prevent William Jennings Bryan from expunging the teaching of evolution from American schools. Yet we are constantly being told that systematic work is only worthy of inferior intellects, and that great intellects turn their attention to genes or tropisms, or other superior subjects.

The fact that animals have adapted themselves so wonderfully to their environment, independently arriving at similar resuts on more than one occasion, would make one believe that Lowell's famous lines:

> ''Some flossifers think that a fakkilty's granted the minnit its proved to be thoroughly wanted.''

contain more truth than sarcasm.

Everyone who studies the subject must admit that adaptation runs through the whole animal kingdom, and most will admit the frequency of homoplasmy. Nearly every zoologist who believes in evolution will also admit that the environment, in its widest sense, has been the great "potter's thumb," moulding the organisms in form and habit. The great rift comes when biologists begin to discuss the manner in which this moulding has taken place. This has divided them into two great camps, one following Weismann and the other Lamarck.

Weismann contended that the germ plasm passed from generation to generation continuously, without a break, absolutely uninfluenced by the body cells or soma. Thus, any influence which the environment might have upon the soma could not be impressed upon the germ plasm. As the soma arises from the germ plasm at each generation, it follows that the only means by which heritable variation can arise is by an alteration of the germ plasm. While Weismann considered that the environment might produce modifications of the germ plasm similar to that produced on the soma (parallel modification) many of his followers do not admit this, but maintain that the germ plasm cannot be influenced by the environment either directly or indirectly. According to this extreme school, all variation arises through the mixing and sorting out of the genes during the mating of the sperm and egg. In this kaleidoscopic shifting of the genes, or particles of the chromosomes, the chances of the combinations of characters that are necessary arising in the necessary consecutive order, without any inimical combinations, are so enormous that one's faith falters, and one turns to seek a solution which requires a smaller draft upon our credulity. That similar sequences should have occurred two, three, or more times quite independently is still harder to believe. This has been aptly called the "lucky throw of the Mendelian dice," but the dice are not six-sided, but very many-sided, and many sides bear death upon their face, and others bear indifference, and among the remainder only certain sequences are allowable, and the banker is Death and Oblivion.

But even to those whose faith is greater than mine there are other obstacles. While there is a large amount of negative evidence to support Weismann, there is also some positive evidence which is against him. That the continuity of the germ plasm is not so universal as he thought, is evident from work such as Gatenby's on the formation of new egg cells during sexual maturity in frogs. Kammerer's work cannot be ignored by his opponents, and the work of Guyer and Smith on the eyes of rabbits is a strong point against him. The more recent work of Garrett and Harrison on melanism among British moths is of great interest, for here we find that melanism caused by certain metal salts is inherited, and follows the Mendelian law.*

Turning to the other school of thought, we find few today who hold the crude views of a past generation. Early in the development of animal life a mechanism must have been developed to guard against individual mutilations becoming incorporated into the race, otherwise we should have nothing but maimed and helpless races of animals.

Fortunately, we have a few leaders who can see the virtues and vices of both of these extreme schools of thought, and who are combining the best in each into a more workable theory. In the study of the development of the phylum, as well as the individual, the great task is to discover the mechanism by which similar cells develop into totally different organs, having vastly

* Melanism in the Lepidoptera and its Possible Induction, Nature, August, 1923, p. 240. See, also, Nature, September 16, 1922, p. 380.

different functions and shapes. This cannot be due to the chromosomes and genes, for all the cells are equally endowed, but it must be due to forces external to these chromosomes, by which some of the latent capacities of growth are suppressed, while others are encouraged. Some light is being thrown upon this most interesting problem by recent discoveries in cell activities and harmones, and in the harmonic relationship of various parts of an organism. This most important and fascinating subject is but in its infancy, but already it appears to have thrown some little light upon Lamarckian factors and the inheritance of acquired characters. The post-pituitary harmone is responsible for the change of color in the skin of the frog which is of a protective nature, and, if we accept Kammerer's experiments, individuals born of parents that have lived in dark or light surroundings are correspondingly light or dark, which most likely is caused by the influence of the harmones on the germ plasm. Guyer and Smith's experiments on the eyes of rabbits may also be due to similar influences. Along this line of thought we may eventually find the mechanism by which we can understand, to some extent, the effect of use and disuse upon the organism. But we must co-ordinate the studies of form, function and development, or morphology, physiology and embryology.

This subject also has direct bearing upon the subject of this address, viz., Homoplasmy, for if environment in its widest meaning can affect certain organs or characters in one animal it is likely to do so in many others. The reduction of eyes in cave-dwelling animals may then be due to the absence of stimuli and not to "chance throws of the Mendelian dice"; and if we admit the possibility or probability of this, then the reduction of organs in parasitic animals may also be due to the absence of stimuli. And then it is not a long step to the production of similar characters in different animals living under similar conditions. That they do develop such is common knowledge. The question at present at issue is whether this is due to harmonic relationship between the animal and its environment or to "chance throws of the Mendelian dice."