Parasitism and Symbiosis in Relation to Evolution

A Criticism of Prof. Portier's Theory of Universal Symbiosis

By Prof. Maurice Caullery, of the Sorbonne

Prof. Caullery is a distinguished member of the Faculty of Sciences of the Sorbonne, and is an eminent authority on the science of evolution. Both he and Prof. Portier have done valuable, original research work in biology and we are glad to give our readers the opportunity to compare their contrasting views with respect to the interesting subject of parasitism. The following paper delivered at the Sorbonne, Nov. 5, 1919, *is the opening address of a series of lectures entitled "Evolution of Living Organisms."*—EDITOR.

I WILL begin my subject by stating briefly the reasons for its choice.

Everyone is cognizant at the present time of the critical phase through which the transformist problem is now passing, a phase indicated by F. Le Dantes in 1909, in the title of one of his books: *The Crisis of Transformism.* This crisis, while a very real one, is undoubtedly merely a crisis of growth. For my part I do not seek to solve this problem, as does Le Dantes and I am ready to acknowledge that the great solutions in which more than one generation of naturalists have had entire faith, namely, Lamarckism and Darwinism, are today quite inadequate, at any rate, in their orthodox forms.

The study of all nature tends to impress upon our minds the conviction that living organisms have undergone a process of evolution and that they have passed through manifold stages before becoming the species whose fossil remains we find and those which are now living under our very eyes. But we do not yet know, it must be acknowledged, the nature of the essential factors in this evolution. All of the experiments hitherto made in the endeavor to furnish experimental proof of the possibility of transformation by natural selection or of the heredity of acquired characters have yielded but meagre results. And in the presence of these results the experimental study of heredity and of variation which have been pursued so actively and so fruitfully since the beginning of the 20th century, lead us provisorily at least, to conclusions which it is difficult to harmonize either with Darwinism or with Lamarckism. It is true that they themselves lead—at least when carried to extremes, to singular paradoxes, as was shown by W. Bateson, in 1914.[1] It is true, also, that what have seemed the best founded hypotheses in the world of science, such as that of universal gravitation or of the principles of electro-magnetism, have also finally encountered objections which have temporarily arrested our opinions with regard to them.

As regards living organisms the conformity of their structure to the conditions in which they live—their *adaptation* in a word, a fact of such general occurrence in nature and so impressively illustrated in the structure of living creatures, can no longer be explained with the beautiful simplicity of Lamarck's theory as being due to the direct action of the surrounding medium modeling the organism by means of its own activities. It seems rather more probable in fact that when the organism undergoes variations it reacts in a manner which is proper to itself and which is derived from its own constitution through the most varied factors which are capable of inciting it to action, and furthermore, that it passes either continuously or discontinuously through a series of forms which progress towards a definite end.

ORTHOGENESIS.

It is this idea which Eimer has tried to express by the word *orthogenesis* and this idea holds a place of prime importance in biology. Thus, one branch of the *Ondulidae*, starting from some ancestor analogous to the *Phaenacodus*, finally produced the horse, the *equidus* and in the same way the elephant type was gradually developed from the *Paleomastodon.* At the present time we have more and more numerous examples of series of this sort. The surrounding medium can have had at most merely an indirect action upon the development of these series . . . accelerating them, perhaps, or retarding them, or possibly exerting upon them a relative effect of elimination.

Under the influence of these data we have seen the reappearance even among those biologists who are rather strong partisans of evolution concepts similar to those which opposed Darwinism upon its origin. Thus D. Rosa has recently published under the title Hologenesis,[2] a theory in which he expresses upon the whole ideas similar to those of Naegeli, and in which he attributes evolution entirely to the interplay of the initial factors in the constitution of the organism.

HOLOGENESIS.

If adaptation is not necessarily a direct and normal effect of the action of the milieu upon the organism, we are led to conclude that it results secondarily from the choice by the latter of a mode of life suited to its previous constitution. This is what Cuénot has called *Pre-Adaptation.* The idea is by no means new; Darwin sought to ascertain how selection could have brought about the tongue of the wood-pecker, which is so marvellously adapted for the search for insects in the bark of trees. But Buffon, one of the forerunners of the transformationists, had already, in describing the behavior of these birds, come to the conclusion that "thus is the instinct of a bird bounded by a miserable and wretched life. He has received from nature organs and instruments appropriate to this destiny, or *rather he derives this destiny from the very organs with which he is born.*" Thus it is in the organ which creates the function instead of vice versa as in the aphorism of Lamarck.

Even if this explanation be fitting in certain cases, as might be suggested by modern experimental researches upon heredity, one would hesitate to assume its general application in view of the mass of adaptation arrangements which exist in nature and in view especially of the graduated series which they present. Would it be possible for a harmony so close and so thoroughly coördinated with the milieu to exist if the latter played no part in its accomplishment? Could a fact of such general occurrence possibly be due to a simple series of coincidences between the mileu on the one hand, and the constitution peculiar to the organism on the other, together with the laws necessary to their transformation? This is aside from a theological or creationist idea.

What still more gives us pause is, that under our very eyes we perceive that the reaction of the individual to the milieu is in a large measure adaptative; the transformation which a plant undergoes in passing from a lowland environment to a mountain environment, or vice versa, furnishes proof of this, but its adaptative modifications do not appear to be hereditary. Perhaps the solution of the difficulty lies in the general indications furnished by paleontology. The different types have not varied in a uniform and permanent fashion. Each one seems to have had its period of variability. During this period we may ask whether the hereditary variations were really independent of the milieu as we observe them to be to-day in organisms which are, perhaps, in a certain phase of stability, or is it true, on the contrary, that the individual adaptative reaction was hereditary.

[1] Presidential address delivered before the British Association for the Advancement of Science (The Australia meeting, 1914).

[2] D. Rosa, Ologenesi (Nuova Teoria dell Evoluzione, etc.) (Hologenesis—New Theory of Evolution, etc.). Florence, 1917.

However this may be the problem of the adaptation remains of prime importance. The phenomenon of parasitism affords an excellent domain in which to study this question, at the same time examining in this connection the question of variation in all its manifold aspects. Furthermore, there is a physiological as well as a morphological problem.

PREDATORYISM AND PARASITISM

From the physiological point of view, in fact, the phenomenon of parasitism presents a series of problems of the greatest possible interest as regards general biology.

To begin with it affords an excellent domain for the study of the reciprocal influence exerted by organisms. All organisms are separate entities and they are mutually engaged in the struggle for existence. The latter is a capital phenomenon, the investigation of which is one of Darwin's greatest titles to fame. But the bond between the parasite and its host is a definite one and the reciprocal action of the two antagonistic parties is definitely limited. But it is necessary here to define parasitism. A parasite is an organism which lives at the immediate expense of another organism, feeding upon the substance of the latter or utilizing the activity of the host's organs in order to obtain the substance of its own body and to accomplish its biological cycle. Except in the case of plants, which assimilate directly the carbon or the nitrogen of the atmosphere and the mineral substances of the earth, all living creatures nourish themselves at the expense of other organisms, and thus might be said to be parasites in a certain sense. But in ordinary conditions the animal kills and devours its prey; it destroys the latter in fact. This sort of life is called *predatoryism* and is properly distinguished from parasitism. The parasite feeds upon the organism at whose expense it lives without destroying it; it exploits the host to a certain degree in a methodical manner by turning aside to its own profit a part of the energy expended by the latter, thus occasioning more or less damage and exerting an action which is often more or less pathogenic in nature, but which is sometimes, on the contrary, perfectly tolerated.

One finds in nature a continuous sliding scale of stages intermediate between predatoryism and parasitism. Sometimes also two living creatures are associated together in a dependent relation, which constitutes to a certain degree an exploitation of one by the other, without there being, however, any direct borrowing by the second organism from the first.

COMMENSALISM

This phenomenon is known as *commensalism*, in other words, as the Latin origin implies, two organisms "eat at the same table." Thus for example, the *Nereilepas fucata*, a polychete, Annelid which is always found at the bottom of the shells of Gastropods (such as the Buccins) inhabited by the Pagures (*Pagurus bernhardus*) profits by the current of water which the Pagure creates in order to draw towards itself the prey upon which it feeds; some of the latter are thus turned aside from the Pagure to the Annelid. But the latter is not a parasite, it is merely a table companion, i.e., a *commensal*. It is difficult, therefore, to draw a definite line between commensalism and parasitism. Certain creatures, such as many of the Infusoria, like the Urceolaria, the Trichodins, and the Vorticellæ live in the homes of other animals of necessity; they are termed *Epizoa;* they are likewise commensals while at the same time borrowing directly from the animal which bears them the power of locomotion as well as very often the condition of aeration and of renewed water supply which are assured by the play of the gills of the host.

One of the characteristics of parasitism is the *fixed nature* and the *necessity* of the relations between the host and the parasite. A true parasite cannot fulfil its vital cycle without the aid of its host and lives at the expense of the latter. These associations are very precise in their nature, however, and are more or less intimate. But it is not always easy to say that in such an association one of the associates suffers at the hands of the other; there are certain very distinct cases in which it can be demonstrated that there is a physiological advantage, in, sometimes a *necessity* for, such an association on both sides. Thus these complexes of two organisms which mutually benefit each other and have a reciprocal intimacy constitute *symbiosis.*

SYMBIOTES.

In a recent book by M. P. Portier, *Les Symbiotes* (Prof. Portiers' views were described and discussed at some length in an article entitled Symbiosis, by May Tevis, which appeared in the *Scientific American Supplement* for November 15th, 1919), the author endeavors to establish the view that symbiosis is not only a phenomenon of general character but one of the fundamental bases of the life of a cellular organism. He regards the cell which is unanimously considered by modern biologists as the fundamental and indivisible organic unit, as being in truth a symbiotic association. In other words his idea is that the cell alone is incapable of existing without containing within it certain bacteria—true symbiotes—whose power of direct assimilation is employed for the benefit of the cell as well as for their own advantage, and M. Portier believes that he can recognize in the organites known to histologists as mitochondria, these symbiotic bacteria or bacteriods.

Autotrophs and Heterotrophs.—According to this author, therefore, living organisms are divided into two classes, namely autotrophs, i.e., bacteria, which are sufficient to themselves and heterotrophs, i.e., organisms having a cellular structure which assimilate their nourishment by the aid of autotrophs.

The capital importance of such a concept is at once evident. Its partisans declare that it will bring about a transformation of the primordial ideas of biology comparable in importance only to the revolution produced by the discoveries of Pasteur. But no matter how clearly expressed and how suggestive a theory may be, it is of value only in case it has been verified by the facts in the case . . . I do not hesitate to declare formally that up to the present time the author has not demonstrated anything convincing as to the justice of his hypothesis, and I believe that objections of fundamental importance may be proved in opposition to it. I make this statement unreservedly, but I am, of course, bound to prove the objections I advance.

OBJECTIONS TO THE THEORY OF UNIVERSAL SYMBIOSIS.

From the physiological point of view the study of parasitism includes a number of other problems. A parasite always lives upon a special sort of host and this specificity, which is always comparatively definite, is sometimes absolutely so. Thus the *Conospora longissima*, a gregarine studied by M. Mensil and myself[3], is constant and abundant in one of the forms of the *Dodecaceria concharum*, which we have designated by B; but it is never found in the A form, and yet this is the same species or, at any rate, a very closely related species of Annelid. Entomophagous (insect eating) Hymenoptera never deposit their eggs except in a denite species of insect. Girard believes, with apparent justice, that the general run of the species of the Epicarid Isopods are parasitic, each upon single species of Crustaceans, and that two similar parasites found upon related species belong to distinct species, even when the precise morphological difference in structure or in form is imperceptible.

The parasite Copepod which M. Mesnil and myself have just been studying[4] under the name of the *Xenocoeloma brumpti* is found only upon a single species of Polycirrus and not upon related species which are found near it. What is the mechanism of this specificity? In these cases, as among

[3] Caullery and Mesnil. Les Formes Epitoques et l'Evolution des Cirratulians (The Epitochal Forms and the Evolution of the Cirratulians) Ann. Univ. Lyon, Vol. XXXVIII, 1898.

[4] *Bull. Biol. de la France et de le Belgique.* Vol. LIII, 1919.

the insects, where the parasite actively penetrates the host, how does the parasite succeed in finding the proper host amid the immensity of nature, and how does it distinguish between related species? Is it through some form of tropism, by some olfactory sensation, for example, as is believed by J. Loeb? In the case of the passive ingestion of spores, as with the gregarine mentioned above, wherein the two forms of the host which live side by side, must certainly ingest the same sporocysts, why does the infection occur only in the B form? And this is closely related to another question, namely: How do the internal parasites, whether in the alimentary canal, in the deep lying organs, or in the colloma manage to exist within their host, maintaining immunity with respect to the humors of the latter's body, or to the phagocytes, whose function it is to digest or destroy the foreign substances or organisms which have made their way into the body? At this point the entire problem of immunity presents itself for our consideration.

And in what manner does the parasite exert an effect upon its host—an effect which is so definite in the case of certain organs. Thus in many instances the parasite produces, from a distance, alterations in the metabolism of its host, thus destroying the genital glands of the latter and producing *parasitic castration.* And after having produced the aforesaid effect, the parasite proceeds by way of good measure to occasion morphological modifications, particularly in the secondary sexual characters. It is a remarkable fact that the transformations thus produced by parasitism sometimes occur in groups such as the Arthropods, in which experimental castration, no matter at how early a stage has never been observed thus far to produce any alteration in these sexual characters. And yet the Sacculina, which more or less tardily infests the Crab, often profoundly modifies the secondary sexual characters of its abdomen and its abdominal claws. These facts, which were first pointed out by A. Girard, have been extended and strikingly illustrated by G. Smith.

In short, the list of important questions in physiology suggested by parasitism could be readily lengthened.

DEGRADATION DUE TO PARASITISM.

But let us return to problems of morphology and their connection with the more general problem of Evolution—as a matter of fact they are by no means independent of physiological problems. The reaction of parastism upon morphology is very striking. There is, in fact, no category of analogous facts in the realm of biology which affords the same breadth of vision. Parasites are distinguished from forms belonging to the same groups by traits so marked that the affinities of these parasites often become unrecognizable. Furthermore, there is an evident parallelism between the transformations which are produced in the various groups.

Parasitic *degradation* is a long established idea. The more profound the nature of the parastism, i.e., the more use the parasite makes of the host's activities to secure his own nutrition, the more the parasite becomes deformed and simplified. Thus, as a general thing the organs of locomotion and those of the senses tend to retrograde and even disappear. In some cases there is even no longer any trace of the original nervous system. The digestive organs become simplified, since the parasite, which absorbs only substances which are already fully elaborated and perfectly assimilable, needs not go to the trouble of making such transformations; there merely occurs a hypertrophy of some organs whose function it is to store up reserve material, such as the hepato-pancreas. The alimentary canal on the other hand, sometimes disappears completely, as among the Cestods, and the animal, immersed in assimilable nourishment, feeds itself by means of simple osmosis through its external tegument; the reproductive organs, in particular, are altered and are generally hypertophied, but in various manners. Sometimes the parasitism manifestly produces hermaphroditism. Sometimes, on the other hand, it exaggerates sexual bi-morphism, making of the female, stuffed with eggs, a giant upon which the dwarfed male lives as a sort of parasite. In one case as well as in the other the number of eggs produced by parasites is enormous—in this enormous production of eggs there is a compensation for the extreme mortality of those embryos and larvae which do not succeed soon enough in finding the indispensable host. This compensation is essentially adaptative and suggests theological illusions. Thus, parasites sometimes consist of little more than enormous egg sacks and the cycle of the parasite, starting from its meeting with the host is summed up in forming the substance of the eggs, laying them, and finally, incubating them until the hatching of the larvae.

There is, therefore, a very great simplification of the various apparatus which take no part in reproduction; there is a *degradation* if one choses so to express it, in comparison with free forms, but this term merely expresses a subjective point of view, and one might be equally justified in saying that parasites exhibit a specialization carried to a greater or less extent and upon the whole a peculiar adaptation which often attains a very great degree of perfection. In their own way these highly adapted forms might be regarded as being very highly organized. I will illustrate these ideas by a few examples and we shall observe, in particular, how a single group often exhibits successive stages of transformation connecting the forms ultimately attained with the normal forms although scarcely any perceptible resemblance between the former and the latter is apparent. Parasites, present together, more than any other category whatever of organisms a collective and striking illustration of adaptation. Nowhere else is the structure so clearly brought out as molded by the kind of life and nowhere else does pre-adaptation seem less probable.

Not only the adult has been thus influenced; the immature stages are no less so, and the requisite conditions in the finding of the host, which often involve a necessary passage by means of a provisory host (and consequently an enormous destruction of individuals in the process of development) are in correlation with the adaptative peculiarities of the larvae and frequently with the phenomenon of embryonic multiplication involving asexual reproduction. The comparison of various groups is, therefore, suggestive in this respect because we can thus observe parallel divergences with respect to normal embryogeny appearing in series which are entirely distinct, as if the action of the environment were effectively shaping in a direct manner the development and structure of the parasites, in a purely Lamarckian sense.

However, the problem is by no means so simple as it may appear. Conditions which are apparently similar sometimes bring about the most opposite results. A very striking example of this is found in the parasite Copepods. They attach themselves to their host after a period of free existence, during which they generally pass through the principal stages of larval development, like the free forms, attaining the stages which are known as syclopoid; they then attach themselves to the host and become deformed and degraded in the usual sense of the words. M. Mesnil and I have just finished the study of the truly astonishing retrogression of the genus which we have called *Xenocoeloma*, which actually succeeds in borrowing from its host, in the literal sense of the word, a portion of the latter's organs! It is impossible to imagine a more complete degradation and a more intensive parasitism. On the other hand let us consider another type of Copepods, the *Monstrillidae.* These peneterate the host as soon as they reach the Nauplius stage. They then lose all their appendages, forming a simple non-differentiated cellular mass which proceeds to develop within the circulatory system of an Annelid,[5] i.e., in conditions of supreme parasitism. One would expect a creature as degraded as possible from this mode of life. But this is by no means the case. From this parasitism, on the contrary, there issues a Copepod magnificently endowed for a free existence and provided with power-

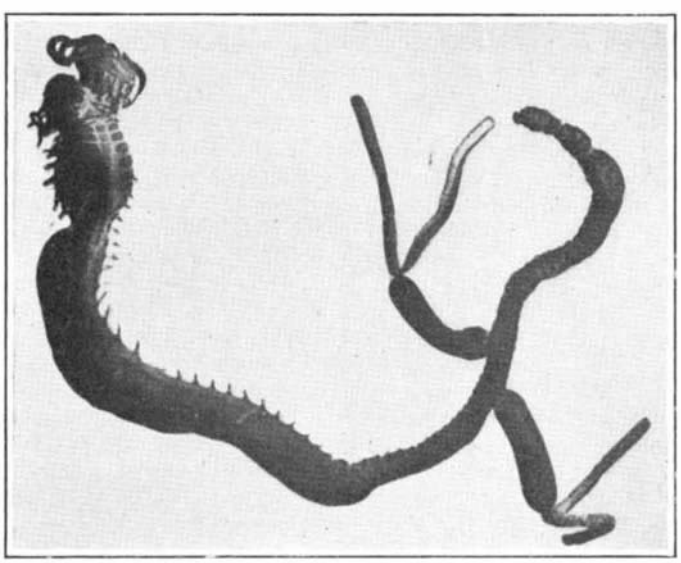
[5]A parasite species has been observed in a mollusc (*Odostomia*). Pelseneer, Bull. Biol. Vol. XLVII, 1913.

ful appendages for its pelagic life. A single feature of its organism, however, appears paradoxical, and was an enigma before the initial parasitic stages had been studied. The alimentary canal of these adult Monstrillidae is atrophied. We now explain this peculiarity by the fact that the animal accomplished its complete development in the form of a parasite, while its life in the adult stage is merely a brief pause at whose very beginning the sexual products are altogether mature and require only to be disseminated. The animal has no longer any need to assimilate nourishment. In the same manner the innumerable entomophagous insect included principally among the Hymenoptera and Diptera lay their eggs within the bodies of other species, where the eggs develop in the form of parasites producing free and perfect Imagos. In the same way also there is found among the Annelids a series of Eunicians which develop as internal parasites in other Annelids, ending in a free form in the adult state which is in no wise degraded by the parasitism. This shows that the mere fact of parasitism does not necessarily involve simple and uniform transformation.

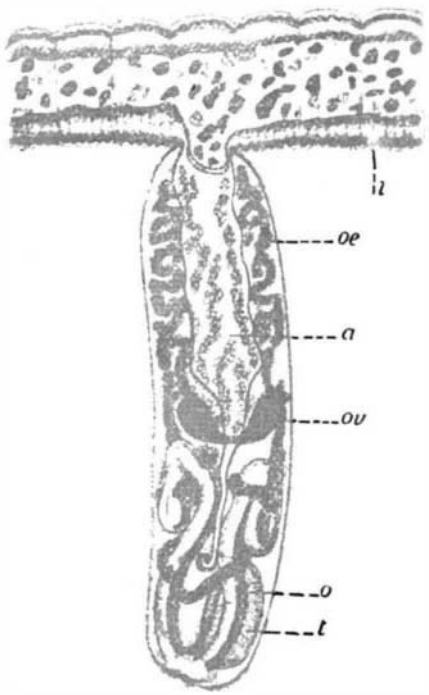
Thus it is not evident that the striking adaptation of parasites is explicable any more than is the case with free forms by the simple Lamarckian mechanism as was formerly supposed. Here, too, parasites have been able to react according to the successive degrees of a vast orthogenesis. However, it is surely very remarkable to observe that parasitism produces in the most diverse groups parallel modifications which cannot possibly be completely independent of circumstances external to the organisms proper. When a Rhizocephalus crustacean exhibits the asexual modification demonstrated by F. A. Potts[6], is it possible to imagine that this result was an inevitable evolution resulting from the internal factors alone of these organisms independent of external circumstances? Can we refuse to believe that the progressive action of parasitism which, in the general evolution of types can be only a contingency, has been, at least, an external factor of considerable weight, and which has many times produced similar results under similar conditions, but in entirely independent series?

Doubtless free organisms present analogous problems, but parasitism is of peculiar character. The constitution of the fundamental types of the animal kingdom goes back into a practically inaccessible past. But the differentiation of parasites is a secondary evolution subsequent to the first. It is not reasonable to suppose that the parasites, with their intensive anatomical, embryological, and physiological deformations appeared originally in their present form. They are evidently derived from normal forms and nowhere have we stronger evidence of the truth of the theory of evolution . . . This secondary evolution is less remote than the original one, hence the study of parasitic forms is of peculiar interest with reference to the laws of evolution . . .

[6]Carnegie Institution, publication No. 215, 1915.



ANNELID WORM *POLYCIRRUS* HAVING TWO SPECIMENS OF THE *XENOCOELOMA BRUMPTI* ATTACHED TO OPPOSITE SIDES OF THE BODY AS PARASITES



CROSS SECTION OF *XENOCOELOMA BRUMPTI* ATTACHED TO HOST. 14 DIAMETERS

i intestine of *Polycirrus* full of sand and forming slight hernia in the crustacean; *a*, axial cavity of *Xenocoeloma*; *ov*, ovary; *oe*, strings of ripening eggs; *o*, oveduct; *t*, testicle.

. . . We have now arrived at a period in the history of the biological sciences when we are able to form a precise idea of the difficulties presented by their great problems. In the classic period of Darwinism it was generally believed that embryology would reveal all the secrets of morphology. Today, we no longer hold this view . . . On the other hand, in the domain of physiology which is constituted by factors existing at the present time . . . the progress of all the experimental sciences daily proffers possibilities of new investigations. For example, cellular physiology is today in its prime and is making rapid progress. . . .

The tremendous researches which have been carried on since 1859, under the impulse of Darwin's book, have not enabled us to discover the essential solution of the transformist problem . . . But these researches have given us an incomparably greater knowledge of the forms of animals, of their intimate structure, and of the course of their development. It is thanks to this progress that we now perceive the inadequacy of certain solutions which seemed almost obvious in the years immediately following 1859. And the very difficulties offered by the problem of adaptation have proved that the science of morphology cannot be reduced to a few simple laws. Moreover, it is this progress which has enabled us to formulate the most vitally interesting questions in the realms of physiology . . . An infinite amount remains to be discovered in the domain of morphology and these discoveries may prove decisive for the direction of physiological researches . . . Even to-day we must profoundly admire the information given us by Claude Bernard in his celebrated work, "*Lessons Concerning the Phenomena of the Common Life of Animals and Plants*," with regard to the respective rôles of morphology and physiology . . . In our opinion future researches concerning parasitism show that the last word has by no means been said in morphology and in zoölogy.