ECOLOGY OF ANIMAL PARASITES

Ecology of animal parasites

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ECOLOGY OF ANIMAL PARASITES

TO DR. CHARLES JOYEUX, EMERITUS PROFESSOR OF PARASITOLOGY AT THE UNIVERSITY OF AIX-MARSEILLE, WITH WHOM MOST OF THE IDEAS EXPRESSED IN THIS BOOK HAVE BEEN OFTEN DISCUSSED IN THE COURSE OF OUR COLLABORATION FOR TWENTY-FIVE YEARS

INTRODUCTION

Dans la nature, les non-réussites, les échecs, sont éliminés et par conséquent nous ne voyons que les réussites.
L. CUENOT

The title of this book may seem somewhat pretentious to students of ecology accustomed to collecting data and observations on organisms concentrated within a given area. It has been chosen intentionally to stress the fact that today our knowledge of parasites is much more extensive than might be supposed from current textbooks, and even from those that are devoted entirely to the medical or veterinary aspects of the question.

An attempt has been made to review the field of parasitology from all possible angles and to show that parasites are subject to the same general laws that govern all free-living organisms. The latter, however, are adapted in various ways to widely different biotopes whereas parasites have adapted themselves to a very specialized, and consequently limited, environment. The association of the parasite with its host is also a problem of ecology and all the more interesting in that, in many cases, it is possible to furnish indisputable evidence that such associations originated several thousands of centuries ago.

It is the writer's contention that a taxonomic background is absolutely essential to a complete understanding of the relationships between the parasites and their hosts. This is the broad basis on which modern parasitology has been built up and to overlook it would be an unpardonable error.

The materials collected for this book represent two courses in parasitology that the writer was invited to give as Visiting Professor in the Graduate College of the University of Illinois. They do not pretend to furnish an exhaustive review of the subject; many facts are assumed to be known and consequently have been omitted. Several of the ideas expressed are not new but are presented in a different manner; some may be premature and others may be proved to be erroneous. The aim of this book is to stimulate the reader's thoughts in new fields and to encourage him to consider old problems from new angles.

In the following chapters, the writer has found it necessary to define certain terms that are usually used in a somewhat loose sense but that really correspond to very definite types of animal associations. Adaptations to parasitism are examined from both the morphological and the biological angles, the stress being laid on the latter rather than on the former—especially in groups that are entirely parasitic, where there are no free-living species with which the parasites can be compared. Such a general outline furnishes the basis for examining the ecology of host-parasite relationships and will also enable the reader to gain a more complete understanding of the physiological peculiarities of parasites. Using the data available, the writer has attempted to discern how parasitism in animals has arisen.

During his stay at Urbana the writer has continuously benefitted from the support and encouragement of Dr. Harley J. Van Cleave, and the ensuing friendship has led to the editing of these lectures in their present form. He has enjoyed the hospitality of Dr. Van Cleave's laboratory, the generous loan of his personal library, and the stimulating atmosphere of his research program. In the world of today, such gifts as these are landmarks in the life of a man.

The writer is also greatly indebted for their wholehearted collaboration to the members of the staff in the department of zoology and to those in the Natural History library. Their friendly attitude toward a fellow scientist has done much toward a better understanding of the problems shared in common.

The drawings have been prepared by Mrs. Katherine Hill Paul, department artist, who with her usual skill has contributed much to making the text attractive.

LANDMARKS IN PARASITOLOGY

The following dates and facts have no pretense of being complete. They have been chosen more for the new ideas that subsequently resulted from the discovery than for the importance of the discovery itself. To stress the historical aspect of the data presented, they have been arranged in chronological order, regardless of their nature.

1603. The first recognizable description of *Diphyllobothrium latum* is published by Felix Platter of Basle.

1666. First mention of parasitic crustaceans, argulids, by F. Baldner of Strassburg (France).

1675. A protozoan is described for the first time by the Flemish craftsman, Antony van Leeuwenhoeck.

1700. Publication in Paris of the first treatise on human helminths by Nicolas Andry.

1781. First experimental life cycle of a tapeworm is obtained by Peter Abildgaard in Copenhagen.

1835. Richard Owen discovers *Trichinella* in London.

1837. *Trichomonas vaginalis* is discovered by Alfred Donné in Paris.

1841. Description of the first blood parasite, a trypanosome, by Gustav Valentin of Bern.

1845. Felix Dujardin of Rennes shows the relationships between cysticerci and taenia.

1852. In Dresden, Friederich Küchenmeister obtains the experimental cycle of the dog tapeworm, *Taenia pisiformis*.

1852. The first parasitic snail is discovered and named *Entoconcha* by Johannes Müller of Berlin.

1853. First pig is rendered measly experimentally by Edouard Van Beneden of Liège.

1854. First experimental infestation of man by *Taenia solium* by Carl Vogt of Geneva.

1861. Rudolf Leuckart of Leipzig infests a calf with *Taenia saginata* cysticerci.

1869. H. Krabbe, a Danish physician, discovers that each order of birds possesses its particular tapeworms.

1870. Discovery of human intestinal amoebae in Calcutta by T. R. Lewis.

1877. The life cycle of *Wuchereria bancrofti* is established by Patrick Manson in China. This is the first case of an insect vector of a larval parasite.

1880. Alphonse Laveran, a French army doctor, discovers the protozoan nature of the malarial parasite.

1880. G. Evans, in the Punjab, discovers that the disease known in elephants as "Surra" is caused by trypanosomes, thus establishing their pathogenecity.

1881. Simultaneously, R. Leuckart in Germany and G. Thomas in Great Britain discover the life cycle of *Fasciola hepatica* and describe for the first time the larval development of trematodes.

1882. Max Braun of Koenigsberg furnishes experimental proof of the plerocercoid nature of the larvae of *Diphyllobothrium latum*.

1883. Rudolf Leuckart discovers the heterogonic life cycle of *Strongyloides stercoralis*.

1884. In Paris, Yves Delage describes the life cycle of a rhizocephalan (*Sacculina*) and establishes its affinities with cirripeds.

1886. Alfred Giard, a French biologist, introduces the notion of parasitic castration.

1889. The role of ticks in the transmission of Texas Fever is demonstrated by Frederick L. Kilborne in the United States.

1892. The first direct life cycle of a tapeworm is described by B. Grassi and G. Rovelli in Italy.

1895. Ronald Ross discovers the transmission of bird malaria through a mosquito in India.

1898. Ross's discovery is substantiated for human malaria by Grassi and his collaborators in Italy.

1902. The first human trypanosome is described by J. E. Dutton from Africa.

1904. Arthur Looss, in Cairo, accidentally infests himself with larvae of *Ancylostomum duodenale* and thus discovers their penetration through the skin.

1911. The life cycle of *Trypanosomum gambiense* is worked out for the first time by F. K. Kleine and M. Taute in Germany.

1913. The first complete life cycle of a schistosome is worked out by K. Miyairi and M. Suzuki in Japan.

1916. F. Stewart and B. H. Ransom, in the United States, discover the migration of ascaris larvae through the lungs.

1918. F. Rosen and C. von Janicki in Neuchâtel discover that the life cycle of *Diphyllobothrium latum* requires two intermediate hosts.

CONTENTS

To understand the true meaning of a parasitic adaptation, and consequently the nature of the association that has arisen between two partners, it is necessary to examine briefly the principal types of associations that have been recorded so far.

When analyzing animal associations, one must keep in mind both the morphological and the physiological aspects of the problem. It is very important to be able to form an unbiased opinion of the association and especially in regard to its necessity for either of the two partners.

Far too many anthropocentric ideas have been introduced into several of the definitions currently used, because the older authors were influenced primarily by the morphological rather than by the physiological aspect of the association. Consequently, they usually failed to discover to what extent the associations were of a permanent or of a transitory type.

All animal associations may be divided into two groups which differ fundamentally (see diagram p. 7). In the first case, all the associates belong to the same species, they tend to form colonies, and within these there appears a very definite type of specialization. This affects both the morphology and the physiology of the individuals which, in turn, influence the ecology of the specialized individuals. A colony of termites, for instance, contains a queen, workers, soldiers, males and, sporadically, young females. All work together and lead a socially organized life, yet each group possesses its own particular type of morphology and ecology. Such specialized colonies are found, of course, among other hymenopterons which lead a highly socialized existence.

It is important to emphasize that within these colonies, each individual has arisen from a distinct egg whereas a colony of hydroids is the result of the cleavage of a single egg. It is not a colony in the true sense of the word, but a primitive metazoan, low in degree of specialization.

The varied aspects of parasitism, symbiosis, commensalism, and phoresis are as truly within the scope of ecology as are the problems of predation, succession, geographical distribution, and relations with the physical environment.

PHORESIS AND COMMENSALISM

The second type of association is characterized by the fact that its members belong to different species. An analysis of such associations is much more difficult than that of the previous ones since they should be subjected, as far as possible, to experimental conditions to determine the true nature of the bond between the different partners.

There is no doubt that such associations originated from species having similar ecological needs in regard to both food and environment, these conditions being the only bond between them. This is especially true of sedentary organisms. A typical association of this kind would be an oyster bed, for the organization of which there exists no fundamental necessity. The type and number of the associates may vary a great deal and differ from one region to another, but the ultimate chances for the entire association to subsist in a more or less permanent fashion will depend on the successful adaptation of each individual species.

It is only natural that such ecological associations attract all kinds of predatory animals, since they have every chance of finding there their favorite food. The predators in turn are followed by scavengers and in this way very complex associations are formed.

Scavengers, hiding from predators, burrow in among the various members of the association. Probably in such cases protozoans and coelenterates, and other organisms also, attach themselves to the scavengers. The latter, thus camouflaged, would stand a greater chance of survival than those not so protected. The protective coating of a crab would of course vary according to the species that compose the association into which it has introduced itself as a scavenger. There is nothing teleological about such associations. Their successful survival is the outcome of natural selection, since they benefit the individuals so protected.

It is important to emphasize that camouflage is entirely accidental. An oyster covered with a growth of hydroids derives no evident benefit from this covering. But it is quite possible that an organism which attaches itself indiscriminately to another of a different kind may eventually gain an advantage from this support. Attachment to an animal which moves around continually may be advantageous, as it would provide a greater and more varied food supply or raise its metabolic rate to a higher level by an increase in oxygen intake resulting from the continual movements through water. Here again there would be a selective influence that might eventually lead to some degree of specialization.

Numerous species of sedentary infusorians, vorticellids for example, are found attached to the surface of the body of water fleas and some other aquatic arthropods. They have become specialized in that movement has become indispensable for their metabolism. If fragments of chitin together with the attached protozoans are kept motionless in water, the protozoans die. They will survive, however, if the fragments are moved about continually. Although the nature of the supporting partner is indifferent, the other associate has become physiologically specialized. There is no kind of specificity in such associations, since the only condition for them to be effective is that the supporting partner be continually moving.

Such associations are usually termed *phoresis* and the supporting partner is spoken of as the host. Phoretic associations may be permanent, as above, or they may be transitory, arising at definite stages of the life cycle of free-living or parasitic organisms.

The triunguloid, the first larval instar of the so-called Spanish fly, attaches itself to the body of a bumblebee as it comes to feed on flowers. In this way, the larva is transported to the bee's nest where it leaves the host to penetrate into one of the cells. It devours both the bee larva and the honey and enters into a new larval instar. Phoresis is absolutely necessary for the larval cantharid which finally becomes a predator and should never be called a parasite, especially since it lives within the nest and not upon the host.

Phoresis does not necessarily imply that one of the two partners is attached in a more or less permanent fashion to the other. For instance, a small European fish known as the fierasfier is found inside the so-called respiratory tree and the intestine of sea cucumbers. To feed, the fish emerges only at night and then for short periods, returning immediately to its shelter (Fig. 1). If such fish are kept in an aquarium they may remain alive even when the holothurians are removed, but only if no other

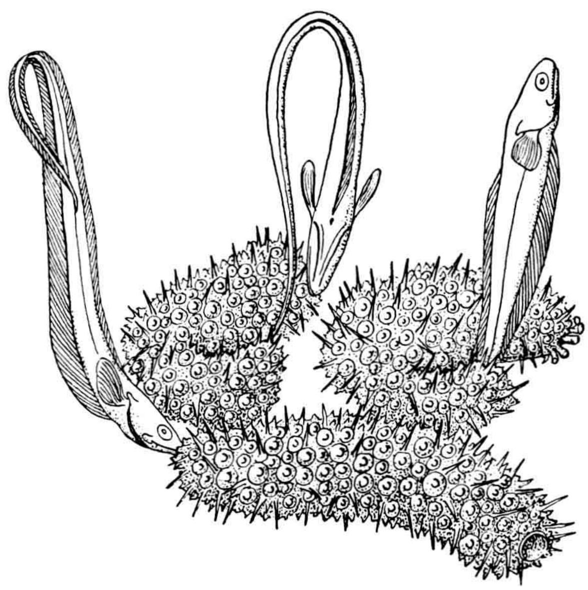


FIG. 1. A case of endophoresis. Holothurians with fierasfier leaving and entering via the cloaca (Emery).

species of fish be introduced—since these invariably eat the fierasfier. Such an association might be termed endophoresis; it is vital for the fish but indifferent for the holothurian. In several cases, it has been found that the fierasfier may become predator and feed on the organs in which it lives, but since these regenerate rapidly the host suffers no irreparable damage.

One of the most extraordinary cases of what might also be called endophoresis is that of the vorticellid ciliate, *Ellobiophrya donacis* Chat. & Lwoff, which is found in certain species of mussels. It has so far been reported from only the wedge shell, *Donax vittatus* da Costa, where it is found attached in a very peculiar manner (Fig. 2). The usual single stalk found in other vorticellids is duplicated in this species. The two stalks are locked together in such a way that they embrace the gill-grid. The protozoan is literally padlocked to the gills of its host, yet it is able to turn around its base like other sedentary vorticellids. When *Ellobiophrya* divides longitudinally, the individual that is detached remains free-swimming and is provided with a double crown of cilia. It swims around within the mantle cavity. Some individuals are probably expelled through the excurrent siphon. The two "legs" appear gradually and at the same time the posterior crown of cilia gradually degenerates and disappears completely as soon as the individual is padlocked to the gill-grid.

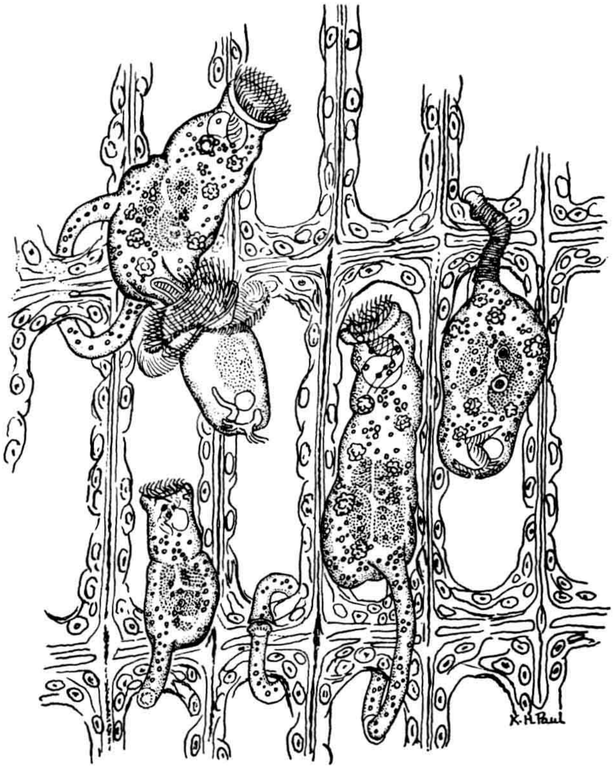


FIG. 2. *Ellobiophrya donacis* Chatt. & Lwoff attached to the gill-grid of its host. Upper left, an individual with a bud that has resulted from a longitudinal fission, showing the posterior circle of cilia (Chatton & Lwoff).

The food of *Ellobiophrya* apparently consists of small organisms and perhaps also mucus, filtered out from the sea water. This protozoan appears to be a highly specialized phoretic organism, adapted in a teleological fashion to a particular support. There is no evidence so far of the possible transfer of *Ellobiophrya* to other hosts. Such experiments would be particularly important since they might show whether this peculiar adaptation is only morphological or also physiological, and whether *Ellobiophrya* is specialized in its food habits.

Numerous cases of phoresis have been recorded and most authors usually regard this association as leading ultimately to true parasitism. One cannot deny that this might be the case, yet there is no factual evidence so far.

Turbellarian-like organisms known as temnocephalans occur within the branchial chamber or on other parts of the body of certain fresh-water crayfish. Tentacles and a sucker-like organ enable them to crawl about on their hosts and they feed on the minute organisms that occur in their environment (Fig. 3). They can also abandon their host and pass

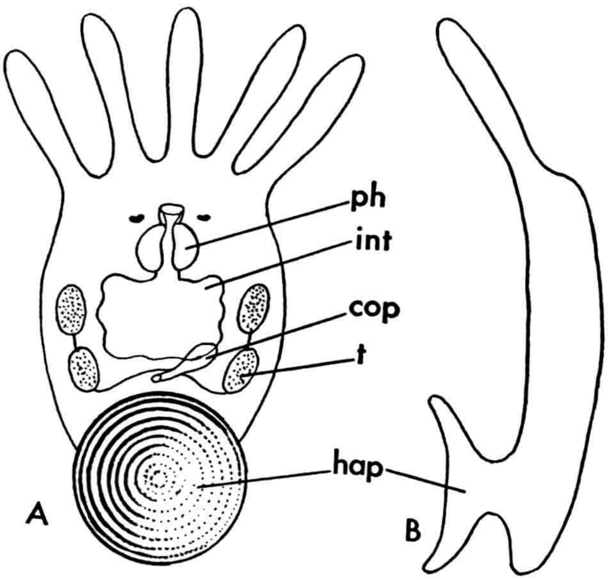


FIG. 3. Diagrammatic morphology of a temnocephalan. A. Ventral view. B. Lateral view. cop.—male copulatory organ. hap.—haptor. int.—gut. ph.—pharynx. t.—testis.

on to another one. However, since the eggs are attached to the surface of the crayfish, on hatching the young temnocephalans immediately find suitable conditions for their existence. The fact that several authors have successfully maintained these flatworms in daily renewed water, without their hosts, and have been able to observe that they live normally and produce eggs, indicates that this is again a case of phoresis comparable to those mentioned above. Here, however, it is possible to obtain some evidence as to the length of time during which these organisms have been associated with their hosts.

Temnocephalans are found principally on species of parastacids that possess a very peculiar geographical distribution. They occur in streams and rivers of Australia, New Zealand, Madagascar, and of some of the Polynesian Islands and are also found in South America. Carcinologists who have studied this particular problem come to the conclusion that the ancestors of present-day parastacids first appear-ed as such during early Cretaceous times. At that time Australia, New Zealand, and Madagascar, as well as South America, were united by the paleantarctic continent and became detached from one another in the middle of Tertiary times.

Since sea water presents an insurmountable barrier to most fresh-water organisms, it is possible to conclude that the present-day parastacids are derived from a common stock. Since South American, Australian, New Zealand, and Madagascar crayfishes all harbor temnocephalans, it is evident that these flatworms were associated with the ancestors of the recent crayfishes and that this form of phoresis arose sometime during late Secondary times. The thousands of centuries that have elapsed since would be considered by most evolutionists as sufficient for such an association to develop into parasitism. That this is not the case furnishes a very pertinent argument against the assumption that phoresis necessarily leads to parasitism.

Hermit crabs are unfortunate creatures that have been left with soft-shelled abdomens which invite other animals to seek them as food. They have succeeded in surviving by resorting to expedients, i.e., by introducing the abdomen into an empty snail shell into which the crab can withdraw almost completely. These crabs are true psychopaths, endowed with a flight-complex that incites them to hide themselves. This complex is satisfied whenever they discover shells already overgrown with other organisms. Their sense of camouflage is so developed that a hermit crab, grown too large for its shell and obliged to seek a larger one, may detach part of the original epizoic growth and implant it on the new abode.

The sea anemone *Sagartia parasitica* Gosse is found attached to rocks and also to empty shells where it doubtlessly finds the necessary support for its well-being. Should such a shell be chosen by a hermit crab, the sea anemone usually detaches itself and seeks a more stable support. Should the hermit crab, however, belong to the species *Pagurus arrosor* Herbst the anemone remains, and a durable partnership is formed. Whenever the crab is obliged to seek a larger shell, it first detaches the anemone and places it on the new shelter. Apparently neither of the two partners profits by the other's presence and each is quite capable of living by itself. This is consequently not even a case of phoresis.

Numerous different associations of hermit crabs and actinians have been recorded, yet their true nature has hardly ever been studied experimentally and very little is known about it. But the association of *Eupagurus prideauxi* Leach with the anemone *Adamsia palliata* Forbes is of an intimate kind, since the crab uses the pedal disc of the actinian to protect its abdomen (the crab always crowds itself into a shell too small to contain it completely). Moreover, the relative position of the two partners is such that they literally feed out of the same dish (Fig. 4).

This association has become so intimate that

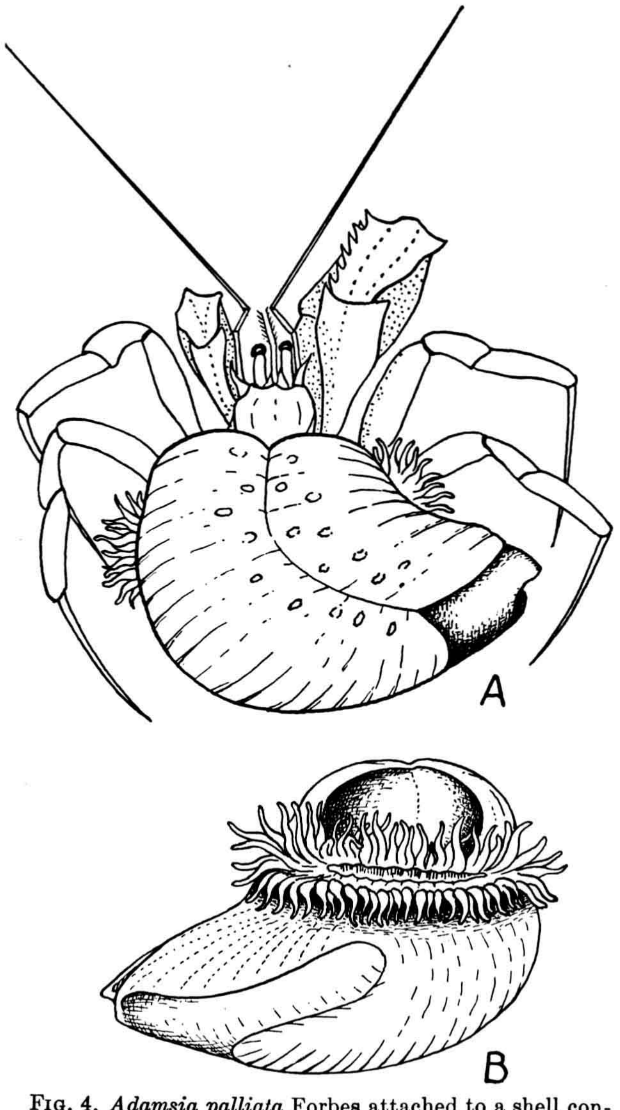


FIG. 4. *Adamsia palliata* Forbes attached to a shell containing *Eupagurus prideauxi* Leach. A. Dorsal view; the foot of the actinian protects the dorsal surface of the crab's abdomen. B. Shell from which the crab has been removed, showing the actinian's mouth opposite that of the crab (Faurot).

neither of the partners is able to survive alone. *Adamsia palliata* produces toxins that are deadly when injected into crabs, but *Eupagurus prideauxi* appears so far to be the only species that possesses natural antibodies toward these toxins. This may be interpreted in two ways. In the first case, it is possible to envisage the presence of antibodies as being the outcome of a very long association, a gradual adaptation of one of the partners to the other. In the second case, one might assume that the blood of *E. prideauxi* has always contained these antibodies and that this species was preadapted to living in close association with *Adamsia*.

From what is known of the habits of hermit crabs and their association with sea-anemones, one is inclined to adopt the second of the two ideas. This would also account for the almost permanent nature of this particular association as compared to the others. In such cases, it is usual to speak of the two partners as messmates or commensals and the association is named *commensalism*.

Commensalism implies that the association is to the mutual benefit of both partners. In the case just mentioned, for instance, the hermit crab profits by the presence of the sea-anemone which enables it to enlarge its shelter and keep off undesirable predators. The sea-anemone benefits directly, as it may digest easily the food that the crab tears up into small pieces.

It is clear that such animal associations must be carefully analyzed, using experimental methods whenever possible. One cannot classify them into distinct categories without knowing the exact nature of the association and, especially, to how great an extent it is obligatory to either of the two partners. It is more than likely that both phoresis and commensalism have arisen from ecological associations in which certain members were protected, either accidentally or intentionally, by camouflage. But in no case does one of the partners provide the other with vital foodstuffs without which it could not survive. This means that both partners have retained their entire physiological independence, although they may, for ecological reasons, be unable to survive when separated.

Commensalism never leads to parasitism and it is also fundamentally distinct from symbiosis with which it is sometimes confused.

SYMBIOSIS

The paunch of ruminants and the cecum of members of the horse tribe contain enormous numbers of ciliates belonging to many species and to several genera. The rumen of a cow may contain as many as 50,000 ciliates per cubic centimeter and this means that the average weight of infusorians contained in the entire rumen would be approximately 2.8 kilos.

The nature of this association has been the matter of much speculation, and it is in only comparatively recent years that it has been determined on an experimental basis.

Cultures *in vitro* show that probably there exist at least two distinct groups of these protozoans, one represented by the genera *Diplodinium* and *Eudiplodinium* which produces cellulase and cellobiase and the other, which includes *Entodinium*, that cannot produce these two enzymes and consequently cannot utilize cellulose directly but must rely on cellulose-splitting bacteria (Fig. 5). In cultures the

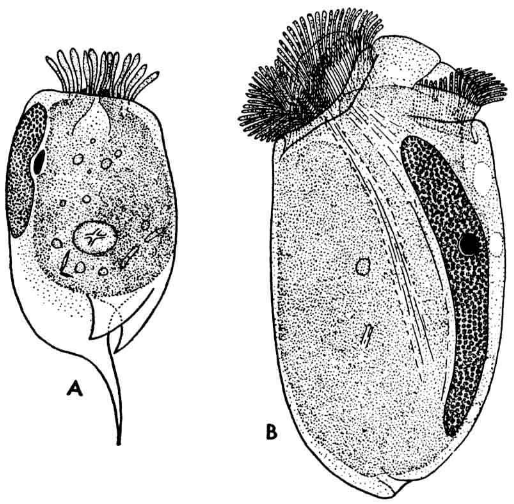


FIG. 5. Symbiotic ciliates from cattle. A. *Entodinium caudatum* Stein. B. *Diplodinium hegneri* Becker & Talbot (Becker & Talbot).

rate of fission of these ciliates is about once every twenty-four hours and approximately 69 per cent, by weight, of *Protozoa* is produced daily (Hungate). When these die and disintegrate they provide the host with about 20 per cent of its total nitrogen requirements. Consequently, these ciliates are concerned both with the carbohydrate and protein metabolisms of the host.

Defaunated ruminants, i.e., those that have been deprived of their ciliates, are able to utilize cellulose only if cellulose-splitting bacteria have developed sufficiently to replace the infusorians.

It is clear that the association of protozoans and herbivorous mammals is of a very intricate nature. Since the ciliates die in the presence of oxygen, they find in the methane gas-filled rumen almost perfect conditions, including a source of their indispensable food. Their metabolism consequently is intense and enables them to multiply very rapidly although their longevity is only about one day. Their total number therefore remains fairly constant and proportionate to the amount of food available. The host that harbors such ciliates profits by their presence. It can use larger amounts of carbohydrates than it could if the cellulose were split up by bacteria alone and it also derives a notable quantity of animal protein from the dead bodies of the ciliates.

Consequently, this type of association is of mutual benefit to both partners who have each lost their physiological independence. Such an association is termed *symbiosis*.

Symbiosis also exists between wood-eating insects, especially termites, and their intestinal flagellates (Fig. 6). In this case, evidence of their providing the host with notable amounts of nitrogen and probably also carbohydrates is derived from the fact that defaunated termites fail to survive and also that the higher termites, those that cultivate fungi and certainly use them as a source of nitrogen, do not harbor flagellates.

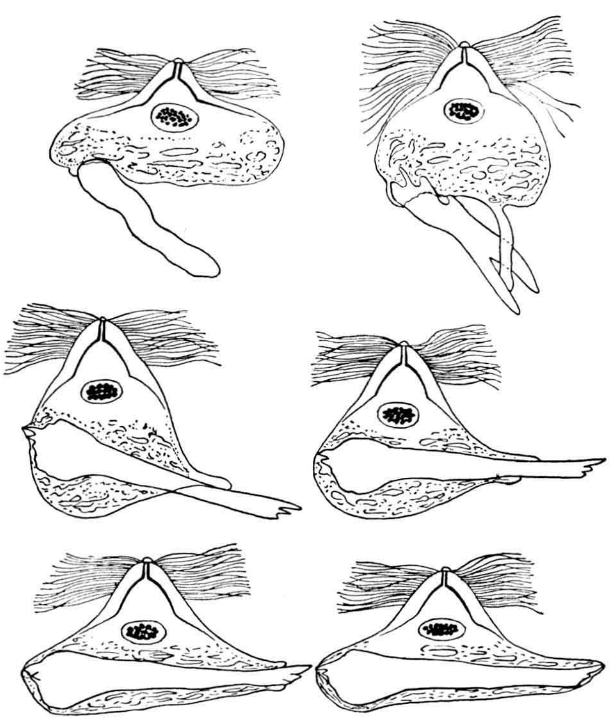


FIG. 6. *Trichonympha* sp. from the gut of a termite showing mode of ingesting fragments of wood (Swezy).

There is no conclusive evidence of symbiosis having ever led to parasitism, although several authors assume this to be the case.[1] It is possible that both symbiosis and parasitism have originated in a somewhat similar way and have evolved on parallel lines. Evidence shows that flagellates evolved together with their hosts, so that it would be reasonable to assume that these symbionts were already present in termites during the Carboniferous period. The approximately three hundred million years that have elapsed since then do not appear to have been sufficient to turn the symbionts into parasites!

PARASITISM

Parasitism is an association of an entirely different kind in which the host provides the parasite with substances that it has elaborated and that are essential for the parasite's nutritional requirements. A parasite has usually lost to some degree the power to synthesize certain vital substances and must therefore rely on the host to furnish them. Consequently, such an association is even more intimate than any of those mentioned above since it implies the reliance of the parasite upon its host. The greater the loss of the power to synthesize its essential nutritional requirements, the more intricate will be the relationship between the parasite and the host. This is known as host specificity, the knowledge of which is fundamental to establishing the degree of parasitic adaptation.

Parasitism so defined implies that a state of unstable balance exists between the two partners since they necessarily react upon each other, even if, normally, neither is a menace to the other. Should, however, the parasite produce toxins prejudicial to the host, or injure it in some other way, the balance will be upset in favor of the parasite. On the other hand, if the host reacts to the presence of the para-

[1] A curious instance of parasitism being transformed into symbiosis is that recorded by Vuillemin and Legrain (*C. R. Acad. Sc. Paris*, 118:549–551). Plants from the Sahara desert that harbor the root nematode *Heterodera radicicola* Greef are able to withstand the drought much better than those not so infested, since under the attack of the parasite, the plants lignify the walls of giant cells and use these cavities as water reservoirs.

site by producing antibodies or other substances that interfere with normal development, the balance will be upset in favor of the host.

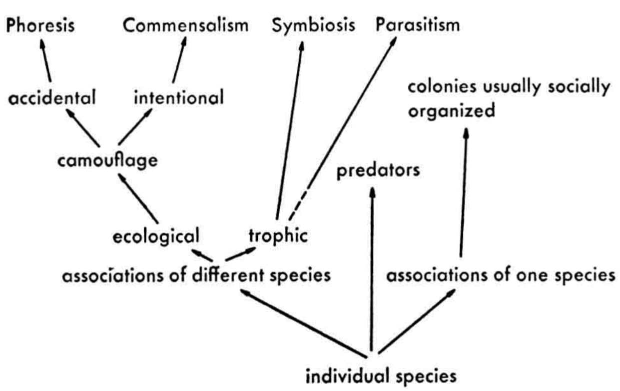
Consequently, what might be termed the ideal parasite, that is, the successfully adapted parasite, exists only in theory since both the parasite's and the host's existence may be jeopardized by extraneous factors independent of either.

No mention will be made of vertebrates as parasites, since in no single instance has the significance of such possible associations been analyzed.

The males of ceriatoid fishes are, it is true, grafted onto the bodies of the females, but so far there exists no indication of the way in which this occurs. Moreover, from preserved materials it appears that this association might be considered as secondary hermaphroditism, since the males are reduced to the state of a testis.

Social parasitism, as it is sometimes called, is found among birds, cowbirds and some cuckoos, but this bears no relationship to animals that are both physiologically and morphologically adapted to parasitism.

It has often been assumed that the embryos of mammals are parasites, parasitic within the maternal organism. But, if this were the case, it would also



be necessary to consider all abnormal growths that appear either on the surface or within the body as parasites. This would apply equally well to all fertilized ova that have not yet left the maternal organism or that develop partly therein, as in certain fishes and amphibians.

The preceding diagram illustrates the different types of associations mentioned.

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