TEXTBOOKS OF ANIMAL BIOLOGY

PARASITISM AND SYMBIOSIS

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PREFACE TO THE ENGLISH EDITION

In the present work I have dealt with parasitism from the point of view of general biology. Parasitism is a relationship of direct and limited importance between two organisms, each usually having a clearly defined role, either of host or parasite; the parasite lives at the expense of the host. It is really a special case of the relationship of every organism to its environment, in this instance to another organism, an association which is particularly precise. There exist other associations between organisms, less restricted—but which are also very often specific—that are described as commensalism and mutualism. There are others again which are, on the contrary, more restricted, more constant and less unilateral, to which the name symbiosis has been given. Commensalism, parasitism and symbiosis are man-made categories which in nature are not discontinuous but are really different aspects of the same general laws. This book seeks to make this clear by reviewing these types of association one by one, within the framework of the theory of evolution. Ignorant as we still are of the mechanisms by which evolution is brought about, its reality cannot easily be controverted, and it imposes itself on us more and more as our knowledge increases. Parasites are perhaps the organisms in which this is most evident. In effect they are closely adapted to the very peculiar conditions in which they live, and their organization, specialized as it may be, always appears not like that of autonomous types forming an independent class of beings but as the transformation of various types of animals living under normal conditions. The world of parasites was formed gradually, after the differentiation of the various groups of animals. It is the result of a secondary evolution which is less remote. If this were not so it would be necessary to assume that a capricious Providence had specially attached to each animal a cortège of parasites curiously malformed according to a predetermined plan. And, in this case,

why should not these parasites constitute special groups ? The study of parasitism is a particularly clear illustration of evolution.

This book does not aim at an equivalent treatment of parasitism among animals and among plants, which might logically be expected. As a zoologist, I have not been able to avoid giving preponderance to facts drawn from the animal kingdom, if only because I feel myself more competent to deal with them. Also there is a vast domain intimately connected with parasitism which remains almost completely outside the scope of this book, namely bacteriology. Most bacteria, pathogenic or not, are parasites. Their relationships with their hosts involve above all else the major problem of immunity, natural or acquired, and it is perhaps astonishing that it should not occupy here the place to which it appears to be entitled. In point of fact bacteriology and the problems it raises have on account of their theoretical and practical importance their place in other works; in this one, therefore, they have been left on one side.

It goes without saying that questions of a general character can only be treated through facts that are concrete and exact. In the field of biology the general exists only through the particular. It is necessary, therefore, to bring all the ideas expressed back to precise facts. Thus, in order to give an idea of the malformations due to parasitism, instead of keeping to affirmations of principle, or to general aspects, a certain number of especially characteristic examples have been chosen. They have been selected as far as possible from recent researches, thus avoiding the detailed repetition of examples which have become classical.

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COMMENSALISM

PARASITISM may be defined as the condition of life which is normal and necessary for an organism nourishing itself at the expense of another—called the host—without destroying it as the predator does its prey. In fact there is a complete series of transitions between the two conditions. In order to live regularly on its host, the parasite, save in exceptional cases, remains in permanent contact with it, perhaps on its outer surface, perhaps within it. Parasitism is then an association, generally continuous, between two different organisms, one of which lives at the expense of the other. The association has an essentially unilateral character: it is necessary to the parasite, which dies for lack of nourishment if separated from the host; it is not in the least necessary to the host. The organization of the parasite is modified according to the conditions under which it lives on the host: adaptation is the hallmark of parasitism.

But one can imagine, and there exist in fact, associations not having the same unilateral character: two species associating regularly but without the one living on the other. One of them may indeed benefit in protection or nutrition without the other's gaining any advantage. These associations are grouped under the term *commensalism*. In some of them, which come under the heading of *mutualism*, there are clearly reciprocal advantages for both associates. In addition, the regular localization of one species within the interior of another one may have a peculiar spatial significance without any physiological relationship being involved. Associations of this nature come under the heading of *inquilinism*. It is clear that there are many transitions between these associations and parasitism which is no more than a unilateral deviation from them. The study of commensalism, inquilinism and mutualism is then the natural prelude to that of parasitism and will allow us to grasp the

diversity of the relationships which can become established between two species.

Very similar in meaning to commensalism is the term synœcy (*σύν* with, *οἶκος* house), which has been suggested for certain particular cases. Synœcy implies, however, more than a simple spatial relationship, which would be a much more widespread phenomenon. There is, indeed, in the grouping of organisms, a general relationship, closely bound up with the laws of their interdependence, which is beyond the scope of the present work and which gives rise to the general facies of flora and fauna, that is, organic populations. It leads to what the botanists call *formations of plants*; the zoologist will easily find analogous groupings which are termed *biocœnoses*. A coral reef comprises a major association of this kind, which entails a certain persistent stability among all the creatures which live there and come constantly into contact. It would be possible to cite from the sea shores of Europe many other associations of the same kind but more limited, each comprising a definite population. The terrestrial fauna shows them equally clearly; we shall have to return to those concerned with the social insects, particularly ants and termites. On an isolated plant, particularly a tree, a whole series of species associates regularly. These general associations, however, involve a very loose relationship, much less precise than that denoted by the term commensalism.

COMMENSALISM IN MARINE ANIMALS

Commensalism implies a regular association between two species, recurring constantly in widely separated localities. On analysis it is found that this simple relationship involves very marked modifications, particularly of a psychophysiological nature. The double danger of research into this type of phenomenon lies, on the one hand, in bringing to them preconceived ideas of too subjective a nature, bordering on an illusory anthropomorphism and, on the other hand, in trying to reduce complex facts to simple elementary reactions.

Let us consider the classical case of the commensalism of sharks and the pilot fish (*Naucrates ductor*) or the remora (*Echeneis remora*). These scombrids accompany the sharks, the

remora attaching itself to them temporarily by means of its dorsal fin, modified to form a sucker. This mode of life presupposes a very precise adaptation of nervous reflexes which can be surmised when a remora and a *Carcharias* are seen together, as I have seen them in an aquarium at Bermuda. The first follows the other as a piece of iron does a magnet, obeying instantly the incessant and irregular changes of direction shown by the shark in an aquarium. The synchronism of the remora's swimming with that of the shark must be associated with a close adaptation of sensory organs and nerve centres, an adaptation as considerable as that of the sucker in the morphological field. From this instance it is clear that the facts of commensalism must be studied from life, and as far as possible through experiment.

Apparently quite simple, but probably very complex, is the similar association between anemones and fishes known in many localities in tropical seas, and studied carefully by Sluiter [48] in Batavia. A fish of the genus *Trachichthys* (or *Amphiprion*) always remains amongst the tentacles of a large anemone. Plate has also seen this association in the Red Sea, where the anemone is, according to him, *Crambactis arabica*, more than 30 cm. in diameter. If the anemone closes up, the fish is imprisoned and momentarily vanishes within its digestive cavity. Now, it is only necessary to be present when an anemone's prey comes into contact with the tentacles and is enclosed within them to see how formidable contact with the nematocysts can be. The fishes cited here must thus possess an immunity against the urticarious poisons of the anemones that they frequent, an immunity which has, no doubt, been gradually acquired and which, by itself alone, witnesses to the very definite nature of an association which appears to be purely casual. This association satisfies two different needs, nutrition and protection. Concerning nutrition, the authors do not give very precise information but it may be supposed that when the anemone engulfs its prey and, at the same time, closes over the fish, the latter gets a share of the food. As for protection, Sluiter has demonstrated it directly. For several months he was able to keep living *Trachichthys* in an aquarium where he had placed carnivorous fishes and also the anemone. The *Trachichthys* never left the latter. On the other hand, when

placed alone with the carnivorous species in an aquarium they were always eaten after a few hours. The anemone, then, truly shelters the fish. Thus here we have an example of a highly efficient association comprising precise physiological immunity and, very probably, co-ordination of the reflexes of the two associates.

It is evident that a similar interpretation must be given to an association, easily observed on French coasts, between acraspedote medusæ, in particular *Rhizostoma cuvieri*, and the amphipod *Hyperina medusarum*, or young fishes, mainly *Caranx trachurus*.

Hyperina swims in shoals under the umbrella of the medusa, and takes shelter in the sub-genital cavities. *Caranx* forms fair-sized shoals with the same habit, never leaving the medusa and sometimes taking refuge within it, as do the amphipods. The same association has been met with in very distant regions. It has been found between a *Caranx* and a crambessid in the Gambier Islands in the Australian Pacific by Seurat, and between *Caranx melampygus* and *Crambessa palmipes* near Mauritius by Lunel[36].

The members of the genus *Physalia*, whose nematocysts are particularly urticarious, are frequently accompanied by little fishes (*Nomeus gronovii*) related to *Caranx* and apparently immune to the poison of the siphonophore;* they evidently derive protection from its proximity and possibly profit by sharing its prey.

Associations of this type are very common on coral reefs. Coutière [22] has seen a number of examples at Djibouti. A transparent pontoniid prawn, *Periclimenes*, constantly remains, like the fishes cited above, within the zone of protection formed by the tentacles of a large anemone; anchovies, *Engraulis*, take refuge amongst the long spines of a sea urchin, *Diadema setosum*; a large asteroid, *Culcita*, permanently shelters a hippolytid prawn beneath its disc. Many alpheids live in the shelter of madrepore corals (*Pocillopora*, *Porites*, etc.). In the Gambier

* The various aspects of commensalism raise many complex problems of immunity each of which demands special study. I shall limit myself here to recalling the work of J. Cantacuzène on immunity in invertebrates, and his report on this subject at the 75th anniversary of the Société de Biologie (1923,pp. 48–219). This work provides a starting point for research into immunity amongst commensals.

Islands, Seurat (in Coutière [22]) has seen an alpheid prawn, *Arete dorsalis*, living beside a sea urchin (*Heterocentrotus mamillatus*) in holes occupied by the latter within a coral, and the prawn is of the same colour as the urchin (homochromous); a similar phenomenon occurs in many of the examples already given. Potts [45] says that in Torres Straits *Synalpheus brucei* lives in pairs (male and female) in the arms of a comatulid (*Comanthus annulatus*) and he has seen many other crustaceans (alpheids, pontoniids, *Galathea*, *Cirolana*, etc.), annelids and gastropods, which are commensal with crinoids under the same conditions on reefs. In Madagascar Geay has observed a crab, *Lissocarcinus orbicularis*, living permanently at the mouth of a holothurian, which, when the tentacles are retracted, is surrounded by these and momentarily trapped within the buccal cavity just as the fishes discussed above are trapped by the anemones. Here again the crab is homochromous with the holothurian. Borradaile has seen the same kind of phenomenon in the Maldives.

Sometimes the commensal even produces a malformation in the animal with which it shelters, causing a kind of gall. Such is the case with the crab *Eumedon convictor*, observed by Seurat [15] in the Gambier Islands; this animal lives in quite a large cavity, almost enclosed and formed by the folding back of the apical region of a sea urchin (*Echinothrix turca*), with which the crab is homochromous.

Similar malformations are produced in *Pocillopora* by another crab (*Hapalocarcinus marsupialis*), first noted by Semper in the Philippines and studied again later by Potts [267] in Torres Straits.

A very curious association (Fig. 1) is that of the sipunculid *Aspidosiphon* with a solitary polyp of the genus *Heteropsammia* (=*Heterocyathus*). It has been studied principally by Bouvier [14] and by Sluiter [49]. The *Aspidosiphon* begins by establishing itself in a little empty gastropod shell as if it were a hermit crab; the larval polyp settles on the shell, covers it and grows beyond it, forming a considerable mass in which the worm would be immured did it not establish within it a gallery with a terminal opening as well as a series of lateral ones. The *Aspidosiphon* is thus effectively protected by the polyp whose mobility is assured by it; it can, in fact, project its anterior extremity and,